Gayana Bot. 63(1): 13-74, 2006 ISSN 0016-5301

RIBOSOMAL AND CHLOROPLAST DNA EVIDENCE FOR DIVERSIFICATION OF WESTERN AMERICAN PORTULACACEAE IN THE ANDEAN REGION

EVIDENCIA DE ADN RIBOSOMAL Y DEL CLOROPLASTO PARA LA DIVERSIFICACION DE LAS PORTULACACEAS DE AMERICA OCCIDENTAL EN LA REGION ANDINA

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ABSTRACT

Sequences of the ribosomal DNA internal transcribed spacer (ITS) region and the chloroplast DNA *ycf*3-*trn*S intergenic spacer were determined for 183 samples representing Chilean and non-Chilean taxa of western American Portulacaceae and their outgroups. The data refine previous inferences of generic circumscriptions and interrelations. In particular, the data reveal that an earlier circumscription of *Cistanthe* Spach is polyphyletic and also reveal a North American clade comprising *Claytonia* L., *Lewisia* Pursh, *Lewisiopsis* R. Govaerts, and *Montia* L. Within the South American genera, two patterns emerge from the data: (1) in some cases, interspecific divergence is remarkably low given the markers employed and estimated number of species; and (2) where divergence of one or both markers offer phylogenetic resolution, there is conflict between them and/or with morphology. The patterns can be evaluated in terms of two phenomena: (1) morphological/ecological radiation proceeding much faster than sequence divergence; and (2) frequent hybridization. In the latter case, the gene tree patterns may distort the true timing and cladistic pattern of morphological and ecological diversification. At present, the degree to which evidence for hybridization among the Chilean Portulacaceae will prove to be the rule or the exception is unclear. Nonetheless, spatial and temporal ecological patterns in Chile generally favor hybrid formation and persistence.

KEYWORDS: Portulacaceae, Chile, ITS, *ycf*3-*trn*S, hybridization.

RESUMEN

Se determinaron las secuencias del espaciador interno (ITS) del ADN ribosomal y del espaciador intergénico de *ycf*3-*trn*S del ADN del cloroplasto para 183 muestras de taxas, chilenos y no chilenos, de Portulacaceae de América occidental, y sus grupos externos. Los datos permiten refinar previas inferencias sobre la circunscripción e interrelaciones de los géneros estudiados. En particular estos datos revelan que una circunscripción anteriormente publicada de *Cistanthe* Spach es polifilética y también revelan la existencia de un clado norteamericano compuesto por *Claytonia* L., *Lewisia* Pursh, *Lewisiopsis* R. Govaerts, and *Montia* L. De los datos de los géneros sudamericanos surgieron dos patrones: (1) en algunos casos la divergencia interespecífica es notablemente baja dado los marcadores empleados y el número estimado de especies; y (2) en cuanto la divergencia de uno o de los dos marcadores ofrecen resolución filogenética, existen conflictos entre ellos y/o entre la morfología. Estos patrones pueden ser interpretados en términos de dos fenómenos: diversificación morfológica/ecológica siguiendo más rápida que la divergencia en las secuencias; y (2) frecuente hibridación. Este alto grado de hibridación sugiere que el árbol filogenético molecular puede representar mal el patrón temporal, morfológico y ecológico de diversificación de estas especies. Al presente no es claro si la hibridación es una regla o una excepción entre las Portulacaceae chilenas. No obstante, en Chile las condiciones ecológicas, espaciales y temporales, son en general favorables para la formación y persistencia de híbridos.

PALABRAS CLAVES: Portulacaceae, Chile, ITS, *ycf*3-*trn*S, hibridización.

INTRODUCTION

The term "western American Portulacaceae" refers to a group of ca. 120-150 species of closely interrelated genera of traditional Portulacaceae (e.g., *sensu* Carolin 1993) distributed predominantly in the Americas from the cordillera westward to the Pacific coast (Hershkovitz 1991a, 1993). Genera included in this group are *Calandrinia* Kunth, *Calyptridium* Nutt., *Cistanthe* Spach, *Claytonia* L., *Lenzia* Phil., *Lewisia* Pursh, *Lewisiopsis* Govaerts (= *Cistanthe* sect. *Strophiolum* Hershk.), *Montia* L., and *Montiopsis* Kuntze. Monophyly of the group remains unresolved and depends upon the relations of *Phemeranthus* Raf., distributed mainly in North America from the cordillera eastward, and the Australian calandrinias (*Parakeelya* Hershk.; these species should be classified in *Rumicastrum* Ulbr. according to J. G. West, pers. comm., cf. Carolin 1987, 1993). However, molecular evidence indicates that these taxa together form a well-supported clade within the portulacaceous alliance (Hershkovitz & Zimmer 1997, 2000).

Species diversity of western American Portulacaceae is divided approximately equally between North America and South America, and much of it is concentrated in California and northern Chile. Notwithstanding several amphitropical disjunctions, most of the genera can be characterized as predominantly or completely North American or South American. However, the present data indicate that the largely South American *Cistanthe* sect. *Amarantoides* (Reiche) Carolin ex Hershk. and *Cistanthe* sect. *Philippiamra* (Kuntze) Hershk. are more closely related to the North American *Calyptridium* than to the largely South American *Cistanthe* sect. *Cistanthe*. The data suggest that the first two sections may be preferably classified in *Calyptridium*. However, this and other nomenclatural actions supported by the present analyses will be deferred pending revision of type material.

This work presents analysis of diversity of both ITS and *ycf*3-*trn*S spacer sequences. ITS, a typically 600 base-pair sequence, is the most widely applied molecular marker in interspecific phylogenetic analyses in angiosperms (Hershkovitz *et al.* 1999). The *ycf*3-*trn*S intergenic spacer separates an open reading frame of unknown function (*ycf*3) from the chloroplast transfer RNA for serine bearing the anticodon GGA (*trn*S-GGA). These sequences have been determined for ca. 275 samples of western American Portulacaceae, ca. 145 of which represent South American (mostly Chilean) samples. The present analyses incorporate 183 of these samples, emphasizing the South American samples but including sufficient samples from outside this region to provide appropriate phylogenetic reference. Superficial examination of some of the gene trees suggests evolutionary radiation too rapid to reconstruct cladistically. This would be a reasonable scenario given evidence of relatively recent, rapid, and catastrophic events that shaped modern Chilean habitats (Arroyo *et al.* 1988; Villagrán 1995). More detailed examination of the data in light of field observations, however, reveals evidence for an alternative scenario, in which the gene trees reflect not rapid diversification, but effective homogenization of the marker sequences via gene flow, thus obscuring a pattern of ecological and morphological specialization that occurred over a longer historical period. This paper presents evidence for both of these models and consequent implications for diversification of the Chilean flora.

MATERIALS AND METHODS

Plant materials

Table I provides collection data for the analyzed specimens. For field collections, above-ground parts (variously, leaves, stems, flower buds, but not open flowers) from one or a few identical individuals, free from insect or other apparent damage or infection, were washed thoroughly with tap water and dried in clean paper towels prior to silica preservation. Herbarium specimens were prepared at the same time. Floristic, monographic, and other taxonomic references (see below) and museum specimens were used to identify the materials. For a variety of reasons, identification of many of the Chilean samples of *Cistanthe* was difficult and in many cases not successful: (1) of all the South American taxa, only *Montiopsis* subg. *Montiopsis* has been monographed (Ford 1992); (2) the most recent comprehensive floristic revision of the Chilean taxa is that of Reiche (1898, 1905); this treatment notes numerous taxonomic problems and, nonetheless, its reliability is questionable given the degree of discordance with the monograph of Ford (1992); (3) succulent members of *Cistanthe* preserve poorly as

herbarium specimens; (4) type specimens of many *Cistanthe* species are missing at SGO, and many of those present are too poorly preserved to aid in identification; (5) several types of *Cistanthe* species represent populations now extinct in areas later urbanized (and current observations of this group indicate that localized populations are morphologically distinctive); (6) as noted by Ford-Werntz & Peralta (2002), infrequency and irregularity of rain in the north of Chile hampers efforts to relocate populations from which taxa were described; and (7) notwithstanding the above, several collections from between 1998-2002 do not appear to correspond with any described taxa. The difficulty in identifying the species of the succulent taxa has been noted by Hershkovitz (1991b) and Ford-Werntz & Peralta (2002). The latter synopsis (without key) of *Cistanthe* includes 22 species of Chile/Argentina/Peru but also a list of names of 28 taxa of unresolved application "where more studies as to relationship and circumscription are necessary before the appropriate combinations or synonymizations can be published". In fact, as noted in the discussion, the historical taxonomic difficulties and present inability to identify numerous specimens can be interpreted as an expectation of the diversification scenarios proposed.

Eighteen of the DNA samples are not associated with voucher specimens. Data associated with such specimens should be interpreted circumspectfully, but not dogmatically. Several vouchers for DNA samples published on previously (Hershkovitz & Zimmer 1997, 2000) appear to have been accidentally discarded. Other DNA samples represent cultivated material that was accessioned but not vouchered. The unvouchered materials are principally those of the outgroup and North American taxa and are hence peripheral to the theme of the present work. In any case, all samples in the present work have some degree of documentation verifying their source and identity. Furthermore, I have handled and determined nearly all of the plant materials personally and have performed all of the DNA extractions.

Molecular methods

DNA was extracted using the DNeasy Mini protocol (Quiagen, Inc.) and quantified using agarose gels. In some cases, additional purification was necessary and accomplished via either PEG precipitation or by a silica suspension (Boyle & Lew 1995). The PEG protocol used equal volumes of sample and a fresh (< 2 weeks at 4C) solution of 20% PEG 8000 (Sigma)/ 2.5M NaCl. Following thorough mixing, the solution is maintained at 37 °ðC for ca. 20 min, followed by high-speed centrifugation, careful (and thorough) removal of the supernatant, three washes of the pellet with ca. 80% EtOH, drying, and resuspension in water or AE buffer from the DNeasy kit (Quiagen). To minimize the risk of cross contamination, especially by PCR products, extraction supplies and reagents, as well as PCR reagents, were maintained separately from those of post-PCR procedures. In addition, all surfaces (including equipment, pipettors, and reagent containers) contacted during extraction and PCR reaction preparation were thoroughly washed with 10% chlorine bleach solution prior to performing these procedures. In several cases, DNA was extracted from the herbarium specimen corresponding to the previously-extracted silica specimen in order to confirm sequencing results (Table I).

Amplification of ITS for sequencing generally followed Hershkovitz and Zimmer (2000), i.e., double-strand amplification followed by separate asymmetric amplification of each strand using primers internal to the first. The amplification and sequencing primers are listed in Table 2. The amplification products were sequenced according to the Big-Dye Dye Terminator (Applied Biosystems) or DYEnamic ET Terminator (Pharmacia) cycle sequencing protocols. Sequencing reactions were electrophoresed on a 3100 Gene Analyzer (Applied Biosystems). Most specimens were sequenced in both directions. Exceptions were made for chromatograms that were especially clean in a single direction and which matched completely those of samples sequenced in both directions. Many sequences of *Cistanthe* samples were sequenced in essentially one direction, because an internal poly-T microsatellite-like repeat obliterated clarity of the downstream signal.

Phylogenetic analysis

Phylogenetic analyses were performed using PAUP 4.0 (Swofford 2002) version b10. Analyses were undertaken at the level of western American Portulacaceae and at the level of each of the South American clades. ITS and *ycf*3-*trn*S sequences were analyzed separately and in combination. The

intergeneric analysis was performed as an update of Hershkovitz & Zimmer (2000) with additional critical samples and a cpDNA sequence. This analysis included representative sequences of the South American genera analyzed in greater detail at the infrageneric level and fewer representative sequences of the North American genera analyzed in greater detail elsewhere (Hershkovitz, submitted ms.). This analysis provides an outgroup perspective relative to each of the primarily South American genera. Alignment was optimized manually. Unambiguous gaps were treated as independent characters. Up to four unordered states were permitted for superposed (multistate) gaps. In general, when more than four gap states occurred, the alignment was ambiguous. Length variable regions that could not be aligned unambiguously were scored as unknown in all sequences or at least in the sequences that could not be unambiguously aligned. Likewise, substitutions in length variable regions were scored as substitutions among the alignable sequences and as unknown in the unalignable sequences. Unweighted parsimony and associated bootstrap (500 replicates) were applied with stepwise addition and tree bisection-reconnection. Bootstrap replicates held ten trees at each addition step with maxtrees at 100 trees per replicate. Partition homogeneity tests (500 replicates, maxtrees = 100) were performed to evaluate conflict in the two data sets. To visualize the total conflict in the combined data, split decomposition was performed using SplitsTree 2.4 (Huson 1997) using «p» distances and refining for the maximum number of possible quartets.

Maximum likelihood and minimum evolution methods were considered unnecessary for the present analyses. Previous analyses involving these taxa (Hershkovitz & Zimmer 1997, 2000) found that all methods yielded largely unresolved intergeneric-level relations. At the infrageneric level, both the number of sequences and substitutions are very low, so that the variance in estimates of Markov model substitution parameters used in distance and maximum likelihood analysis would be very high (e.g., Posada 2001). Likewise, the short branch lengths at the infrageneric level and separating several poorly resolved intergeneric nodes can mislead current implementations of Bayesian likelihood methods (Suzuki *et al.* 2002; Cummings *et al.* 2003; P. O. Lewis, oral comm., 2003). In addition, practical implementations of distance and likelihood analysis cannot take into account length variation characters, which provide a considerable proportion of the information, especially in the *ycf*3-*trn*S sequences. Finally, statistical inconsistency that results from using inaccurate substitution models is expected mainly when divergence is high, e.g., when there are long branches.

RESULTS

ITS AND *YCF*3-*TRN*S SEQUENCE CHARACTERISTICS

Variability of the ITS region and *ycf*3-*trn*S spacer are compared in Table III. Infra-and intergeneric ITS sequence divergences were calculated by Hershkovitz & Zimmer (2000) this table is not reproduced here. Corrected intergeneric ITS sequence divergence (using ML distances as in Hershkovitz & Zimmer 2000) among the South American genera is generally on the order of 5%, except for that of *Calandrinia* sect. *Calandrinia*. Divergences of the latter to the other genera ranges from 10-13%. Maximum ITS divergence within the relevant taxa are on the order of: 4% (*Calandrinia* sect. *Calandrinia*); 2% (*Calandrinia* sect. *Acaules* Reiche); 1% (*Cistanthe* sect. *Cistanthe*, *Montiopsis* subg. *Montiopsis* and *Montiopsis* subg. *Dianthoideae* (Reiche) D.I.Ford); and 0.5% (*Cistanthe* sections *Amarantoides* and *Philippiamra*). Thus, net rates from a common ancestor are especially higher in the first taxon and especially low in the last. Divergences within taxa of the *ycf*3-*trn*S sequences are approximately in proportion to the number of variable sites relative to ITS.

As noted previously (Hershkovitz & Zimmer 2000), the variable regions of ITS in western American Portulacaceae are GC-rich except for *Claytonia* and *Montia*, in which the base bias may be absent or AT-rich. The *ycf*3-*trn*S sequences, as is typical of cpDNA spacers in general, are AT-rich, and include numerous poly-A, poly-T, and poly-AT repeats 6-20 bases in length. However, the aligned parsimony-informative sites of the *ycf*3-*trn*S sequences are not AT-, but rather GC-rich: 50-60% in these exemplars and 54% on average. Relative to ITS, variation in the *ycf*3-*trn*S sequences is more frequently in length rather than base substitution. At the intergeneric level, the

*ycf*3-*trn*S spacer sequences include one region, ca. 150 bases downstream of the 3' end and 0-50 bases long, that is unalignable between genera, although largely alignable within genera. At the infrageneric level, the length differences tend to be more easily aligned than in ITS. The length differences commonly correspond to discrete direct repeats of three or more bases. In some cases, length variation occurs in a poly-A and/or –T region, resembling polymorphic microsatellite loci. The majority of the repeat variation observed involved two states or two common states and up to two additional rare states. A poly-T repeat varying in length from 11 to 17 bases occurs in the *ycf*3-*trn*S sequences of samples of *Cistanthe* sect. *Cistanthe*. Because of the high variability and difficulty determining the exact number of Ts in the longer repeats, this region was not included in the phylogenetic analysis.

Intergeneric-level analysis

Figures 1 and 2 show sample parsimony trees and parsimony bootstrap values for the ITS and *ycf*3-*trn*S data, respectively. Figure 3 shows the parsimony bootstrap consensus for the combined data. The ITS tree is considerably longer, indicating an overall higher rate of evolution. However, the ITS tree also has much lower consistency and retention indices than the *ycf*3-*trn*S data, i.e., much of the length difference is in apparently homoplasious changes. The *ycf*3-*trn*S data actually yield a larger number of branches with higher bootstrap proportions. The overall number of branches with higher bootstrap proportions is greater in the combined analysis than in either data set alone. However, individual conflicts between the two data sets can be discerned, as diagnosed by a reduction of particular bootstrap proportions in the combined analysis versus either of the separate analyses.

Circumscriptions of supraspecific taxa. Both ITS and *ycf*3-*trn*S trees show a backbone structure similar to that in the previously published ITS-based analysis (Hershkovitz & Zimmer 2000). Monophyly of *Cistanthe sensu* Hershkovitz 1991a is strongly refuted by the combined data. Each tree shows > 70% bootstrap proportions for the circumscriptions of *Cistanthe* sect. *Cistanthe*, *Lewisia*, *Claytonia*, *Montiopsis*, *Montiopsis* subg. *Montiopsis*, *Calandrinia*, and *Parakeelya*. In one or the other tree, bootstrap proportions are lower, in some cases < 50%, for the circumscriptions of *Calyptridium*, *Cistanthe* sections *Amarantoides* plus *Philippiamra*, *Montia*, and *Montiopsis* subg. *Dianthoideae.* However, bootstrap proportions for the combined data are > 78% for all of these clades. *Intergeneric relations.* Addition of critical samples and the chloroplast data provide support for intergeneric relations not well-supported in the previous analyses (Hershkovitz & Zimmer 1997, 2000). The combined data show reasonably strong support for the existence of a "North American clade" comprising *Lewisiopsis, Lewisia*, *Claytonia*, and *Montia*. Support for this clade is weak in the separate data analyses. The *ycf*3-*trn*S data support a sister relation between *Lewisia* and *Lewisiopsis*, but support is dramatically less in the combined analysis. In both data sets, the branch length from the hypothetical North American clade ancestor to *Lewisiopsis* is much shorter than those of the other taxa. Combined data support is also high for a clade comprising *Lenzia*, *Calyptridium*, and *Cistanthe* sections *Amarantoides* and *Philippiamra.* Again, support is weak in the separate data sets. The relations of *Parakeelya* conflict in the parsimony consensus trees of the ITS and *ycf*3-*trn*S sequences (not shown). In the former, the genus is sister to *Calandrinia*, and in the latter to the North America clade. Oddly enough, neither position is supported in the majority-rule bootstrap consensus of either data set. In fact, the *ycf*3-*trn*S of the bootstrap majority–rule tree (not shown) conflicts with the parsimony consensus in showing the strictly western American Portulacaceae as monophyletic, as in the combined data bootstrap, though with insignificant support (51%).

Relations among species of the predominantly South American clades

1. *Calandrinia*. Parsimony trees for separate and combined data analyses are presented in Figures 4-6. A splits graph is shown in Figure 7. Two samples were polymorphic at single sites in the ITS. The genotypes are indicated by "a" and "b". These trees cannot be rooted confidently by an outgroup criterion, because the outgroups are approximately equally diverged from the *Calandrinia* species (Figures 1-2), and different outgroups root the ingroup differently. The midpoint roots of the ITS and *ycf*3-*trn*S trees are different. The trees are

arbitrarily rooted between the annuals (*Calandrinia* sections *Calandrinia* and *Monocosmia*) and perennials (*Calandrinia* sect. *Acaules*), although the combined data analysis *per se* supports a partition between these groups. The ITS and *ycf*3-*trn*S trees are incongruent at certain points, but complementary at others, as evidenced by the much larger number of branches with higher bootstrap proportions in the combined versus the separate analysis. Total incongruence can be visualized with the splits graph. The partition homogeneity test indicates that the two data sets conflict (p = 0.001). Divergence among the perennials is uniformly low. Some interspecific divergences among annuals are higher than others. Divergences between nearest neighbors are generally proportional between ITS and *ycf*3-*trn*S, except for *Calandrinia monandra* DC. which shows much higher ITS than *ycf*3-*trn*S divergence.

The combined analysis supports three interspecific groups: (1) *C. menziesii* (Hook.) Torr. & A. Gray and *C. breweri* S. Watson; (2) *Calandrinia ciliata* (Ruiz & Pav.) DC. and *Calandrinia compressa* Schrad. ex DC.; and (3) *Calandrinia axilliflora* Barnéoud and the unidentified collections from the Falkland Islands (Islas Malvinas). The first group is temperate North American, although *Calandrinia menziesii* is introduced in the southern hemisphere. The second group is Central American and South American, and the last is temperate South American. Support for the third group is from the ITS data. The *ycf*3-*trn*S sequences support a different relationship for the Falklands plants. This incongruence is evident in the splits graph. The ITS of one collection of *Calandrinia breweri* is different from the remainder and slightly more similar to those of *Calandrinia ciliata* and *Calandrinia compressa*. Neither data set supports a close relationship of *Calandrinia monandra* to any particular annual taxon. Sequence divergence among the perennial species is less than among the annuals and interspecific relations are mostly poorly supported. The morphologically diagnosed hybrid *Calandrinia caespitosa* x *compacta* has both the ITS and *ycf*3-*trn*S sequences of the sympatric *Calandrinia compacta* Barnéoud samples, but the two *Calandrinia compacta* samples are divergent in both sequences. The splits graph shows considerable reticulation among the *Calandrinia compacta* and *Calandrinia caespitosa* Gillies ex Arn. samples.

2. *Cistanthe* sections *Amarantoides* and *Philippiamra*. The separate and combined ITS and *ycf*3-*trn*S trees are shown in Figures 8-10. Support for monophyly of the two sections together is sensitive to sampling and sequence and depends on the relationships of *Cistanthe ambigua* (S.Watson) Carolin ex Hershk. Support for monophyly of the two sections minus *Cistanthe ambigua* is strongest (98% bootstrap support) in the combined data infrageneric-level analysis and weakest in the ITS intergeneric-level analysis (less than 50% bootstrap support). Support for monophyly of *Calyptridium* is strongest in the combined data intergeneric-level analysis (80% bootstrap support) and weakest in both of the *ycf*3-*trn*S analyses (less than 50% bootstrap support). The bootstraps do not support the inclusion of *Cistanthe ambigua* in either section. The trees are outgroup-rooted with *Lenzia* (cf. Figs. 1-2). Relations among species of *Calyptridium* will be considered in more detail elsewhere (Hershkovitz, in prep). The divergence among species of *Cistanthe* sections *Amarantoides* and *Philippiamra* is extremely low, hence the monophyly of each section is neither supported nor strongly refuted. However, the *ycf*3-*trn*S sequences of *Cistanthe* (*Philippiamra*) *amarantoides* (Phil.) Carolin ex Hershk. and most samples of *Cistanthe* (*Amarantoides*) *calycina* (Phil.) Carolin ex Hershk. are identical and share at least two differences from all other samples.

3. *Cistanthe* sect. *Cistanthe*

3a. Grandiflora group (*Calandrinia* sect. *Cistanthe* sensu Reiche 1897). Figures 11-12 show the MP trees for the ITS and *ycf*3-*trn*S data. Figure 13 shows the splits graph for the combined data. The combined data bootstrap is not shown because it includes only a single partition, that separating *Cistanthe* sp. indet., aff. *Calandrinia crassifolia* Phil. and *Cistanthe* sp. 00-51 from the remaining taxa (84% support). Both trees are arbitrarily midpoint rooted, but the midpoint in the ITS tree is among the many equally parsimonious roots possible using the Rosulatae group as the outgroup. As is evident, divergence of both sequences is low overall, and many samples have identical sequences. The ITS data do not yield substantial bootstrap support for any relationships. Even though the informative variation is much less, the *ycf*3-*trn*S data produce one reasonably strong bootstrap partition. This partition is absent, however, in the combined data bootstrap consensus, whereas the combined data show stronger support for a partition less strongly

supported in each of the separate data sets. The lack of shared agreement between the two data sets is indicated by the reduced rescaled consistency index in the combined versus separate data analyses, a significant score in the partition homogeneity test (p = 0.03) notwithstanding the low variation, and the reticulate appearance of the splits graph.

3b. Rosulatae group *(= Calandrinia* sections *Andinae*, Arenarie and Rosulatae *sensu* Reiche 1897). Figures 14-16 show the MP trees for the ITS and *ycf*3-*trn*S data. The ITS tree is arbitrarily midpoint rooted, but the root shown is among many equally parsimonious roots possible using the Grandiflora group sequences as outgroups. The midpoint root of the ITS data is the unequivocal root of the *ycf*3-*trn*S data using outgroup rooting. However, this is not the same root produced by midpoint rooting of the *ycf*3-*trn*S data. As with the Grandiflora group, variation is low for both sequences, and only the *ycf*3-*trn*S data produce any relatively high bootstrap proportions. Likewise, the combined data show generally reduced support for partitions in the separate data sets. However, conflict appears to be less than in the Grandiflora group, as indicated by the partition homogeneity test (p = 0.17). The splits graph (not shown) shows only one internal quadrangle. In three cases, support is increased in the combined data relative to the separate data. One case is trivial, that involving *Cistanthe* sp. indet., aff. *Calandrinia oblongifolia* Barnéoud and its putative hybrid offspring, which have identical ITS and *ycf*3-*trn*S sequences. Two other cases involve increased support for intertaxon relations between *Cistanthe* sp. indet., aff. *Calandrinia thyrsoidea* Reiche, *Cistanthe cephalaphora* (I.M.Johnst.) Carolin ex Hershk., and *Cistanthe maritima* (Nutt. ex Torr. & A.Gray) Carolin ex Hershk., and between *Cistanthe* sp. indet., aff. *Calandrinia chamissoi* Barnéoud and a sample of *Cistanthe arenaria* (Cham.) Carolin ex Hershk. However, *Cistanthe arenaria* appears as polyphyletic in both trees. Likewise, the samples of *Cistanthe longiscapa* (Barnéoud) Carolin ex Hershk. appear as polyphyletic, and one sample of *Cistanthe cymosa* (Phil.) Carolin ex Hershk. (from near the type locality) shares the same ITS sequence as a sample of *Cistanthe longiscapa* collected at the same locality.

4. *Montiopsis*. ITS and *ycf*3-*trn*S parsimony trees are illustrated in Figures 17-19. Each subgenus is outgroup-rooted with the other, although it is conceivable that high divergence between the subgenera could produce rooting artifacts within them. In fact, the ITS and *ycf*3-*trn*S trees conflict in the placement of the root of each subgenus. However, the two data sets conflict in numerous aspects, evidenced in part by the reduction of bootstrap proportions in the combined versus separate analysis. In addition, the conflict is demonstrated by the partition homogeneity test (p = 0.004).

4a. *Montiopsis* subgenus *Dianthoideae*. The ITS and *ycf*3-*trn*S trees conflict in their placement of the taxa. The *ycf*3-*trn*S sequences of the *Montiopsis gayana* (Barnéoud) D.I.Ford samples are closely related to those of *Montiopsis* sp. indet., aff. *Calandrinia tricolor* Phil., but the ITS sequences are more divergent. The combined data consensus favors the *ycf*3-*trn*S result.

4b. *Montiopsis* subgenus *Montiopsis*. The samples of *Montiopsis* x *trifida*, *Montiopsis uspallatensis* (Phil.) D.I.Ford, and one of the samples of *Montiopsis trifida* (Hook. & Arn.) D.I.Ford were polymorphic for ITS, and the last of these was also polymorphic for *ycf*3-*trn*S. The genotypes are indicated with letters, as above. The polymorphic samples of *Montiopsis* x *trifida* and *Montiopsis trifida* were each polymorphic for two positions in the ITS. This creates four possible genotypes, of which two possible extremes (different at both positions) were arbitrarily designated for analysis. Without cloning, it cannot be determined which sequences actually exist. Sequence divergence, especially of the ITS, is low relative to the number of taxa. Nonetheless, the combined data suggests that the two data sets conflict. This conflict is less evident in the splits graph (not shown). Of the two clades supported by 81% bootstrap support in the *ycf*3-*trn*S data, only one is present in the combined data bootstrap consensus, and the support is lower. The sample *Montiopsis* x *trifida* has both the ITS and *ycf*3-*trn*S sequence of *Montiopsis trifida*. One sample of *Montiopsis parviflora* (Phil.) D.I.Ford has the *ycf*3-*trn*S sequence of *Montiopsis trifida* but the ITS sequence of the other *Montiopsis parviflora* samples. However, the ITS divergence between the *Montiopsis trifida* and *Montiopsis parviflora* samples is as little as one change.

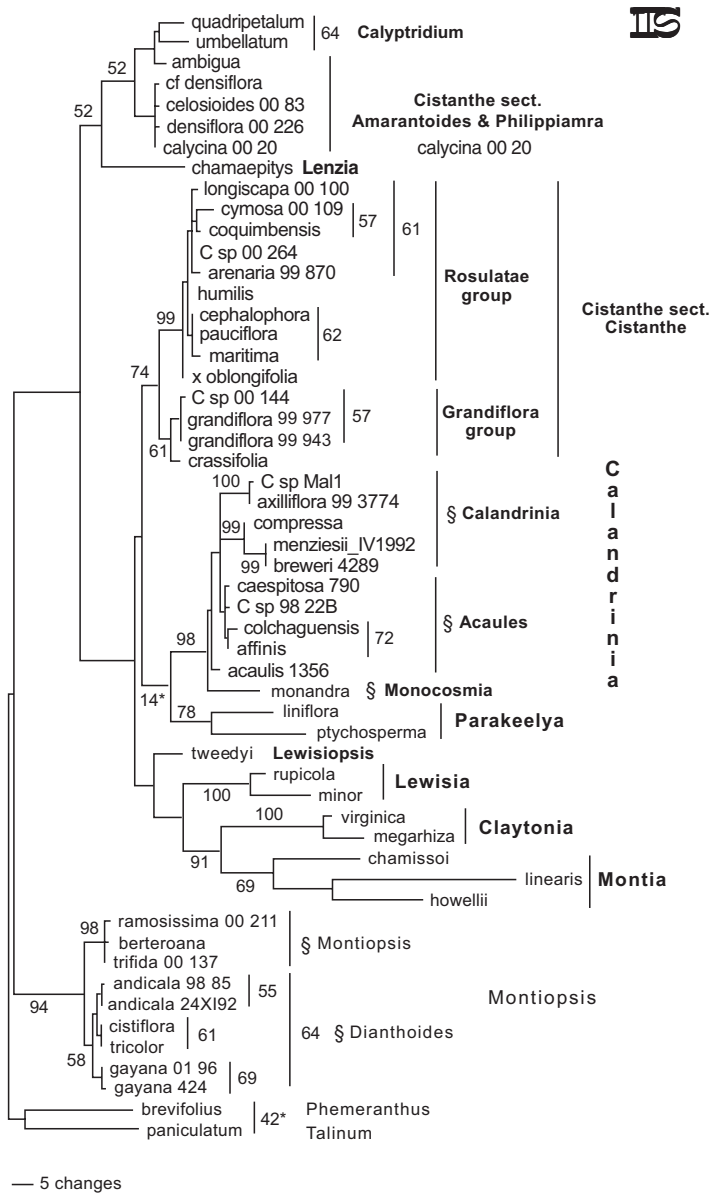

FIGURE 1. Most parsimonious (MP) tree for ITS data for western American Portulacaceae. Sample names are defined in Table I. One of 7146 trees, length 479. Rescaled consistency index (RC) 0.52, retention index (RI) 0.80. The tree is outgroup rooted with samples of *Phemeranthus* and *Talinum* (cf. Hershkovitz & Zimmer 1997, 2000). Bootstrap proportions (BP; 500 replicates) greater than 50% are indicated. Two BP values less than 50% are indicated with an asterisk: these branches are in conflict with branches in the MP strict consensus. Note the longer branch lengths associated with samples of *Claytonia* and *Montia* and, to a lesser degree, *Lewisia*. The bootstrap consensus includes 13 branches with BP values >70%.

FIGURA 1. Arbol más parsimonioso (MP) de los datos de ITS de Portulacaceae de América occidental. Los nombres de muestras se presentan en la Tabla I. Uno de 7146 árboles, largo 479, índice de consistencia rescalado (RC) 0,52, índice de retención (RI) 0,80. El árbol está enraizado con las muestras de *Phemeranthus* y *Talinum* (cf. Hershkovitz & Zimmer 1997, 2000). Se indican las proporciones de "bootstrap" (BP, 500 réplicas) mayores que 50%. Se indican con un asterisco dos valores BP menores que 50%: estas ramas están en conflicto con las ramas en el árbol de MP del consenso estricto. Nótese las ramas largas asociadas con muestras de *Claytonia* y *Montia* y, en menor grado, *Lewisia*. El consenso de bootstrap incluye 13 ramas con valores de BP >70%.

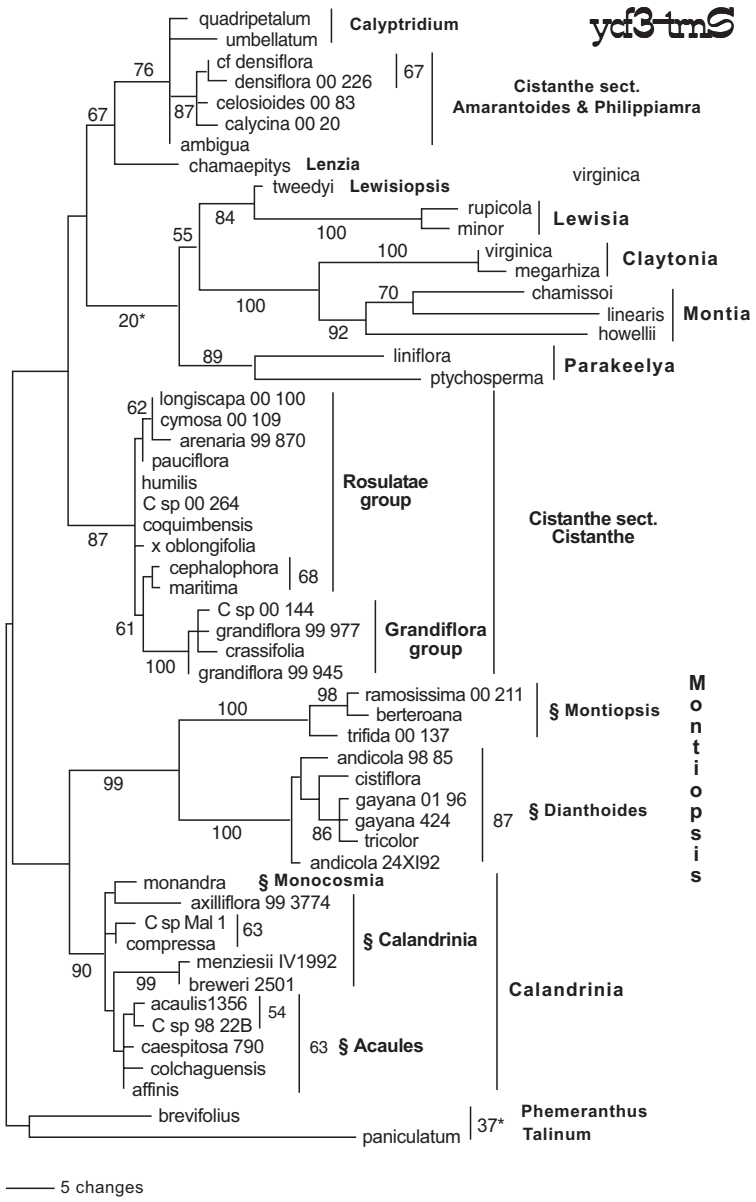

Figure 2. Most parsimonious (MP) tree for *ycf*3-*trn*S data for western American Portulacaceae. Sample names are defined in Table I. One of 120 trees, length 384, RC 0.71, RI 0.88. The tree is outgroup rooted as in Fig. 1. BP values (500 replicates) greater than 50% are indicated. Two BP values less than 50% are indicated with an asterisk: these branches are in conflict with branches in the MP strict consensus, Western American Portulacaceae (all taxa minus the outgroups and *Parakeelya*) are partitioned in the bootstrap consensus (BP = 51%). Note the longer branch lengths associated with samples of *Claytonia*, *Montia*, and *Lewisia* (cf. Fig. 1). Note also longer branches associated with samples of *Montiopsis* (cf. Fig. 1). The bootstrap consensus includes 19 branches with BP values >70%.

Figura 2. Arbol más parsimonioso (MP) para los datos de *ycf*3-*trn*S de Portulacaceae de América occidental. Los nombres de muestras se presentan en la Tabla I. Uno de 120 árboles, de largo 384, RC 0,71 y RI 0,88. El árbol está enraizado como en la Figura 1. Se indican valores de BP (500 réplicas) mayor que 50%. Se indican con un asterisco dos valores BP menores que 50%: estas ramas están en conflicto con ramas en el árbol de MP del consenso estricto. Se separa en el consenso de bootstrap (BP = 51%) Portulacaceae de América occidental (todos los taxa menos los grupos externos y *Parakeelya*). Nótese las ramas largas asociadas con muestras de *Claytonia*, *Montia* y *Lewisia*. Nótese también las ramas largas asociadas con muestras de *Montiopsis* (cf. Figura 1). El consenso de bootstrap incluye 19 ramas con valores de BP >70%.

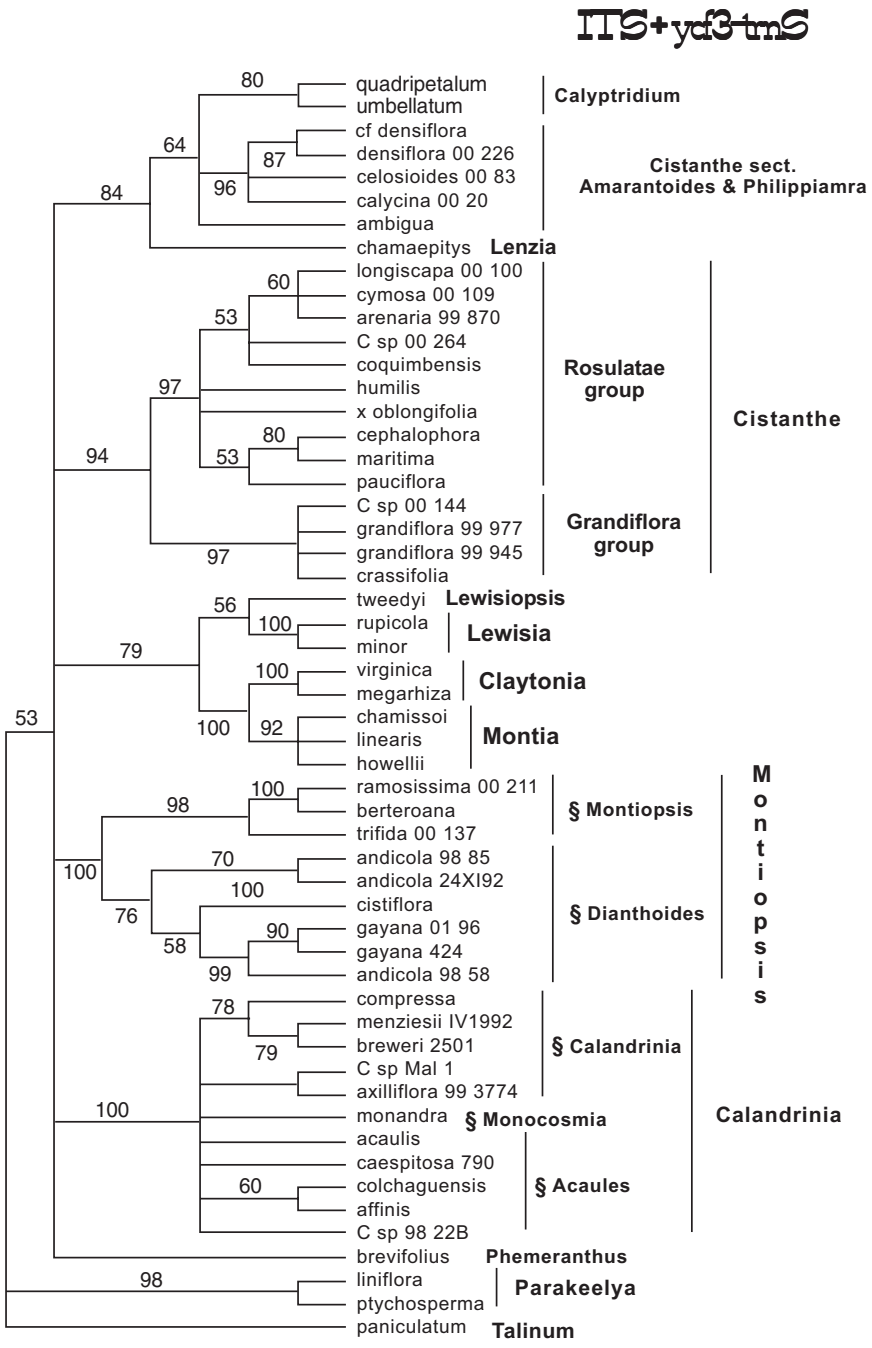

FIGURE 3. Bootstrap consensus for combined ITS and *ycf*3-*trn*S data for western American Portulacaceae. Sample names are defined in Table I. Analysis of the combined data yielded 104 MP trees, length 888, RC 0.58, RI 0.82. BP values (500 replicates) greater than 50% are indicated. The bootstrap consensus includes 25 branches with BP values >70%.

FIGURA 3. Consenso de bootstrap para los datos combinados de ITS y *ycf*3-*trn*S de Portulacaceae de América occidental. Los nombres de las muestras se presentan en la Tabla I. El análisis produjo 104 árboles de MP, de largo 888, RC 0,58 y RI 0,82. Se indican valores de BP (500 réplicas) mayores que 50%. El consenso de bootstrap incluye 25 ramas con valores de BP >70%.

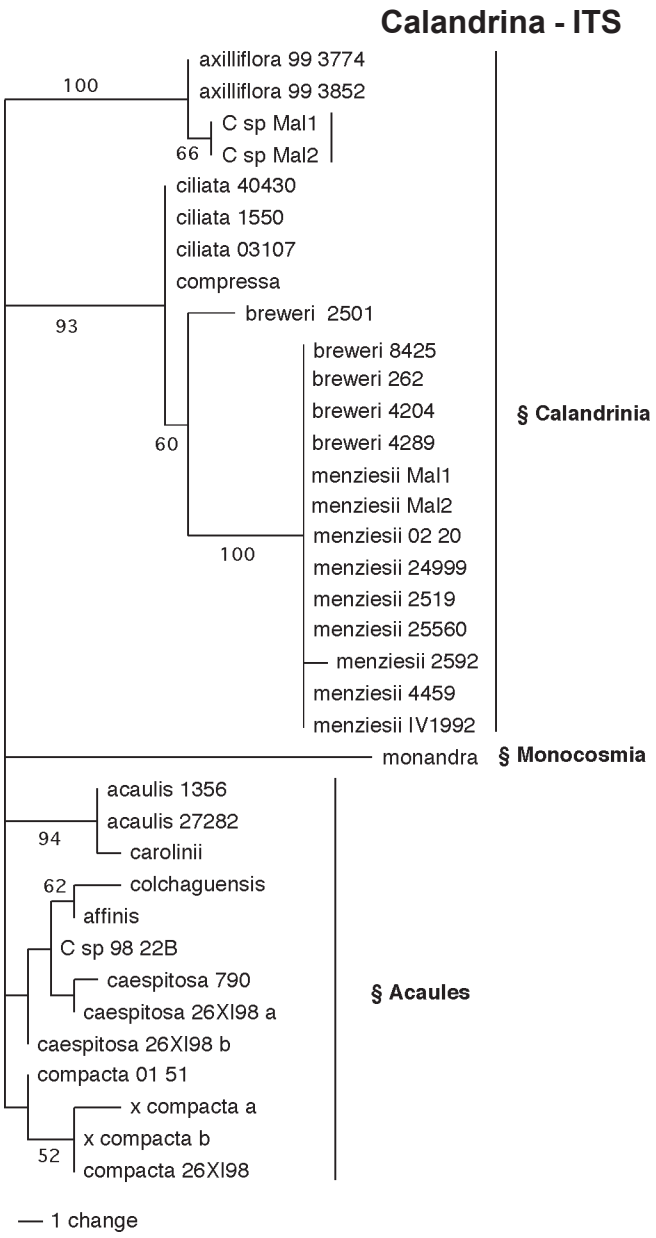

Figure 4. MP tree for ITS data for *Calandrinia*. Sample names are defined in Table I. One of 101,179 trees, length 57, RC 0.91, RI 0.98. BP values (500 replicates) greater than 50% are indicated. Lower case letters following duplicated sample names denote samples having more than one ITS genotype. The tree is rooted with samples of *Calandrinia* sect. *Acaules* as outgroup. Midpoint rooting of this tree places the root between *Calandrinia monandra* (the longest branch) and the remaining taxa. The bootstrap consensus includes 4 branches with BP values >70%.

Figura 4. Arbol más parsimonioso (MP) para los datos de ITS de *Calandrinia*. Los nombres de muestras se presentan en la Tabla I. Uno de 101.179 árboles, de largo 57, RC 0,91 y RI 0,98. Se indican los valores de BP (500 réplicas) mayores que 50%. Las letras en minúsculas que acompañan los nombres de muestras corresponden a muestras con más de un genotipo de ITS. El árbol se enraíza con las muestras de *Calandrinia* sect. *Acaules* como grupo externo. Si se enraíza el árbol por el criterio de "midpoint", la raíz se encuentra entre *Calandrinia monandra* (la rama más larga) y el remanente de los taxa. El consenso de bootstrap incluye 4 ramas con valores de BP >70%.

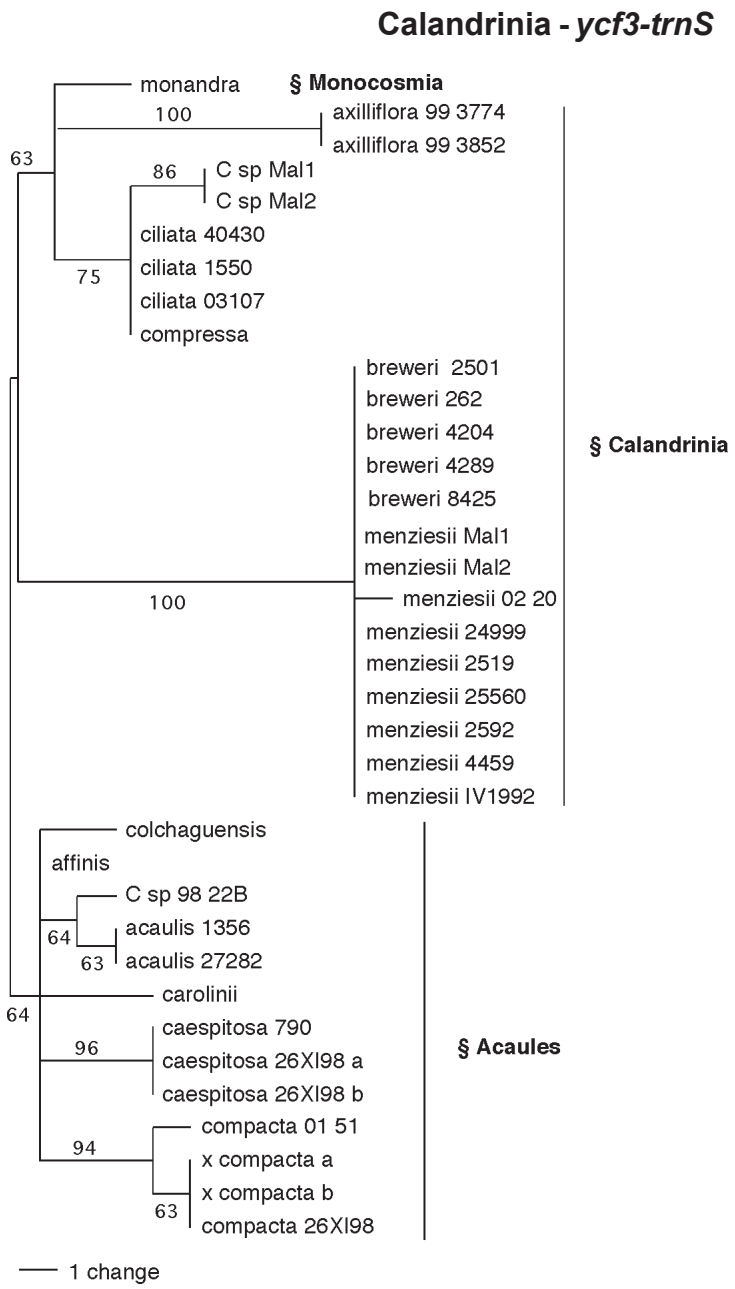

FIGURE 5. MP tree for *ycf*3-*trn*S data for *Calandrinia*. Sample names are defined in Table I. One of 2 trees, length 41, RC 1.0, RI 1.0. BP values (500 replicates) greater than 50% are indicated. Lower case letters following duplicated sample names denote samples having more than one ITS genotype (cf. Fig. 4). The tree is rooted with samples of *Calandrinia* sect. *Acaules* as outgroup. The bootstrap consensus includes 6 branches with BP values >70%.

FIGURA 5. Arbol más parsimonioso (MP) para los datos de *ycf*3-*trn*S de *Calandrinia*. Los nombres de las muestras se presentan en la Tabla I. Uno de 2 árboles, de largo 41, RC 1,0 y RI 1,0. Se indican los valores de BP (500 réplicas) mayores que 50%. Las letras en minúsculas que acompañan los nombres de muestras corresponden a muestras con más de un genotipo de ITS (cf. Figura 4). El árbol se enraíza con las muestras de *Calandrinia* sect. *Acaules* como grupo externo. El consenso de bootstrap incluye 6 ramas con valores de BP >70%.

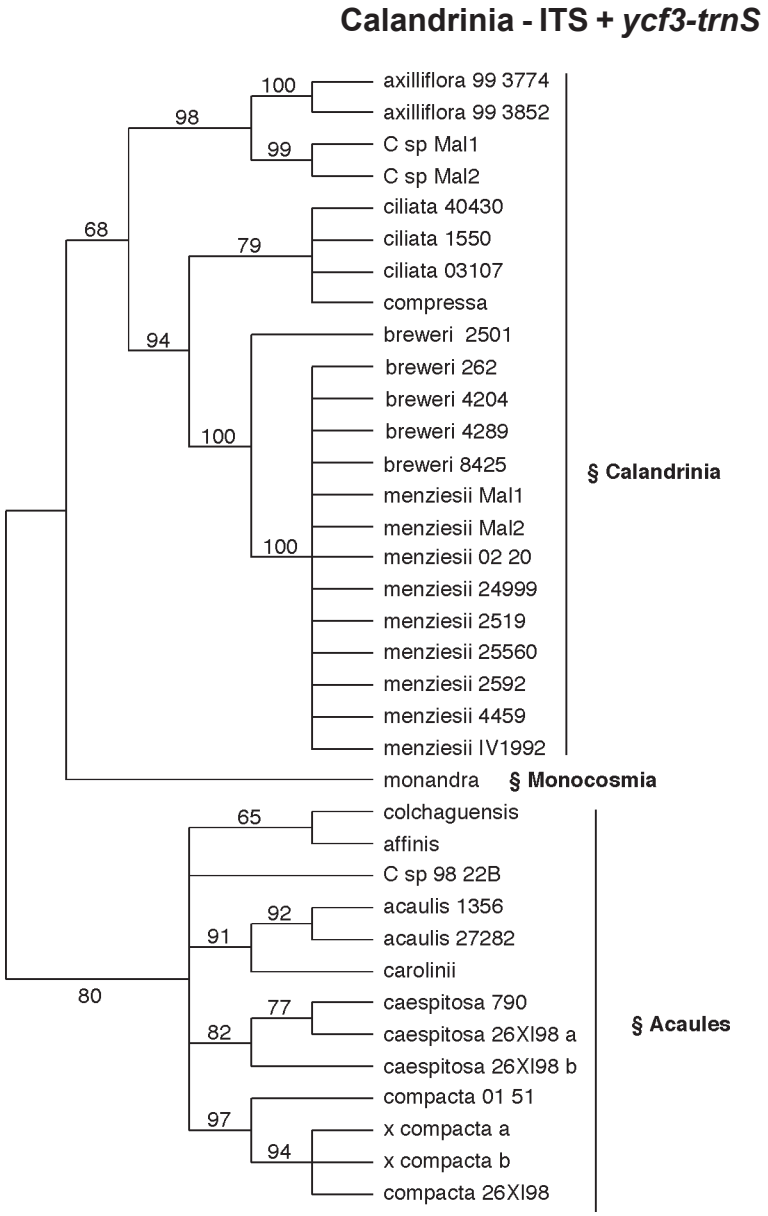

Figure 6. Bootstrap consensus for combined ITS and *ycf*3-*trn*S data for *Calandrinia*. Sample names are defined in Table I. BP values (500 replicates) greater than 50% are indicated. Lower case letters following duplicated sample names denote samples having more than one ITS genotype (cf. Figure 4). The tree is rooted with samples of *Calandrinia* sect. *Acaules* as outgroup. Analysis of the combined data yielded 19 MP trees, length 103, RC 0.89, RI 0.98. The bootstrap consensus includes 14 branches with BP values >70%.

Figura 6. Consenso de bootstrap para los datos combinados de ITS y *ycf*3-*trn*S de *Calandrinia*. Los nombres de las muestras se presentan en la Tabla I. Se indican los valores de BP (500 réplicas) mayores que 50%. Las letras en minúsculas que acompañan los nombres de muestras corresponden a muestras con más de un genotipo de ITS (cf. Figura 4). El árbol se arraiga con las muestras de *Calandrinia* sect. *Acaules* como grupo externo. El análisis de los datos combinados produjo 19 árboles de MP, de largo 103, RC 0,89 y RI 0,98. El consenso de bootstrap incluye 14 ramas con valores de BP >70%.

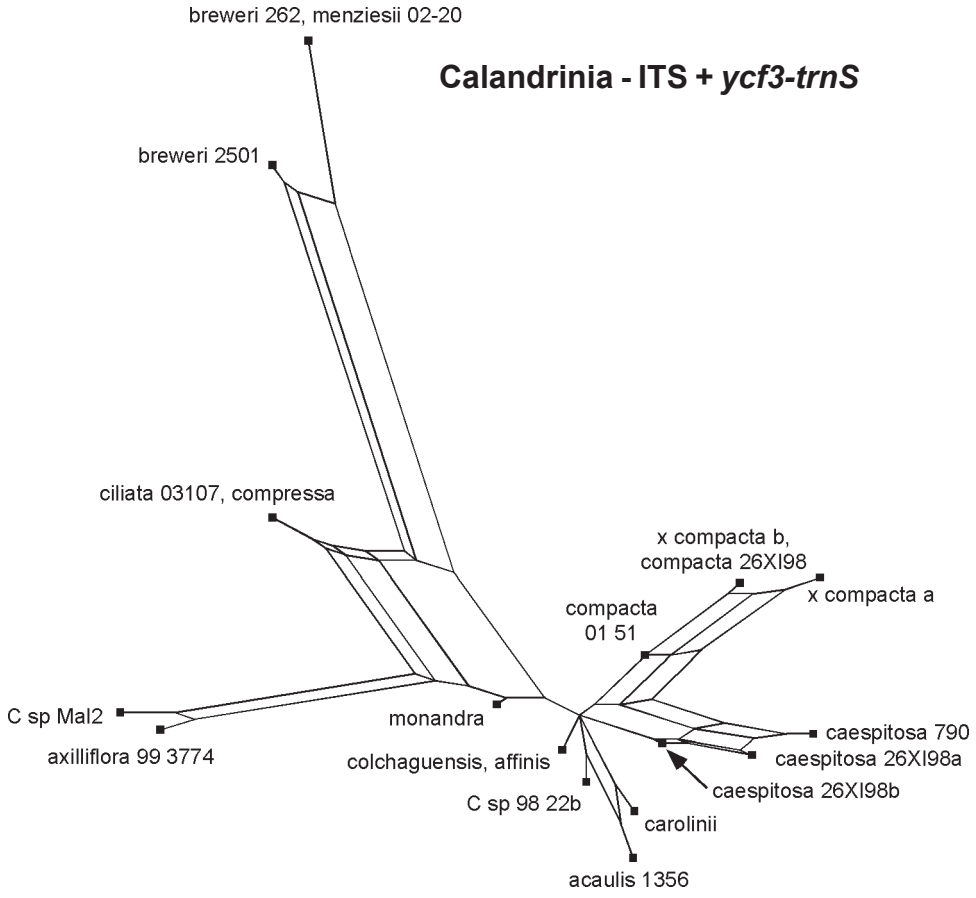

FIGURE 7. Splitsgraph for combined ITS and *ycf*3-*trn*S data for *Calandrinia*. For simplicity, duplicate samples of the same taxon identical for both sequences were omitted. The omitted samples can be deduced from Figures 4 and 5. The splits analysis used "p" distances and was refined over the maximum possible number of quartets.

FIGURA 7. Splitsgraph de los datos combinados de ITS y *ycf*3-*trn*S de *Calandrinia.* Para simplicidad, muestras duplicadas del mismo taxón, e iguales para las dos secuencias fueron eliminadas. Las muestras eliminadas pueden ser deducidas desde las Figuras 4 y 5. El análisis de "splits" incorporó distancias de "p" y fue refinado sobre el número máximo de cuartetos posibles.

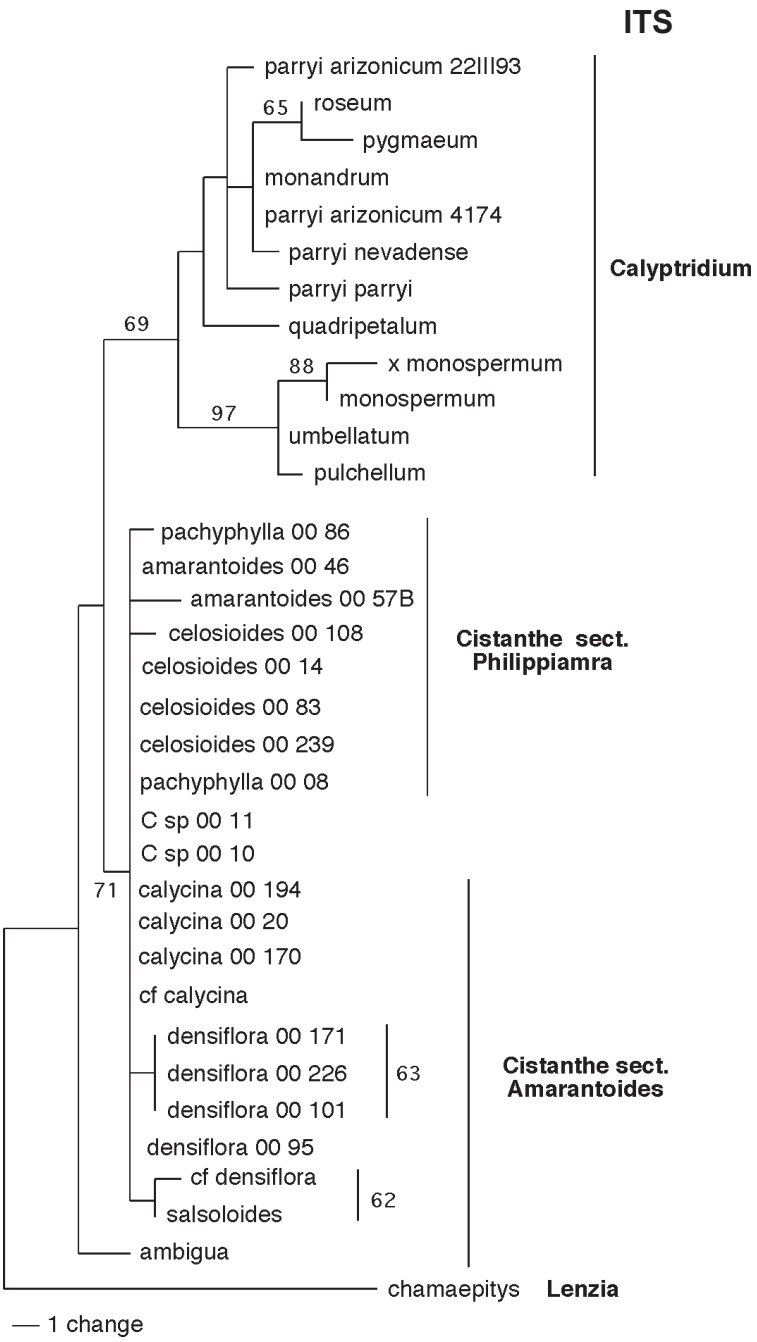

Figure 8. MP tree for ITS data for *Lenzia*, *Calyptridium* and *Cistanthe* sections *Amarantoides* and *Philippiamra*. Sample names are defined in Table I. One of 16 trees, length 55, RC 0.83, RI 0.93. BP values (500 replicates) greater than 50% are indicated. The tree is outgroup-rooted using *Lenzia* (cf. Figs. 1-3). The bootstrap consensus includes 3 branches with BP values >70%.

Figura 8. Arbol más parsimonioso para los datos de ITS de *Lenzia*, *Calyptridium* y *Cistanthe* secciones *Amarantoides* y *Philippiamra*. Los nombres de las muestras se presentan en la Tabla I. Uno de 16 árboles, de largo 55, RC 0,83 y RI 0,93. Se indican los valores de BP (500 réplicas) mayores que 50%. El árbol se enraíza con las muestras de *Lenzia* como grupo externo (cf. Figuras 1-3). El consenso de bootstrap incluye 3 ramas con valores de BP >70%.

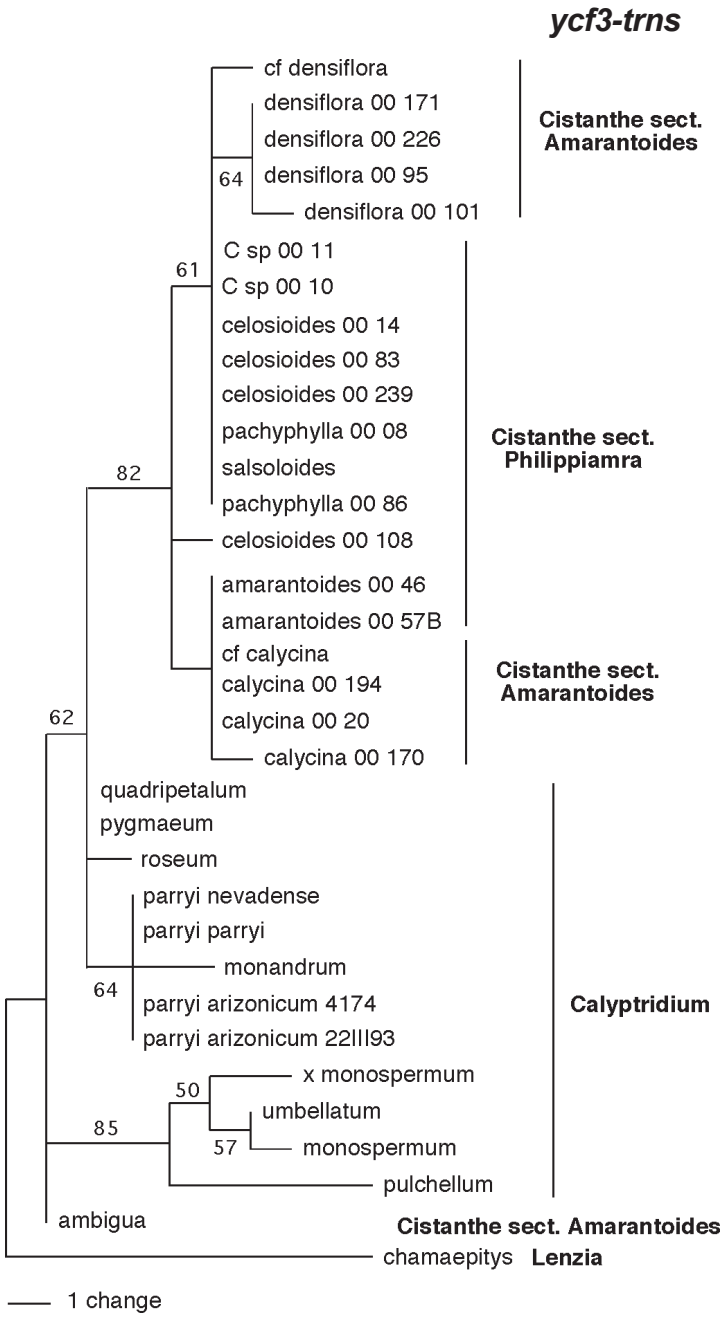

FIGURE 9. MP tree for *ycf*3-*trn*S data for *Lenzia*, *Calyptridium* and *Cistanthe* sections *Amarantoides* and *Philippiamra*. Sample names are defined in Table I. One of 1 tree, length 37, RC 0.88, RI 0.96. BP values (500 replicates) greater than 50% are indicated. The tree is outgroup-rooted using *Lenzia* (cf. Figs. 1-3). The bootstrap consensus includes 2 branches with BP values >70%.

FIGURA 9. Arbol más parsimonioso para los datos de *ycf*3-*trn*S de *Lenzia*, *Calyptridium* y *Cistanthe* secciones *Amarantoides* y *Philippiamra*. Los nombres de las muestras se presentan en la Tabla I. El árbol más parsimonioso, de largo 37, RC 0,88 y RI 0,96. Se indican los valores de BP (500 réplicas) mayores que 50%. El árbol se enraíza con las muestras de *Lenzia* como grupo externo (cf. Figuras 1-3). El consenso de bootstrap incluye 2 ramas con valores de BP >70%.

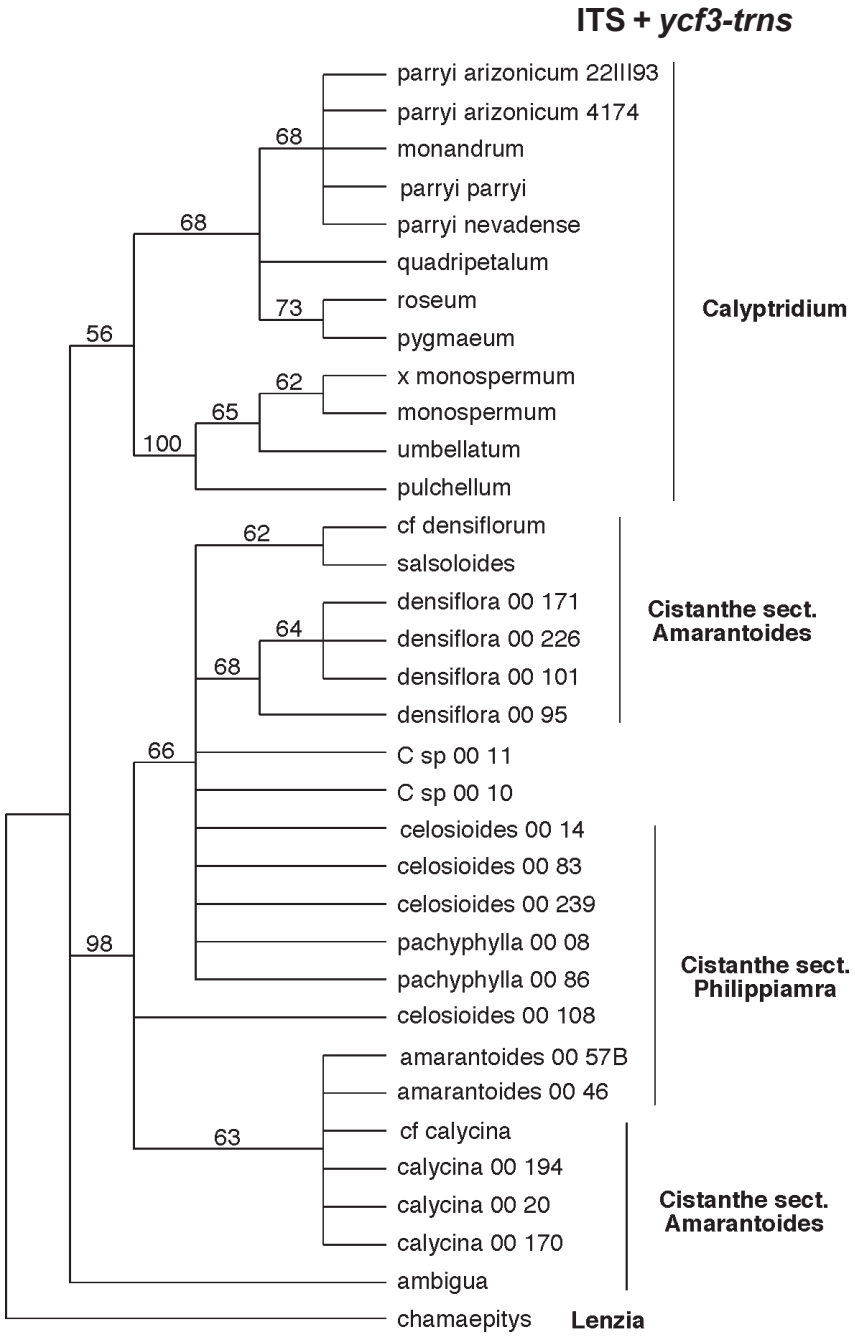

Figure 10. Bootstrap consensus for combined ITS and *ycf*3-*trn*S data for *Lenzia*, *Calyptridium* and *Cistanthe* sections *Amarantoides* and *Philippiamra*. Sample names are defined in Table I. BP values (500 replicates) greater than 50% are indicated. The tree is outgroup-rooted using *Lenzia* (cf. Figs. 1-3). Analysis of the combined data yielded 8 MP trees, length 94, RC 0.82, RI 0.93. The bootstrap consensus includes 3 branches with BP values >70%.

Figura 10. Consenso de bootstrap para los datos combinados de ITS y *ycf*3-*trn*S de *Lenzia*, *Calyptridium* y *Cistanthe* secciones *Amarantoides* y *Philippiamra.* Los nombres de las muestras se presentan en la Tabla I. Se indican los valores de BP (500 réplicas) mayores que 50%. El árbol se enraíza con las muestras de *Lenzia* como grupo externo (cf. Figuras 1-3). El consenso de bootstrap incluye 3 ramas con valores de BP >70%.

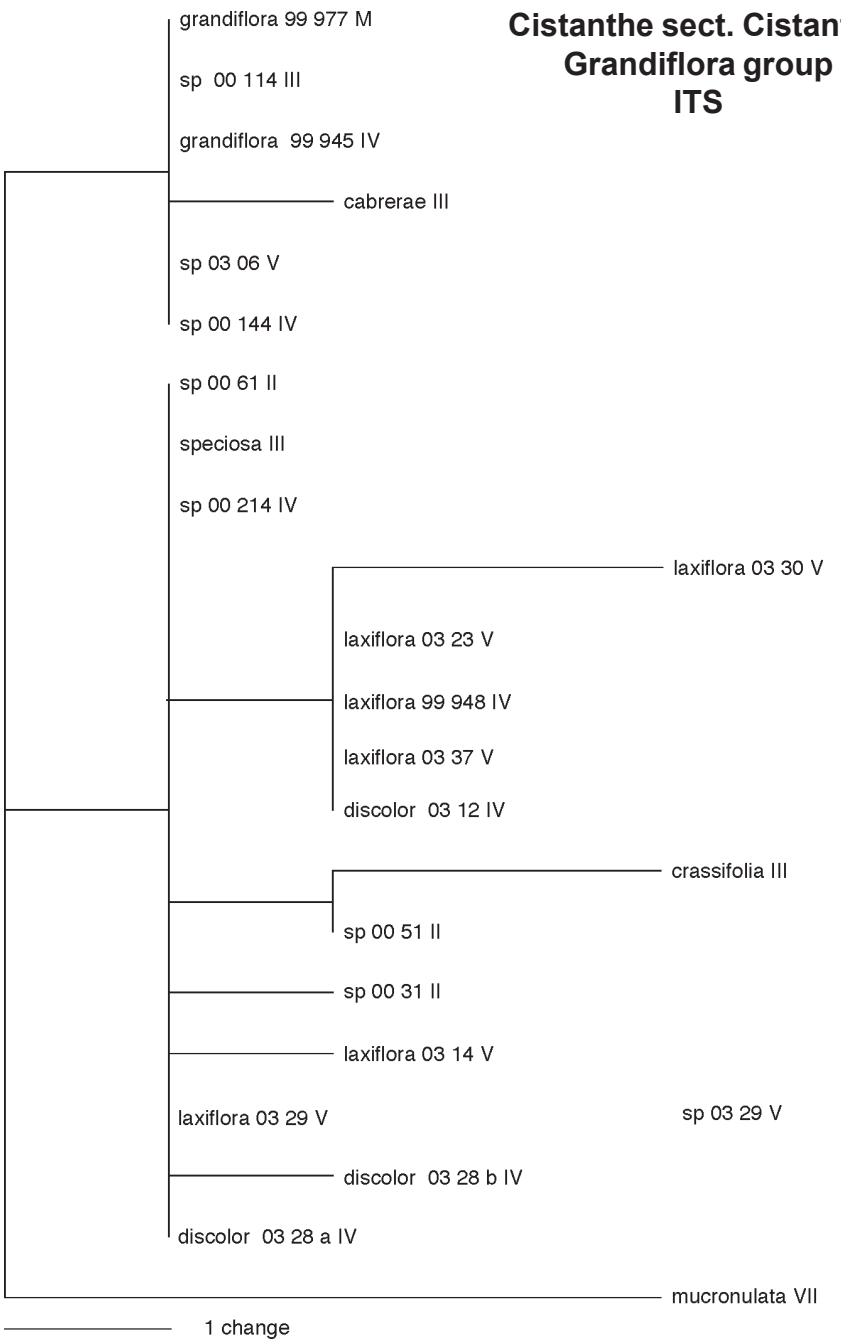

FIGURE 11. MP tree for ITS data for *Cistanthe* sect. *Cistanthe*, Grandiflora group. Sample names are defined in Table I. Roman numerals refer to Chilean Region of origin; M refers to the Metropolitan Region (see Table I). One of 251 trees, length 16, RC 0.78, RI 0.89. BP values (500 replicates) greater than 50% are indicated. The tree is midpoint-rooted.

FIGURA 11. Arbol más parsimonioso para los datos de ITS de *Cistanthe* sect. *Cistanthe*, grupo Grandiflora. Los nombres de las muestras se presentan en la Tabla I. Los números romanos se refieren a la región de Chile; M se refiere a la Región Metropolitana (ver Tabla I). Uno de 251 árboles, de largo 16, RC 0,78 y RI 0,89. Se indican los valores de BP (500 réplicas) mayores que 50%. El árbol se enraíza con el criterio de "midpoint".

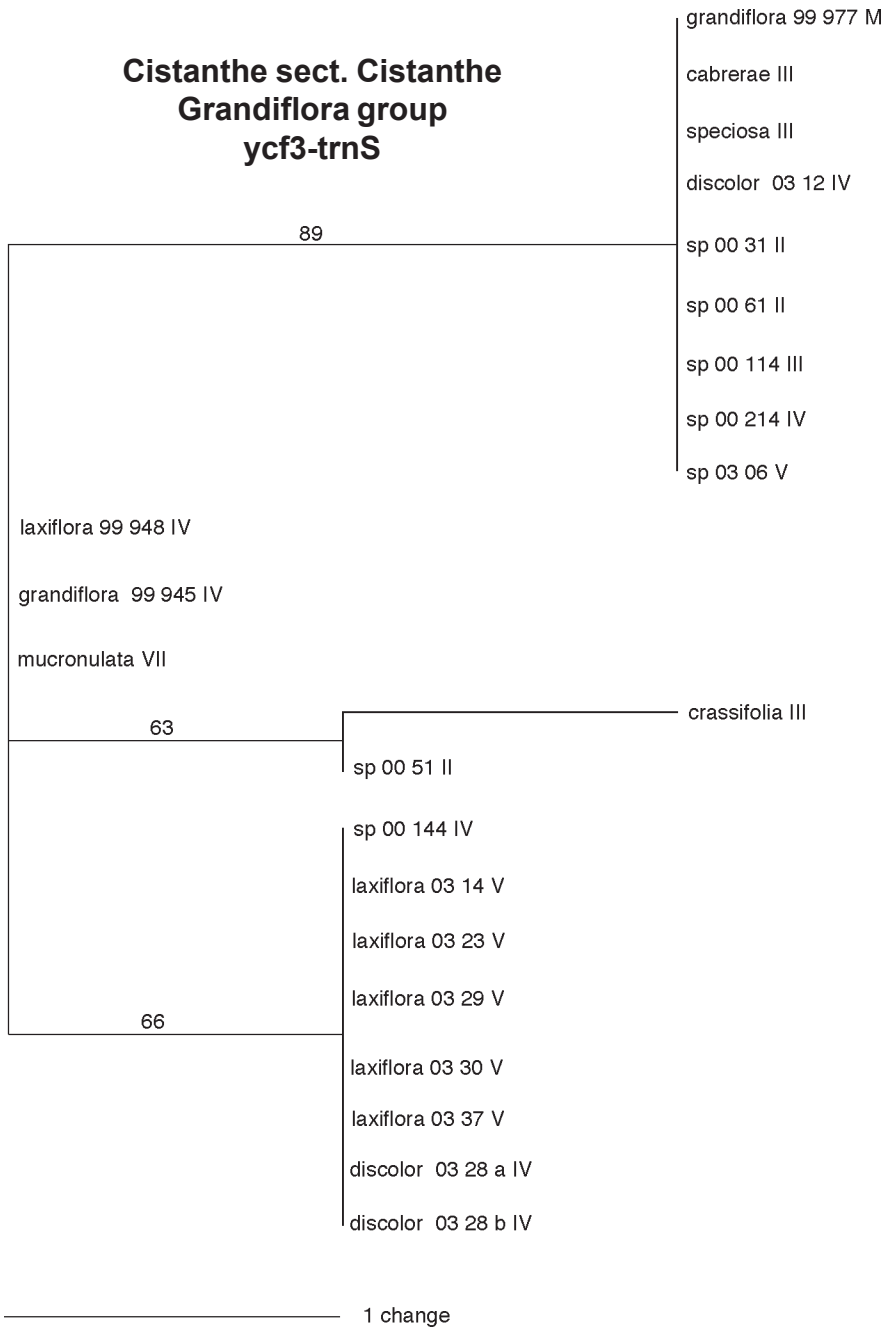

Figure 12. MP tree for *ycf*3-*trn*S data for *Cistanthe* sect. *Cistanthe*, Grandiflora group. Sample names are defined in Table I. Roman numerals refer to Chilean Region of origin; M refers to the Metropolitan Region (see Table I). Single MP tree, length 5, RC 1.0, RI 1.0. BP values (500 replicates) greater than 50% are indicated. The tree is midpoint-rooted.

Figura 12. Arbol más parsimonioso para los datos de *ycf*3-*trn*S de *Cistanthe* sect. *Cistanthe*, grupo Grandiflora. Los nombres de las muestras se presentan en la Tabla I. Los números romanos se refieren a la región de Chile; M se refiere a la Región Metropolitana (ver Tabla I). El único árbol más parsimonioso, de largo 5, RC 1,0 y RI 1,0. Se indican los valores de BP (500 réplicas) mayores que 50%. El árbol se enrraíza con el criterio de "midpoint".

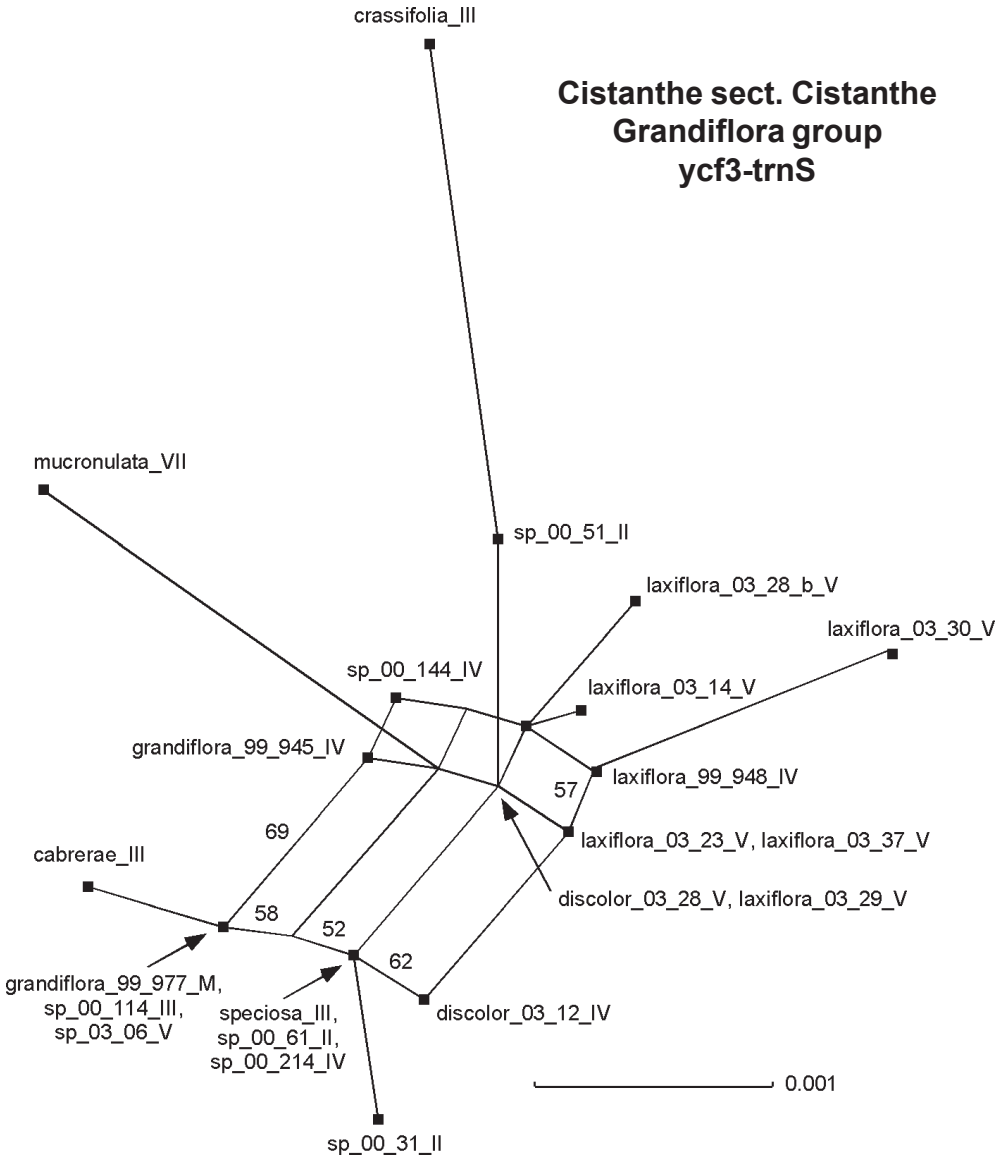

FIGURE 13. Splitsgraph for combined ITS and *ycf*3-*trn*S data for *Cistanthe* sect. *Cistanthe*, Grandiflora group. Sample names are defined in Table I. Roman numerals refer to Chilean Region of origin; M refers to the Metropolitan Region (see Table I). The splits analysis used "p" distances and was refined over the maximum possible number of quartets.

FIGURA 13. Splitsgraph para los datos combinados de ITS y *ycf*3-*trn*S de *Cistanthe* sect. *Cistanthe*, grupo Grandiflora. Los nombres de las muestras se presentan en la Tabla I. Los números romanos se refieren a la región de Chile; M se refiere a la Región Metropolitana (ver Tabla I). El análisis de "splits" incorporó distancias de "p" y fue refinado sobre el número máximo de cuartets posibles.

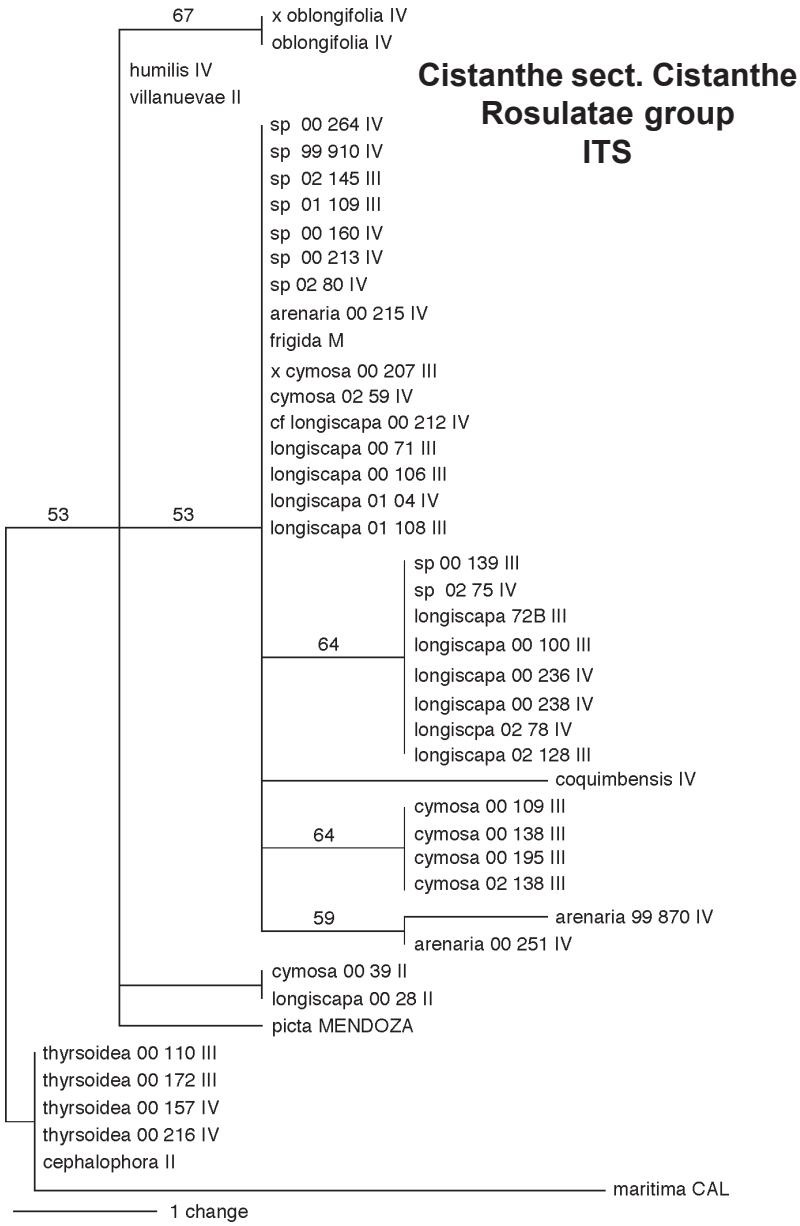

Figure 14. MP tree for ITS data for *Cistanthe* sect. *Cistanthe*, Rosulatae group. Sample names are defined in Table I. Roman numerals refer to Chilean Region of origin; M refers to the Metropolitan Region; MENDOZA refers to Mendoza Province, Argentina; CAL refers to California, USA (see Table I). One of 5 trees, length 34, RC 0.84, RI 0.96. BP values (500 replicates) greater than 50% are indicated. Rooting is arbitrarily in agreement with Figure 15, but the midpoint root occurs along the basal split shown.

Figura 14. Arbol más parsimonioso para los datos de ITS de *Cistanthe* sect. *Cistanthe*, grupo Rosulatae. Los nombres de las muestras se presentan en la Tabla I. Los números romanos se refieren a la región de Chile; M se refiere a la Región Metropolitana; MENDOZA a la provincia de Mendoza, Argentina; CAL a California, EEUU (ver Tabla I). Uno de 5 árboles, de largo 34, RC 0,84 y RI 0,96. Se indican los valores de BP (500 réplicas) mayores que 50%. El árbol se enraíza en una manera arbitraria en acuerdo con Figura 15, pero la raíz de midpoint se encuentra en la divergencia basal.

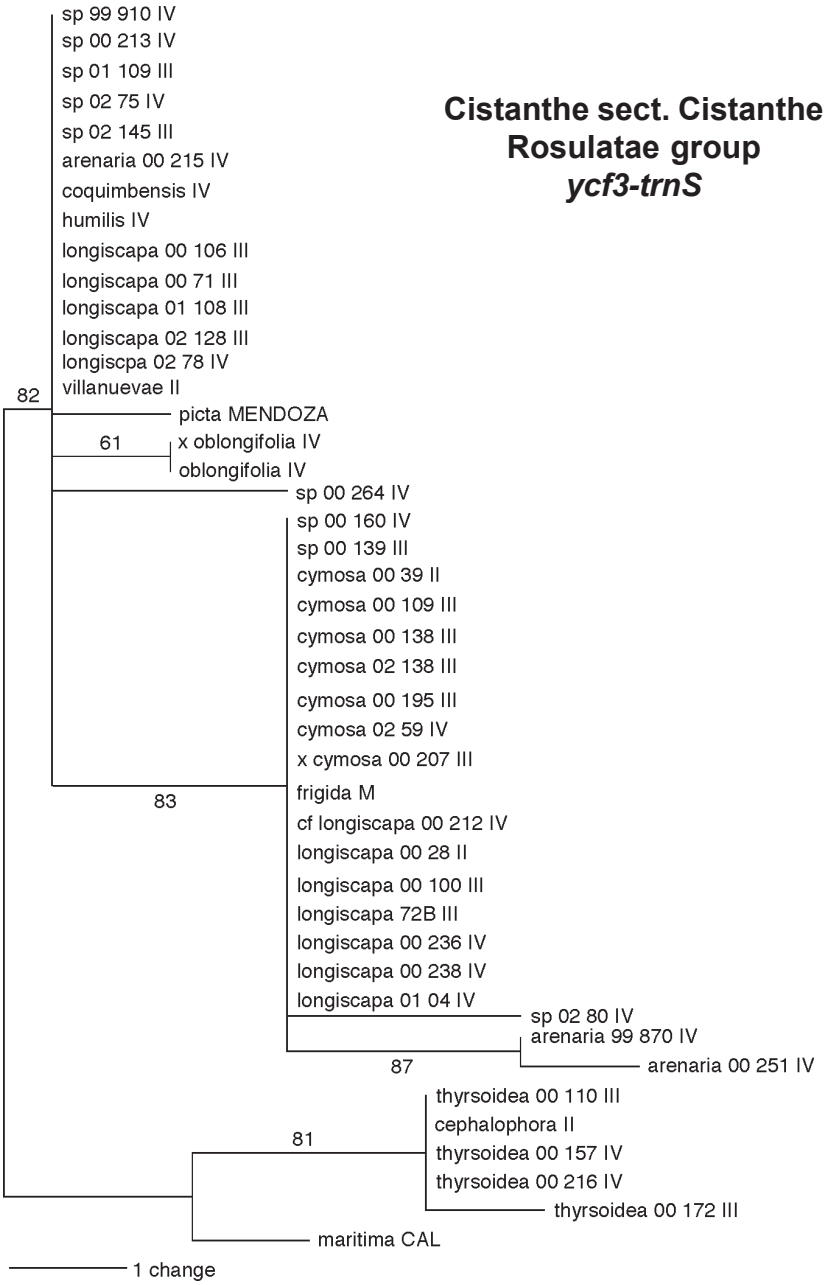

FIGURE 15. MP tree for *ycf*3-*trn*S data for *Cistanthe* sect. *Cistanthe*, grupo Rosulatae. Sample names are defined in Table I. Roman numerals refer to Chilean Region of origin; M refers to the Metropolitan Region; MENDOZA refers to Mendoza Province, Argentina; CAL refers to California (see Table I). Single MP tree, length 17, RC 0.93, RI 0.98. BP values (500 replicates) greater than 50% are indicated. The root is based on outgroup rooting using the *Cistanthe* sect. *Cistanthe,* Grandiflora group *ycf*3-*trn*S data.

FIGURA 15. Arbol más parsimonioso para los datos de *ycf*3-*trn*S de *Cistanthe* sect. *Cistanthe*, grupo Rosulatae. Los nombres de las muestras se presentan en la Tabla I. Los números romanos se refieren a la región de Chile; M se refiere a la Región Metropolitana; MENDOZA a la provincia de Mendoza, Argentina; CAL a California, EEUU (ver Tabla I). El árbol más parsimonioso, de largo 17, RC 0,93 y RI 0,98. Se indican los valores de BP (500 réplicas) mayores que 50%. El árbol se enraíza con los datos de *ycf*3-*trn*S de *Cistanthe* sect. *Cistanthe*, grupo Grandiflora.

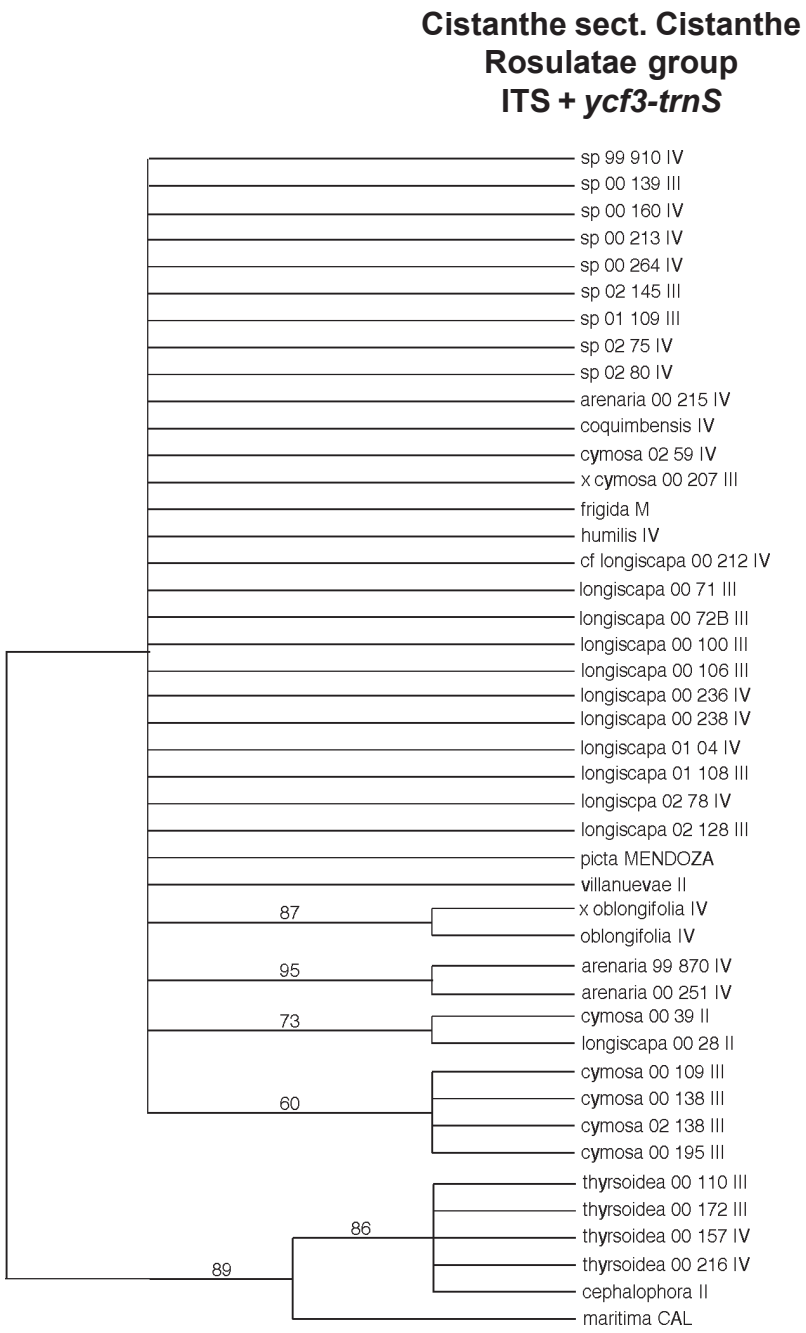

Figure 16. Bootstrap consensus for combined ITS and *ycf*3-*trn*S data for *Cistanthe* sect. *Cistanthe*, Rosulatae group. Sample names are defined in Table I. Roman numerals refer to Chilean Region of origin; M refers to the Metropolitan Region; MENDOZA refers to Mendoza Province, Argentina; CAL refers to California, USA (see Table I). BP values (500 replicates) greater than 50% are indicated. The tree is midpoint-rooted.

Figura 16. Consenso de bootstrap para los datos combinados de ITS y *ycf*3-*trn*S de *Cistanthe* sect. *Cistanthe*, grupo Rosulatae. Los nombres de las muestras se presentan en la Tabla I. Los números romanos se refieren a la región de Chile; M se refiere a la Región Metropolitana; MENDOZA a la provincia de Mendoza, Argentina; CAL a California, EEUU (ver Tabla I). Se indican los valores de BP (500 réplicas) mayores que 50%. El árbol se enraíza con el criterio de midpoint.

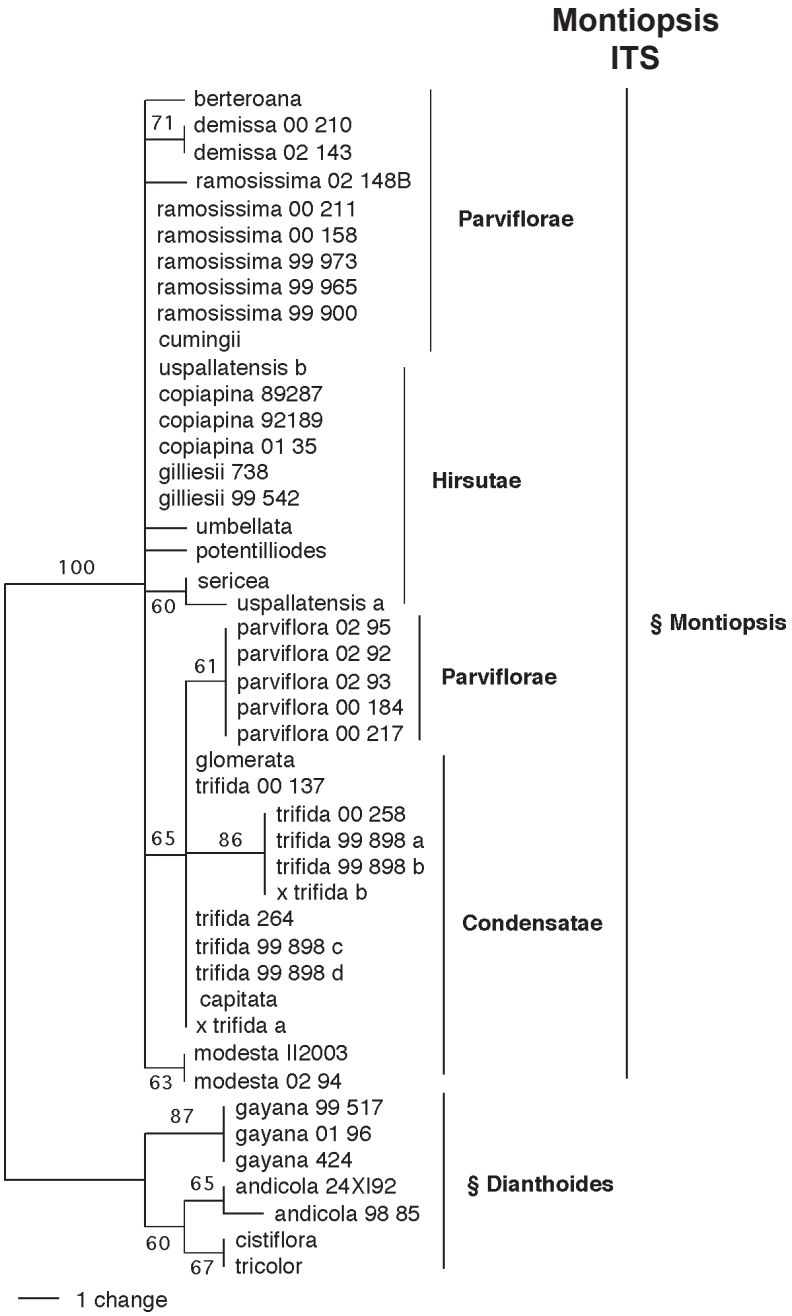

FIGURE 17. MP tree for ITS data for *Montiopsis*. Sample names are defined in Table I. One of 2 trees, length 27, RC 1.0, RI 1.0. BP values (500 replicates) greater than 50% are indicated. Lower case letters following duplicated sample names denote samples having more than one ITS genotype. The tree is rooted between subgenera *Montiopsis* and *Dianthoides*. The bootstrap consensus includes 4 branches with BP values >70%.

FIGURA 17. Arbol más parsimonioso para los datos de ITS de *Montiopsis*. Los nombres de las muestras se presentan en la Tabla I. Uno de 2 árboles, de largo 27, RC 1,0 y RI 1,0. Se indican los valores de BP (500 réplicas) mayores que 50%. Las letras en minúsculas que acompañan los nombres de muestras corresponden a muestras con más de un genotipo de ITS. El árbol se enraíza entre los subgéneros *Montiopsis* y *Dianthoideae*. El consenso de bootstrap incluye 4 ramas con valores de BP >70%.

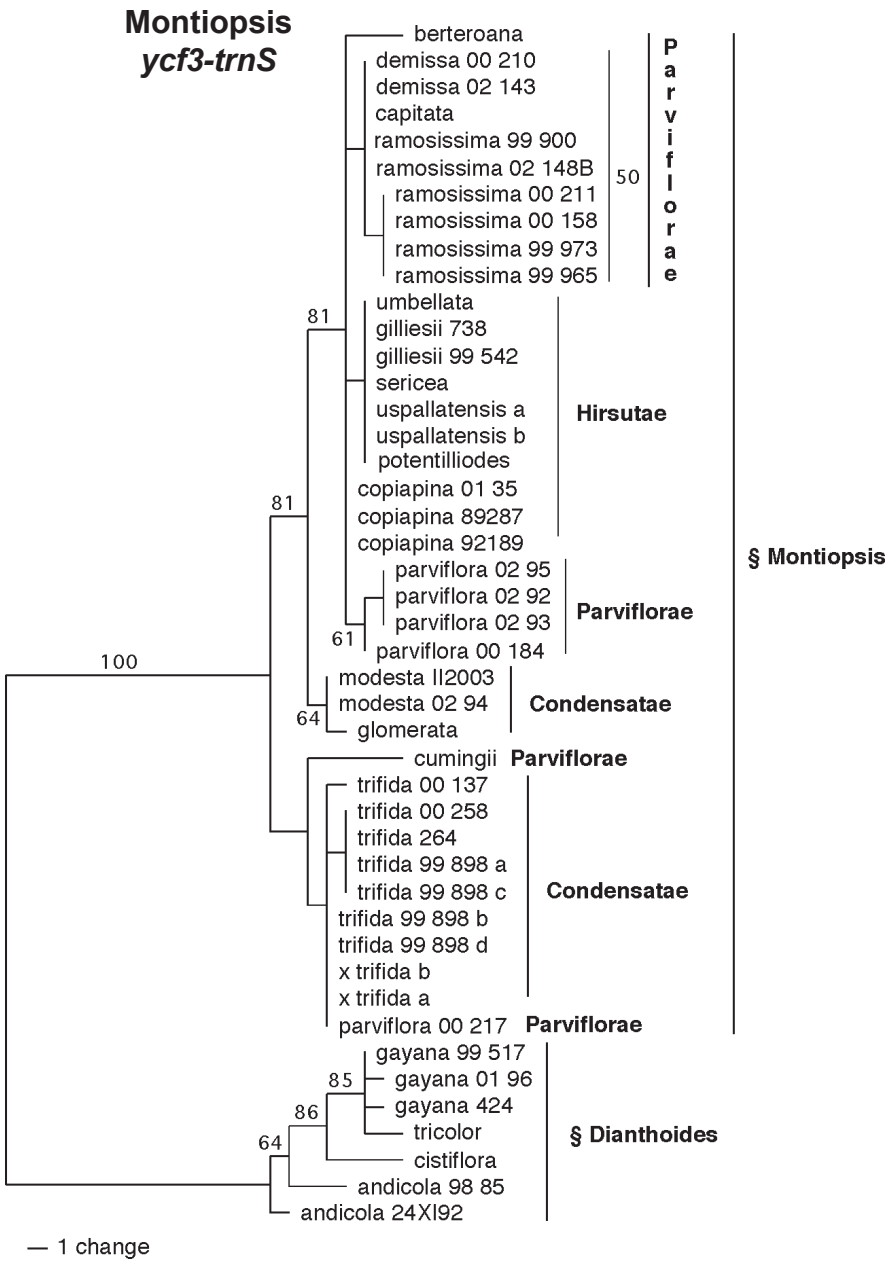

Figure 18. MP tree for *ycf*3-*trn*S data for *Montiopsis*. Sample names are defined in Table I. One of 174 trees, length 69, RC 0.93, RI 0.99. BP values (500 replicates) greater than 50% are indicated. Lower case letters following duplicated sample names denote samples having more than one ITS genotype. The tree is rooted between subgenera *Montiopsis* and *Dianthoides*. The bootstrap consensus includes 5 branches with BP values >70%.

Figura 18. Arbol más parsimonioso para los datos de *ycf*3-*trn*S de *Montiopsis*. Los nombres de las muestras se presentan en la Tabla I. Uno de 174 árboles, de largo 69, RC 0,93 y RI 0,99. Se indican los valores de BP (500 réplicas) mayores que 50%. Las letras en minúsculas que acompañan los nombres de muestras corresponden a muestras con más de un genotipo de ITS. El árbol se enraíza entre los subgéneros *Montiopsis* y *Dianthoideae*. El consenso de bootstrap incluye 5 ramas con valores de BP >70%.

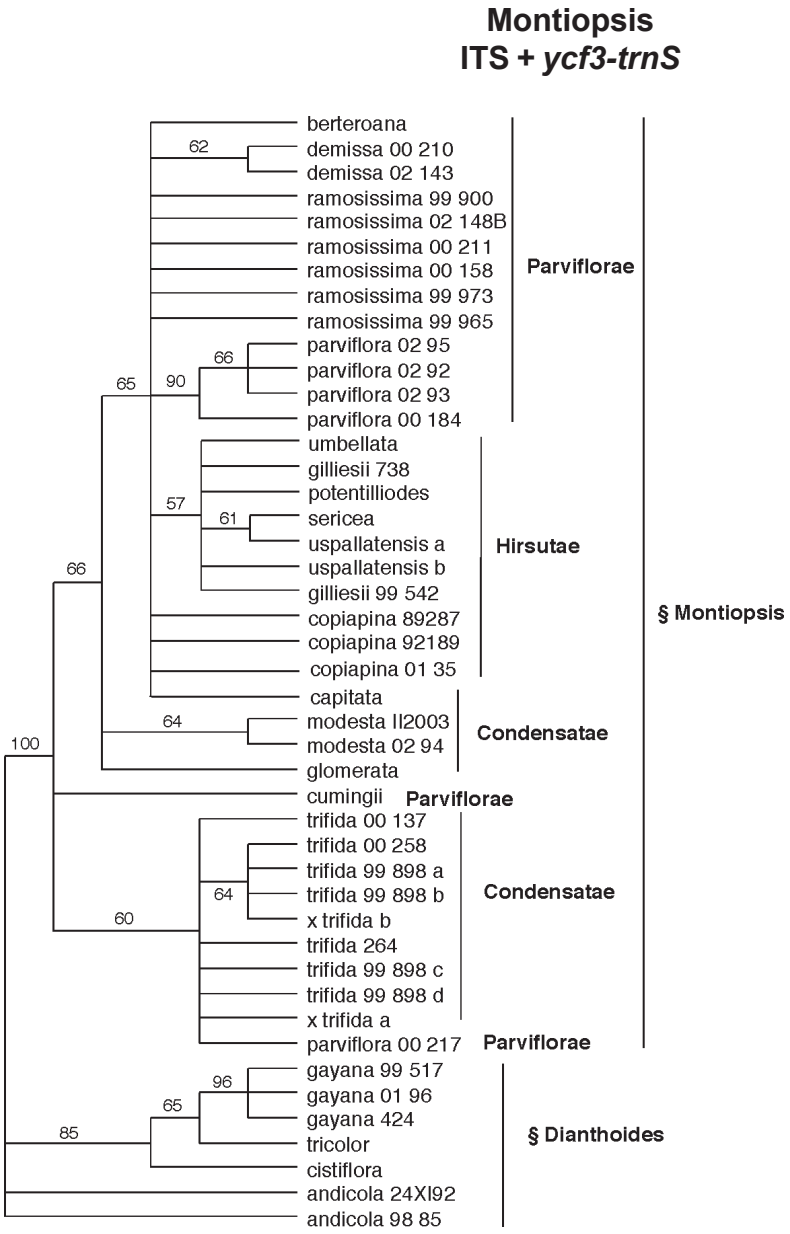

FIGURE 19. Bootstrap consensus for combined ITS and *ycf*3-*trn*S data for *Montiopsis*. Sample names are defined in Table I. BP values (500 replicates) greater than 50% are indicated. Lower case letters following duplicated sample names denote samples having more than one ITS genotype. The tree is rooted between subgenera *Montiopsis* and *Dianthoides.* Analysis of the combined data yielded > 1,000,000 MP trees, length 104, RC 0.86, RI 0.97. The bootstrap consensus includes 4 branches with BP values >70%.

FIGURA 19. Consenso de bootstrap para los datos combinados de ITS y *ycf*3-*trn*S de *Montiopsis*. Los nombres de las muestras se presentan en la Tabla I. Se indican los valores de BP (500 réplicas) mayores que 50%. Las letras en minúsculas que acompañan los nombres de muestras corresponden a muestras con más de un genotipo de ITS. El árbol se enraíza entre los subgéneros *Montiopsis* y *Dianthoideae*. Los análisis de los datos en combinación produjo > 1.000.000 árboles más parsimoniosos, de largo 104, RC 0,86 y RI 0,97. El consenso de bootstrap incluye 5 ramas con valores de BP >70%.

DISCUSSION

Comparison of its and *ycf*3-*trn*S sequence data in phylogenetic reconstruction of western american portulacaceae

For western American Portulacaceae as a whole, informative variability of the *ycf*3-*trn*S spacer is approximately 10% greater than that of ITS (cf. Small *et al.* 1998). At the generic level, the variation is approximately equal. These comparisons include informative variation in sequence length (indels), but these characteristics must be considered a priori at least as robust as substitutions, if not more so. In particular, assuming that the probability of insertion or deletion of particular sequence lengths is, at least within the range of observed length differences, not systematically biased, then the probability of a particular length variation is related to the probability of all possible length variants. In contrast, a substitution has three possible outcomes. Thus, the high information content of indels balances their possible disadvantages, e.g., lack of well-developed methods of incorporating indels into stochastic models of sequence evolution. In parsimony analysis, the *ycf*3-*trn*S sequences also showed equal or, in the case of all western American Portulacaceae, substantially lower levels of homoplasy than ITS. Although the two sequences appear to be substantially complementary in their phylogenetic signal, several cases of conflict were noted. Cronn *et al.* (2002) also found that chloroplast sequence characters showed lower homoplasy than that of various nuclear sequences, and that chloroplast and nuclear sequences yielded conflicting phylogenetic signal. Interpretation of the conflict in this case was problematic. The authors doubted but could not reject that the conflict was the result of interspecific gene flow. They also noted that analysis of length variation versus substitution in the chloroplast sequences also conflicted, but they were unable to detect evidence that substitutions in the chloroplast sequences were systematically biased in a way that would yield spurious interpretation of synapomorphies. In the present infrageneric-level analyses, the number of informative substitutions and length variations was too low to evaluate statistically their degree of consistency.

The ITS tree shows relatively longer branches leading to the North American genera *Claytonia*, *Montia*, and less markedly, *Lewisia*. Longer branches for these taxa also occur in the *ycf*3-*trn*S tree. Hershkovitz & Zimmer (2000) proposed that rates of ITS evolution are higher in these taxa, and that the rate difference was related to a shift in base composition at the parsimony–informative sites from a strong GC to a strong AT bias. The *ycf*3-*trn*S data might suggest that the rate increase in the ITS and chloroplast are also related. However, no comparable shift in base composition is apparent in the *ycf*3-*trn*S sequences: informative sites in the North American taxa are 50-54% GC, generally below average for the exemplars as a whole, but not lower than in samples from the other genera. In contrast to the apparent correlation of rates for the North American taxa, the branch lengths leading to *Montiopsis* are different in the two data sets, relatively short in the ITS data and relatively long in the *ycf*3-*trn*S data. In any case, differences in branch lengths in either data set at the intergeneric level are not related to life form, i.e., a shift to the annual habit. The North American taxa are all perennial (*Lewisia*) or include both perennial and annual species (*Claytonia* and *Montia*). Likewise, species of *Montiopsis* subg. *Dianthoideae* are all perennials, so it is not clear why their *ycf*3-*trn*S divergences are greater than among the Rosulatae group of *Cistanthe* sect. *Cistanthe*, which are mainly annuals. However, differences in divergence coincident with differences in life form were evident within some of the genera (see below).

Intergeneric relations among western american portulacaceae

Unfortunately, increased ITS sampling and the addition of a chloroplast marker did little to improve resolution of relations among genera beyond what was reported by Hershkovitz & Zimmer (2000). The explanation proposed previously was that the genera radiated explosively. An alternative possibility, viz., the gene trees reflect artifacts of hybridization, is considered following discussion of the individual genera. However, the new data do clarify relations involving *Lewisiopsis* and *Lenzia*, as discussed below. Because of the poor resolution, the analysis provides only limited justification for rooting of the various infrageneric trees, and no justification at all in the case of *Calandrinia*. The intergeneric tree appears to provide clear rooting points or outgroups for the Grandiflora and Rosulatae groups of

Cistanthe sect. *Cistanthe* (each other), *Montiopsis* (between subgenera *Montiopsis* and *Dianthoideae*), and *Calyptridium* plus *Cistanthe* sections *Amarantoides* and *Philippiamra* (*Lenzia*), but these rootings may be misleading. Specifically, the branch lengths of the root branches are long relative to the respective ingroup branch lengths. This may introduce long-branch artifacts.

1. *Lewisiopsis* and the North American clade. Evidence for the North American clade is relevant to the understanding of the relation between the Andean and non-Andean taxa. *Lewisiopsis tweedyi* (A.Gray) Govaerts historically was classified in *Lewisia*. Morphological analysis (Hershkovitz 1992) indicated that this species lacked synapomorphies of *Lewisia* and, on the balance, was more similar to species of *Cistanthe* than to any species of *Lewisia*. For this reason, the species was transferred to *Cistanthe*. In fact, that analysis indicated that *Lewisiopsis tweedyi* was not more similar to any *Lewisia* species than to *Claytonia* species. The previous ITS analysis (Hershkovitz & Zimmer 2000) provided no support for relations to *Cistanthe* and only weak support for a "North American" clade comprising *Lewisiopsis tweedyi*, *Lewisia*, and the *Claytonia*/*Montia* clade. However, the molecular data were remarkably parallel to the morphological in that the ITS sequence of *Lewisiopsis* was highly plesiomorphic relative to *Lewisia* and *Claytonia*/*Montia*. In fact, it is more similar to the *Cistanthe* than to the North American taxa sequences. The present ITS analysis is in agreement. The *ycf*3-*trn*S sequence data provide relatively strong support for a sister-relation between *Lewisiopsis* and *Lewisia*, although, as with ITS, the *ycf*3-*trn*S sequence of *Lewisiopsis tweedyi* is also plesiomorphic. Support for the *Lewisiopsis*-*Lewisia* clade, however, is sensitive to sampling in the other North American genera (data not shown). The analysis of the combined data provide strong support for the North American clade but weak support for the *Lewisiopsis*-*Lewisia* clade. The reduction of support for the latter clade in the combined analysis suggests that the ITS and *ycf*3-*trn*S sequences conflict somewhat. The relictuality of *Lewisiopsis* among the North American taxa is discussed in greater detail elsewhere (Hershkovitz, in prep.)

2. The relations of *Lenzia*. Surprising given its morphology (cf. Hershkovitz 1993), the monotypic *Lenzia* appears as the sister group to *Calyptridium* plus *Cistanthe* sections *Amarantoides* and *Philippiamra*. *Lenzia chamaepitys* Phil. is an acaulescent high alpine chaemophyte distributed between ca. 22-31°ð S. At ca. 30°ð S, it was observed to occur among the highest elevation plant species (4200 m). The plant is a 2-3 cm tall tuft of largely membranous awl-shaped leaves. Reportedly, it has solitary, axillary flowers (Carolin 1993). The plants are connected by slender rhizomes (pers.observ.), a characteristic not previously reported. Among western American Portulacaceae, this acaulescent, perennial growth form is most suggestive of *Calandrinia* sect. *Acaules*, especially the diminutive and rhizomatous *Calandrinia compacta* that occurs in the alpine zone in the same region. *Cistanthe* sections *Amarantoides* and *Philippiamra*, in contrast, are all succulent, ramified lowland desert annuals with multiflorous (20-100 flowers) inflorescences. As noted in Hershkovitz (1991a, c; see also Carolin 1987), the plants have the same vegetative and inflorescence morphology and leaf anatomy as in *Cistanthe*. The flowers of *Calyptridium* plus *Cistanthe* sections *Amarantoides* and *Philippiamra* are smaller and more congested and the sepals more membranous than in most *Cistanthe* species, but these characteristics intergrade in the two. *Calyptridium* are also mainly low-elevation annuals. The higher-elevation condition and perenniality appear to be derived in this genus (Hershkovitz in prep.). The only reported characteristic of *Lenzia* that is coincident with *Calyptridium* plus *Cistanthe* sections *Amarantoides* and *Philippiamra* is membranous sepal texture (Reiche 1905). However, the leaves of *Lenzia* are also membranous. Thus, even in hindsight, morphology and ecology provide little if any hint of the sister relation between *Lenzia* and *Calyptridium* plus *Cistanthe* sections *Amarantoides* and *Philippiamra*. Although the evidence for the relations of *Lenzia* refute the hypothesized monophyly of *Cistanthe sensu* Hershkovitz 1991a, the molecular data support the previously hypothesized close relationship between the North American *Calyptridium* and South American *Cistanthe* sections *Amarantoides* and *Philippiamra* (Carolin 1987; Hershkovitz 1993).

Infrageneric relations among western american portulacaceae

1. *Calandrinia*. As noted, the rooting of the *Calandrinia* trees remains problematic, but the ITS and *ycf*3-*trn*S data are at least consistent with the classification of *Calandrinia* in three sections. In particular, the annual and perennial taxa are partitioned, and the data do not indicate a clear relationship for *Calandrinia* sect. *Monocosmia* Hershk. As noted in Hershkovitz (1993), *Calandrinia* (*Monocosmia*) *monandra* resembles the annuals vegetatively, but its inflorescence and flowers are distinctive, so much so that the species was traditionally classified not only in the separate genus *Monocosmia* Fenzl, but in a different tribe of Portulacaceae. The ITS and *ycf*3-*trn*S data conflict at certain points, which is consistent with other information that hybridization may occur among certain taxa, as discussed below. The data also contribute to the taxonomic understanding of *Calandrinia menziesii*, *Calandrinia feltonii* Skotts., and two unidentified forms.

Calandrinia menziesii, which is distributed from Baja California to British Columbia, historically has been considered as a variety of the Central American and South American *Calandrinia ciliata* (e.g., Macbride 1931; Munz & Keck 1968) or even as the same species (e.g., Kelley 1993). *Calandrinia menziesii* also has been considered as a variety or as the same species as *Calandrinia caulescens* Kunth (e.g., Gray 1887), but the latter is generally considered a taxonomic synonym of *Calandrinia ciliata*. In any case, there has never been a clear morphological distinction between the temperate North American versus the Central American and South American plants. The characteristics of *Calandrinia menziesii* mentioned by Macbride (1931), "more numerous stamens (often) and larger flower," are actually highly polymorphic in this species. In fact, the taxonomic recognition of *Calandrinia menziesii* appears to have been among North American populations rather than between these and those of Central America and South America (e.g., Gray 1887; Rydberg 1928). Both the ITS and *ycf*3-*trn*S data show that the *Calandrinia menziesii* samples (spanning Baja California to British Columbia) are divergent from those of *Calandrinia ciliata* (Mexico and Argentina). Ironically, the *Calandrinia ciliata* sequences are identical to those of *Calandrinia compressa*, a morphologically distinctive species endemic to central/southern Chile, at least 1000 km disjunct from *Calandrinia ciliata*. However, some herbarium collections from northernmost Chile and in the range of *Calandrinia cililata* appear to be intermediate in morphology between *Calandrinia ciliata* and *Calandrinia compressa*. Thus, the possibility of hybridization involving *Calandrinia compressa* should be considered.

It is further ironic that evidence for hybridization involving *Calandrinia compressa* emerges from the study of *Calandrinia menziesii* apparently introduced to the Falkland Islands (Islas Malvinas), where it has been known as *Calandrinia feltonii*. *Calandrinia feltonii* had been presumed to be an endemic species that was extirpated in the wild because of grazing and other human activity (Davidson 1975; Woods 1994, 2000a). I had considered this species to be the same as *Calandrinia ciliata* (*sensu* Kelley 1993, including *Calandrinia menziesii*), as indicated in my 1992 annotation of the type (*Skottsberg 1910*, UPS!, SGO!). The same opinion was shared by Peralta (1999). Circumstantial evidence suggested that this plant may have been introduced to the Falkland Islands: the absence of populations in undisturbed localities, its long history of cultivation on the islands, the remoteness of the Falklands from the nearest wild populations of *Calandrinia ciliata sensu lato* (in the highlands west of Buenos Aires), the introduction and subsequent establishment of this species in Australia, New Zealand, and, most recently, India (Pande 2001), the frequent cultivation of this species in European botanical gardens in the late 19th century, and the strategic location of the Falkland Islands in the shipping route between Europe and the American Pacific coast. Nonetheless, *Calandrinia feltonii* became a keystone species of Falklands Islands conservation efforts, even featured on a conservation-themed Falkland Islands postage stamp. The search for wild populations of *Calandrinia feltonii* led to the discovery of an apparently distinct *Calandrinia* (Woods 2000b). Actually, the "new" form [e.g., *R. W. Woods, s.n. 24 Dec 2001* (Falkland Islands National Herbarium, photo!)] had been cultivated and collected as early as 1895 [*L. H. Firman s.n.* (K, received June 1895), R. Woods, pers. comm.], but the earlier collection was presumed to be *Calandrinia feltonii*. From

photographs (courtesy of R. Woods), the unidentified taxon more closely resembles the Chilean endemic *Calandrinia axilliflora*, but nonetheless appears distinct. The present data show that the Falkland Island specimens purporting to be *Calandrinia feltonii* have ITS and *ycf*3-*trn*S sequences identical to *Calandrinia menziesii*. Given the genetic distinction between *Calandrinia menziesii* and *Calandrinia ciliata*, this corroborates the hypothesis of introduction. The data for the purportedly new form (C_sp_Mal1 and C_sp_Mal2) are conflicting. The ITS tree corroborates the close relationship of this plant with *Calandrinia axilliflora* of Chile, but the *ycf*3-*trn*S sequences are more similar to those of *Calandrinia ciliata* and *Calandrinia compressa*. Although materials used in the present study were not vouchered, the authenticity of their identity is supported circumstantially by the DNA data. In particular, sequences of the samples purported to be *Calandrinia feltonii* conform as expected to *Calandrinia menziesii*, and ITS sequences of the samples purported to be the form similar to *Calandrinia axilliflora* likewise conform to this species. Moreover, the sequence data indicate that these samples may be hybrids.

Subsequent examination of herbarium material has revealed that plants resembling the unidentified Falkland Islands form have been collected in coastal southern Chile, mainly between Concepción and Valdivia [e.g., *Lechler 585* (P!), *C. Gay 65* (P!)]. A possible scenario supported by the sequence data is that the unidentified form is actually a hybrid between *Calandrinia axilliflora* and either *Calandrinia compressa* or *Calandrinia ciliata*, and that, like *Calandrinia menziesii*, it has been introduced into the Falkland Islands. Also consistent with the data is the possibility that *Calandrinia compressa* itself is of hybrid origin. This would explain why this ecologically and morphologically distinctive species shares genotypes with *Calandrinia ciliata*.

As noted in Table I, another unidentified calandrinia, *Hershkovitz 99-22B*, occurs among the perennial species, described and illustrated in Hoffmann *et al.* (1998, pp. 56-57). This plant is known only from two small populations (< one hectare) in a ski area east of Santiago. It has a jointed peduncle characteristic of (sub)tropical perennial calandrinias that occur only north of the arid diagonal, a virtually plantless region that transects the Andes at ca. 24°S S. This natural phytogeographic barrier separates the southern Andes, which receives moisture in winter via an Antarctic polar front, from the central Andes, which receives moisture in the summer months via the Intertropical Convergence (Arroyo *et al.* 1988). Relatively few species (as currently recognized) are distributed on both sides of the diagonal (Arroyo *et al.* 1988, unpublished data), and among *Calandrinia* species, only *Calandrinia compacta*, distributed from Bolivia to central Chile and Argentina (Peralta 1999). The presence of the unidentified form in central Chile could be explained by numerous scenarios involving, variously, dispersal, relictuality, human influence, and/or homoplasy. ITS and *ycf*3-*trn*S sequence divergences are low among the perennials, hence insufficient to definitively corroborate one hypothesis over another. Nonetheless, the ITS sequence of the unidentified form is more similar to those of central Chilean species while the *ycf*3-*trn*S sequence is more similar to that of the northern species, *Calandrinia acaulis* Kunth. This introduces the possibility that the unidentified form represents a hybrid.

The sampling also includes a natural morphologically intermediate hybrid between *Calandrinia compacta* and *Calandrinia caespitosa* that was collected where the two species were growing in intimate association in their range of overlap in the Andes of Mendoza Province, Argentina. The hybrid resembles *Calandrinia caespitosa* more than *Calandrinia compacta* (see Table I for comments regarding this hybrid). The *ycf*3-*trn*S sequence is that of the resident sample of *Calandrinia compacta*, whereas the ITS is dimorphic. One ITS sequence corresponds to *Calandrinia compacta* and the other is possibly recombinatorial, with two positions shared by the resident *Calandrinia caespitosa*. The resident *Calandrinia caespitosa* shares the same dimorphism at the same two positions. (These dimorphisms were diagnosed by superimposed peaks in the chromatograms. The ITS was not cloned.) The polymorphisms resolve as homoplasy in the Figure 4 topology. In the consensus of the 100,000-plus ITS MP trees, all of the *Calandrinia caespitosa* and *Calandrinia compacta* branches collapse into a polytomy. The lack of resolution is evident in the splits graph (Figure 7). Nonetheless, the combined data bootstrap supports both the

Calandrinia caespitosa and *Calandrinia compacta* clades, with the putative hybrid grouping with the latter. It is also noteworthy that both the ITS and *ycf*3-*trn*S sequences of a sample of *Calandrinia compacta* from Region III of Chile, north of the range of *C. caespitosa*, are different from those of the more southerly samples.

Finally, it is important to note that not all forms of *Calandrinia* have been sampled in the present work. Three recognized taxa not available are *Calandrinia acaulis* var. *magna* Macbride, *Calandrinia alba* (Ruiz & Pav.) DC., and *Calandrinia acutisepala* Añon. An internet search reveals another species distributed worldwide by alpine garden enthusiasts as *Calandrinia ranunculina* (nom. invalid.), originally from seed collected by John M. Watson and Ana Flores in Patagonia. In addition, further study of *Calandrinia* should sample the entire ranges of especially widespread taxa and also intermediate forms associated with two species pairs. One pair is *Calandrinia acaulis* and *Calandrinia carolinii* Hershk. & D.I.Ford. As noted by Hershkovitz & Ford (1993), many specimens from Peru and Bolivia are difficult to assign to one or the other taxon. The other pair is *Calandrinia affinis* Gillies ex Arn. and *Calandrinia colchaguensis* Barnéoud. These taxa have overlapping ranges in central Chile, and many herbarium specimens are intermediates.

2. *Calyptridium* plus *Cistanthe* sections *Amarantoides* and *Philippiamra*. Because the relations of *Cistanthe ambigua* are unresolved, it is not clear if the most recent common ancestor of extant members of this clade was North American or South American, even though the sister group, *Lenzia*, is South American. Indeed, the relatively low sequence divergence among samples of *Cistanthe* sections *Amarantoides* and *Philippiamra* may implicate a secondary origin from North America (but see also below).

Because of the low sequence divergence, the data do not provide strong support for interspecific relations among taxa of *Cistanthe* sections *Amarantoides* and *Philippiamra*, nor even the distinction between these. This lack of divergence is remarkable for a group traditionally circumscribed as including 14 species in two genera [12 spp. listed by Reiche (1898), including *Cisanthe densiflora* (Barnéoud) Carolin ex Hershk., plus *Cistanthe arancioana* Peralta and *Cistanthe minuscula* (Añon) Peralta]. As discussed by Hershkovitz (1993), these taxa were at one time classified not only in separate genera, but in different tribes of the family. The strongest bootstrap value links *Cistanthe calycina* of *Cistanthe* sect. *Amarantoides* with *Cistanthe amarantoides* of *Cistanthe* sect. *Philippiamra*. The data do not even support monophyly of samples of particular species. The combined data provide at least weak support for monophyly of the Chilean samples of *Cistanthe densiflora*, but a specimen from San Juan Province, Argentina, does not cluster with these. As noted in Table I, one collection appears to be intermediate between plants of *Cistanthe calycina* and *Cistanthe densiflora* growing together in the same locality. The possibility that gene flow can account for the apparent uniformity of sequences in this and other genera is elaborated further below.

3. *Cistanthe* sect. *Cistanthe*

3a. Grandiflora group. The taxonomy of the Grandiflora group is difficult for reasons described in the Materials and Methods, and because types of three species, including the type species of the genus, are iconotypes that illustrate plants cultivated in Europe from seed of provenance no more specific than "Chile." Given the tremendous variation among populations, it may be necessary to designate neotypes. As indicated by the trees and splits graph, sequence divergence among the samples is low, but somewhat conflictive. The graphics show proximity among the samples of *Cistanthe* sp. indet., aff. *Calandrinia laxiflora* Phil., but the samples themselves were geographically proximal.

The combination of the data and field observations suggest that interspecific gene flow may be occurring in the Grandiflora group. For example, samples of *Cistanthe* sp. indet., aff. *Calandrinia laxiflora* and *Cistanthe discolor* (Schrad.) Spach collected from the same site share both sequences. As here interpreted, the former species occurs strictly on coastal cliffs and bluffs, has narrow and very succulent leaves, petals with red blotches in the claw, and a well exserted style. The latter species ranges from coastal matorral to at least 50 km inland, has broad and flat leaves, whitish petal claws, and a style not exserted. I have observed intermediates where the two occur proximally, e.g., *Cistanthe discolor* with petals that are red to maroon at the base and somewhat exserted styles. One of the present

samples of *Cistanthe* sp. indet., aff. *Calandrinia laxiflora*, *Hershkovitz 99-948*, has unusually broad leaves for this species, and plants in this population have supernumerary petals (6-8 rather than five). These anomalous characteristics may be indicative of hybrid origin.

3b. Rosulatae group. As in the Grandiflora group, sequence divergence is low in Rosulatae group, and interspecific relations generally are not resolved. The poor resolution of the sequence data is more surprising for the Rosulatae group than for the Grandiflora group, because morphological and ecological variation in the former group is greater. Reiche (1898) recognized 15 species divided among three sections of *Calandrinia*. Neither of the two sequences groups samples of some of the reasonably distinct species, let alone the morphologically similar species corresponding to Reiche´s sections. The only exceptions are the partitions supporting relationships of *Cistanthe maritima*, *Cistanthe cephalaphora*, and *Cistanthe* sp. indet., aff. *Calandrinia thyrsoidea*. These last two taxa differ from other members of the section in their congested inflorescences of relatively small flowers with short pedicels. They are nonetheless clearly distinct taxa. There does not appear to be a morphological character that unites *Cistanthe maritima* with these species, however. *Cistanthe maritima*, which is disjunct in California, has the more open inflorescence and larger flowers of other members of the section. However, support for monophyly of this partition depends upon the unresolved location of the root, i.e., *Cistanthe maritima* may be the sister of the remainder of the section.

As evident in Table I, most of the unidentified samples fall into two morphological categories. One form resembles oversize plants of *Cistanthe arenaria*. These commonly occur in association with other taxa, and I have found them only in highly disturbed sites, especially in or near avocado plantations. The other form somewhat resembles *Cistanthe* sp. indet., aff. *Calandrinia thyrsoidea* in having linear leaves and an erect rather than prostrate or ascending habit, but the flowers may be similar to those of *Cistanthe longiscapa* or, alternatively, *Cistanthe arenaria*. These plants occur occasionally in desert habitats in sites that may be disturbed but not under cultivation.

As in the Grandiflora group, the molecular data, morphology, and/or field observations suggest interspecific gene flow in this group. The evidence includes observations of plants that are either aberrant or intermediate between other species, and that occur in sympatry with potential parental types and/or are restricted to human-transformed habitats that presumably were not part of the prehuman history of the group. The unidentified plants described above fit these criteria. As indicated in Table I, another aberrant collection, *Cistanthe* sp. 02-80, resembles a dwarf or stunted plant of the Grandiflora group. The finding of both ITS and *ycf*3-*trn*S sequences of the Rosulatae group in this collection was somewhat surprising. In 2002, a few hundreds of individuals were found near the peak of Cuesta Pajonales, along the main highway that links the cities of Coquimbo and Vallenar. The form apparently was first collected in the late 1950s, but it has been collected perhaps three times since then. Cuesta Pajonales forms both a political and rain-shadow border between Regions III and IV of Chile. This is also a natural border of Chile's "desierto florido". In rainy years, vast expanses of *Cistanthe longiscapa* appear immediately on the Region III side of Cuesta Pajonales. This species is much more sparsely distributed on the Region IV side. Nonetheless, plants of both the Grandiflora and the Rosulatae groups occur within 50 meters of the population of aberrant plants. The aberrant plants appeared to be fully fertile on the basis of their copious seed production. Other aberrant plants include those of giant-sized *Cistanthe cymosa* found growing in a population of normal plants. The giant plants had ca. 17 stamens in contrast to the nearly invariable five that occur throughout the extensive range of *Cistanthe cymosa*. Again, other forms of the Rosulatae group occur nearby. Another putative hybrid was an aberrant form of *Cistanthe* sp. indet., aff. *Calandrinia oblongifolia* having pink rather than usual white flowers and inordinately higher numbers of petals and stamens. The plants were growing with plants of *Cistanthe* sp. indet., aff. *Calandrinia oblongifolia* and *Cistanthe humilis* (Phil.) Peralta in a 100 m range of altitudinal overlap. *Cistanthe humilis* has pink flowers.

Molecular evidence for gene flow in the Rosulatae group includes conflict among gene trees and conflict between gene trees and morphology, especially when such conflict is coincident with interspecific sympatry. Conflict involving the gene

trees cannot be considered strong given the low divergence, i.e., it could be explained by homoplasy and/or conservation of ancestral polymorphism. In any case, numerous conflicts exist between the ITS and *ycf*3-*trn*S trees for the Rosulatae group. For example, for the 12 samples of *Cistanthe longiscapa*, five can be considered to have conflicting combinations of genotypes, i.e., the different sequences do not circumscribe the same groups of samples. In one case, a collection has the same ITS genotype of a sympatric collection of *Cistanthe cymosa*. The sequence of this *Cistanthe cymosa* sample is, in turn, different from the other four samples of this species. These collections are from a coastal site near the northern limits of the ranges of both species. This site is also near the type locality of *Cistanthe cymosa*. Another noteworthy example of discordance is polyphyly of samples of *Cistanthe arenaria* in both the ITS and *ycf*3-*trn*S sequences. Both trees show one sample grouping with a sample of *Cistanthe* sp. indet., aff. *Calandrinia chamissoi*, which Reiche (1898) considered a variety of *Cistanthe arenaria*. As identified here, the two taxa can be distinguished by numerous characteristics (leaf shape, size of all floral parts, sepal texture and coloration, petal color, stamen number, style length, stigma color, seed pubescence). Populations of each taxon occur separately, but they commonly occur together, invariably with some morphologically intermediate individuals (pers. obs.). Thus, the divergence of the material sampled here may reflect hybridization.

As a final note, the present analysis does not include 3-4 Peruvian taxa and one species from Guadalupe Is., Mexico, all of which probably pertain to this section (see Macbride 1937; Hershkovitz 1991a, 1991b; Hershkovitz & Zimmer 2000).

4. *Montiopsis*

4a. *Montiopsis* subgenus *Dianthoideae*. This group includes at least four species. Two of these, *Montiopsis andicola* (Gillies) D.I.Ford and *Montiopsis gayana*, show considerable variability, as suggested by their extensive synonymy (Peralta 1999). Likewise, each chloroplast haplotype of samples of these taxa was found to be distinct. One species, *Calandrinia tricolor*, has been considered as a synonym of *Montiopsis andicola*, but it is distinct genetically, as well as morphologically (Hoffmann *et al.* 1998, p. 56, fig. 1 vs. fig. 4). It also occurs at lower elevation (pers. obs.) than *Montiopsis andicola*. As in the other genera, the conflict between the ITS and *ycf*3-*trn*S sequences may be indicative of hybridization. However, additional sampling is needed to draw more definitive conclusions.

4b. *Montiopsis* subgenus *Montiopsis*. As in other genera, sequence divergence is too low to resolve relationships and evaluate conflicting signal. As in the Rosulatae group of *Cistanthe* sect. *Cistanthe*, the lack of divergence is somewhat surprising given the morphological and ecological diversity of the taxa, which Reiche (1897, 1898) also divided into three sections within *Calandrinia*. Ford (1992) recognized 15 species. Notwithstanding, as in other genera, some evidence may suggest interspecific gene flow. The molecular data conflict in the relations of the *Montiopsis trifida* samples. The relevant partitions reasonably well-supported in the *ycf*3-*trn*S tree are conflicted by the somewhat weaker partition in the ITS tree. The partitions in the *ycf*3-*trn*S tree are less well supported in the combined data bootstrap consensus. A more peculiar result is that one specimen of *Montiopsis parviflora* (00-217) has the same chloroplast haplotype as the *Montiopsis trifida* specimens and is well-separated from the remaining *Montiopsis parviflora* samples. This particular specimen corresponds morphologically more to the type specimen than the others. In particular, it has densely pubescent eglandular sepals rather than sparsely pubescent glandular sepals characteristic of the other samples. Also, its provenance is much more proximal to the type locality in northern Region IV of Chile than the others, which are all from Region III. However, all of the samples of *Montiopsis parviflora* correspond morphologically and geographically to the diagnosis given by Ford (1992).

The remaining evidence for gene flow in *Montiopsis* sect. *Montiopsis* is more circumstantial. A sample corresponding morphologically and geographically to a putative recurring hybrid between *Montiopsis capitata* (Hook. & Arn.) D.I.Ford and *Montiopsis trifida* (Ford 1992) has both the ITS and *ycf*3-*trn*S sequences of the latter. Ford (1992) also suggested hybridization was responsible for intermediacy among the sympatric perennial species of *Montiopsis*, most of which are identical in both their ITS and *ycf*3-*trn*S sequences. The present work also documents a new case of sympatry between *Montiopsis* species, viz., *Montiopsis*

modesta (Phil.) D.I.Ford (Hershkovitz 02-94) and *Montiopsis parviflora* (Hershkovitz 02-92, 02-93, & 02-95). In fact, the *Montiopsis parvifolia* plants were unusually diverse, and none of the three collections here have what Ford (1992) indicated was the "typical" morphology of the species. One collection (Hershkovitz 02-92) has a pedicel length longer than the extreme recorded by Ford and also plumose sepal trichomes. The other two (Hershkovitz 02-93 and Hershkovitz 02-95) have the sparely pubescent and glandular sepals that Ford regarded as unusual for this species. This particular characteristic is shared with *Montiopsis modesta*, a species never before collected in the same elevational range nor flowering during the same season as *Montiopsis parviflora*.

Rapid radiation, rampant hybridization, or both?

A pervasive theme of the age of DNA sequence phylogenetics is that of "rapid radiation," which can be characterized as apparent morphological/ecological diversity disproportionate to unexpectedly short and often cladistically irresolvable gene tree branches. The previous analysis of western American Portulacaceae ITS data (Hershkovitz & Zimmer 2000) and a considerable number of references cited therein cited rapid radiation as the explanation for this pattern. Among the numerous more recent examples is Cronn *et al.* (2002). In most of these cases, rapid radiation is associated with recency of the development of modern habitats, especially on islands. The rapidity and degree of morphological and ecological diversification possible in a short time and with negligible divergence of "neutral marker" gene sequences is manifest by performing BLAST searches of such domesticated plants as *Brassica* species (pers. observ., data not shown).

Taken at face value, the present data can be interpreted as evidence of successive rapid radiations of taxa, the first resulting in evolution of the modern genera and subsequent resulting in the species diversity within each. At least with the sequence markers used, the radiation would be considered too rapid to evaluate the pattern of phylogeny across the various habitats occupied by the taxa. This is especially the case for *Montiopsis* subg. *Montiopsis*, whose taxa exhibit the broadest range of habitats, from cool temperate to desert and from high alpine to sea level (Ford 1992). The present sequence data reveal relatively few differences among the taxa and practically no phylogenetic resolution. A typical divergence rate for ITS for herbaceous plants (5×10^{-9} substitutions/site/year; see Hershkovitz & Zimmer 2000) would date the diversification of this group at less than 2 million years. This date is not inconceivable, but it suggests that the group diversified more recently than the range (though not necessarily the actual locations) of habitats occupied in Chile. In this case, the outgroup is clearly *Montiopsis* subg. *Dianthoideae*, which includes only alpine perennial species in central and southern Chile. This would suggest that *Montiopsis* subg. *Montiopsis* has such an origin and evolved northwards and into the lowland mediterranean, desert, and coastal regions. At the same time, it must be noted that the *ycf*3-*trn*S divergence between the subgenera is relatively high, thus the rate calibration of one or the other or both sequences may be misleading. However, this does not change the observation that an order in which the species of *Montiopsis* subg. *Montiopsis* evolved into their diverse habitats cannot be discerned from either sequence, i.e., both sequences suggest simul-taneous diversification. The same observations can be extended to the other genera.

Possibly, permeation of the parsimony principle in systematics has promoted the rapid radiation interpretation, viz., there is no need to postulate a DNA sequence diversification period longer than the minimum possible. The more recent implemen-tation of relatively simple likelihood methods in phylogenetics software, has facilitated a conceptual shift away from the "minimal explanation" towards the explanation that best predicts the data under the most realistic model. In this context, it is possible to evaluate, at least intuitively and given certain parameters, an alternative model. In particular, is it possible that the ecological diversification within the genera of Portulacaceae took place earlier than is apparent, but that hybridization has homogeneized the neutral markers within genera, giving the appearance of more recent radiation?

As a preface to consideration of the possible role of hybridization (gene flow between historically individuated lineages that nominally merit taxonomic distinction) as an explanation for the morphological and molecular diversity of Andean Portulacaceae, it should be emphasized that reticulate evolution in a group predisposed to hybridization cannot be considered *a priori* an *ad hoc* assumption. In other words, it does not represent an explanation that is inherently arbitrary relative to other explanations. The

basis for an expectation of cladogenesis is reasonably clear: the lack of panmixia in the face of continual mutation. In practice, however, cladogenesis *de facto* represents *a priori* an *ad hoc* assumption, because the most popular phylogenetic methods constrain for cladogenesis without justification as to why this process should be preferred, much less assumed, in the group in question. It is perhaps more the rule than the exception that, at least in plants, the conditions necessary and sufficient for hybridization exist. Hybridization can be considered as a process that is not necessary in organic evolution, but, like among-site rate heterogeneity, one that occurs at some level. In phylogenetics, hybridization is discriminated against in part because it introduces tremendous mathematical complexity into phylogenetic reconstruction and in part because the relevant parameters are poorly understood or cannot be easily evaluated using common molecular systematic approaches (Linder & Rieseberg 2004). However, reticulate evolution and cladogenetic evolution can be evaluated subjectively in terms of several parameters, including the biotic conditions that regulate hybridization and what genotypic and phenotypic patterns are produced under each model. Some of these parameters will be discussed below and evaluated in the case of Andean Portulacaceae. In many cases, knowledge may not be sufficient to establish or at least conjecture the value of a particular parameter. The value of that parameter, however, should not be set at a value that, *a priori,* either favors or refutes hybridization or cladogenesis.

1. Interfertility

At present, no experimental data exist relating to the interfertility among species within the genera of Portulacaceae. However, several cases of suspected hybrids sympatric with parental taxa have been described above. It is also relevant to note that current interfertility may not be an indicator of past interfertility, i.e., fertility barriers are derived (Kimball *et al.* 2003). On the balance, the putative evidence for hybrids in the absence of evidence for intersterility appears to favor more than refute hybridization scenarios for Portulacaceae.

2. Allopolyploidy

Allopolyploidy is considered to be a consequence of hybridization. However, hybrid taxa may also be diploid (Rieseberg 1997). Among the relatively few chromosome data for Portulacaceae (Nyanyano 1986; Ford 1992), there are no clear cases of allopolyploidy, but there are a few instances of tetraploids and hexaploids. Thus, the existing chromosome data should not influence the hybridization probability one way or another.

3. Morphological evidence

Several cases of morphological intermediates have been discussed above. However, it should be emphasized that hybridization does not always result in morphological intermediacy; hybrids may appear as one or the other parent or as a novel phenotype (McDade 1995, Rieseberg & Welch 2002). Likewise, some of the plants considered in the present analysis appeared to represent novelty.

4. Conflict between genotypes

The present results include several apparent cases of conflict between ITS and *ycf*3-*trn*S genotypes, which may be interpreted as evidence of hybridization. At the same time, lack of conflict between two putatively neutral markers cannot be considered strong evidence contrary to hybridization. A large portion of the genome may be neutral in terms of morphological appearance. Introgression of this portion across species boundaries is regulated mainly by interfertility/opportunity and perhaps fitness of the genotype at the molecular level (Morjan & Rieseberg 2004, Rieseberg *et al.* 2004). Thus, while conflict between putatively neutral DNA sequences favors a hybridization scenario, agreement between two or a few markers may not yield strong evidence to the contrary (see also Linder & Rieseberg 2004). Likewise, the paucity of ITS polymorphism in the present data may not be contrary to hybrid origins. Elimination in hybrids of divergent parental ITS forms appears to take place over the course of relatively few generations, so that the inheritance is essentially uniparental in evolutionary time (Kotseruba *et al.* 2003, Song *et al.* 1995, Smedmark *et al.* 2003, Kovarik, in press).

5. Conflict between genotype and morphology

Aside from cases in which suspected morphological hybrids lack polymorphism in their ITS sequence, two cases were noted in which samples have unexpected

genotypes. One of these was a sample of *Cistanthe cymosa* that shared the ITS genotype of a sympatric sample of *Cistanthe longiscapa*, and the other was samples of *Montiopsis parviflora* with the *ycf*3-*trn*S sequence of *Montiopsis trifida*. The unexpected similarity of the marker sequences in morphologically divergent taxa may itself result from hybridization. Introgression can cause alleles of one age to be replaced by those of another. If younger alleles have a tendency to replace older, the result would be low sequence divergence in a group older than the sequence divergence would suggest. This can be called marker "surfing," because an allele can surf the tips of the phylogeny via introgression.

6. Ecological conditions favoring hybrids

If ecological instability and novelty of habitats favor hybrid success, then current and historical environmental parameters must be considered favorable to hybridization of Andean Portulacaceae. Most of the diversity occurs in central and northern Chile. This region includes altitudinal gradients of commonly 3000-4000 m over relatively short distances. The precipitation gradient ranges from absolute desert to moderate, and temperature regimes range from subtropical to boreal and maritime to continental. The combination of high relief and temperate latitudes provide sharp climatic differences on opposing polar and equatorialfacing slopes. Chile has experienced extreme ecological instability, especially in the period of ca. 10 million – 10,000 ybp (Arroyo *et al.* 1988; Villagrán 1995; Villagrán & Hinojosa 1997; Hinojosa & Villagrán 2005). During this period, Chile´s extreme alpine and desert habitats and its mediterranean type climate developed, these representing novelties for South America. The vegetation zones were substantially and repeatedly perturbed by advancing and retreating glaciers during the Pleistocene. Climatic instability persists today, influenced by the Southern Oscillation, which generates cycles of significant climate differences approximately every 5-10 years. These conditions collectively facilitate contact between species of different environments and promote the availability of unoccupied habitats, both of which favor hybridization.

7. Summary

The above discussion is not intended to prove that hybridization is the principal process underlying diversification of Portulacaceae in the Andean region. However, it does aim to show that frequent hybridization can yield the observed data patterns, that evidence for hybridization exists in some cases, and that evidence against hybridization is generally lacking. Thus, hypotheses of hybridization should not be restricted to those instances where there is no other possible explanation. Evidence that hybridization may have been a recurring event during the evolution of Andean Portulacaceae suggests a different approach to taxonomic and phylogenetic studies of these taxa. Floristic study must pay attention to variability and aberrations in the field. Interpretation of molecular data derived from one or a few samples per taxon and few DNA sequences must allow for the possibility of past gene flow. Possibly more worthwhile would be approaches based on multilocus techniques (e.g., AFLP) with sampling of multiple individuals from multiple populations. Empirical data on taxon interfertility would be useful. A program of artificial hybridization may to establish the extent to which phenotypic diversity can be generated as a result of genetic segregation (e.g., Carr *et al.* 1996, Schwarzbach *et al.* 2001). Such hybrids could be useful for comparison of their multilocus marker profiles with suspected natural hybrids.

ACKNOWLEDGMENTS

I thank C. Zavaleta and C. Domínguez for technical and/or field assistance, C. Hernández-Pellicer, A. Maldonado, and M. K. Arroyo (U. de Chile) and D. Hannon (RSA) for providing particular samples, R. Woods (Falklands Conservation Charity) for samples and discussion, G. Arancio (ULS) for collection information, the curators of CAS, RSA, SBBG, SD, UC, ULS for permission to sample herbarium specimens, and Liz Zimmer and other members of the Laboratory of Systematic Biology, Smithsonian Institution and the staff of Rancho Santa Ana Botanical Garden for invaluable logistical assistance in support of the development of a molecular systematics program in Chile. The molecular research was undertaken in a laboratory developed substantially with support from the Mellon Foundation. The research was financed by CONICYT (Chile) grant number 1000909.

Table I. Taxa, specimens, acronyms, diagnostics, and commentary for plant materials used in this study. Locality data provided is as complete as is available. Diagnostics and commentary are provided primarily in the case where published keys and descriptions are insufficient and/or in the case of unusual, problematic, or otherwise notable taxa or specimens. Locality data include country, first political division, and usually second political division. Except for the Metropolitan Region, main political divisions of Chile are indicated with Roman numerals. Superscripts adjacent to the acronyms refer to DNA extraction procedure: [1]extracted from herbarium material, [2]extracted from silica-dried or frozen tissue, [3]ITS and/or *ycf*3-*trn*S sequences determined from more than one independent extraction.

Tabla I. La Tabla presenta los taxa, especímenes, acrónimos, diagnósticos y comentarios de los materiales usados en este estudio. Los datos de localidad son entregados tan completos como fue posible. Diagnósticos y comentarios son entregados principalmente en el caso donde las claves publicadas y las descripciones son insuficientes y/o en el caso de ser raras o problemáticas, o para taxa y especímenes notables. Los datos de localidad incluyen país, región, provincia. Excepto para la Región Metropolitana, la división política principal de Chile se indica con números romanos. El superíndice junto a los acrónimos se refieren al método de extracción de ADN: [1]extraído desde material de herbario, [2]extraído de tejido secado en sílica o congelado, [3]secuencias de ITS y/o *ycf*3-*trn*S determinadas de más de una extracción independiente.

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
Calandrinia Kunth			
Calandrinia sect. *Acaules* Reiche			
Calandrinia acaulis Kunth	acaulis_1356[1]	MEXICO. **México:** Amecameca, *García 1356* (RSA)	DQ090306 / DQ090285
	acaulis_27282[1]	MEXICO. **México:** Zinacantepec, *Rzedowski 27282* (RSA)	DQ090307 / DQ090286
Calandrinia affinis Gillies ex Arn.	affinis[2,3]	Voucher lost. Original data: CHILE. **Metropolitana:** Cordillera, betw. Santiago & Valle Nevado, *Hershkovitz 92-05*, determined by M. A. Hershkovitz.	DQ090318 / DQ090327
Calandrinia carolinii Hershk. & D. I. Ford	carolinii[1]	ARGENTINA. **Tucuman:** Quebrada los Bemos, *Arroyo 03-108* (CONC)	DQ090308 / DQ090287
Calandrinia caespitosa Gillies ex Arn.	caespitosa_790[2,3]	Cultivated. CHILE. V: ex *Ford 790* (MO).	DQ090319 / DQ090328
	caespitosa_26XI98[2,3]	ARGENTINA. **Mendoza:** San Carlos, rd to Laguna Diamante, *Peralta & Hershkovitz s.n. 26 Nov 1992* (MERL)	DQ090305 / DQ090284

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
Calandrinia caespitosa x *compacta*	x compacta[2,3]	ARGENTINA. **Mendoza:** San Carlos, rd to Laguna Diamante, *Peralta & Hershkovitz s.n. 26 Nov 1992* (MERL). COMMENT: The plant was sympatric with both putative parental species. It had a massive crown of thickened stems resembling that of *C. caespitosa* rather then the slender rhizomes of *C. compacta*. The petals are rose rather than orange as in *C. caespitosa* or pale pink as in *C. compacta*. The leaves and peduncles are intermediate in length between the two parental species.	DQ090309 / DQ090288
Calandrinia colchaguensis Barnéoud	colchaguensis[2,3]	CHILE. **VIII:** Ñuble, Termas de Chillán, dry rocky slopes E of hotel/spa, *Hershkovitz 01-72* (CONC).	DQ090303 / DQ090282
Calandrinia compacta Barnéoud	compacta_01-51[2]	CHILE. **III:** Huasco, rd from Conay to El Nevado (Barrick Mine Proyecto Pascua) at km 36, *Hershkovitz* 01-51 (CONC).	DQ090310 / DQ090289
	compacta_26XI98[2,3]	ARGENTINA. **Mendoza:** San Carlos, rd to Laguna Diamante, *Peralta & Hershkovitz s.n. 26 Nov 1992* (MERL)	DQ090262 / DQ090329
Calandrinia sp. indet. 1	C. sp_98-22B[2]	CHILE. **Metropolitana:** Cordillera, Valle Nevado ski area, *Hershkovitz 98-22B* (CONC).	DQ090304 / DQ090283
Calandrinia sect. *Calandrinia*			
Calandrinia axilliflora Barnéoud	axilliflora_99-3774[1]	CHILE. *Arroyo 99-3774* (CONC)	DQ090290 / DQ090266
	axilliflora_99-3852[1]	CHILE. *Arroyo 99-3852* (CONC)	DQ090291 / DQ090267
Calandrinia breweri S. Watson	breweri_262[1]	USA. **California:** San Diego Co., S Cuyamaca Mts, *Hirschberg 262* (RSA)	DQ090296 / DQ090271

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
	breweri_2501[1]	USA. **California:** Sta. Cruz I., *Junak SC 2501* (SBBG)	DQ090295 / DQ090272
	breweri_4204[1]	USA. **California:** San Luis Obispo Co., Santa Lucia Mts, *Junak 4204* (RSA)	DQ090265 / DQ090273
	breweri_4289[1,3]	USA. **California:** San Luis Obisbo Co., *Junak 4289* (SBBG)	DQ090263 / DQ090274
	breweri_8425[1]	USA. **California:** Riverside Co., Palomar Range, Agua Tibia Wild. Area, *Boyd 8425* (RSA)	DQ090264 / DQ090275
Calandrinia ciliata (Ruiz & Pav.) DC	ciliata_03107[1]	ARGENTINA. **Túcuman**: Quebrada los Bemos, *Arroyo 03-107* (CONC)	DQ090292 / DQ090268
	ciliata_1550[1]	MEXICO. **Tlaxcala**: Nanacamilpa, *Rodríguez 1550* (RSA)	DQ090293 / DQ090269
	ciliata_40430[1,3]	MEXICO. **Chiapas**: Motozintla de Mendoza, 3000 m, *Breedlove 40430* (RSA)	DQ090294 / DQ090270
Calandrinia compressa Schrad. ex DC	compressa[2,3]	Voucher lost. Original data: CHILE. **VIII:** Bío-Bío, rd betw. Concepción & Yumbel ca. 1 km W of jct w/rd to Cabrero, *Hershkovitz 92-10,* determined by M. A. Hershkovitz	DQ090314 / DQ090323
Calandrinia menziesii (Hook.) Torr. & A. Gray	menziesii_02-20[2]	USA. **California:** Amador Co., California Hwy 88 at jct w/Irish Town Rd & Clinton Rd, *Hershkovitz 02-20*	DQ090297 / DQ090276
	menziesii_24999[1]	CANADA. **British Columbia**: Vancouver I., *Calder 29499* (RSA)	DQ090298 / DQ090281

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
	menziesii_2579[1]	MEXICO. **Baja California Norte**: *Rebman 2579* (RSA)	DQ090299 / DQ090277
	menziesii_25560[1]	USA. **Arizona:** Pima Co, *Hitchcock 25560* (RSA)	DQ090300 / DQ090278
	menziesii_2592[1]	USA. **Arizona:** Pima Co., Coronado National Forest, *Schmidt 2592* (RSA)	DQ090301 / DQ090279
	menziesii_4459[1]	USA. **Oregon:** Linn Co., *Halse 4459* (RSA)	DQ090302 / DQ090280
	menziesii_IV1992[2,3]	No voucher. Original data: USA. **California:** Yuba Co., *Hershkovitz s.n. Apr 1992,* determined by M. A. Hershkovitz	DQ090315 / DQ090324
	menziesii_Mal1[1]	No voucher. Original data: Cultivated, United Kingdom. **Falkland Islands:** Stanley. Fragments of the plant were received from Dr. David Broughton, Royal Botanic Garden, Kew	DQ090316 / DQ090325
	menziesii_Mal2[1]	No voucher, Original data: Cultivated, United Kingdom. **Falkland Islands:** Stanley, ex seed from Beaver Island, *S. Poncet, s.n.* Fragments of the plant were received from Dr. David Broughton, Royal Botanic Garden, Kew	DQ090317 / DQ090326
Calandrinia sp. indet. 2	C_sp_Mal1[1]	No voucher, Original data: Cultivated, United Kingdom. **Falkland Islands:** Stanley, ex seed from Tea Island, *S. Poncet, s.n.* Fragments of the plant were received from Dr. David Broughton, Royal Botanic Garden, Kew	DQ090312 / DQ090321
	C_sp_Mal2[1]	No voucher. Original data: United Kingdom. **Falkland Islands.**: NE facing slope of Sabina Point, at head of North Harbor, *R. Woods s.n. Dec. 1999* . DNA extracted from seed sent by R. Woods, Falklands Conservation Charity.	DQ090313 / DQ090322

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
Calandrinia sect. *Monocosmia* (Fenzl) Hershk.			
Calandrinia monandra DC	monandra[2]	Voucher lost. Original data: CHILE. **VIII:** Ñuble, Fundo Las Salvidas, *Hershkovitz 92-08*, determined by M. A. Hershkovitz	DQ090311 / DQ090320
Calyptridium Nutt.			
Calyptridium monandrum Nutt.	monandrum[2]	USA. **California:** San Bernardino Co., California Hwy 138 ca. 1 km W of US Interstate Hwy 15, *Hershkovitz 02-01* (CONC).	DQ090372 / DQ090338
Calyptridium monospermum Greene	monospermum[2]	Voucher lost. Original data: USA. **California:** Alpine Co., along Hwy 88 Sierra Nevada, *Hershkovitz s.n. Apr. 1992*, determined by M. A. Hershkovitz	DQ090375 / DQ090341
Calyptridium monospermum x *umbellatum*	x monospermum[2]	USA. **Oregon:** Jackson Co., Mt. Ashland Rd ca. 0.5 miles E of ski lodge, *Hershkovitz 02-38* (CONC).	DQ090367 / DQ090333
Calyptridium parryi A. Gray var. *nevadense* J. T. Howell	parryi nevadense[1]	USA. **Nevada:** Nye Co., *Tiehm 13605* (CAS)	DQ090374 / DQ090340
Calyptridium parryi var. *parryi*	parryi parryi[2]	USA. **California:** San Bernardino Co., San Bernardino Natl. Forest, *Hershkovitz 02-11* (CONC).	DQ090371 / DQ090337
Calyptridium parryi var. *arizonicum* J. T. Howell	parryi arizonicum_4174[1]	MEXICO. **Baja California Norte:** *Rebman 4174* (SD)	DQ090373 / DQ090339
	parryi arizonicum_22III93[1]	Voucher lost. Original data: MEXICO. **Sonora**: Cerro Colorado, Piñarte Región, *Felger s.n. 22 Mar 1993*	DQ090371 / DQ090330
Calyptridium pulchellum (Eastw.) Hoover	pulchellum[1]	USA. **California:** Madera Co., *Hamon 80-67* (UC)	DQ090370 / DQ090336

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
Calyptridium pygmaeum Parish ex Rydb.	pygmaeum[1]	USA. **California:** *Twisselman 16811* (RSA)	DQ090368 / DQ090334
Calyptridium quadripetalum S. Watson	quadripetalum[2,3]	Voucher lost. Original data: USA. **California:** Lake Co., *Hershkovitz s.n. Apr. 1992*, determined by M. A. Hershkovitz	DQ090365 / DQ090331
Calyptridium roseum S. Watson	roseum	USA. **Nevada:** Lyon Co., *Hershkovitz 02-25* (CONC).	DQ090366 / DQ090332
Calyptridium umbellatum (Torr.) Greene	umbellatum[1]	USA. **California:** Mono Co., Big Sand Flat, *Honer 132* (RSA)	DQ090369 / DQ090335
Cistanthe Spach *Cistanthe* sect. *Amarantoides* Reiche (Hershk.) *Cistanthe ambigua* (S. Watson) Carolin ex Hershk.	ambigua[1]	USA. **California:** San Bernardino Co., *Hannon & Elvin s.n.* (RSA)	DQ090396 / DQ090362
Cistanthe calycina (Phil.) Carolin ex Hershk.	calycina_00-170[2]	CHILE. **III:** Huasco, rd from Vallenar to Junta Valeriana 40 km from ctr of Vallenar, *Hershkovitz 00-170* (CONC).	DQ090387 / DQ090353
	calycina_00-194[2]	CHILE. **III:** Huasco, rd from Domeyko to Caleta Sarco 2 km W of Domeyko, *Hershkovitz 00-194* (CONC).	DQ090382 / DQ090347
	calycina_00-20[2]	CHILE. **II:** Taltal, km 1140 of Panamerican Hwy, betw. Antofagasta & Taltal, *Hershkovitz 00-20* (CONC).	DQ090382 / DQ090348
Cistanthe salsoloides (Barnéoud) Carolin ex Hershk.	salsoloides[2]	CHILE. **II:** Antofagasta, rd from Antofagasta to Mina Escondida betw. km 131 & 135, *Hershkovitz 00-04* (CONC).	
Cistanthe sp. indet. 1, aff. *C. calycina*	aff. calycina[2]	CHILE. **IV:** Elqui, Ruta 41 ca. 36 km E of Vicuña, *Hershkovitz 00-227*	DQ090378 /

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
		(CONC). COMMENT: The habit of this plant was intermediate between the prostrate form of *C. calycina* and the ascending form *C. densiflora*, both of which grow at this site.	DQ090344
Cistanthe densiflora (Barnéoud) Carolin ex Hershk.	densiflora_00-101[2]	CHILE. **III:** Huasco, Panamerican Hwy betw. La Serena & Vallenar ca. 69 km from Vallenar, *Hershkovitz 00-101* (CONC).	DQ090386 / DQ090352
	densiflora_00-171[2]	CHILE. **III:** Huasco, rd from Domeyko to Caleta Sarco 2 km W of Domeyko, *Hershkovitz 00-171* (CONC).	DQ090383 / DQ090349
	densiflora_00-226[2]	CHILE. **IV:** Elqui, Ruta 41 ca. 36 km E of Vicuña, *Hershkovitz 00-226*	DQ090384 / DQ090350
	densiflora_00-95[2]	CHILE. **III:** Copiapó, rd from Paipote to Diego de Almagro ca. 91 km N of Paipote, *Hershkovitz 00-95* (CONC).	DQ090385 / DQ090351
Cistanthe sp. indet. 2, aff. *C. densiflora*	aff. densiflora[2,3]	ARGENTINA. **San Juan:** ex *Kiesling & Peralta s.n.* (MERL)	DQ090376 / DQ090342
Cistanthe sect. *Cistanthe*		COMMENT: When noted, seed surface morphology is as follows: G, glabrous; H, hairy; PT, pusticulate-tomentose.	
Grandiflora group (= *Calandrinia* sect. *Cistanthe* Reiche)			
Cistanthe cabrerae (Añon) I. Peralta	cabrerae[2]	CHILE. **III:** Huasco, rd from Conay to El Nevado (Barrick Mine Proyecto Pascua) ca. 5 km S of Conay, *Hershkovitz 01-33* (CONC).	DQ090250 / DQ090185
Cistanthe discolor (Schrad.) Spach	discolor_03-12[2]	CHILE. **V:** Aconcagua, E of Cabildo, *Hershkovitz 03-12* (CONC).	DQ090261 / DQ090195
	discolor_03-28[2]	CHILE. **V:** Aconcagua, rd betw. Papudo & Zapallar, *Hershkovitz 03-28* (CONC).	DQ090257 / DQ090191

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
Cistanthe grandiflora (Lindley) Carolin ex Hershk.	grandiflora_99-945[2]	CHILE. **IV:** Choapa, Panamerican Hwy ca. 3 km N of Los Vilos, *Hershkovitz 99-945* (CONC). COMMENT: Seeds H.	DQ090246 / DQ090181
	grandiflora_99-977[2]	CHILE. **Metropolitana:** Chacabuco, rd from Tiltil to Limache ca. 2 km E of Puente Santa Laura, *Hershkovitz 99-977* (CONC). COMMENT: Seeds H.	DQ090240 / DQ090175
Cistanthe sp. indet. 3, aff. *Calandrinia crassifolia* Phil.	crassifolia[2]	CHILE. **III:** Huasco, jeep trail ca. 30 air km N of Carrizal Bajo, *Hershkovitz 00-123* (CONC).	DQ090247 / DQ090182
Cistanthe sp. indet. 4, aff. *Calandrinia laxiflora* Phil.	laxiflora_99-948[2]	CHILE. **IV:** Choapa, Panamerican Hwy ca. 5 km N of Los Vilos, *Hershkovitz 99-948* (CONC). COMMENT: Seeds H.	DQ090245 / DQ090180
	laxiflora_03-14[2]	CHILE. **IV:** Choapa, Panamerican Hwy ca. 5 km N of Los Vilos, *Hershkovitz 03-14* (CONC).	DQ090254 / DQ090189
	laxiflora_03-23[2]	CHILE. **V:** Aconcagua, Panamerican Hwy 2 km N of Huenquen, *Hershkovitz 03-23* (CONC).	DQ090255 / DQ090190
	laxiflora_03-29[2]	CHILE. **V:** Aconcagua, rd betw. Papudo & Zapallar, 2km N of N access to Zapallar, *Hershkovitz 03-29* (CONC).	DQ090258 / DQ090192
	laxiflora_03-30[2]	CHILE. **V:** Aconcagua, rd betw. Papudo & Zapallar, 2km N of N access to Zapallar, *Hershkovitz 03-30* (CONC).	DQ090259 / DQ090193
	laxiflora_03-37[2]	CHILE. **V:** Aconcagua, Horcón, *Hershkovitz 03-37* (CONC).	DQ090260 / DQ090194
Cistanthe sp. indet. 5, aff. *Calandrinia mucronulata* Meyen	mucronulata[2]	CHILE. **VII:** Cauquenes, Constitución, *Hershkovitz 03-194* (CONC).	DQ090251 / DQ090186

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
Cistanthe sp. indet. 6, aff. *Calandrinia speciosa* Lehm.	speciosa[2]	CHILE. **III:** Copiapó, rd from Paipote to Diego de Almagro ca. 9 km N of Paipote, *Hershkovitz 00-91* (CONC).	DQ090243 / DQ090178
Cistanthe sp. indet. 7	C. sp_00-114[2]	CHILE. **III:** Copiapó, Panamerican Hwy betw. Copiapó & Vallenar ca. 40 km S of Copiapó, *Hershkovitz 00-114* (CONC). COMMENT: seeds H.	DQ090241 / DQ090176
	C. sp_00-214[2]	CHILE. **IV:** Elqui, rd betwe. Marquesa & Condoriaco km 12 N of Marquesa, *Hershkovitz 00-214* (CONC). COMMENT: seeds H.	DQ090244 / DQ090179
	C. sp_00-31[2]	CHILE. **II:** Taltal, rd betw. Taltal & Paposo ca. 20 km N of Taltal, *Hershkovitz 00-31* (CONC). COMMENT: seeds H.	DQ090249 / DQ090184
	C. sp_00-51[2]	CHILE. **II:** Taltal, rd betw. Taltal & Paposo ca. 26 km N of Taltal, *Hershkovitz 00-51*. COMMENT: stamens ca. 100, seeds G, collected with *Hershkovitz 00-61* (CONC).	DQ090248 / DQ090183
	C. sp_00-61[2]	CHILE. **II:** Taltal, rd betw. Taltal & Paposo ca. 26 km N of Taltal, *Hershkovitz 00-61* (CONC). COMMENT: stamens ca. 50, seeds H, collected with *Hershkovitz 00-51*.	DQ090242 / DQ090177
	C. sp_00-144[2]	CHILE. **IV:** Elqui, Panamerican Hwy betw. Los Vilos & La Serena ca. 1 km N of Las Tacas jct, *Hershkovitz 00-144* (CONC). COMMENT: Plants resemble *Cistanthe grandiflora* except for their unusually broad and lax leaves.	DQ090253 / DQ090188
Rosulatae group Andinae forms (= *Calandrinia* sect. *Andinae* Reiche)			
Cistanthe frigida (Barnéoud) I. Peralta	frigida[2]	CHILE. **Metropolitana:** Cordillera, Valle Nevado ski area, *Hershkovitz 01-28* (CONC).	DQ090215 / DQ090150

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
Cistanthe humilis (Phil.) I. Peralta	humilis[2]	CHILE. **IV:** Elqui, Cordillera Doña Ana, Fundo Olivieres, *Hershkovitz 01-17* (CONC). COMMENT: Flowers 10-15 per inflorescence, stamens 20-25, seeds PT. The identification of this plant is based mainly on the origin of the type ([*F. Peralta s.n.* (SGO!)] "in altissimo monte doña Ana, c. 4000 m.s.m.) and on superficial similarity to the type vegetatively. Ford-Werntz & Peralta (2002) indicated fewer flowers (5-8), fewer stamens (5-6), and glabrous seeds for this species.	DQ090198 DQ090133
Cistanthe sp. indet. 8, aff. *Calandrinia oblongifolia* Barnéoud	oblongifolia[2]	CHILE. **IV:** Elqui, Cordillera Doña Ana, Fundo Olivieres, *Hershkovitz 01-15* (CONC).	DQ090197 / DQ090132
Cistanthe humilis x *Calandrininia oblongifolia*	x oblongifolia[2]	CHILE. **IV:** Elqui, Cordillera Doña Ana, Fundo Olivieres, *Hershkovitz 01-16* (CONC). COMMENT: These plants occur in the elevational zone of overlap between the putative parental taxa. They superficially resemble *Calandrinia oblongifolia*, but have pink petals of the *Cistanthe humilis* rather than white of the former, as well as several floral characteristics distinct from both putative parental forms.	DQ090196 / DQ090131
Cistanthe sp. indet. 9, aff. *Calandrinia villanuevae* Phil.	villanuevae[1]	No voucher. Original data: CHILE. **II-III:** Rd betw. Ex Oficina Flor de Chile & Salar de la Azufrera, *A. Maldonado s.n.*, determined by M. A. Hershkovitz	DQ090199 / DQ090134
Arenarie group (= *Calandrinia* sect. *Arenarie* Reiche)			
Cistanthe arenaria (Cham.) Carolin ex Hershk.	arenaria_00-215[2]	CHILE. **IV:** Elqui, rd betw. Marquesa & Condoriaco km 12 N of Marquesa, *Hershkovitz 00-215* (CONC).	DQ090211 / DQ090146
	arenaria_00-251[2]	CHILE. **IV:** Elqui, rd from Vicuña to Hurtado 10.5 km S of jct w/Ruta 41, *Hershkovitz 00-251* (CONC).	DQ090233 / DQ090174
Cistanthe sp. indet 10, aff. *Calandrinia chamissoi* Barnéoud	chamissoi[2]	CHILE. **IV:** Choapa, rd betw. Illapel & Combarbala, *Hershkovitz . 99-870* (CONC)	DQ090239 / DQ090173

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
Cistanthe sp. indet. 11	C. sp_00-213[2]	CHILE. **IV:** Elqui, rd betw. Marquesa & Condoriaco km 12 N of Marquesa, *Hershkovitz 00-213* (CONC). COMMENT: Resembles giant form of *Cistanthe arenaria*. Seeds H.	DQ090212 / DQ090147
	C. sp_99-910[2]	CHILE. **IV:** Choapa, hillside S of Illapel, *Hershkovitz 99-910* (CONC). COMMENT: Resembles giant form of *Cistanthe arenaria*.	DQ090201 / DQ090136
Rosulatae forms (= *Calandrinia* sect. *Rosulatae* Reiche *sensu* Reiche 1898)			
Cistanthe cephalaphora (I. M. Johnst.) Carolin ex Hershk.	cephalaphora[2]	CHILE. **II:** Taltal, km 1140 of Panamerican Hwy, *Hershkovitz 00-27* (CONC).	DQ090230 / DQ090165
Cistanthe coquimbensis (Barnéoud) Carolin ex Hershk.	coquimbensis[1,2,3]	CHILE. **IV:** Elqui, Panamerican Hwy km 489, ca. 15 km N of main jct in La Serena, *Hershkovitz 00-155* (CONC).	DQ090233 / DQ090168
Cistanthe cymosa (Phil.) Hershk.	cymosa_00-109[2]	CHILE. **III:** Huasco, Panamerican Hwy betw. Vallenar & Copiapó ca. 21 km N of Vallenar, *Hershkovitz 00-109* (CONC). COMMENT: Petals pink, seeds G.	DQ090234 / DQ090169
	cymosa_00-138[2]	CHILE. **III:** Huasco, rd S from Freirina ca. 20 km S of Freirina, *Hershkovitz 00-138* (CONC). COMMENT: Petals pink, seeds G.	DQ090235 / DQ090170
	cymosa_00-195[1,2,3]	CHILE. **III:** Huasco, rd from Domeyko to Caleta Sarco 2 km W of Domeyko, *Hershkovitz 00-195* (CONC). COMMENT: Petals pink, seeds G.	DQ090237 / DQ090172
	cymosa_00-39[1,2,3]	CHILE. **II:** Taltal, rd betw. Taltal & Paposo ca. 20 km N of Taltal, *Hershkovitz 00-39* (CONC). COMMENT: Petals yellow, seeds G.	DQ090216 / DQ090151

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
	cymosa_02-138[1]	CHILE. **III:** Huasco, rd from Domeyko to Caleta Sarco 5 km W of Domeyko, *Hershkovitz 02-138* (CONC). COMMENT: Petals pink, seeds G.	DQ090236 / DQ090171
	cymosa_02-59[1,2,3]	CHILE. **V:** Petorca, Panamerican Hwy nr Los Molles, 40 km S of Los Vilos, *Hershkovitz 02-59* (CONC). COMMENT: Petals white, seeds G.	DQ090205 / DQ090140
Cistanthe sp. indet. 11, aff. *Cistanthe cymosa*	x cymosa[2]	CHILE. **III:** Huasco, rd from Domeyko to Caleta Sarco 5 km W of Domeyko, *Hershkovitz 00-207* (CONC). COMMENT: The plants cooccur with pink-flowered *C. cymosa*, but the flowers are white, the stems and leaves about twice as large, 15-17 stamens vs 5, and seeds PT vs G.	DQ090213 / DQ090148
Cistanthe longiscapa (Barnéoud) Carolin ex Hershk.	longiscapa_00-100[2]	CHILE. **III:** Huasco, Panamerican Hwy betw. La Serena & Vallenar ca. 69 km from Vallenar, *Hershkovitz 00-100* (CONC). COMMENT: Seeds G.	DQ090218 / DQ090153
	longiscapa_00-106[2]	CHILE. **III:** Huasco, Panamerican Hwy betw. Vallenar & Copiapó ca. 21 km N of Vallenar, *Hershkovitz 00-106* (CONC). COMMENT: Seeds G.	DQ090207 / DQ090142
	longiscapa_00-236	CHILE. **IV:** Elqui, Ruta 41 ca. 36 km E of Vicuña, *Hershkovitz 00-236* (CONC).	DQ090221 / DQ090156
	longiscapa_00-238[2]	CHILE. **IV:** Elqui, Ruta 41 ca. 49 km E of Vicuña, *Hershkovitz 00-238* (CONC). COMMENT: Seeds PT.	DQ090222 / DQ090157
	longiscapa_00-28[1,2,3]	CHILE. **II:** Taltal, km 1140 of Panamerican Hwy, betw. Antofagasta & Taltal, *Hershkovitz 00-28* (CONC). COMMENT: Seeds G.	DQ090217 / DQ090152
	longiscapa_00-71[1,2,3]	CHILE. **II:** Taltal, Panamerican Hwy ca. 20 km SE of Taltal, *Hershkovitz 00-71* (CONC). COMMENT: Seeds G.	DQ090209 / DQ090144

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
longiscapa_00-72B[2]		CHILE. **III:** Copiapó, Panamerican Hwy 10 km N of Caldera, *Hershkovitz 00-72B* (CONC). COMMENT: Seeds G.	DQ090219 / DQ090154
	longiscapa_00-212[2]	CHILE. **IV:** Elqui, rd betw. Marquesa & Condoriaco km 12 N of Marquesa, *Hershkovitz 00-212* (CONC). COMMENT: Seeds PT.	DQ090203 / DQ090138
	longiscapa_01-04[2]	CHILE. **IV:** Elqui, Cordillera Doña Ana, Fundo Olivieres, *Hershkovitz 01-04* (CONC). COMMENT: Seeds PT.	DQ090206 / DQ090141
	longiscapa_01-108[2]	CHILE. **IV:** Elqui, Panamerican Hwy betw. Los Vilos & La Serena ca. 1 km N of Las Tacas jct, *Hershkovitz 01-108* (CONC).	DQ090210 / DQ090145
	longiscapa_02-78[2]	CHILE. **IV:** Elqui, Panamerican Hwy betw. La Serena & Vallenar, km 565, ca. 91 km from La Serena, *Hershkovitz 02-78* (CONC). COMMENT: Seeds G.	DQ090225 / DQ090160
	longiscapa_02-128[2]	CHILE. **III:** Copiapó, rd toward Barranquillas 1 km S of Puerto Viejo, *Hershkovitz 02-128* (CONC).	DQ090223 / DQ090158
Cistanthe maritima (Nutt.) Carolin ex Hershk.	maritima[1]	MEXICO. **Baja California Norte**: *Rebman 1616* (SD).	DQ090231 / DQ090166
Cistanthe sp. indet. 12, aff. *Calandrinia thyrsoidea* Reiche	thyrsoidea_00-157[2,3]	CHILE. **IV:** Elqui, Panamerican Hwy ca. 15 km N of main jct in La Serena, *Hershkovitz 00-15* (CONC). *7.*	DQ090228 / DQ090163
	thyrsoidea_00-110[2]	CHILE. **III:** Huasco, Panamerican Hwy betw. Vallenar & Copiapó ca. 21 km N of Vallenar, *Hershkovitz 00-110* (CONC).	DQ090226 / DQ090161
	thyrsoidea_00-172[2]	CHILE. **III:** Huasco, rd from Vallenar to Junta Valeriana 40 km from ctr. of Vallenar, *Hershkovitz 00-172* (CONC).	DQ090227 / DQ090162

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
	thyrsoidea_00-216[2]	CHILE. **IV:** Elqui, rd betw. Marquesa & Condoriaco km 12 N of Marquesa, *Hershkovitz 00-216* (CONC).	DQ090229 / DQ090164
Cistanthe sp. indet. 13	C. sp_00-139[2]	CHILE. **III:** Huasco, rd S from Freirina ca. 20 km S of Freirina, *Hershkovitz 00-139* (CONC). COMMENT: The plant has the erect habit and linear lvs. of *C. thyrsoidea* but large flowers similar to *C. longiscapa.* Seeds PT.	DQ090220 / DQ090155
	C. sp_00-160[2]	CHILE. **IV:** Elqui, Panamerican Hwy ca. 15 km N of main jct in La Serena, *Hershkovitz 00-160* (CONC). COMMENT: The plant has the erect habit and linear lvs. of *C. thyrsoidea* but large flowers similar to *C. longiscapa.* Seeds G.	DQ090204 / DQ090139
	C. sp_00_264[1,2,3]	CHILE. **IV:** Elqui, rd betw. Tambillo & Panamerican Hwy ca. km 8 W of jct w/Ruta 43, *Hershkovitz 00-264* (CONC). COMMENT: The plant has the erect habit and linear lvs. of *C. thyrsoidea* but large flowers similar to *C. arenaria.* Seeds PT.	DQ090200 / DQ090135
	C. sp_01-109[1,2,3]	CHILE. **IV:** Elqui, Panamerican Hwy betw. Los Vilos & La Serena ca. 1 km N of Las Tacas jct, *Hershkovitz 01-109* (CONC). COMMENT: Plant stunted, possibly a stressed seedling.	DQ090208 / DQ090143
	C. sp_02-75[2]	CHILE. **IV:** Elqui, Panamerican Hwy betw. La Serena & Vallenar, km 565, ca. 91 km from La Serena, *Hershkovitz 02-75* (CONC). COMMENT: The plant has the erect habit and linear lvs. of *C. thyrsoidea* but large flowers similar to *C. longiscapa.* Seeds G.	DQ090224 / DQ090159
	C. sp_02-80[2,3]	CHILE. **IV:** Elqui, Panamerican Hwy betw. La Serena & Vallenar, ca. km 584, ca. 6 km E of crest of Cuesta Pajonales, *Hershkovitz 02-80* (CONC). COMMENT: This plant resembles a stunted plant of *C.* sect. *Cistanthe*, in particular in its erect, leafy habit and glaucous texture.	DQ090214 / DQ090149
	C. sp_02-145[2]	CHILE. **III:** Huasco, rd from Domeyko to Caleta Sarco ca. 4 km W of jct to	DQ090202 /

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
		Caleta Chañaral, *Hershkovitz 02-145* (CONC). COMMENT: The plant has the erect habit and linear lvs. of *C. thyrsoidea* but large flowers similar to *C. longiscapa*. Seeds PT.	DQ090137
Cistanthe sect. *Philippiamra* (Kuntze) Hershk.			
Cistanthe amarantoides (Phil.) Hershk.	Amarantoides_00-46[2]	CHILE. **II:** Taltal, along rd betw. Taltal & Paposo ca. 20 km N of Taltal, *Hershkovitz 00-46* (CONC).	DQ090379 / DQ090345
	Amarantoides_00-57B[2]	CHILE. **II:** Taltal, along rd betw. Taltal & Paposo ca. 26 km N of Taltal, *Hershkovitz 00-57b* (CONC).	DQ090380 / DQ090346
Cistanthe celosioides (Phil.) Hershk.	celosioides_00-108[2]	CHILE. **III:** Huasco, Panamerican Hwy betw. Vallenar & Copiapó ca. 21 km N of Vallenar, 17 Sep 2000, *Hershkovitz 00-108* (CONC).	DQ090377 / DQ090343
	celosioides_00-239[2]	CHILE. **IV:** Elqui, Ruta 41 ca. 49 km E of Vicuña, *Hershkovitz 00-239* (CONC).	DQ090392 / DQ090352
	celosioides_00-83[2]	CHILE. **III:** Copiapó, rd from Paipote to Diego de Almagro ca. 55 km N of Paipote, *Hershkovitz 00-83* (CONC).	DQ090391 / DQ090351
	celosioides_02-147[2]	CHILE. **III:** Huasco, Panamerican Hwy betw. Domeyko & La Serena ca. 3 km S of Domeyko, *Hershkovitz 02-147* (CONC).	DQ090388 / DQ090354
Cistanthe sp. 14 aff. *Philippiamra pachyphylla* (Phil.) Kuntze.	pachyphylla_00-08[2]	CHILE. **II:** Taltal, Panamerican Hwy km 1103, betw. Antofagasta & Taltal, *Hershkovitz 00-08* (CONC).	DQ090393 / DQ090359
	pachyphylla_00-86[2]	CHILE. **III:** Copiapó, rd from Paipote to Diego de Almagro ca. 55 km N of Paipote, *Hershkovitz 00-86* (CONC).	DQ090395 / DQ090361

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
Cistanthe sections *Amarantoides* or *Phillipiamra incertae sedis*			
Cistanthe sp. indet. 15	C. sp_00-10[2]	CHILE. **II:** Taltal, Panamerican Hwy km 1103, betw. Antofagasta & Taltal, *Hershkovitz 00-10* (CONC). COMMENT: Plant sterile, stems spreading, stiff, yellow-green, leaves broadly oblanceolate, surface texture abrasive.	DQ090390 / DQ090356
	C. sp_00-11[2]	CHILE. **II:** Taltal, Panamerican Hwy km 1103, betw. Antofagasta & Taltal, *Hershkovitz 00-11* (CONC). COMMENT: Plant sterile, stems prostrate, lax, magenta, leaves spatulate, noticibly cool to touch, surface texture smooth. These sterile plants cooccurred with *Hershkovitz 00-10*. Superficially, they resembled large plants of *Portulaca oleracea*.	DQ090389 / DQ090355
Claytonia L.			
Claytonia sect. Caudicosae A. Gray ex Poellnitz			
Claytonia megarhiza (A. Gray) S. Watson	megarhiza[2,3]	No voucher. Cultivated plant originally collected in Colorado, USA, determined by M. A. Hershkovitz.	DQ090126 / DQ080655
Claytonia sect. *Claytonia*			
Claytonia viriginica	virginica[2,3]	Voucher lost. Original data: USA. **Maryland:** *G. Sattler s.n.* 1993, determined by M. A. Hershkovitz	DQ090125 / DQ080654
Lenzia Phil.			
L. chamaepitys Phil.	chamaepitys[2,3]	CHILE. **III:** Huasco, rd from Conay to El Nevado (Barrick Mine Proyecto Pascua) at km 36, *Hershkovitz 01-40* (CONC).	DQ090397 / DQ090363
Lewisia Pursh			
Lewisia columbiana (Howell ex A. Gray) B. L. Rob. var. *rupicola* (English) C. L. Hitchc.	rupicola[2]	No voucher. Cultivated, University of California (Berkeley) Botanical Garden acc. 89.1410, from wild-collected plant, *S. B. Hogan 1481*, determined by S. B. Hogan.	DQ090123 / DQ080652

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
Lewisia rediviva Pursh var. *minor* (Rydb.) Munz	minor[2]	USA. **California:** Los Angeles Co., Angeles Natl. Forest, *Hershkovitz 02-06* (CONC).	DQ090124 / DQ080653
Lewisiopsis R. Govaerts			
Lewisiopsis tweedyi (A. Gray) R. Govaerts	tweedyi[2,3]	No voucher. Cultivated, University of California (Berkeley) Botanical Garden acc. 89.1401, from wild-collected plant, *S. B. Hogan 1145*, determined by S. B. Hogan.	L78089 / DQ080651
Montia L.			
Montia chamissoi (Sprengel) E. Green	chamissoi[2]	USA. **Oregon:** Jackson Co., ca. 1 mile E of Lincoln, *Hershkovitz 02-40* (CONC).	DQ090127 / DQ080656
Montia howellii S. Watson	howellii[2]	USA. **California:** Trinity Co., Burnt Ranch Campground, *Hershkovitz 02-37* (CONC).	DQ090129 / DQ080658
Montia linearis (Hook.) Greene	linearis[2]	USA. **Maryland:** Prince George's Co., Smithsonian Institution Museum Support Center, *Hershkovitz s.n. 10 May 1986* (US)	DQ090128 / DQ080657
Montiopsis Kuntze			
Montiopsis subg. Dianthoideae (Reiche) D. I. Ford			
Montiopsis andicola (Gillies) D. I. Ford	andicola_24XI92[2,3]	ARGENTINA. **Mendoza:** Las Heras, weather station at La Cumbre, *Peralta & Hershkovitz s.n. 24 Nov 1992* (MERL)	DQ090437 / DQ090478
	andicola_98-85[2]	CHILE. **Metropolitana:** Cordillera, Valle Nevado ski area, *Hershkovitz 98-85* (CONC).	DQ090438 / DQ090479
Montiopsis cistiflora (Gillies ex Arn.) D. I. Ford	cistiflora[2]	CHILE. **VII:** Curicó, rd from Los Queñes to Paso del Planchón (Paso Vergera), 1 rd km from Argentina border, *Hershkovitz 99-546* (CONC).	DQ090439 / DQ090480
Montiopsis gayana (Barnéoud) D. I. Ford	gayana_99-517[2]	CHILE. **VII:** Curicó, rd from Los Queñes to Paso del Planchón (Paso Vergera), 1 rd km from Argentina border, *Hershkovitz 99-517* (CONC).	DQ090434 / DQ090475

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
	gayana_01-96[2]	CHILE. **VIII:** Ñuble, Termas de Chillán, *Hershkovitz 01-96.*	DQ090435 / DQ090476
	gayana_424[2,3]	Cultivated, CHILE. IX: ex *Ford & Rosas 424b* (MO).	DQ090436 / DQ090477
Montiopsis tricolor (Phil.) D. I. Ford	tricolor[2]	CHILE. **Metropolitana:** Cordillera, Valle Nevado hotel parking area, *Hershkovitz 98-58* (CONC).	DQ090440 / DQ090481
Montiopsis subg. *Montiopsis* Hirsutae group (Ford 1992)			
Montiopsis copiapina (Phil.) D. I. Ford	copiapina_01-35[2]	CHILE. **III:** Huasco, rd betw. Conay & El Nevado (Barrick Mine, Proyecto Pascua), ca. km 35 S of Conay, *Hershkovitz 01-35* (CONC).	DQ090404 / DQ090447
	copiapina_89287[1]	CHILE. **IV:** Elqui, Cordillera Doña Ana, ski slope S of Baños del Toro, *Arancio 89287* (ULS).	DQ090411 / DQ090453
	copiapina_92189[1]	CHILE. **IV:** Elqui, Cordillera Doña Ana, Vega Piuquenes, *Squeo 92189* (ULS)	DQ090412 / DQ090454
Montiopsis gilliesii (Hook. & Arn.) D. I. Ford	gilliesii_738[1,3]	ARGENTINA. **Mendoza:** Las Heras, Valle Horcones, Las Cuevas-Uspallata rd 3 miles N of Ruta 7, *Ford & Peralta 738* (MO)	DQ090406 / DQ090449
	gilliesii_99-542[1]	CHILE. **VII:** Curicó, rd from Los Queñes to Paso del Planchón (Paso Vergera), 1 rd km from Argentina border, *Hershkovitz 99-542* (CONC).	DQ090413 / DQ090455
Montiopsis potentillioides (Barnéoud) D. I. Ford	potentillioides[2]	CHILE. **Metropolitana:** Cordillera, Valle Nevado ski area, *Hershkovitz 98-97* (CONC).	DQ090407 / DQ090450
Montiopsis sericea (Hook. & Arn.) D. I. Ford	sericea_12XII03[1]	CHILE. **V:** Quillota, Parque Nacional de La Campana, sector near entrance at Granizo, *Rougier s.n., 12 Dec 2003* (no voucher).	DQ090408 / DQ090451

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
Montiopsis umbellata (Ruiz & Pav.) D. I. Ford	umbellata[2]	Cultivated, ex *Andrews & Archibald 12535* (MO).	DQ090405 / DQ090448
Montiopsis uspallatensis (Phil.) D. I. Ford	uspallatensis[1]	CHILE. **IV:** Limari, Quebrada Larga, S side of Rio Los Molles, *Ford & Arancio 754* (MO).	DQ090409, DQ090410 / DQ090452
Condensatae group (Ford 1992)			
Montiopsis capitata (Hook. & Arn.) D. I. Ford	capitata[1,2,3]	CHILE. **IV:** Elqui, rd betw. Hurtado & Pabellón 24.4 km E of Hurtado, *Hershkovitz 00-257* (CONC).	DQ090403 / DQ090446
Montiopsis glomerata (Phil.) D. I. Ford	glomerata[2,3]	CHILE. **IV:** Elqui, slopes near Baños del Toro, *Hernandez s.n. Feb 2003* (CONC).	DQ090425 / DQ090467
Montiopsis modesta (Phil.) D. I. Ford	modesta_02-94[1,2,3]	CHILE. **III**: Huasco, rd from Vallenar to Los Morteros, *Hershkovitz 02-94* (CONC). COMMENT: This species has never been collected below 3000 m nor before late December in Region III, nor sympatrically with *M. parviflora*.	DQ090420 / DQ090462
	modesta_II2003[2,3]	CHILE. **IV**: Elqui, slopes near Baños del Toro, *Hernandez s.n. Feb 2003* (CONC).	DQ090419 / DQ090461
Montiopsis trifida (Hook. & Arn.) D. I. Ford	trifida_00-137[2]	CHILE. **III**: Huasco, ca. 10.5 km S from Freirina, *Hershkovitz 00-137* (CONC).	DQ090426 / DQ090468
	trifida_00-258[1,2,3]	CHILE. **IV**: Elqui, rd betw. Vicuña & Hurtado 22 km S of Vicuña, *Hershkovitz 00-258* (CONC).	DQ090427 / DQ090469
	trifida_264[2,3]	CHILE. **IV**: Elqui, Mina El Romeral, 3 km from Panamerican Hwy on alternate S access rd, *Ford 264* (MO).	DQ090428 / DQ090470
	trifida_99-898[1,2,3]	CHILE. **IV**: Choapa, rd betw. Illapel & Combarbalá, *Hershkovitz 99-898* (CONC).	DQ090429, DQ090430 /

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
			DQ090471, DQ090472
Montiopsis trifida x *capitata*	x trifida[2,3]	CHILE. **IV:** Limarí, Río Cogatí canyon, *Hershkovitz 02-152* (CONC). COMMENT: The morphology and elevation correspond with those given by Ford (1992) for such interspecific hybrids.	DQ090432 / DQ090473
Parviflorae group (Ford 1992)			
Montiopsis berteroana (Phil.) D. I. Ford	berteroana[2,3]	Voucher lost. Original data: CHILE. **VIII:** Bío-Bío, Rd betw. Yumbel & Estación Yumbel at bridge over Río Claro, *Hershkovitz 92-11,* determined by M. A. Hershkovitz.	DQ090398 / DQ090441
Montiopsis cumingii (Hook. & Arn.) D. I. Ford	cumingii[1]	CHILE. **I:** Parinacota, Vegas de Caquena, *Arancio 92691* (ULS).	DQ090399 / DQ090442
Montiopsis demissa (Phil.) D. I. Ford	demissa_00-210[2]	CHILE. **IV:** Elqui, Panamerican Hwy betw. La Serena & Vallenar, km 62 N of main jct in La Serena, *Hershkovitz 00-210* (CONC).	DQ090400 / DQ090443
	demissa_02-143[1,2,3]	CHILE. **III:** Huasco, rd from Domeyko to Caleta Sarco ca. 4 km W of jct to Caleta Chañaral, *Hershkovitz 02-143* (CONC).	DQ090401 / DQ090444
Montiopsis parviflora (Phil.) D. I. Ford	parviflora_00-184[1,2,3]	CHILE. **III:** Huasco, rd from Vallenar to Junta Valeriana 4 km E of Conay, *Hershkovitz 00-184* (CONC).	DQ090424 / DQ090466
	parviflora_00-217[1,2,3]	CHILE. **IV:** Elqui, rd betw. Marquesa & Condoriaco, *Hershkovitz 00-217* (CONC).	DQ090433 / DQ090474
	parvifolia_02-92[1,2,3]	CHILE. **III:** Huasco, rd from Vallenar to Los Morteros, *Hershkovitz 02-92* (CONC).	DQ090422 / DQ090464

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
	parvifolia_02-93[1,2,3]	CHILE. **III:** Huasco, rd from Vallenar to Los Morteros, *Hershkovitz 02-93* (CONC).	DQ090423 / DQ090465
	parvifolia_02-95[1,2,3]	CHILE. **III:** Huasco, rd from Vallenar to Los Morteros, *Hershkovitz 02-95* (CONC).	DQ090421 / DQ090463
Montiopsis ramosissima (Hook. & Arn.) D. I. Ford	ramosissima_00-158[2]	CHILE. **IV:** Elqui, Panamerican Hwy betw. La Serena & Vallenar, km 62 N of main jct in La Serena, *Hershkovitz 00-158* (CONC).	DQ090416 / DQ090458
	ramosissima_00-211[2]	CHILE. **IV:** Elqui, Panamerican Hwy betw. La Serena & Vallenar, km 62 N of main jct in La Serena, *Hershkovitz 00-211* (CONC).	DQ090415 / DQ090457
	ramosissima_ 02-148B[1,2,3]	CHILE. **IV:** Limarí, rd betw. Punitaqui & Combarbalá 36 km N of Combarbalá, *Hershkovitz 02-148B* (CONC).	DQ090414 / DQ090456
	ramosissima_99-900[2]	CHILE. **IV:** Choapa, rd betw. Illapel & Combarbala, *Hershkovitz 99-900* (CONC).	DQ090402 / DQ090445
	ramosissima_ 99-965[1,2,3]	CHILE. **Metropolitana:** Chacabuco, rd betw. Polpaico & Tiltil ca. 9 km N of Polpaico, *Hershkovitz 99-965* (CONC).	DQ090418 / DQ090460
	ramosissima_ 99-973[1,2,3]	CHILE. **Metropolitana:** Chacabuco, Rd betw. Tiltil & Quebrada Alvarado 1 km W of Tiltil, *Hershkovitz 99-973* (CONC).	DQ090417 / DQ090459
Parakeelya Hershk.			
Parakeelya liniflora (Fenzl) Hershk.	liniflora[1]	AUSTRALIA. **Western Australia**: rd from Mandurah to Bunbury ca. 14 mi N of jct w/rd to Waroona, *Deburh 3468* (RSA)	DQ090130 / DQ080659
Parakeelya ptychosperma (F. Muell.) Hershk.	ptychosperma[2,3]	Cultivated, ex *J. G. West* 4244 (CANB)	L78050 / DQ080660

Table I, continued

Taxon	Acronym	Specimen and collection data and commentary	GenBank sequence accession (ITS/*ycf*3-*trn*S)
Phemeranthus Raf.			
Phemeranthus brevifolius (Torr.) Hershk.	brevifolius[2,3]	No voucher. Original data: Cultivated, University of California Botanical Garden, not accessioned, original collection, USA. **Arizona:** Coconino Co., Marble Canyon, *S. B. Hogan s.n.*, determined by S. B. Hogan.	L78038 / DQ080661
Talinum Adans.			
Talinum paniculatum (Jacq.) Gaertn.	paniculatum[2,3]	No voucher. Original data Cultivated, USA. **Texas**: Bexar Co., San Antonio, courtyard of the Menger Hotel, *Hershkovitz s.n. Aug 1991,* determined by M. A. Hershkovitz.	L78094 / DQ080662

Table II. Amplificafion and sequencing primers used in the present study.

Tabla II. Partidores de amplificación y secuenciación usadas en el presente estudio.

Primer name	Sequence	Comment or reference
ITS6	5'-TTTCTTTTCCTCCGCTTA-3'	3' (reverse) primer for double-stranded (ds) amplification of the ITS region; complementary to 26S rDNA
ITS7	5'-GAAGGAGAAGTCGTAACAAG-3'	5' (forward) primer for ds amplification of the ITS region; complementary to 18S rDNA
ITS4	5'-TCCTCCGCTTATTGATATGC-3'	Internal to ITS6 primer and used to generate ITS region noncoding strand in single-strand (ss) PCR and or sequencing of coding strand ss PCR product.
N18L18	5'-AAGTCGTAACAAGGTTTC-3'	Internal to ITS7 primer and used to generate ITS region noncoding strand in single-strand (ss) PCR and for sequencing of coding strand ss PCR product.
PORTITS4R	5'-GGTCGCAACGGTTTGTG-3'	Portulacaceae-specific primer used to generate ITS region noncoding strand in asymmetric PCR and for sequencing of coding strand ss PCR product. This primer was useful for DNA extractions from herbarium specimens, where possible contamination with non-Portulacaceae DNA was a problem.
SP43095F	5'-TTTCTCCTGAAGTTGTCGGAAT-3'	5' (forward) primer used for ds amplification of the cpDNA *ycf*3-*trn*S intergenic spacer.
SP43122F	5'-ATTGGCYACAAYTGAAAAGG-3'	Primer used for generation of the *ycf*3-*trn*S noncoding strand in ss PCR and for sequencing of coding strand ss PCR product.
SP44097R	5'-ATTCGAACCCTCGGTAAACA-3'	3' (reverse) primer used for ds PCR of the cpDNA *ycf*3-*trn*S intergenic spacer.

TABLE III. Variation in aligned western American Portulacaceae ITS & *ycf3-trn*S sequences. The table lists the number of variable/informative characters and informative indel characters at various phylogenetic levels. The number of informative characters is inclusive of the number of informative indels. The number of informative indels refers to those indels that were considered unambiguously alignable. Addition indels occur in the data. The bp numbers include only variation at aligned positions, e.g., a region of *ycf3-trn*S was unalignable at the intergeneric level (see results), hence variation in this region is not included in the sums below. The data are intended primarily for comparisons between taxa and between data sets.

TABLA III. Variación de las secuencias alineadas de ITS & *ycf*3-*trn*S de Portulacaceae de América occidental. Se indican el número de caracteres variables/informativos y de inserción/deleción informativos en varios niveles filogenéticos. El número de caracteres incluye el número de inserciones/deleciones informativas. El número de inserciones/deleciones informativos se refiere a aquellos que fueron considerados no ambiguos al alinearse. Inserciones/deleciones adicionales aparecen en los datos. El número pb incluye sólo la variación en las posiciones alineadas, e.g., una región de *ycf3-trn*S no fue alineada a nivel intergenérico (ver resultados), de esta forma la variación en esta región no está incluida. Los datos son principalmente propuestos para comparación entre taxa y entre sets de datos.

	ITS			*ycf3-trnS*			Combined ITS + *ycf3-trn*S		
Taxon	variable	informative	informative indels	variable	informative	informative indels	variable	informative	informative indels
All taxa	231	139	18	282	154	59	513	293	77
western American Portulacaceae	217	131	17	250	147	37	467	278	54
Calandrinia	51	26	4	38	29	11	89	55	15
Montiopsis	25	18	1	62	42	11	87	60	12
Montiopsis subg. *Montiopsis*	12	6	1	19	9	2	31	15	3
Montiopsis subg. *Dianthoides*	6	5	0	16	3	1	22	8	1
Calyptridium + *Lenzia* + *Cistanthe* sects. Amarantoides and *Philippiamra*	47	17	4	33	13	4	80	30	8
Calyptridium	33	16	4	24	12	4	57	28	8
Cistanthe sects. *Amarantoides* and *Philippiamra*	7	2	1	7	3	1	14	5	2
Cistanthe sect. *Cistanthe*	25	17	3	24	16	2	49	33	5
Cistanthe sect. *Cistanthe*, Grandiflora group	7	3	1	5	3	1	12	6	2
Cistanthe sect. *Cistanthe*, Andinae + Arenarie + Rosulatae groups	13	7	1	15	9	1	28	16	2

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Recibido 20.06.05
Aceptado 04.03.06