



Phylogeny and diversification of Valerianaceae (Dipsacales) in the southern Andes

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ABSTRACT

The southern Andean clade of *Valeriana* provides an excellent model for the study of biogeography. Here we provide new data to help clarify phylogenetic relationships among the South American valerians, with special focus on taxa found in the southern Andes. We found that the southern Andean taxa formed a clade in maximum likelihood and maximum parsimony analyses, and used a Bayesian relaxed clock method to estimate divergence times within Valerianaceae. Our temporal results were similar to other studies, but we found greater variance in our estimates, suggesting that the species of *Valeriana* have been on the South American continent for some time, and have been successful at exploiting new niche opportunities that reflects the contemporary radiation. Regardless of the time frame for the radiation of the clade, the uptick in the rate of diversification in Valerianaceae appears correlated with a dispersal event from Central to South America. The appearance of *Valeriana* in the southern Andes (13.7 Ma) corresponds with the transition from closed forest on the western side of the Andes in central Chile to a more open Mediterranean woodland environment. This would suggest that the high species richness of Valerianaceae in South America is the result of multiple, smaller radiations such as the one in the southern Andes, that may or may not be geographically isolated. These smaller radiations may also be driven by species moving into new biomes (migration from a temperate to a more Mediterranean-type climate and into alpine). The degree to which different ecological and geological factors interact to drive diversification is difficult to ascertain. Likewise, without a better-resolved phylogeny it is impossible to determine the directionality of dispersal in this group; did they colonize the southern Andes first, then move northward as the central Andean alpine habitat became more widely available or vice versa?

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1. Introduction

The Andes are the dominant physiographic feature of western South America, extending almost the entire length of the continent for some 9000 km, largely unbroken for more than 66° of latitude. On strict geological grounds, the Andes have been divided into the northern (11°N–5°S), central (5–47°S) and southern Andes (47–55°S) (Gansser, 1973). Biologists, however, tend to use the terms central and southern Andes differently, referring to the first as the part of the Andean chain occurring in most of Peru, Bolivia, northern Chile and north-western Argentina, and the southern Andes as occurring south of central Chile and corresponding latitudes in Argentina.

On a global scale the Andean region is characterized by significant vegetation diversity and high species-richness and endemism (Barthlott et al., 2005). At elevations above tree line (or its phytogeographic equivalent), is found the world's largest

continuous corridor of andean (alpine) vegetation comprised of páramo (11°N–8°S), puna (8–27°S), and southern Andean steppe (27–55°S), (Arroyo et al., 2010). On both the western and eastern flanks the páramo is subtended by humid montane cloud forest, Andean rainforest and tropical rainforest, and occasionally by drier deciduous forest lower down on its eastern side. The main organizing component of the mid- and low-elevation vegetation types at the latitudes occupied by the puna vegetation and southern Andean steppe is the so-called “Arid Diagonal” of South America (Garleff et al., 1991; Villagrán and Hinojosa, 1997). This arid zone is a product of two severe rain shadows (Arroyo et al., 1988; Placzek et al., 2009) that produce contrasting climates and a wide range of ecological conditions and vegetation types on either side of the Andes at any given latitude.

The biogeographical consequences of the Andean uplift during the mid-Miocene–Pliocene (Gregory-Wodzicki, 2000; Ramos and Ghiglione, 2008; Rech et al., 2006; Graham, 2009) have been investigated in a number of genera (e.g., Simpson and Todzia, 1990; Ezcurra, 2002; Rauscher, 2002; Sánchez-Baracaldo, 2004; Bell and Donoghue, 2005a; Hughes and Eastwood, 2006; Jaramillo et al., 2006; Hershkovitz et al., 2006; Hoot et al., 2008; Scherson

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et al., 2008; Simpson et al., 2009). However, most studied to date are restricted to a few vegetation types or are predominantly tropical or temperate groups, thus impeding a broader understanding of the evolutionary connection between different habitats and a more complete view of Andean biogeography.

Among the South American taxa, species of Valerianaceae are well represented in the high, mid, and low elevation habitats throughout the entire length of the Andean region. With approximately 350 species, Valerianaceae represents the largest radiation within Dipsacales (Borsini, 1966; Backlund, 1996; Bell, 2004, 2007; Bell and Donoghue, 2005a). The family contains annual and perennial herbs and shrubs characterized by: (1) thyrse inflorescences with perfect or unisexual, symmpetalous, asymmetric flowers; (2) corolla epigynous, sometimes with a gibba or spur at the base of corolla tube; (3) basically three-carpelate ovaries with one fertile carpel with axillary placentation and one anatropous ovule; and (4) fruits with the persistent pappus-like calyx (sometimes leafy or absent) and lack of endosperm in the ripe seed (except *Triplostegia*) (Borsini, 1966; Eriksen, 1989a, 1989b; Kutschker, 2009). Although Valerianaceae, like many dipsacalean taxa, occur widely in the northern hemisphere, the bulk of the species are found in the Andean region of South America where several introductions from the northern hemisphere have occurred (Bell, 2004, 2007; Bell and Donoghue, 2005a). The distribution of Valerianaceae in many Andean vegetation types and throughout the length of the South American Andes makes it ideal for detailed phylogenetic analyses of the association between habitat types.

Of the approximately 250 species of Valerianaceae in South America, 40 taxa are restricted to the Andes of Argentina and Chile. Species in the southern Andes are found mostly in mid- and low-elevation habitats, with some alpine species and a least two restricted to the upper alpine. These grow mainly in open to shaded habitats and exceptionally in wet boggy areas. Species in northern Chile and northwestern Argentina, in contrast, are mostly inhabitants of the puna, and are taxonomically affiliated to species occurring in the northern Andes. Although extensive phylogenetic work has been done on South American Valerianaceae (Hidalgo et al., 2004; Bell and Donoghue, 2005b; Bell, 2007), to date no southern Andean species has been included in any molecular phylogenetic analysis. Consideration of these species is critical to providing a clearer picture of the diversification of South American Valerianaceae and for estimating the time of arrival of the family on the continent. With this in mind, in this paper we present data from one nuclear and nine chloroplast regions to further clarify phylogenetic relationships within Valerianaceae, placing special emphasis on where the southern Andean taxa fit into the phylogeny. In addition, we consider the biogeographic history of Valerianaceae species in the Andean region as a whole to determine the number of times Valerianaceae may have colonized South America and the time of origin of the major clades in relation to the date of appearance of the major vegetation types where they are found.

2. Materials and methods

DNA extraction, PCR amplification, cloning, sequencing, and alignment—For this study, we sampled 155 samples of Valerianaceae representing 142 of the currently accepted species (Table A.1).

We extracted total DNAs using the CTAB methods or with Qiagen DNeasy plant mini extraction kits (Qiagen). We then amplified all regions using standard Polymerase Chain Reaction (PCR) in 10 μ L volume reactions. Reaction conditions were as follows: an initial denaturation at 94 °C for 3 min; then 35 cycles consisting of 94 °C for 1.5 min, 48–56 °C for 2 min, and 72 °C for 3 min. Next, we cleaned all amplified PCR products prior to sequencing using ExoSap-IT (USB-Affymetrix).

We amplified and sequenced 9 chloroplast regions, 6 of which have not previously been examined in Valerianaceae, including: *trnS-trnG* intergenic space with primers of Hamilton (1999), and the *psbM-trnD* intergenic spacer was amplified using the primers of Lee and Wen (2004). We used primers published by Ford et al. (2009) for amplification and sequencing the *rpoC1*, *accD*, *ndhJ*, and *accD* regions. Information about primers for the *matK*, *trnK* intron, and *trnL-F* region can be found in Bell (2007).

In addition to the chloroplast genome markers, we amplified and sequenced the nuclear ribosomal ITS region using the primers ITS2, ITS3 (in some cases, ITS3B), ITS4, and ITS5. For the ITS region, we cloned many of the PCR products using an Invitrogen Topo-TA cloning kit (Invitrogen, Inc., Carlsbad, California). We then screened 8–16 clones per sample to evaluate sequence heterogeneity.

We sequenced all regions via dye terminator cycle sequencing using the protocol specified by the manufacturer and then visualized on an ABI 3100 capillary sequencer. Next, we visualized and edited sequence fragments using the computer package Sequencher (Gene Codes Corporation, Ann Arbor MI) to build contig sequences. Finally, we aligned all sequences visually with the help of MacClade version 4.0 (Maddison and Maddison, 2000). All aligned matrices are available in TreeBase (Accession #S1117; www.treebase.org) or on request from the authors and all sequences were deposited in GenBank (see Appendix 1).

2.1. Phylogenetic analyses and divergence time estimation

Maximum parsimony searches were conducted using heuristic search methods with tree bisection reconnection (TBR) branch swapping, collapse of zero-length branches, and all characters weighted equally. The analyses were repeated 100 times with the RANDOM ADDITION option. Sets of equally most parsimonious trees were summarized with a strict consensus tree. Bootstrap tests (Felsenstein, 1985) were performed using 300 replicates with heuristic search settings identical to those of the original search. All parsimony analyses were performed using the computer software PAUP* vers. 4.0b10 for UNIX (Swofford, 2002).

In addition to maximum parsimony, we used maximum likelihood (ML), and Bayesian analysis to infer phylogeny. For each region that we sequenced, we used PAUP* and MrModelTest 2.2 (Nylander, 2004) to evaluate the appropriate evolutionary model for each partition. Partitions were established in RAxML and BEAST (see below) based on the model selected by the Akaike Information Criterion (AIC). For the maximum likelihood analyses (ML) we employed the program RAxML ver. 7.0.4 (Stamatakis, 2006). RAxML performs maximum likelihood heuristic phylogenetic searches under the GTR model of nucleotide substitution, in addition to models that incorporate among-site rate variation with either assuming a gamma (Γ) distribution or a proportion of invariable sites (I), or both. We performed analyses on two separate datasets: (1) a **concatenated** dataset that assume a single model of molecular evolution, and (2) a second that **partitioned** the data by gene region. In addition, we performed likelihood analyses for the ITS dataset and cpDNA dataset separately. Heuristic searches were performed 100 times from different random starting trees. We calculate maximum likelihood bootstrap analyses with the default parameters with 500 replicates.

2.2. Hypothesis testing

To test the monophyly of the South American taxa, we built constraint trees enforcing their monophyly in MacClade ver. 4.0. We also built trees enforcing the monophyly of all *Valeriana* species that occur in South America (e.g., the suffrutescens taxa, the southern South American valerians, as well as the high elevation páramo species). We searched under each of these constraints using, both,

Table A.1
Samples and voucher information.

Species	Collection details	ITS	trnL-F	matK	trnK	trnG	psbM-trnD	accD	ndhJ	rpoC1	ycf5
<i>Centranthus ruber</i> (L.) DC.	USA, California, San Francisco, Lucky 13, Market St & Church. Bell #203 (YU)	AY236196	AF446990	AY794225	AY794225	HQ878176	JF269664	JF269311	JF269510	JF269818	JF270019
<i>Centranthus macrosiphon</i> Boiss.	Cult., National Bot. Gard. Belgium. FB/H1433	AY792823	AY792885	AY794224	AY794224	HQ878175	JF269663	JF269310	JF269509	JF269817	JF270018
<i>Centranthus sieberi</i> Heldr.	Cultivated at the Mediterranean Agricultural Institute of Crete, Chania, Crete, MAICH 6083. (YU)	DQ354162	DQ354195	DQ354179	DQ354179	HQ878177	JF269665	JF269312	JF269511	JF269819	JF270020
<i>Centranthus calcitrapae</i> Dufur.	Crete, Giouchtas Mountain, Cellinese 1002 (YU)	DQ354164	DQ354197	DQ354182	DQ354182	HQ878172	JF269660	JF269307	JF269505	JF269814	JF270015
<i>Centranthus calcitrapae</i> Dufur.	Spain, La Roja. 108755 (SALA)	DQ354163	DQ354196	DQ354181	DQ354181	HQ878171	JF269659	JF269306	JF269506	JF269813	JF270014
<i>Centranthus lecoqii</i> Jord.	Spain, San Esteban. Amich & Diez 108751 (SALA)	DQ354165	DQ354198	DQ354184	DQ354184	HQ878173	JF269661	JF269308	JF269507	JF269815	JF270016
<i>Centranthus longiflorus</i> Steven	Republic of Georgia, Merello et al. 2237 (MOBOT)	HQ878124	JF269259	JF269459	JF269967	HQ878174	JF269662	JF269309	JF269508	JF269816	JF270017
<i>Fedia cornucopiae</i> (L.) Gaertn.	Cult. Bergius Bot. Gard., Sweden. Eriksson, 806 (SBT)	AY236193	AF447013	AY794226	AY794226	HQ878179	JF269667	JF269314	JF269513	JF269821	JF270022
<i>Fedia cornucopiae</i> (L.) Gaertn.	Africa	HQ878123	JF269260	JF269460	JF269968	HQ878178	JF269666	JF269313	JF269512	JF269820	JF270021
<i>Nardostachys jatamansi</i> DC.	China, Sichuan Province. Boufford et al., #28099 (A)	AY236190	AF447010	AY794227	AY794227	HQ878180	JF269668	JF269315	JF269514	JF269822	JF270023
<i>Patrinia gibbosa</i> Maxim.	Cult. Zurich Bot. Gard., Switzerland. (A. Mast) #19885022	AY792824	AY792886	AY794229	AY794229	HQ878181	JF269669	JF269316	JF269515	JF269823	JF270024
<i>Patrinia saniculifolia</i> Hemsl.	South Korea, Kang-won Prov. Chase 19250 (Kew)	HQ878125	JF269261	JF269461	JF269969	HQ878182	JF269670	JF269317	JF269516	JF269824	JF270025
<i>Patrinia scabiosifolia</i> Link	Cult. Yale Univ. Bell #104 (YU)	AY792825	AY792887	AY79430	AY79430	HQ878183	JF269671	JF269318	JF269517	JF269825	JF270026
<i>Patrinia triloba</i> Miq.	Cult. Bergius Bot. Gard., Sweden. Eriksson 807 (SBT)	AY236191	AF447011	AY794228	AY794228	HQ878184	JF269672	JF269319	JF269518	JF269826	JF270027
<i>Patrinia villosa</i> Juss.	Cult. Zurich Bot. Gard., Switzerland. (A. Mast) #19910230	AY792826	AY792888	AY794403	AY794403	HQ878185	JF269673	JF269320	JF269519	JF269827	JF270028
<i>Plectritis brachystema</i> Fisch. & C.A. Mey.	USA, California, Sierra Co. Timme #015 (SFSU)	AY792828	AY79290	AY794232	AY794232	HQ878186	JF269674	JF269321	JF269520	JF269828	JF270029
<i>Plectritis congesta</i> (Lindl.) DC.	USA, Oregon, Benton Co. Shenk #308 (YU)	AY792827	AY792889	AY794231	AY794231	HQ878187	JF269675	JF269322	JF269521	JF269829	JF270030
<i>Plectritis macroceras</i> Torr. & A. Gray	USA, California, San Mateo Co. Patterson, 2000 (SFSU)	AY236195	AF447015	AY794233	AY794233	HQ878188	JF269676	JF269323	JF269522	JF269830	JF270031
<i>Triplostegia glandulifera</i> Wall. ex DC.	China, Sichuan Province. Boufford et al., #28440 (A)	AY236189	AF447009	AY794234	AY794234	HQ878189	JF269677	JF269324	JF269523	JF269831	JF270032
<i>Valeriana acutiloba</i> Rydb.	USA, Colorado. Grand, Co. Barrie 826 (YU)	AY792829	AY792891	AY794235	AY794235	HQ878190	JF269678	JF269325	JF269524	JF269832	JF270033
<i>Valeriana adscendens</i> Turcz.	Ecuador, Napo. Bell, #EC006 (YU)	AY792830	AY792892	AY794236	AY794236	HQ878191	JF269679	JF269326	JF269525	JF269833	JF270034
<i>Valeriana albonervata</i> B.L. Rob.	Mexico, Tamaulipas. Barrie & Nixon, #1279 (YU)	AY792831	AY792893	AY794237	AY794237	HQ878192	JF269680	JF269327	JF269526	JF269834	JF270035
<i>Valeriana apiifolia</i> A. Gray	Mexico, Durango. Barrie & Gage, #1263 (YU)	AY792832	AY792894	AY794238	AY794238	HQ878193	JF269681	JF269328	JF269527	JF269835	JF270036
<i>Valeriana arborea</i> Killip & Cuatrec.	Colombia, Boyaca. Madrinan #2070 (YU)	AY360096	AY360116	AY794239	AY794239	HQ878194	JF269682	JF269329	JF269528	JF269836	JF270037
<i>Valeriana aretioides</i> Kunth	Ecuador, Tungurahua. Sklenar & Laegaard #7224 QCNE (157584)	AY792833	AY792895	AY794240	AY794240	HQ878195	JF269683	JF269330	JF269529	JF269837	JF270038
<i>Valeriana arizonica</i> A. Gray	USA, Arizona, Pima Co. Barrie et al., # 272 (YU)	AY792834	AY792896	AY794241	AY794241	HQ878196	JF269684	JF269331	JF269530	JF269838	JF270039
<i>Valeriana asarifolia</i> Dufur.	Crete, Asterousia Mountain, Heraklion Province, Cellinese 1000. (YU)	DQ354167	DQ354200	JF269461	JF269969	HQ878197	JF269685	JF269332	JF269531	JF269839	JF270040
<i>Valeriana barbataefolia</i> M. Martens. & Galeotti	Mexico, Veracruz. Barrie & Luckow, #1470 (YU)	AY792835	AY792897	AY794242	AY794242	HQ878198	JF269686	JF269333	JF269532	JF269840	JF270041

Table A.1 (continued)

Species	Collection details	ITS	trnL-F	matK	trnK	trnG	psbM-trnD	accD	ndhJ	rpoC1	ycf5
<i>Valeriana boelckei</i> Rossow	Argentina: Neuquén. Dpto Huiliches. A.L.V. 122 (BCRU)	HQ878126	JF269262	JF269462	JF269970	HQ878199	JF269687	JF269334	JF269533	JF269841	JF270042
<i>Valeriana bracteata</i> Benth.	Ecuador, Azuay. Bell # EC018 (YU)	AY792836	AY792898	AY794243	AY794243	HQ878200	JF269688	JF269335	JF269534	JF269842	JF270043
<i>Valeriana bracteosa</i> Phil.	Chile: VI Region. Prov. Cachapoal. Arroyo et al. # 210433 (CONC)	HQ878127	JF269263	JF269463	JF269971	HQ878201	JF269689	JF269336	JF269535	JF269843	JF270044
<i>Valeriana bridgesii</i> Hook. & Arn.	Chile: VI Region. Prov. Cachapoal. Arroyo et al. # 993921 (CONC)	HQ878128	JF269264	JF269464	JF269972	HQ878202	JF269690	JF269337	JF269536	JF269844	JF270045
<i>Valeriana bryophila</i> Barrie	Mexico, Guerrero. Barrie et al., 956 (paratype) (YU)	AY792837	AY792899	AY794244	AY794244	HQ878203	JF269691	JF269338	JF269537	JF269845	JF270046
<i>Valeriana bulbosa</i> Wedd.	Bolivia, La Paz. Eriksen & Molau, #540	AY792838	AY792900	AY794245	AY794245	HQ878204	JF269692	JF269339	JF269538	JF269846	JF270047
<i>Valeriana candolleana</i> Gardner	Mexico, Oaxaca. Barrie & Nixon, 1363 (YU)	AY792839	AY792901	AY794247	AY794247	HQ878206	JF269694	JF269341	JF269540	JF269848	JF270049
<i>Valeriana californica</i> A. Heller	USA, California, Sierra Co. Timme #016	AY360098	AY360118	AY794246	AY794246	HQ878205	JF269693	JF269340	JF269539	JF269847	JF270048
<i>Valeriana carnososa</i> Sm.	Argentina: Chubut. Dpto. Futaleufú. Kutschker 801 (BCRU)	HQ878130	JF269266	JF269466	JF269974	HQ878208	JF269696	JF269343	JF269542	JF269850	JF270051
<i>Valeriana carnososa</i> Sm.	Chile. XII Region, Prov. Ultima Esperanza. Arroyo et al. 92253 (CONC)	HQ878129	JF269265	JF269465	JF269973	HQ878207	JF269695	JF269342	JF269541	JF269849	JF270050
<i>Valeriana celtica</i> L.	Switzerland, Valais. Bell, #SWITZ002 (YU)	AY360101	AY360121	AY794248	AY794248	HQ878209	JF269697	JF269344	JF269543	JF269851	JF270052
<i>Valeriana ceratophylla</i> Kunth	Mexico, Hidalgo. Barrie #888 (YU)	AY792840	AY792902	AY794249	AY794249	HQ878210	JF269698	JF269345	JF269544	JF269852	JF270053
<i>Valeriana chaerophylloides</i> Sm.	Ecuador, Loja. Bell # EC023 (YU)	AY360103	AY360126	AY794250	AY794250	HQ878211	JF269699	JF269346	JF269545	JF269853	JF270054
<i>Valeriana chilensis</i> Borsini	Argentina: Chubut. Dpto. Futaleufú. Kutschker 808 (BCRU)	HQ878131	JF269267	JF269467	JF269975	HQ878212	JF269700	JF269347	JF269546	JF269854	JF270055
<i>Valeriana clarionifolia</i> Phil.	Argentina: Chubut. Dpto. Futaleufú. Kutschker 802 (BCRU)	HQ878132	JF269268	JF269468	JF269976	HQ878213	JF269701	JF269348	JF269547	JF269855	JF270056
<i>Valeriana clematitis</i> Kunth	Argentina: Salta. Ahumada & Ahumada 8282 (SI)	HQ878133	JF269269	JF269469	JF269977	HQ878215	JF269702	JF269350	JF269549	JF269856	JF270058
<i>Valeriana clematitis</i> Kunth	Colombia, Boyaca. Madrinan # 2111 (YU)	AY792841	AY792903	AY794251	AY794251	HQ878214	JF269703	JF269349	JF269548	JF269857	JF270057
<i>Valeriana coarctata</i> Ruiz & Pav.	Peru, Dept. Cuzco. Davis et al. # 1571 (A)	AY792884	AY792904	AY794252	AY794252	HQ878216	JF269704	JF269351	JF269550	JF269858	JF270059
<i>Valeriana connata</i> Ruiz & Pav.	Peru, Dept. Cajamarca. Molau & Eriksen #3464 (YU)	AY792842	AY792905	AY794253	AY794253	HQ878217	JF269705	JF269352	JF269551	JF269859	JF270060
<i>Valeriana crispa</i> Ruiz & Pav.	Chile, Metropolitan Region, Prov. Melipilla. Arroyo et al. # 207074 (CONC)	HQ878134	JF269270	JF269470	JF269978	HQ878218	JF269706	JF269353	JF269552	JF269860	JF270061
<i>Valeriana densiflora</i> Benth.	Mexico, Mexico. Barrie #907 (YU)	AY792843	AY792906	AY794254	AY794254	HQ878219	JF269707	JF269354	JF269553	JF269861	JF270062
<i>Valeriana decussata</i> Ruiz & Pav. ssp. <i>polemonioides</i> (Kunth) B. Eriksen	Peru, Tungurahua. Villacres # 183 (Glaxo Group Research) (FMNH #2179954)	AY792845	AY792919	AY794279	AY794279	HQ878220	JF269708	JF269355	JF269554	JF269862	JF270063
<i>Valeriana dioica</i> L.	Cult. Zurich Bot. Gard., Switzerland. #16910745 (YU)	AY360107	AY360119	AY794255	AY794255	HQ878221	JF269709	JF269356	JF269555	JF269863	JF270064
<i>Valeriana edulis</i> Nutt.	USA, Colorado, Park Co. Barrie #822 (YU)	AY360104	AY360127	AY794256	AY794256	HQ878222	JF269710	JF269357	JF269556	JF269864	JF270065
<i>Valeriana effusa</i> Griseb.	Argentina, La Rioja. Dpto. Capital. Biurrun et al. 4664 (SI)	HQ878135	JF269271	JF269471	JF269979	HQ878223	JF269711	JF269358	JF269557	JF269865	JF270066
<i>Valeriana fauriei</i> Briq.	Japan. Yokekura #96175 (A)	AY792844	AY792907	AY794257	AY794257	HQ878224	JF269712	JF269359	JF269558	JF269866	JF270067
<i>Valeriana flaccidissima</i> Maxim.	Japan, Honshu, Kyoto. Tsugara # 17730 (A)	AY792845	AY792908	AY794258	AY794258	HQ878225	JF269713	JF269360	JF269559	JF269867	JF270068
<i>Valeriana fonckii</i> Phil.	Argentina, Chubut. Dpto. Futaleufú. Kutschker 803 (BCRU)	HQ878136	JF269272	JF269472	JF269980	HQ878226	JF269714	JF269361	JF269560	JF269868	JF270069
<i>Valeriana gallinae</i> Barrie	Mexico, Guerrero. Barrie et al. #951 (YU)	AY792846	AY792909	AY794259	AY794259	HQ878227	JF269715	JF269362	JF269561	JF269869	JF270070

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Table A.1 (continued)

Species	Collection details	ITS	trnL-F	matK	trnK	trnG	psbM-trnD	accD	ndhJ	rpoC1	ycf5
<i>Valeriana graciliceps</i> Clos	Chile, Metropolitan Region . Prov. Santiago. Arroyo & Humaña 991851 (CONC 167197)	HQ878137	JF269273	JF269473	JF269981	HQ878228	JF269716	JF269363	JF269562	JF269870	JF270071
<i>Valeriana grandifolia</i> Phil.	Chile, VIII Región. Prov. Ñuble, Matthei 679 (CONC 151723)	HQ878138	JF269274	JF269474	JF269982	HQ878229	JF269717	JF269364	JF269563	JF269871	JF270072
<i>Valeriana hebecarpa</i> DC.	Chile, VIII Región. Prov. Bio-Bío. Mihoc 3163 (CONC 159222)	HQ878139	JF269275	JF269475	JF269983	HQ878230	JF269718	JF269365	JF269564	JF269872	JF270073
<i>Valeriana henrici</i> (Graebn.) B. Eriksen	Peru, Depto. Ancash. Molau & Eriksen #3497 (YU)	AY360105	AY360128	AY794260	AY794260	HQ878231	JF269719	JF269366	JF269565	JF269873	JF270074
<i>Valeriana hirtella</i> Kunth	Ecuador, Loja. Cotton et al. #1548 (MO)	AY360114	AY360134	AY794261	AY794261	HQ878232	JF269720	JF269367	JF269566	JF269874	JF270075
<i>Valeriana hornsuschiana</i> Walp.	Chile, Metropolitana Region. Prov. Santiago. Arroyo & Humaña 980630 (CONC 162930)	HQ878141	JF269276	JF269476	JF269984	HQ878233	JF269721	JF269368	JF269567	JF269875	JF270076
<i>Valeriana hornsuschiana</i> Walp.	Chile, Metropolitan Region. Prov. Cordillera. Arroyo et al. 210625 (CONC)	HQ878140	JF269277	JF269477	JF269985	HQ878234	JF269722	JF269369	JF269568	JF269876	JF270077
<i>Valeriana interrupta</i> Ruiz & Pav.	Peru, Depto. Cajamarca. Molau & Eriksen #3331 (YU)	AY792847	AY792910	AY794262	AY794262	HQ878235	JF269723	JF269370	JF269569	JF269877	JF270078
<i>Valeriana kawakamii</i> Hayata	Taiwan, Hualien Hsein. Chih-Chiu Wang #1089 (A)	AY792848	AY792911	AY794263	AY794263	HQ878236	JF269724	JF269371	JF269570	JF269878	JF270079
<i>Valeriana lancifolia</i> Hand.-Mazz.	China, Sichuan. Boufford et al. 38699 (AA)	HQ878142	JF269278	JF269478	JF269986	HQ878237	JF269725	JF269372	JF269571	JF269879	JF270080
<i>Valeriana lapathifolia</i> Vahl	Argentina, Chubut. Dpto. Futaleufú. Kutschker 812 (BCRU)	HQ878143	JF269279	JF269479	JF269987	HQ878238	JF269726	JF269373	JF269572	JF269880	JF270081
<i>Valeriana laurifolia</i> Kunth	Ecuador, Imbabura. Bell #EC011 (YU)	AY360112	AY360133	AY794264	AY794264	HQ878239	JF269727	JF269374	JF269573	JF269881	JF270082
<i>Valeriana laxiflora</i> DC.	Chile: VIII Region. Prov. Ñuble. Termas de Chillán. ca. 2000 m. 22 January 1983 (CONC)	HQ878145	JF269280	JF269481	JF269989	HQ878241	JF269729	JF269376	JF269575	JF269882	JF270084
<i>Valeriana laxiflora</i> DC.	Argentina, Chubut. Dpto. Futaleufú. Kutschker 806 (BCRU)	HQ878144	JF269281	JF269480	JF269988	HQ878240	JF269728	JF269375	JF269574	JF269883	JF270083
<i>Valeriana lepidota</i> Clos	Chile, VII Región. Prov. Talca, Arroyo & Becerra 209668 (CONC)	HQ878146	JF269282	JF269482	JF269990	HQ878242	JF269730	JF269377	JF269576	JF269884	JF270085
<i>Valeriana leucocarpa</i> DC.	Argentina, Río Negro. Rechencq s.n. (BCRU)	HQ878147	JF269283	JF269483	JF269991	HQ878243	JF269731	JF269378	JF269577	JF269885	JF270086
<i>Valeriana lobata</i> Phil.	Chile, V Region. Prov. Petorca. Arroyo & Humaña 992267 (CONC)	HQ878148	JF269284	JF269484	JF269992	HQ878244	JF269732	JF269379	JF269578	JF269886	JF270087
<i>Valeriana mexicana</i> DC.	Mexico, Oaxaca. Barrie & Leidig # 1080 (YU)	AY792849	AY792912	AY794265	AY794265	HQ878245	JF269733	JF269380	JF269579	JF269887	JF270088
<i>Valeriana microphylla</i> Kunth	Ecuador, Cotapaxi. Bell #EC007 (YU)	AY360113	AY360122	AY794266	AY794266	HQ878246	JF269734	JF269381	JF269580	JF269888	JF270089
<i>Valeriana minutiflora</i> Hand.-Mazz.	China, Sichuan Province. Boufford et al., #28646 (AA)	AY236192	AF447012	AY794267	AY794267	HQ878247	JF269735	JF269382	JF269581	JF269889	JF270090
<i>Valeriana montana</i> L.	Switzerland, Valais. Nyffeler, 1063 (YU)	AY360100	AY360124	AY794268	AY794268	HQ878248	JF269736	JF269383	JF269582	JF269890	JF270091
<i>Valeriana moyanoi</i> Speg.	Argentina, Chubut. Kutschker 804 (BCRU)	HQ878149	JF269285	JF269485	JF269993	HQ878249	JF269737	JF269384	JF269583	JF269891	JF270092
<i>Valeriana naidae</i> Barrie	Mexico, Oaxaca. Barrie & Nixon, #1368 (YU)	AY792850	AY792913	AY794269	AY794269	HQ878250	JF269738	JF269385	JF269584	JF269892	JF270093
<i>Valeriana niphobia</i> Briq.	Ecuador, Azuay. Bell # EC022 (YU)	AY360106	AY360129	AY794270	AY794270	HQ878251	JF269739	JF269386	JF269585	JF269893	JF270094
<i>Valeriana nivalis</i> Wedd.	Bolivia, La Paz. Eriksen & Molau, 4830 (YU)	AY792851	AY792914	AY794271	AY794271	HQ878252	JF269740	JF269387	JF269586	JF269894	JF270095
<i>Valeriana occidentalis</i> A. Heller	USA, Oregon, Lake Co. Schenk #477 (YU)	AY792852	AY792915	AY794272	AY794272	HQ878253	JF269741	JF269388	JF269587	JF269895	JF270096
<i>Valeriana officinalis</i> L.	China, Sichuan Province. Boufford, et al., #28695 (AA)	AY360110	AY360120	AY794273	AY794273	HQ878254	JF269742	JF269389	JF269588	JF269896	JF270097
<i>Valeriana palmeri</i> A. Gray	Mexico, Guerrero. Barrie et al., #948 (YU)	AY792853	AY792916	AY794274	AY794274	HQ878255	JF269743	JF269390	JF269589	JF269897	JF270098

Table A.1 (continued)

Species	Collection details	ITS	trnL-F	matK	trnK	trnG	psbM-trnD	accD	ndhJ	rpoC1	ycf5
<i>Valeriana papilla</i> Bertero ex DC.	Chile, Metropolitan Region. Prov. Maipo. Cerro Cantillana, A. Marticorena 585 (CONC 165496)	HQ878150	JF269286	JF269486	JF269994	HQ878256	JF269744	JF269391	JF269590	JF269898	JF270099
<i>Valeriana papilla</i> Bertero ex DC.	Chile, Metropolitan Region, Prov. Melipilla. Arroyo et al. # 205909 (CONC)	HQ878151	JF269287	JF269487	JF269995	HQ878257	JF269745	JF269392	JF269591	JF269899	JF270100
<i>Valeriana pauciflora</i> Michx.	USA, Florida, Lauderdale Co. Webb #5098 (A)	AY792878	AY792944	AY794275	AY794275	HQ878258	JF269746	JF269393	JF269592	JF269900	JF270101
<i>Valeriana philippiana</i> Briq.	Argentina, Chubut, Kutschker 809 (BCRU)	HQ878152	JF269288	JF269488	JF269996	HQ878259	JF269747	JF269394	JF269594	JF269901	JF270102
<i>Valeriana philippiana</i> Briq.	Argentina, Prov. Neuquén, Dpto. Los Lagos, Cerro Bayo, S40 45 00, W071 36 47. Weigend et al. 6859 (KEW)	HQ878153	JF269289	JF269489	JF269997	HQ878260	JF269748	JF269395	JF269593	JF269902	JF270103
<i>Valeriana pilosa</i> Ruiz & Pav.	Ecuador, Napo. Bell #EC002 (YU)	AY360109	AY360131	AY794276	AY794276	HQ878261	JF269749	JF269396	JF269595	JF269903	JF270104
<i>Valeriana pilosiuscula</i> M. Martens & Galeotti	Mexico. Berrie, Ramamoorthy, & Esquivel 900 (YU)	HQ878154	JF269290	JF269490	JF269998	HQ878262	JF269750	JF269397	JF269596	JF269904	JF270105
<i>Valeriana pinnatifida</i> Ruiz & Pav.	Peru, Depto. La Libertad. Leiva & Salinas #1788 (FMNH)	AY792854	AY792917	AY794277	AY794277	HQ878263	JF269751	JF269398	JF269597	JF269905	JF270106
<i>Valeriana plantaginea</i> Kunth	Ecuador, Napo. Bell #EC001 (YU)	AY792855	AY792918	AY794278	AY794278	HQ878264	JF269752	JF269399	JF269598	JF269906	JF270107
<i>Valeriana polemoniifolia</i> Phil.	Argentina, Río Negro. Puntieri s.n. (BCRU)	HQ878156	JF269292	JF269492	JF270000	HQ878266	JF269754	JF269400	JF269599	JF269907	JF270109
<i>Valeriana polemoniifolia</i> Phil.	Chile, Prov. Quillota. Arroyo et al. # 992939 (CONC)	HQ878155	JF269291	JF269491	JF269999	HQ878265	JF269753	JF269401	JF269600	JF269908	JF270108
<i>Valeriana polystachya</i> Sm.	Argentina, Buenos Aires. Hurrell et al. 5336 (SI)	HQ878157	JF269293	JF269493	JF270001	HQ878267	JF269755	JF269402	JF269601	JF269909	JF270110
<i>Valeriana prionophylla</i> Standl.	Costa Rica. Hill #17547 (A)	AY792857	AY792920	AY794280	AY794280	HQ878268	JF269756	JF269403	JF269602	JF269910	JF270111
<i>Valeriana procera</i> Kunth	Mexico, Durango. Barrie & Leidig #1001 (YU)	AY792858	AY792921	AY794281	AY794281	HQ878269	JF269757	JF269404	JF269603	JF269911	JF270112
<i>Valeriana pseudofficinalis</i> C.Y. Cheng & H.B. Chen	China, Sichuan, Xiangcheng Xian. Boufford et al. # 30689 (AA)	HQ878158	JF269294	JF269494	JF270002	HQ878270	JF269758	JF269405	JF269604	JF269912	JF270113
<i>Valeriana pyramidalis</i> Kunth	Ecuador, Napo. Bell #EC005 (YU)	AY792859	AY792922	AY794282	AY794282	HQ878271	JF269759	JF269406	JF269605	JF269913	JF270114
<i>Valeriana pyrenaica</i> L.	Cult. Zurich Bot. Gard., Switzerland. (A. Mast) #23659628	AY360111	AY360132	AY794283	AY794283	HQ878272	JF269760	JF269407	JF269606	JF269914	JF270115
<i>Valeriana radicalis</i> Clos	Chile, Metropolitan Region. Prov. Santiago. Arroyo et al. 201442 (CONC 162967)	HQ878159	JF269295	JF269495	JF270003	HQ878273	JF269761	JF269408	JF269607	JF269915	JF270116
<i>Valeriana retrorsa</i> Fern.	Mexico. Berrie et al. 395 (YU)	HQ878160	JF269296	JF269496	JF270004	HQ878274	JF269762	JF269409	JF269608	JF269916	JF270117
<i>Valeriana rigida</i> Ruiz & Pav.	Ecuador, Azuay. Bell # EC016 (YU)	AY360108	AY360130	AY794284	AY794284	HQ878275	JF269763	JF269410	JF269609	JF269917	JF270118
<i>Valeriana robertianifolia</i> Briq.	Mexico, Oaxaca, Barrie & Leidig #1058 (YU)	AY792860	AY792923	AY794285	AY794285	HQ878276	JF269764	JF269411	JF269610	JF269918	JF270119
<i>Valeriana rumicoides</i> Wedd	Ecuador, Carchi. Molau et al., #2579 (YU)	AY792861	AY792924	AY794286	AY794286	HQ878277	JF269765	JF269412	JF269611	JF269919	JF270120
<i>Valeriana rzedowskiorum</i> Barrie	Mexico, Mpio. Barrie #442 (YU)	AY792862	AY792925	AY794287	AY794287	HQ878278	JF269766	JF269413	JF269612	JF269920	JF270121
<i>Valeriana scandens</i> Loeffl ex L. var. <i>scandens</i>	Argentina, Jujuy. Dpto. Slanis et al. 67 (SI)	HQ878161	JF269297	JF269497	JF270005	HQ878280	JF269768	JF269415	JF269613	JF269922	JF270123
<i>Valeriana scandens</i> Loeffl ex L.	Mexico, San Luis Potosi. Barrie & Nixon, #1293 (YU)	AY792863	AY792926	AY794288	AY794288	HQ878279	JF269767	JF269414	JF269614	JF269921	JF270122
<i>Valeriana scouleri</i> Rydb.	USA, Oregon. Schenk #208 (YU)	AY792864	AY792927	AY794289	AY794289	HQ878281	JF269769	JF269416	JF269615	JF269923	JF270124
<i>Valeriana secunda</i> B. Eriksen	Ecuador, Azuay. Bell # EC015 (YU)	AY792865	AY792928	AY794290	AY794290	HQ878282	JF269770	JF269417	JF269616	JF269924	JF270125

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Table A.1 (continued)

Species	Collection details	ITS	trnL-F	matK	trnK	trnG	psbM-trnD	accD	ndhJ	rpoC1	ycf5
<i>Valeriana selerorum</i> Graebn. & Loes.	Mexico, Mexico. Barrie et al., #901 (YU)	AY792866	AY792929	AY794291	AY794291	HQ878283	JF269771	JF269418	JF269617	JF269925	JF270126
<i>Valeriana sichuanica</i> D.Y. Hong	China, Sichuan. Boufford et al. 36803 (AA)	HQ878162	JF269298	JF269497	JF270006	HQ878284	JF269772	JF269419	JF269618	JF269926	JF270127
<i>Valeriana sitchensis</i> Bong.	USA, Oregon, Wallawa Co. Schenk #388 (YU)	AY360097	AY360117	AY794292	AY794292	HQ878285	JF269773	JF269420	JF269619	JF269927	JF270128
<i>Valeriana sorbifolia</i> Kunth	Mexico, Guerrero. Barrie #418 (YU)	AY360102	AY360125	AY794293	AY794293	HQ878286	JF269774	JF269421	JF269620	JF269928	JF270129
<i>Valeriana stenophylla</i> Killip	Colombia, Cundinamarca. Zapata #67 (YU)	AY792868	AY792930	AY794295	AY794295	HQ878287	JF269775	JF269422	JF269621	JF269929	JF270130
<i>Valeriana stenoptera</i> Diels	China, Yunnan Province. Murata et al., #620 (A)	AY792865	AY792931	AY794294	AY794294	HQ878288	JF269776	JF269423	JF269622	JF269930	JF270131
<i>Valeriana stricta</i> Clos	Chile, III Region. Prov. del Huasco. Teillier & Delaunoy 5583 (CONC 166871)	HQ878163	JF269299	JF269498	JF270007	HQ878289	JF269777	JF269424	JF269623	JF269931	JF270132
<i>Valeriana stricta</i> Clos	Chile, Metropolitan Region. Prov. Santiago. Arroyo et al. 980654 (CONC 167045)	HQ878164	JF269300	JF269499	JF270008	HQ878290	JF269778	JF269425	JF269624	JF269932	JF270133
<i>Valeriana stricta</i> Clos	Chile, IV Region, Prov. Choapa. Arroyo et al. # 991438 (CONC)	HQ878165	JF269301	JF269500	JF270009	HQ878291	JF269779	JF269426	JF269625	JF269933	JF270134
<i>Valeriana subincisa</i> Benth.	Mexico, Hidalgo. Berrie 935 (YU)	HQ878166	JF269302	JF269501	JF270010	HQ878292	JF269780	JF269427	JF269626	JF269934	JF270135
<i>Valeriana supina</i> Ard.	Switzerland, Valais. Nyffeler, 1076 (YU)	AY360099	AY360123	AY794296	AY794296	HQ878293	JF269781	JF269428	JF269627	JF269935	JF270136
<i>Valeriana tanacetifolia</i> F.G. Mey.	Mexico, Mexico. Barrie et al., #904 (YU)	AY792869	AY792932	AY794297	AY794297	HQ878294	JF269782	JF269429	JF269628	JF269936	JF270137
<i>Valeriana texana</i> Steyerl.	USA, New Mexico, Lincoln CO. Barrie et al. #267 (YU)	AY792870	AY792933	AY794298	AY794298	HQ878295	JF269783	JF269430	JF269629	JF269937	JF270138
<i>Valeriana tomentosa</i> Kunth	Ecuador, Loja. Luteyn & Romoleraux, 14471. (QCNE #105107)	AY792871	AY792934	AY794299	AY794299	HQ878296	JF269784	JF269431	JF269630	JF269938	JF270139
<i>Valeriana trichostoma</i> Hand.-Mazz.	China, Yunnan Province. Boufford et al., #29190 (A)	AY792872	AY792935	AY794300	AY794300	HQ878297	JF269785	JF269432	JF269631	JF269939	JF270140
<i>Valeriana triphylla</i> Kunth	Colombia, Boyaca. Madrinan # 2107 (YU)	AY792873	AY792936	AY794301	AY794301	HQ878298	JF269786	JF269433	JF269632	JF269940	JF270141
<i>Valeriana tripteris</i> L.	Switzerland, Valais. Bell, #SWITZ005 (YU)	AY792874	AY792937	AY794302	AY794302	HQ878299	JF269787	JF269434	JF269633	JF269941	JF270142
<i>Valeriana tuberosa</i> L.	Spain, Villafranca-Montes de Oca, F. Amich & S. Bernardos (SALA 108754)	DQ354166	DQ354199	DQ354185	DQ354185	HQ878300	JF269788	JF269435	JF269634	JF269942	JF270143
<i>Valeriana urticifolia</i> Kunth	Mexico, Jalisco. Barrie & Gage #1197 (YU)	AY792875	AY792938	AY794303	AY794303	HQ878301	JF269789	JF269436	JF269635	JF269943	JF270144
<i>Valeriana urticifolia</i> Kunth	Ecuador, Loja. Bell # EC024 (YU)	AY792876	AY792939	AY794304	AY794304	HQ878302	JF269790	JF269437	JF269636	JF269944	JF270145
<i>Valeriana urticifolia</i> Kunth var. <i>scorpioides</i> (DC.) Barrie	Mexico, Michoacan. Barrie & Leidig #1049 (YU)	AY290019	AY290008	AY794441	AY794441	HQ878303	JF269791	JF269438	JF269637	JF269945	JF270146
<i>Valeriana vaga</i> Clos	Chile, V Region, Prov. Quillota. Arroyo et al. 994006 (CONC)	HQ878167	JF269303	JF269502	JF270011	HQ878304	JF269792	JF269439	JF269638	JF269946	JF270147
<i>Valeriana verticillata</i> Clos	Chile, VII Region. Prov. Talca. Arroyo et al. # 209817 (CONC)	HQ878168	JF269304	JF269503	JF270012	HQ878305	JF269793	JF269440	JF269639	JF269947	JF270148
<i>Valeriana virescens</i> Clos	Argentina, Chubut. Dpto. Kutschker 807 (BCRU)	HQ878169	JF269305	JF269504	JF270013	HQ878306	JF269794	JF269441	JF269640	JF269948	JF270149
<i>Valeriana wallrothii</i> Kreyer	Cult., National. Bot. Gard. Belgium. F. Billiet V782	AY792877	AY792940	AY794305	AY794305	HQ878307	JF269795	JF269442	JF269641	JF269949	JF270150
<i>Valerianella amarella</i> Krok	USA, Brown Co., Texas, Carr 12722 (TEX)	DQ354177	DQ354205	DQ354205	DQ354205	HQ878308	JF269796	JF269443	JF269642	JF269950	JF270151
<i>Valerianella carinata</i> Loisel.	Crete, Omalos Plateau, Chania Province., Cellinese 1001 (YU)	DQ354169	DQ354207	DQ354180	DQ354180	HQ878309	JF269797	JF269444	JF269643	JF269951	JF270152
<i>Valerianella coronata</i> (L.) DC.	Cult. Yale Univ. Bell #105 (YU)	AY792879	AY792941	AY794306	AY794306	HQ878310	JF269798	JF269445	JF269644	JF269952	JF270153
<i>Valerianella dentata</i> (L.) Loisel.	Cult. Yale Univ. Bell #106 (YU)	AY792880	AY792942	AY794307	AY794307	HQ878311	JF269799	JF269446	JF269645	JF269953	JF270154
<i>Valerianella discoidea</i> (L.) Loisel.	Spain, Tosantos, F. Amich & S. Bernardos (SALA 108752)	DQ354171	DQ354202	DQ354187	DQ354187	HQ878312	JF269800	JF269447	JF269646	JF269954	JF270155
<i>Valerianella eriocarpa</i> Desv.	Cult. Yale Univ. Bell #107 (YU)	AY792881	AY792943	AY794308	AY794308	HQ878313	JF269801	JF269448	JF269647	JF269955	JF270156
<i>Valerianella florifera</i> Shinnery	USA, Texas, Fayette Co., Carr 12663 (TEX)	DQ354178	DQ354206	DQ354190	DQ354190	HQ878314	JF269802	JF269449	JF269648	JF269956	JF270157

Table A.1 (continued)

Species	Collection details	ITS	trnL-F	matK	trnK	trnG	psbM-trnD	accD	ndhJ	rpoC1	ycf5
<i>Valerianella locusta</i> (L.) Laterr.	Cult. San Francisco State Univ., Patterson, 2001 (SFSU)	AY236194	AF447014	AY794309	AY794309	HQ878315	JF269803	JF269450	JF269649	JF269957	JF270158
<i>Valerianella locusta</i> (L.) Laterr.	Spain, Villafranca-Montes de Oca, F. Amich & S. Bernardos, (SALA 108755)	DQ354168	DQ354201	DQ354186	DQ354186	HQ878316	JF269804	JF269451	JF269650	JF269958	JF270159
<i>Valerianella muricata</i> M. Bieb. ex W. Baxt.	Spain, Tosantos, F. Amich & S. Bernardos (SALA 108750)	DQ354172	DQ354203	DQ354188	DQ354188	HQ878317	JF269805	JF269452	JF269651	JF269959	JF270160
<i>Valerianella pumila</i> DC	Cult. Yale Univ. Bell #108 (YU)	AY792882	AY792945	AY794310	AY794310	HQ878318	JF269806	JF269453	JF269652	JF269960	JF270161
<i>Valerianella radiata</i> Duf.,	USA, TEXAS, Bosque Co. Carr 9672 (TEX)	DQ354176	DQ354204	DQ354189	DQ354189	HQ878319	JF269807	JF269454	JF269653	JF269961	JF270162
<i>Valerianella radiata</i> Duf.,	Bosque Co. Texas, USA, Carr 9672 (TEX)	HQ878170	JF269305	JF269306	JF269307	HQ878320	JF269808	JF269455	JF269654	JF269962	JF270163
<i>Valerianella stenocarpa</i> Krok,	USA, Texas, Blanco Co. Carr 11642 (TEX)	DQ354175	DQ354211	DQ354191	DQ354191	HQ878321	JF269809	JF269457	JF269655	JF269963	JF270164
<i>Valerianella texana</i> Dyal,	USA, Texas, Llano Co. Carr 11052 (TEX)	DQ354173	DQ354209	DQ354193	DQ354193	HQ878322	JF269810	JF269456	JF269656	JF269965	JF270165
<i>Valerianella vesicaria</i> Moench	Cult. Yale Univ. Bell #109 (YU)	AY792883	AY792946	AY794311	AY794311	HQ878323	JF269812	JF269458	JF269658	JF269966	JF270167

MP and ML in PAUP*. All ML searches assumed a GTR + I + Γ model of sequence evolution and a single underlying partition (see above). To assess whether certain alternative relationships among clades of *Valeriana* could be statistically rejected, we performed a series of approximately unbiased (AU) tests (Shimodaira, 2002) as implemented in CONSEL v. 0.1i (Shimodaira and Hasegawa, 2001) for the best ML topology and various alternative topologies that constrained the monophyly of the South American species.

We used a Bayesian method (Drummond et al., 2006) implemented in the program BEAST ver. 1.6.2 to estimate divergence times within Valerianaceae. Due to problems with convergence among individual Markov chains when simultaneously estimating divergence times and topology, we fixed the tree topology to estimate divergence times in BEAST. In our case, we used the ML tree from the partitioned RAXML search (see above). We performed two analyses similar to the maximum likelihood ones: (1) in the first, we assumed a single common model across the concatenated dataset, and (2) in a second analysis, in which we partitioned the data set by gene, we estimated separate rates and rate-change parameters for each partition. Bayes factors, as calculated in Tracer, favored the uncorrelated lognormal (UCLN) model for rate change over the strict clock model (see Nylander, 2004, and references therein).

We set the underlying model of molecular evolution to be GTR + I + Γ , for each of the individual genes. We also used the UCLN model, which allows for rates of molecular evolution to be uncorrelated across the tree. BEAST also allows for uncertainty in the age of calibrations to be represented as prior distributions rather than as strict/fixed calibration points. For each analysis, we initiated four independent MCMC analyses from starting trees with branch lengths that satisfied the priors on divergence times. A starting tree with branch lengths satisfying the fossil prior con-

straint was created using r8s v.1.7 with nonparametric rate smoothing (NPRS). For each MCMC analysis, we ran six independent chains for 100 million generations and assessed convergence and stationarity of each chain to the posterior distribution using Tracer v.1.3 (Drummond and Rambaut, 2003) and by plotting time series of the log posterior probability of sampled parameter values. After stationarity was achieved, we sampled each chain every 1000 steps until an effective sample size (ESS) of greater than 200 samples was obtained. If convergence between the independent chains was evident, we combined the samples from each run using Log-Combiner v.1.4.7 (part of the BEAST distribution).

Divergence times for Valerianaceae have been estimated in the broader context of Dipsacales evolution (Bell and Donoghue, 2005b). For the analyses here we set the age of the root node (i.e., the most recent common ancestor [mrca] of *Triplostegia* + Valerianaceae) to a uniform prior between 44 and 62 million years. These values represent a range in mean values obtained by Bell and Donoghue (2005b) across different dating estimation methodologies. Nevertheless, without a reliable fossil record divergence time estimation in Valerianaceae remains tentative.

2.3. Diversification analyses

We investigated patterns of diversification through time using the APE package (Paradis et al., 2004). We did this by plotting a lineage through time (LTT) plot for our MCC tree. To evaluate whether our data was significantly different from a pattern of constant diversification, we generated a null distribution of 10,000 trees under a pure-birth process assuming a constant diversification rate. To account for our incomplete taxon sampling, we assumed a total of 350 extant tips and then randomly sampled 142 tips (as was the case for our empirical dataset).

Table 1
Sequence characteristics.

	ITS	accD	matK	ndhJ	psbM-trnD	rpoC1	trnK intron	trnL IGS	trnG	ycf5
Length of aligned sequences	758	305	1245	419	613	596	1230	1059	637	304
# of variable characters	532	119	705	131	309	219	860	727	344	71
# of parsimony informative characters	396	68	462	75	212	137	585	499	249	47
Best fitting model of molecular evolution	GTR + I + Γ	HKY + I + Γ	GTR + Γ	GTR + I + Γ	GTR + Γ	GTR + I + Γ	GTR + Γ	GTR + Γ	GTR + Γ	GTR + I + Γ

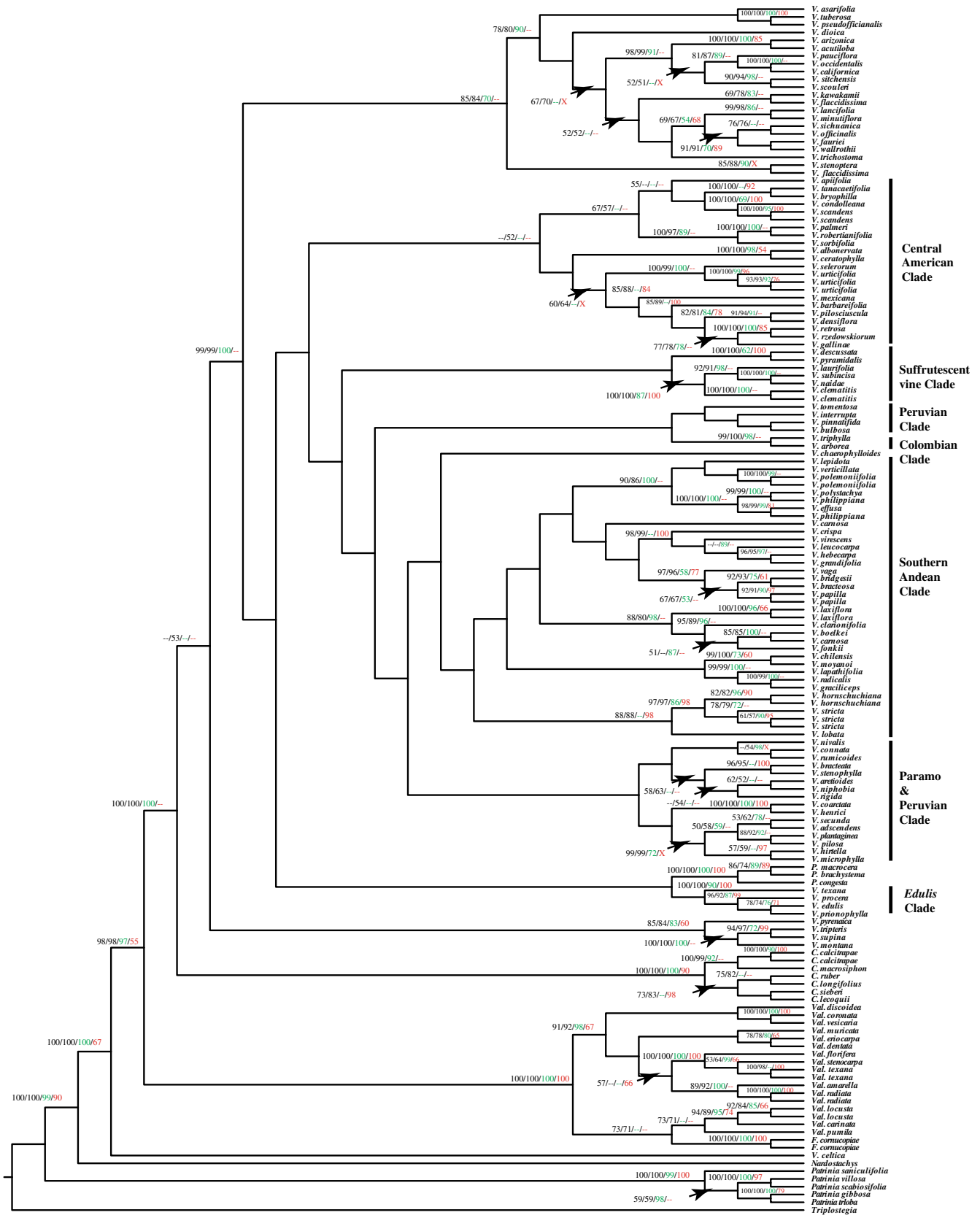


Fig. 1. Phylogeny of Valerianaceae. Maximum likelihood tree topology inferred with RAxML using a concatenated dataset. Numbers above the branches represent bootstrap values greater than 50% for both maximum likelihood concatenated, maximum likelihood partitioned, chloroplast (green), and ITS (red) datasets, respectively. *P.* = *Plectritis*; *C.* = *Centranthus*; *Val.* = *Valerianella*; *F.* = *Fedia*.

3. Results

3.1. Properties of gene regions

We were able to amplify and sequence all 10 regions for all 142 taxa. Statistics for individual regions are listed in Table 1. The results from parsimony and maximum likelihood bootstrap analyses of individual chloroplast regions are not presented here. A concatenated dataset consisted of 7166 aligned base pairs; of which 4027 were variable, and 2730 were parsimony informative. Each dataset showed some degree of among-site rate heterogeneity, and with the exception of the *accD* partition, all datasets seem to favor a general time reversible (GTR) model of base substitutions (see Table 1 for more detail).

3.2. Parsimony analyses

Maximum parsimony searches resulted in 319 equally parsimonious trees with lengths of 13,681 steps (CI = 0.448 RI = 0.659). Although a broader sampling of species was included in this study, the primary focus of our investigation was the phylogenetic and biogeographic relationships of South American taxa. The remainder of the paper focuses on this group in particular. All most parsimonious trees found a clade consisting of the southern Andean taxa, and a clade comprising mostly high elevation páramo and some puna species, and mostly low elevation species centered in Peru. In a strict consensus tree, these two South American clades then formed a dichotomy with a clade consisting of *Valeriana chaerophylloides*, *V. interrupta*, *V. rumicoides*, and the three sampled species of *Plectritis*. This clade was sister to the Colombian–Venezuelan clade. Bootstrap values for the relationship among these major clades were weak (<70%).

3.3. Likelihood analyses

Maximum likelihood searches of the combined data recovered log likelihood (*lnL*) scores of –92,792.42 and –91,811.64 for the

concatenated and partitioned analyses respectively. The tree with the best likelihood across the 100 runs of the concatenated data is presented in Fig. 1. The best trees from the two analyses were in strong agreement. In areas of the tree where topologies differed, they were not strongly supported (i.e., bootstrap values <50%). Like the maximum parsimony analyses, maximum likelihood searches recovered trees with the major South American clades (southern Andean, páramo–puna, Peruvian, and Colombian). Again, there was poor statistical support for these clades (with the exception of the Colombian clade) and the relationships among them. The majority of the South American taxa formed a monophyletic group that was sister to a clade of suffrutescent vines, whose members are distributed in both Central and South America, mainly below the treeline at mid-low elevations in forest habitats. Unlike parsimony analyses, likelihood analysis using the concatenated data placed the North American species of *Plectritis* sister to the *Edulis* clade, and not nested within the South American taxa.

Bootstrap values are presented (Fig. 1) for the likelihood analyses that looked exclusively at either the cpDNA data, or the ITS data. In few cases did we find major clades supported in one dataset and not the other. In general, when we found strong support for relationships for one dataset and not the other, it was for relationships near the tips of the tree. This suggests that the incongruence may be due to incomplete lineage sorting at one, or both of the loci. The overall lack of support from the combined dataset is more than likely due to the short (rapid) time frame at which this clade diversified.

3.4. Hypothesis testing

In all cases, tree topologies enforcing the monophyly of all the South American taxa were rejected ($p < 0.001$).

3.5. Divergence times

Divergence time estimates suggest the origin of the South American taxa occurring some 12–20 million years ago (mya), with

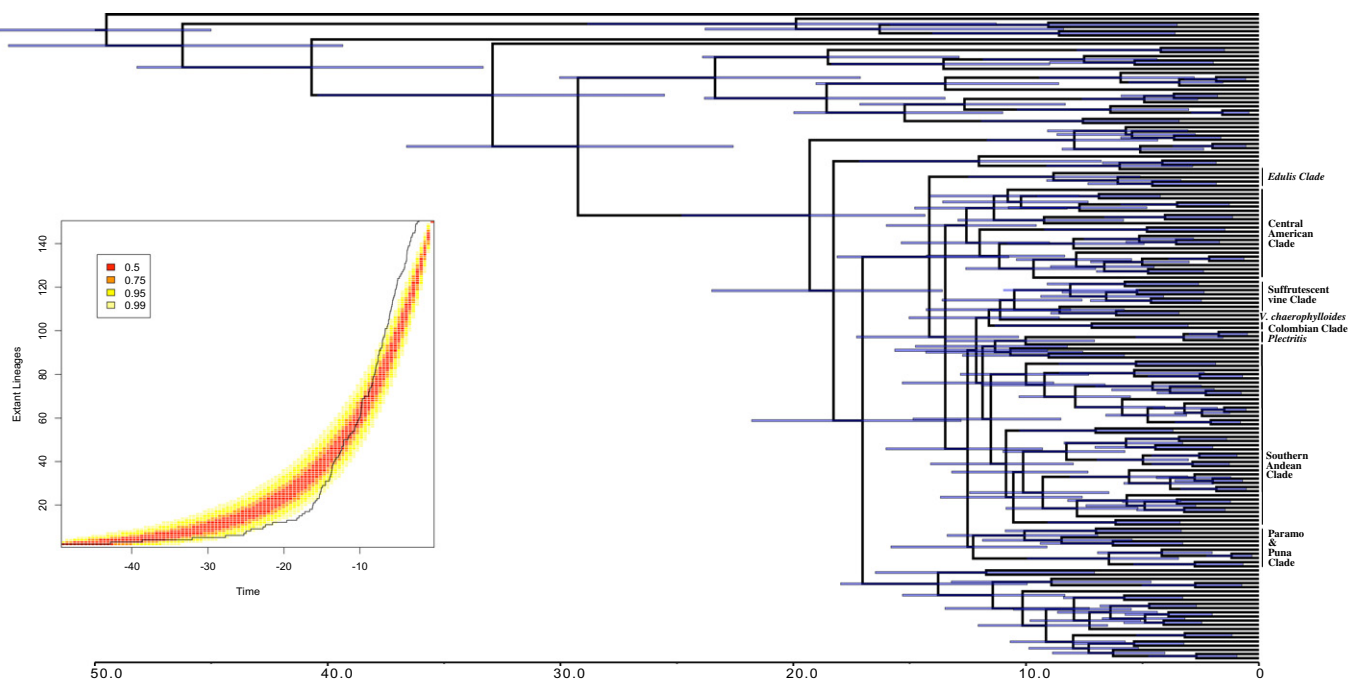


Fig. 2. Valerianaceae chronogram. (A) A chronogram inferred with BEAST using a dataset partitioned by gene and an uncorrelated log-normal (UCLN) model of rate change on the fixed partitioned topology inferred with RAxML (see text). (B) Lineage through time (LTT) plot of maximum clade credibility (MCC) phylogeny inferred with BEAST. Null distribution was generated using 10,000 simulated trees assuming a pure-birth model.

a mean age estimate from the posterior distribution of 15.7 mya. This is followed by a rapid diversification into the other major lineages; páramo–puna and Peruvian clade (14.1 mya), Southern Andean clade (13.7 mya), Colombian clade (8.1 mya), and the “suffrutescent vine” clades I and “suffrutescent vine” clade II at 7.8 and 13.8 mya, respectively. Ninety-five percent highest posterior densities (95% HPD) around mean age estimates were considerable, ranging from 8 to 10 million years.

3.6. Diversification analyses

A graphical presentation of diversification through time (or lineage through time: LTT) is presented in Fig. 2. The initial diversification of the Valerianaceae appears to be significantly lower than expected, followed by an increased uptick in diversification about 16 million years ago.

4. Discussion

Valerianaceae is a family amply represented in temperate latitudes in the northern and southern hemispheres as well as at tropical latitudes in the New World, and thus provides an outstanding opportunity for tracking patterns of plant diversification over a large geographical scale. This study is the most extensive attempt to infer the phylogeny of Valerianaceae, not only in number of taxa and genes sampled, but of the geographic areas covered; taxa from the southern Andes (Chile and Argentina) have been represented in a molecular phylogenetic analysis for the first time. Not surprisingly, some of the conclusions from this study are not significantly different to that of Bell and Donoghue (2005a) and Bell (2007) where sampling in South America was limited to the northern

and central Andes. The main focus of our discussion, however, will be on the placement of southern South American species of *Valeriana* and on how the uplift of the Andes and its impacts on vegetation differentiation and climatic barriers on the west and east slopes of the southern and central Andes has affected the distribution and diversification of *Valeriana*.

At the broad continental scale, a significant finding, confirming earlier work by Bell and Donoghue (2005a) and Bell (2007), is that South American species Valerianaceae do not form a monophyletic group. At least four colonizations of South America are suggested: two by widespread taxa found nested within the “Central American clade”; one corresponds to the “suffrutescent vine clade”; and the other to most high and low elevation South American taxa (see Fig. 1). The age estimates suggest that these four introductions of valerians into South America occurred sometime in the early Miocene (15.7 mya, 20–12 95% HPD). This date corresponds with the increase in diversification rates (16 mya) for Valerianaceae as a family in our lineage (Fig. 2). The Miocene was not only the time of mountain building in many parts of the world, but also of large global climate shifts in the Middle Miocene Climatic Optimum (MMCO) at around 16 mya (Flower and Kennett, 1994), followed by a reduction of 6–7 °C measured at high southern latitudes over the middle Miocene climate transition (14.2–13.8 mya) (Shevenell et al., 2004). There is some evidence for accelerated radiation rates across a range of taxa in the Cape flora of South Africa (Linder, 2008) that was also affected by major vegetation changes and aridification in the Miocene–Pliocene. More specifically, the dating here suggests that valerians first entered South America during the transition from the MMCO to much cooler temperatures at a time when the latitudinal and altitudinal differences in vegetation as seen today were already beginning to take shape.

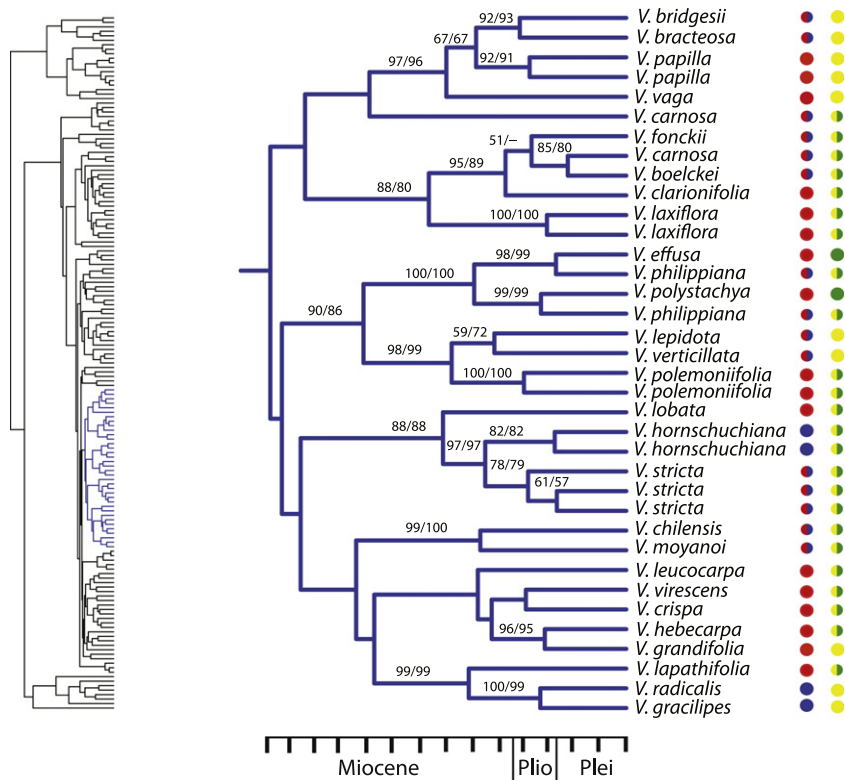


Fig. 3. Southern Andean clade. Zoom in on southern Andean clade from maximum likelihood phylogeny inferred from the partitioned dataset using RAxML with branch lengths transformed using the UCLN model in BEAST. Circles represent observed “altitudinal” and “longitudinal” distributions: Blue = alpine, Red = below alpine; Yellow = west of Cordillera, Green = east of Cordillera. Time scale is drawn in intervals of 1 million years. Plio = Pliocene; Plei = Pleistocene. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4.1. Phylogenetic placement and diversification of the southern South American valerians

Although the southern South American taxa form a clade in all analyses, support values (either bootstrap or posterior probabilities) are not high. This is also the case for more northern clades (e.g., the páramo–puna, Peruvian, and Colombian–Venezuelan clades; see Figs. 1–3) and given the wide geographic separation of some of these clades, begs an explanation. The short internal branches separating clades suggest that these lineages may have radiated rapidly (on the order of 2–3 million years). Inferring species relationships that result from such rapid diversification remain a challenge, and suggest that additional data (both in the form of new DNA markers, as well as more taxa) are required to infer evolutionary relationships of these taxa.

The southern Andean clade (Fig. 3) includes 9 species endemic to Chile distributed in the western Andes from Region VII to Region IV (*V. bridgesii*, *V. bracteosa*, *V. papilla*, *V. vaga*, *V. lepidota*, *V. verticillata*, *V. grandifolia*, *V. radicalis* and *V. graciliceps*). Two species are exclusive to the eastern Andes, *V. polystachya* which is distributed in Argentina, Uruguay and Brazil (Pampa province - Neotropical region) and *V. effusa* in Argentina and Bolivia, in the provinces of the Puna and Prepuna, which are closely related to the North Andean páramo province (Morrone, 2001). The remaining 17 species occur on both sides of the Andes in a variety of habitats including above treeline above and/or below tree-line, on lower slopes, in coastal areas, foothill valleys, Patagonian steppe and riparian habitats (Kutschker, 2009).

The time of appearance of *Valeriana* in the southern Andes (13.7 mya) corresponds with the transition from closed forested environments on the western side in central Chile to a more open Mediterranean woodland environment, which began around 15 mya in the Middle Miocene (Armesto et al., 2007). At this same time (16.5 mya) a transition from a mixture of closed forest and more open woodland to Patagonian Steppe with the concomitant expansion of C4 grasses was taking place on the eastern side of the Andes (Blisniuk et al., 2005) where cold dry environments with vegetation resembling today's Patagonian steppe had fully developed by the Late Miocene (Barreda and Palazzesi, 2007). Of the 17 species that occur on both the west and east sides of the southern Andes (Fig. 3), all with the exception of *V. hornschiuchiana* (found exclusively in the alpine) occur in lowland and/or mid-elevation habitats. Among these, 7 also reach the alpine, but in most cases only as far as the lower alpine. These distributional features, added to the fact that there are few exclusively alpine species on either sides of the Andes (e.g., *V. hornschiuchiana*, *V. radicalis*, *V. graciliceps*) suggest: (a) *Valeriana* entered southern South America originally as a lowland lineage; and (b) the Andes were not high enough, nor altitudinal differentiation of the vegetation sufficiently marked, to constitute an east–west barrier for the early spread of *Valeriana* in southern South America. With respect to uplift history, the southern Patagonian Andes had undergone 1.3 km of surface uplift by 16.5 mya (Blisniuk et al., 2005). In central Chile most uplift occurred after 10 mya (Farías et al., 2010). This uplift history and warmer than present temperatures suggests that a barrier to east–west migration did not exist at the time of initial diversification of *Valeriana* in the southern Andes.

Although it is difficult to pinpoint the exact area in the southern Andean region where *Valeriana* first appeared, the timing of development of the Arid Diagonal (Patagonia steppe, hyper-arid areas in the Atacama Desert and intervening high elevation areas) is believed to have played a major role in isolating the southern Andean clade from mixing with other more northerly clades. Different lines of evidence suggest that climate has been semi-arid in the present location of the Atacama Desert for as long as 150 mya (Hartley et al., 2005) with the Atacama being one of the oldest arid areas

in the world. However, development of a hyper-arid climate occurred more recently, although there is still some debate concerning the exact time. Hartley and Chong (2002) suggested that hyper-aridity did not set in until the late Pliocene. However this has been challenged by Rech et al. (2006) who came to the conclusion that the transition from semi-aridity to hyper-aridity occurred between 19 and 13 mya. Schlunegger et al. (2010) consider that existing and ongoing hyper-arid conditions in northern Chile date to 20 mya (see also Placzek et al., 2009). Thus the possibility of north–south migration across the present mid and lowland areas of the desert would have already have been difficult at the time of the arrival of *Valeriana* in the southern Andean region. The situation on the eastern side of the Andes, however, is less clear given the lower degree of aridity. Looking from the north, the general consensus seems to be that the northern part of the central Andes was uplifted one-third to one-half the present altitude by 10 mya (Graham, 2009). Thus the later date of differentiation of páramo and puna lineages with respect to South American alpine taxa would have impeded easy crossing of the driest part of the arid diagonal at around 24–25°S. Although our sampling of the more southerly puna taxa is limited, the taxonomic relationships of species occurring in the southern part of the puna suggests that they belong to the páramo–puna clade. The southern Andean clade of *Valeriana* contains only two upper alpine species (*V. radicalis*, sampled; *V. sedifolia* from the Patagonian alpine, not sampled). As mentioned earlier, all other alpine species tend to occur in the lower alpine belt and many just make it there and/or are found more abundantly below this zone. Thus a potential high elevation route for moving lineages northward across the driest part of the high Andes (24–25°S) also seems unlikely in *Valeriana* due to lack of differentiation of alpine-adapted lineages at an early stage in southern South America. In summary, given the timing of arrival of *Valeriana* in the southern Andes, especially on the western side of the Andes, as well as at high elevations, there would have been limited possibilities for migration and mixing of clades from the northern and southern Andean regions. Interestingly our “southern Andean clade” contains a recently derived species, *V. effusa*, that occurs only on the eastern flanks of the Andes below the puna belt in northern Argentina, suggesting a northward migration out of southern South America.

It has been suggested that the Tertiary uplift of the Andes may have generated vicariant diversification by isolating populations on either side (Chapman, 1917) or by influencing the lowland Amazon River network (Hoorn et al., 1995; Hooghiemstra and Van der Hammen, 1998), but could have also been a dispersal route for boreotropical lineages (Bell and Donoghue, 2005a) providing a refugia during climatic fluctuations in the Pleistocene (Hooghiemstra and Van der Hammen, 2004; Villagrán and Hinojosa, 2005). During this time the páramo and puna vegetation became widespread and *Valeriana* are believed to have been a common herb. Yet the taxa currently endemic to the páramo and puna region share an ancestry that dates to the Miocene (approx. 15 mya). The subsequent greater radiation of *Valeriana* at high elevations in the Northern and Central Andes compared to the southern Andes possibly relates to differences in time of appearance of high elevation habitat in tropical/subtropical and temperate Andes. In the southern South America, the tree line is much lower than in tropical and subtropical latitudes. Given that uplift of the Patagonian Andes occurred very early, the alpine belt (and its flora) in this part of the southern Andes would have appeared at a significantly earlier date. Under these circumstances, *Valeriana* lineages dispersing directly into páramo and puna by long-distance dispersal, or arriving via upward migration would have encountered a less competitive environment and more space for *in situ* radiations than those colonizing high elevations in southern South America around this time. This general principal (or variants of it) seems to pertain

to other plants groups in high elevation habitats that are thought to have arrived in South America by long-distance dispersal (e.g., *Lupinus* and *Astragalus*).

In summary, the southern Andean clade of *Valeriana* provides a model for the study of the biogeography of this region. Without a good fossil record, dating specific branching events in the phylogeny is problematic. Our data suggest that species of *Valeriana* have been in the South American continent for some time (>13 MY), and have potentially exploited new niche opportunities allowing for the radiation we see today. Regardless of the time frame for the radiation, the uptick in rate of diversification of Valerianaceae seems to be correlated with dispersal from Central to South America (Bell and Donoghue, 2005b; Moore and Donoghue, 2007). However, results from our relative cladogenesis test suggest that the explosion in diversity within the South American Valerianaceae may not have occurred until 3–5 million years after initial colonization of the continent. These data tend to suggest that the high species diversity of Valerianaceae in South America is the result of multiple, smaller radiations such as the one in the southern Andes, that may or may not be geographically isolated. These smaller radiations may also be driven by species moving into new habitats (migration from a temperate to a more Mediterranean-style climate).

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Appendix A

See Table A.1.

References

- Armesto, J.J., Arroyo, M.T.K., Hinojosa, L.F., 2007. The Mediterranean Environment of central Chile. In: Veblen, T.T., Young, K.R., Orme, A.R. (Eds.), *The Physical Geography of South America*. Oxford University Press, New York, pp. 184–199.
- Arroyo, M.T.K., Squeo, F.A., Armesto, J.J., Villagrán, C., 1988. Effects of aridity on plant diversity in the northern Chile Andes: results of a natural experiment. *Ann. Miss. Bot. Gard.* 75, 55–78.
- Arroyo, M.T.K., Dudley, L.E., Pliscoff, P., Cavieres, L.A., Squeo, F.A., Marticorena, C., Rozzi, R., 2010. A possible correlation between the altitudinal and latitudinal ranges of species in the high elevation flora of the Andes. In: Spehn, E.M., Corner, C. (Eds.), *Data Mining for Global Trends in Mountain Biodiversity*. CRC Press, Taylor and Francis, Boca Raton, pp. 39–47.
- Backlund, A., 1996. *Phylogeny of the order Dipsacales*. PhD Thesis. Uppsala University, Uppsala.
- Barreda, V., Palazzesi, L., 2007. Patagonian vegetation turnovers during the Paleogene–Early Neogene: origin of arid-adapted floras. *Bot. Rev.* 73 (1), 31–50.
- Barthlott, W., Mutke, J., Rafiqpoor, M.D., Kier, G., Kreft, H., 2005. Global centres of vascular plant diversity. *Nova Acta Leopold.* 92, 61–83.
- Bell, C.D., 2004. Preliminary phylogeny of Valerianaceae (Dipsacales) inferred from nuclear and chloroplast DNA sequence data. *Mol. Phylogenet. Evol.* 3, 340–350.
- Bell, C.D., 2007. Phylogenetic placement and biogeography of the North American species of *Valerianella* (Valerianaceae: Dipsacales) based on chloroplast and nuclear DNA. *Mol. Phylogenet. Evol.* 44, 929–941.
- Bell, C.D., Donoghue, M.J., 2005a. Phylogeny and biogeography of Valerianaceae (Dipsacales) with special reference to the South American valerians. *Org. Div. Evol.* 5, 147–159.
- Bell, C.D., Donoghue, M.J., 2005b. Dating the Dipsacales: comparing models, genes, and evolutionary implications. *Am. J. Bot.* 92, 284–296.
- Blisniuk, P.M., Stern, L.A., Chamberlain, C.P., Idelman, B., Zeitler, K., 2005. Climatic and ecological changes during Miocene surface uplift in the southern Patagonian Andes. *Earth Planet. Sci. Lett.* 230, 125–142.
- Borsini, O.E., 1966. Valerianáceas de Chile. *Lilloa* 32, 375–476.
- Chapman, F.M., 1917. The distribution of bird-life in Colombia. *Bull. Am. Mus. Nat. Hist.* 36, 1–729.
- Drummond, A.J., Rambaut, A., 2003. BEAST: Bayesian Evolutionary Analysis Sampling Trees. <<http://evolve.zoo.ox.ac.uk/Beast/>>.
- Drummond, A.J., Ho, S.W.Y., Phillips, M.J., Rambaut, A., 2006. Relaxed phylogenetics and dating with confidence. *PLoS Biol.* 4, 699–710.
- Eriksen, B., 1989a. Notes on generic and infrageneric delimitation in the Valerianaceae. *Nord. J. Bot.* 9, 179–187.
- Eriksen, B., 1989b. Valerianaceae. In: Harling, G., Andersson, L. (Eds.), *Fl. Ecuador*, vol. 34, pp. 1–59.
- Ezcurra, C., 2002. Phylogeny, morphology, and biogeography of *Chuquiraga*, an Andean–Patagonian Genus of Asteraceae–Barnadesioideae. *Bot. Rev.* 68 (1), 153–170.
- Fariás, M., Comte, D., Charrier, R., Martinod, J., Claire, D., Tassara, A., Tapía, F., Fock, A., 2010. Crustal-scale structural architecture in central Chile based on seismicity and surface geology: implications for Andean mountain building. *Tectonics*, 29, TC3006. doi:10.1029/2009TC002480.
- Felsenstein, J., 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39, 783–791.
- Flower, B.P., Kennett, J.P., 1994. The middle Miocene climatic transition: East Antarctic ice sheet development, deep ocean circulation and global carbon cycling. In: Cronin, T., Ogasawa, K., Wolfe, J. (Eds.), *Cenozoic Climate and Paleoclimatographic Changes in the Pacific Region*. Palaeo, Palaeo, Palaeo, vol. 108, pp. 537–555.
- Ford, C.S., Ayres, K.L., Toomey, N., Haider, N., Van Alphen Stahl, J., Kelley, L.J., Wikstrom, N., Hollingsworth, P.M., Duff, R.J., Hoot, S.B., Cowan, R.S., Chase, M.W., Wilkinson, M.J., 2009. Selection of candidate coding DNA barcoding regions for use in land plants. *Bot. J. Linn. Soc.* 159, 1–11.
- Gansser, A., 1973. Facts and theories on the Andes. *J. Geol. Soc.* 129, 93–131.
- Garleff, K., Schabitz, F., Stingl, H., Veit, H., 1991. Jungquartäre Landschaftsentwicklung und Klimageschichte beiderseits der Ariden Diagonaler Südamerikas im Jungquartär. *Bamberger Geogr. Schr.* 11, 359–394.
- Graham, A., 2009. The Andes: a geological overview from a biological perspective. *Ann. Miss. Bot. Gard.* 96, 371–385.
- Gregory-Wodzicki, K.M., 2000. Uplift history of the Central and Northern Andes: a review. *Geo. Soc. Am. Bull.* 7, 1091–1105.
- Hamilton, M.B., 1999. Four primers pairs for the amplification of chloroplast intergenic regions with intraspecific variation. *Molec. Ecol.* 8, 521–525.
- Hartley, A.J., Chong, G., 2002. A late Pliocene age for the Atacama Desert: implications for the desertification of western South America. *Geology* 30, 43–46.
- Hartley, A.J., Chong, G., Houston, J., Mather, A.E., 2005. 150 Million years of climate stability: evidence from the Atacama Desert, northern Chile. *J. Geol. Soc.* 162 (3), 421–424.
- Herskovitz, M.A., Arroyo, M.T.K., Bell, C.D., Hinojosa, L.F., 2006. Phylogeny of *Chaetanthera* (Asteraceae: Mutisieae) reveals both ancient and recent origins of the high elevation lineages. *Mol. Phylogenet. Evol.* 41, 594–605.
- Hidalgo, O., Garnatje, T., Susanna, A., Mathez, J., 2004. Phylogeny of Valerianaceae based on *matK* and ITS markers with reference to *matK* individual polymorphism. *Ann. Bot.* 93, 283–293.
- Hooghiemstra, H., Van der Hammen, T., 1998. Neogene and Quaternary development of the neotropical rain forest: the forest refugia hypothesis, and a literature overview. *Earth Sci. Rev.* 44, 147–183.
- Hooghiemstra, H., Van der Hammen, T., 2004. Quaternary ice-age dynamics in the Colombian Andes: developing an understanding of our legacy. *Phil. Trans. Roy. Soc. Lond. B* 359, 173–181.
- Hoorn, C., Guerrero, J., Sarmiento, G.A., Lorente, M.A., 1995. Andean tectonics as a cause of changing drainage patterns in Miocene northern South America. *Geology* 23, 237–240.
- Hoot, S.B., Kramer, J., Arroyo, M.T.K., 2008. Phylogenetic position of the South American dioecious genus *Hamadryas* and related Ranunculaceae (Ranunculaceae). *Int. J. Plant Sci.* 169, 433–443.
- Hughes, C., Eastwood, R., 2006. Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proc. Natl. Acad. Sci. U.S.A.* 103 (27), 10334–10339.
- Jaramillo, C., Rueda, M.J., Mora, G., 2006. Cenozoic plant diversity in the Neotropics. *Science* 311 (5769), 1893–1896.
- Kutschker, A., 2009. *Valeriana* L. (Valerianaceae) en Sudamérica Austral: taxonomía, aspectos biogeográficos y fitoquímicos. Tesis Doctoral. Universidad Nacional de la Patagonia SJB, Comodoro Rivadavia.
- Lee, C., Wen, J., 2004. Phylogeny of *Panax* using chloroplast *trmC*–*trnD* intergenic region and the utility of *trmC*–*trnD* in interspecific studies of plants. *Molec. Phylogenet. Evol.* 31, 894–903.
- Linder, P., 2008. Plant species radiations: where, when, why? *Phil. Trans. Roy. Soc. Lond. B* 363 (1506), 3097–3105.
- Maddison, D.R., Maddison, W.P., 2000. *MacClade Version 4: Analysis of Phylogeny and Character Evolution*. Sinauer Associates, Sunderland Massachusetts.
- Moore, B.R., Donoghue, M.J., 2007. Correlates of diversification in the plant clade Dipsacales: geographic movement and evolutionary innovations. *Am. Nat.* 170, S29–S55.
- Morrone, J.J., 2001. *Biogeografía de América Latina y el Caribe. M&T-Manuales & Tesis SEA. Sociedad Entomológica Aragonesa*, Zaragoza.
- Nylander, J.A.A., 2004. *MrModelTest v2*. Program Distributed by the Author. Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden.

- Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20, 289–290.
- Placzek, C., Quade, J., Betancourt, J.L., Patchett, P.J., Rech, J.A., Latorre, C., Matmon, A., Holmgren, C., English, N.B., 2009. Climate in the dry central Andes over geologic, millennial, and interannual timescales. *Ann. Miss. Bot. Gard.* 96, 386–397.
- Ramos, V.A., Ghiglione, M.C., 2008. Tectonic evolution of the Patagonian Andes. In: Rebasca, J. (Ed.), *The Late Cenozoic of Patagonia and Tierra del Fuego*. Elsevier, Oxford, pp. 57–71.
- Rauscher, J.T., 2002. Molecular phylogenetics of the *Espeletia* complex (Asteraceae): evidence from nrDNA ITS sequences on the closest relatives of an Andean adaptative radiation. *Am. J. Bot.* 89, 1074–1084.
- Rech, J.A., Currie, B.S., Michalski, G., Cowan, A.M., 2006. Neogene climate change and uplift in the Atacama Desert, Chile. *Geology* 34 (9), 761–764.
- Sánchez-Baracaldo, P., 2004. Phylogenetics and biogeography of the neotropical fern genera *Jamesonia* and *Eriosorus* (Pteridaceae). *Am. J. Bot.* 91, 274–284.
- Scherson, R.A., Vidal, R., Sanderson, M.J., 2008. Phylogeny, biogeography, and rates of diversification of New World *Astragalus* (Leguminosae) with an emphasis on South American radiations. *Am. J. Bot.* 95, 1030–1039.
- Schlunegger, F., Kober, F., Zeilinger, G., von Rotz, R., 2010. Sedimentary-based reconstructions of paleoclimate changes in the Central Andes in response to the uplift of the Andes, Arica region between 19 and 21°S latitude, northern Chile. *Int. J. Earth Sci (Geol. Rundsch)* 99 (Suppl. 1), S123–S137.
- Shevenell, A.E., Kennett, J.P., Lea, W.L., 2004. Middle Miocene Southern Ocean cooling and Antarctic cryosphere expansion. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 108, 537–555.
- Shimodaira, H., 2002. An approximately unbiased test of phylogenetic tree selection. *Syst. Biol.* 51, 492–508.
- Shimodaira, H., Hasegawa, M., 2001. CONSEL: for assessing the confidence of phylogenetic tree selection. *Bioinformatics* 17, 1246–1247.
- Simpson, B.B., Todzia, C.A., 1990. Patterns and processes in the development of the high Andean flora. *Am. J. Bot.* 77, 1419–1432.
- Simpson, B.B., Arroyo, M.T.K., Sipe, S., de Moraes, M.D., McDill, J., 2009. Phylogeny and evolution of *Perezia* (Asteraceae: Mutisieae: Nassauviinae). *J. Syst. Evol.* 47, 431–443.
- Stamatakis, A., 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22, 2688–2690.
- Swofford, D.L., 2002. PAUP*: Phylogenetic Analysis Using Parsimony (* and Other Methods), Version b4. Sinauer Associates, Sunderland, Massachusetts.
- Villagrán, C., Hinojosa, L.F., 1997. Historia de los bosques del sur de Sudamérica, Análisis fitogeográfico. *Rev. Chil. Hist. Nat.* 70, 241–267.
- Villagrán, C., Hinojosa, L.F., 2005. Esquema biogeográfico de Chile. In: Bousquets, J.L., Morrone, J.J. (Eds.), *Regionalización biogeográfica en Iberoamérica y tópicos afines*. Ediciones de la Universidad Nacional Autónoma de México, Jiménez Editores, México.