Systematic Botany (2006), 31(2): pp. 310–319

Molecular Evidence Resolving the Systematic Position of *Hectorella* (Portulacaceae)

WENDY L. APPLEQUIST,[1,5] WARREN L. WAGNER,[2] ELIZABETH A. ZIMMER,[3] and MOLLY NEPOKROEFF[4]

[1]William L. Brown Center for Plant Genetic Resources, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A.;
[2]Smithsonian Institution, Department of Botany, MRC 166, P.O. Box 37012, Washington, DC 20013-7012, U.S.A. and National Tropical Botanical Garden, 3530 Papalina Rd., Kalaheo, Hawaii 96741, U.S.A.;
[3]Smithsonian Institution, Laboratories of Analytical Biology, Museum Support Center, 4210 Silver Hill Rd., Suitland, Maryland 20746, U.S.A.;
[4]Dept. of Biology, 177 Churchill-Haines, University of South Dakota, 414 E. Clark St., Vermillion, South Dakota 57069-2390, U.S.A.
[5]Author for correspondence (wendy.applequist@mobot.org)

Communicating Editor: James F. Smith

ABSTRACT. The taxonomic position of *Hectorella caespitosa* and *Lyallia kergelensis*, caespitose plants endemic to New Zealand and to the Kerguélen Archipelago of Antarctica, respectively, remains controversial. Some authors place them within Portulacaceae, but a slight majority of recent authorities treat them as a separate family, Hectorellaceae. Sequences of the chloroplast genes *rbcL*, *ndhF*, and *matK* were obtained from *H. caespitosa* and added to previously published sequences from Portulacaceae and related families. These data strongly supported the derived position of *Hectorella* within a clade consisting of western American members of Portulacaceae; the sister group of *Hectorella* was a clade including *Montia*, *Claytonia*, and *Lewisia*. Implications for taxonomy are discussed. In order to accomodate monophyly in tribal-level classification while preserving current tribes Montieae and Lewiseae, the new tribe **Hectorelleae** is proposed for the family Portulacaceae.

KEYWORDS: Caryophyllales, *Hectorella*, Hectorellaceae, *Lyallia*, *matkK*, *ndhF*, Portulacaceae.

The large, core eudicot order Caryophyllales has long held interest among botanists as reflecting one of the earliest applications of chemical characters to ordinal classification: all but two families of Caryophyllales as traditionally defined (or Centrospermae; Harms 1934) produce betalain pigments instead of the more broadly distributed anthocyanin pigments (Clement and Mabry 1996). Several molecular studies of caryophyllalean taxa have been published in recent years (e.g., Hershkovitz and Zimmer 1997; Meimberg et al. 2000; Applequist and Wallace 2001; Cuenoud et al., 2002; Nyffeler 2002) and broader-scale analyses have contributed toward a major reshaping of the circumscription and classification of the order (e.g., Angiosperm Phylogeny Group 2003; Soltis et al. 2005). One of the well-supported major clades within Caryophyllales comprises a mainly succulent group of families including Portulacaceae, Cactaceae, Didiereaceae, Basellaceae, and two families segregated from Portulaceae, Halophytaceae and Hectorellaceae. Together, these families are commonly referred to as the ''portulacaceous alliance'' (Hershkovitz 1993) or ''portulacaceous cohort'' (Rodman et al. 1984; excluding Aizoaceae, which were included in the original circumscription).

The relationships and classification of one critical taxon within the portulacaceous cohort, *Hectorella caespitosa* Hook. f., have long been in doubt. *Hectorella* is an unusual cushion-forming plant endemic to New Zealand. Its undisputed closest relative is a similar plant, *Lyallia kergelensis* Hook. f., which is endemic to the Antarctic Archipelago of Kerguélen and probably in danger of extinction (Lourteig 1994). Hooker (1847, 1864) initially classified both species within Portulacaceae, as did Gray (1876). Bentham (1862), while acknowledging that *Lyallia* was poorly known, placed it within Caryophyllaceae based largely on its general resemblance to *Pycnophyllum*, which had also been noted by Hooker (1847). Pax (1889a, 1889b) placed *Hectorella* doubtfully in Portulacaceae and *Lyallia* in Caryophyllaceae, although he made note of their resemblance in discussing the former. Diels (1897) seems to have been the first author to place *Hectorella* in Caryophyllaceae, again noting its resemblance to *Pycnophyllum* as well as *Lyallia*; Pax and Hoffmann (1934) followed the same opinion. Skipworth's (1961) studies of *Hectorella* provided sufficient morphological evidence to firmly reject the possibility of placement within Caryophyllaceae, but also found inadequate similarities to selected species of Portulacaceae, so *Hectorella* and *Lyallia* were segregated as Hectorellaceae (Philipson and Skipworth 1961; Philipson 1993).

Characters such as sieve-element plastids similar to those of Portulacaceae (Behnke 1975), wood anatomy resembling that of *Lewisia* (Carlquist 1997), and the ability to produce betalain pigments under certain circumstances (Mabry et al. 1978) have since demonstrated that *Hectorella*'s closest affinities are certainly with

Portulacaceae rather than Caryophyllaceae. However, there is still no consensus as to whether Hectorellaceae are a sister group meriting recognition at the familial level or whether they belong within Portulacaceae as presently defined. *Hectorella* and *Lyallia* have been excluded from most recent treatments of Portulacaceae (e.g., McNeill 1974; Carolin 1987; Carolin 1993) and recognized at the family level in several classifications of the flowering plants (e.g., Takhtajan 1973; Dahlgren 1975; Thorne 1976). However, they were included in Portulacaceae by Allan (1961), Cronquist (1981), Rodman (1990), Nyananyo (1990), and the Angiosperm Phylogeny Group (1998, 2003). Hershkovitz (1993) was unable to include Hectorellaceae in a morphological analysis, but suggested that they might prove to be derived from within the ''eastern American'' and African members of Portulacaceae (e.g., *Portulaca* and *Talinum*).

As material of *Hectorella* suitable for extraction of DNA was recently made available by W. R. Sykes, the present study intends to resolve its phylogenetic relationships and proper classification through the use of sequence data from three chloroplast genes.

Materials and Methods

DNA was extracted from leaf material of *Hectorella caespitosa*, *Pycnophyllum spathulatum*, *Scleranthus annuus* L., and *Mollugo verticillata* L. using the DNeasy Plant Mini Kit (Qiagen Inc., Valencia, California, USA), following the manufacturer's instructions.

ndhF. PCR amplification and sequencing of *ndhF* from *Hectorella* used primers, PCR conditions, and cycle sequencing conditions as specified in Applequist and Pratt (2005). The *Hectorella ndhF* sequence was added to a previously published *ndhF* dataset (Applequist and Wallace 2001) that included 25 representatives of Portulacaceae, three of Cactaceae, two of Basellaceae, and five of Didiereaceae (sensu lato, as defined by Applequist and Wallace 2003), with nine outgroups from five other caryophyllalean families, for a total of 48 taxa (Appendix 1). Of the raw data set, 5.22% was coded as missing; after the first 59 positions, for which many taxa were missing data, and 39 positions representing insertions in one or a few taxa were excluded from the analyses, 1.56% of the data set was coded as missing, which disproportionately reflected missing data in *Maihuenia* and a 699-bp gap (previously reported; Applequist and Wallace 2001) in *Anacampseros*. Heuristic maximum parsimony (MP) analyses were performed using PAUP* 4.0b10 (Swofford 2001) using TBR branch swapping. Clade support was estimated via bootstrap (1000 replicates; Felsenstein 1985) and decay analyses (Bremer 1988; Donoghue et al. 1992) to 10 steps.

matK. New *matK* sequences were obtained from *Hectorella*, *Mollugo*, *Scleranthus*, and *Pycnophyllum spathulatum* Mattf. (Caryophyllaceae), which was included to examine Hooker's (1847) suggestion of a relationship between *Hectorella* and *Pycnophyllum*. The entire *matK* exon, *trnK* introns and a portion of the *trnK* 5′ and 3′ coding regions were amplified in 50 μl volume, using the following conditions: 0.5 l Taq polymerase (ProMega Corp., Madison, WI), 35μl sterile distilled water, 4 μl dNTPs (2.5 μM), 5 μl 10X Buffer, 5 μl $MgCl_2$ (25 mM), 1 μl BSA (10 mg/ml, 0.5 μl 20 μM primer trnK1F (Johnson and Soltis 1994) or 710F (Manos and Steele 1997) as forward primer, and 0.5 μl 20 μM trnK2R (Johnson and Soltis 1994; Steele and Vilgalys 1994) as reverse primer. Amplification parameters were: 94C for 5 minutes; 25 cycles of: 94°C for 1 minute, 50°C for 1 minute, 72°C for 2 minutes; 72°C for 7 minutes; 4°C indefinite hold. An approximately 890 bp portion of the *matK* coding region was sequenced, including about 57% of the total coding region, located from approximately bp 419 through 1309 (out of 1535 total sites). Sequencing reactions were performed using BigDye Terminator v3.0 Cycle Sequencing Ready Reaction kit (Applied Biosystems, Foster City, CA) following the manufacturer's instructions, with the modification of using 4 μl (1/2 volume) Ready Reaction mix. Sequencing reactions were run on an ABI Prism 373 DNA Sequencer. Sequencing primers included 710F (Manos and Steele 1997), 816F (GCYCTTCTTGAACGMAT, used only in *Pycnophyllum*), 455F (GCGATCAATTCATTCAATAT), Car11R (CGAGCCAAAGTTCTAGCAC), 980F (TGGTCTCAACCAAGAAGAAT) and 980R (ATTTCTTCTTGGTTGAGACCA).

A dataset was assembled from the newly obtained sequences and previously published sequences of caryophyllalean taxa (Meimberg et al. 2000; Cuenoud et al. 2002; Nyffeler 2002; Müller and Borsch 2005) available on GenBank. The complete dataset included *Hectorella* plus 12 representatives of Portulacaceae, four of Cactaceae, one of Basellaceae, five of Didiereaceae, and one of Halophytaceae (*Halophytum* Speg., putatively placed near or even within Portulacaceae), with 15 outgroups representing nine related families and *Corbichonia* Scop. (traditionally placed in Molluginaceae, but apparently not closely related; Cuenoud et al. 2002), for a total of 39 taxa (Appendix 1). The raw data set had 0.63% missing data, which was reduced to 0.38% after the first 34 and last 27 bp were excluded due to missing data in many taxa. MP analyses were performed using only parsimony informative characters, employing the four-step search method (Olmstead et al. 1993; Conti et al. 1996); bootstrap analyses (1000 replicates) and decay analyses (8 steps) were performed.

rbcL. PCR amplification of *rbcL* in *Hectorella* was done using puRE™ Taq Ready to Go™ PCR Beads (Amersham Biosciences, Piscataway, NJ), following the manufacturer's instructions with the following modifications: 2 l of genomic DNA, 0.5 l each primer at 10 M, and 22 l water. Primers used were rbcL5′ of Zurawski (DNAX Research Institute, Palo Alto, California, USA) and P1782 (Levin et al. 2003); amplification parameters used were: 94°C for 10 minutes, 35 cycles of 95°C for 30 s, 57°C for 15 s, 72°C for 45 s; followed by 72°C for 7 min and 4°C indefinite hold. Sequencing primers included Z674, Z674R, Z895, and Z234 of Zurawski (DNAX Research Institute), 955F (CGTATGTCTGGTGGAGATC), 1352R (AAGCAGCAGCTAGTTCCGGGCTCC), and 854R (AAGTAGACCATTTCTCGGC). Sequencing reactions were performed using BigDye Terminator v3.0 Cycle Sequencing Ready Reaction kit (Applied Biosystems, Foster City, CA) following the manufacturer's instructions, with the modification of using 2 μl (1/4 volume) Ready Reaction mix, and total volume of 15 μl, using the following cycle sequencing parameters: 30 cycles of 94°C for 30 s, 55°C for 15 s, 60°C for 4 min followed by 4°C indefinite hold. Sequencing reactions were run on an ABI Prism 373 DNA Sequencer.

The *rbcL* dataset comprised 27 taxa (Appendix 1), with all sequences but *Hectorella* and *Pycnophyllum* previously published (Rettig et al., 1992 Manhart and Rettig 1994; Hoot et al. 1999; Clement and Mabry 1996; Savolainen et al. 2000a, 2000b; Cuenoud et al. 2002; Kadereit et al. 2003) and obtained from GenBank, including two genera each of Portulacaceae, Cactaceae, and Basellaceae, one each of Didiereaceae and Halophytaceae, and additional taxa representing ten outgroup families. The raw data set had 3.04% missing data, reduced to 1.74% after the last 44 positions were excluded; this disproportionately reflected missing data in *Halophytum* (>25% missing). MP analysis was performed as for *matK*, with seven steps of decay analysis.

Maximum Likelihood and Bayesian Analyses. All three data sets were also analyzed under maximum likelihood (ML) and Bayesian criteria. In each case, likelihood searches employed an iterative approach (Sullivan et al. 1997) to evaluate models and then optimize model parameters for an initial set of trees resulting from parsimony analysis. Likelihood searches were then conducted under the fully defined model parameters. The program ModelTest 3.06 (Posada and Crandall 1998) was used to evaluate models of DNA substitution that best fit the data. Likelihood scores for all models were evaluated using the likelihood ratio test statistic (Felsenstein 1981; Goldman 1993; Yang et al. 1995) and the AIC criteria in ModelTest 3.0. The TVM+I+G model was selected as the best fit model of nucleotide substitution for the *ndhF* partition; the TVM+G was selected for both the *rbcL* and *matK* partitions. Heuristic ML analyses were implemented with a starting tree (tree 1 of respective MP searches obtained as described above, chosen arbitrarily as a reasonable starting estimate). Searches were conducted under the fully defined model using ten replicates of TBR branch swapping. Maximum likelihood bootstrap analyses were implemented under the fully defined model, using 100 replicates of random addition sequences addition, and fast-step searching and one tree held at each step. Bayesian analyses were conducted for all three data partitions separately using MrBayes v. 3.0 (Huelsenbeck and Ronquist 2001). Likelihood settings employed nst=6 and rates=gamma (GTR+G model as described above for ML searches). MCMC runs used two analyses, the first of 150,000 generations and the second of 1 million. Four simultaneous Monte Carlo chains were run, saving trees every 100 generations and trees found before stationarity of negative log likelihood scores was achieved (the first 1000 trees) were discarded as part of the burnin period (Huelsenbeck and Ronquist 2001).

Data sets were submitted to TreeBASE (study number S1406; matrix numbers M2529, M2530, and M2531).

Results

ndhF. The aligned *ndhF* data set was 2178 characters long, of which 2080 positions were included in analyses. Among all taxa, 548 characters (ca. 26% of the total) were parsimony informative; within the portulacaceous alliance alone, including *Hectorella*, 396 characters (19%) were parsimony informative. Parsimony analysis resulted in 33 trees of length 1958 (Fig. 1, strict consensus tree). *Hectorella* was sister to a clade including Montieae (*Montia* and *Claytonia*) and *Lewisia*; the sister to this clade consisted of representatives of *Calandrinia* and *Parakeelya*. Support for the monophyly of the clade including all of those taxa was strong (99% MP bootstrap, 9-step decay). A six-bp insertion that was present in all members of the portulacaceous alliance of families (Portulacaceae, Basellaceae, Cactaceae, and Didiereaceae) was also present in *Hectorella* but in no outgroup families. The terminal branch of *Hectorella* was not long in the trees found, indicating that misplacement due to long branch attraction was probably not a concern. Maximum likelihood analyses of the *ndhF* dataset resulted in a single tree, with a −lnL = 13994.90, which was identical in topology to the Bayesian consensus phylogram (Fig. 2). As in MP analyses, the ML and Bayesian analyses place *Hectorella* sister to a clade containing *Montia*, *Claytonia*, and *Lewisia* with moderate (76%) ML bootstrap support and 100% posterior probability. These analyses differed from MP only in the placement of *Mollugo* (Molluginaceae). MP analyses placed *Mollugo* as sister to a clade including the portulacaceous alliance and Nyctaginaceae, Phytolaccaceae, and Aizoaceae, a relationship that was not supported by the MP bootstrap. The ML and Bayesian analyses placed *Mollugo* as sister to the portulacaceous alliance alone, with moderate (78%) ML bootstrap and low (57%) posterior probability support. A long terminal branch for *Mollugo*, coupled with very short internal branches on some clades (Fig. 2), may indicate considerable substitution rate heterogeneity, which, unaccounted for in the parsimony analysis, may contribute to the discrepancy in the placement of *Mollugo* in trees reconstructed under probabilistic models of substitution vs. parsimony.

matK. The aligned *matK* data set was 917 bp in length, and 856 bp after the exclusion of both termini; the alignment required the insertion of seven gaps, all of three bp or more in length, of which five were present in only one taxon. Of the non-excluded characters, 260 (ca. 30% of the total) were parsimony informative and were included in the analysis. Within the portulacaceous alliance of families, including *Hectorella*, alone, 14% were parsimony-informative. Parsimony analyses resulted in 176 trees of length 790 steps (Fig. 3A, strict consensus), distributed on two islands. ML analyses resulted in two trees with −lnL = 6492.64, which differed from each other only in branch lengths and not topology. In all analyses, *Hectorella* was sister to a clade including *Montia*, *Claytonia*, and *Lewisia*, with 88% MP bootstrap, 82% ML bootstrap, and 100% posterior probability support. The sister to this clade was *Calandrinia*, with *Cistanthe* sister to that clade, similar to the relationships seen in the *ndhF* tree. These relationships were recovered in analyses using all three optimality criteria. The ML bootstrap was similar in topology to the MP strict consensus, although in the ML trees *Barbeuia* was resolved as sister to the clade including Phytolaccaceae, Nyctaginaceae and Aizoaceae (not shown). The Bayesian consensus tree was likewise similar except for the placement of *Limeum*, which was sister to the clade containing the portulacaceous alliance plus *Mollugo* in the MP and ML analyses but was well supported in the Bayesian analysis (100% posterior probability) as sister to a clade including the outgroup families Amaranthaceae, Caryophyllaceae, Aizoaceae, Nyctaginaceae, Phytolaccaceae, Barbeuiaceae, Achatocarpaceae, and *Corbichonia* (not shown). Also, in both ML and Bayesian analyses, the clade including *Cistanthe*, *Calandrinia*, *Hectorella*, *Lewisia*, *Claytonia*, and *Montia* was resolved as sister to the remainder of the portulacaceous alliance (not shown), although this position was not well supported in either analysis.

rbcL. The *rbcL* data set was 1380 bp in length, and 1336 bp after exclusion of the 3′ end; 174 of the included nucleotide positions, or 13%, were parsimony informative and were used in the analysis. Parsimony analyses resulted in 69 trees of length 514 steps (Fig. 3B, strict consensus). Resolution among included taxa was limited; *Hectorella* was sister to the included representative of *Claytonia*. Decay analysis was performed to only seven steps, at which point all relevant clades had collapsed; the branch supporting the clade com-

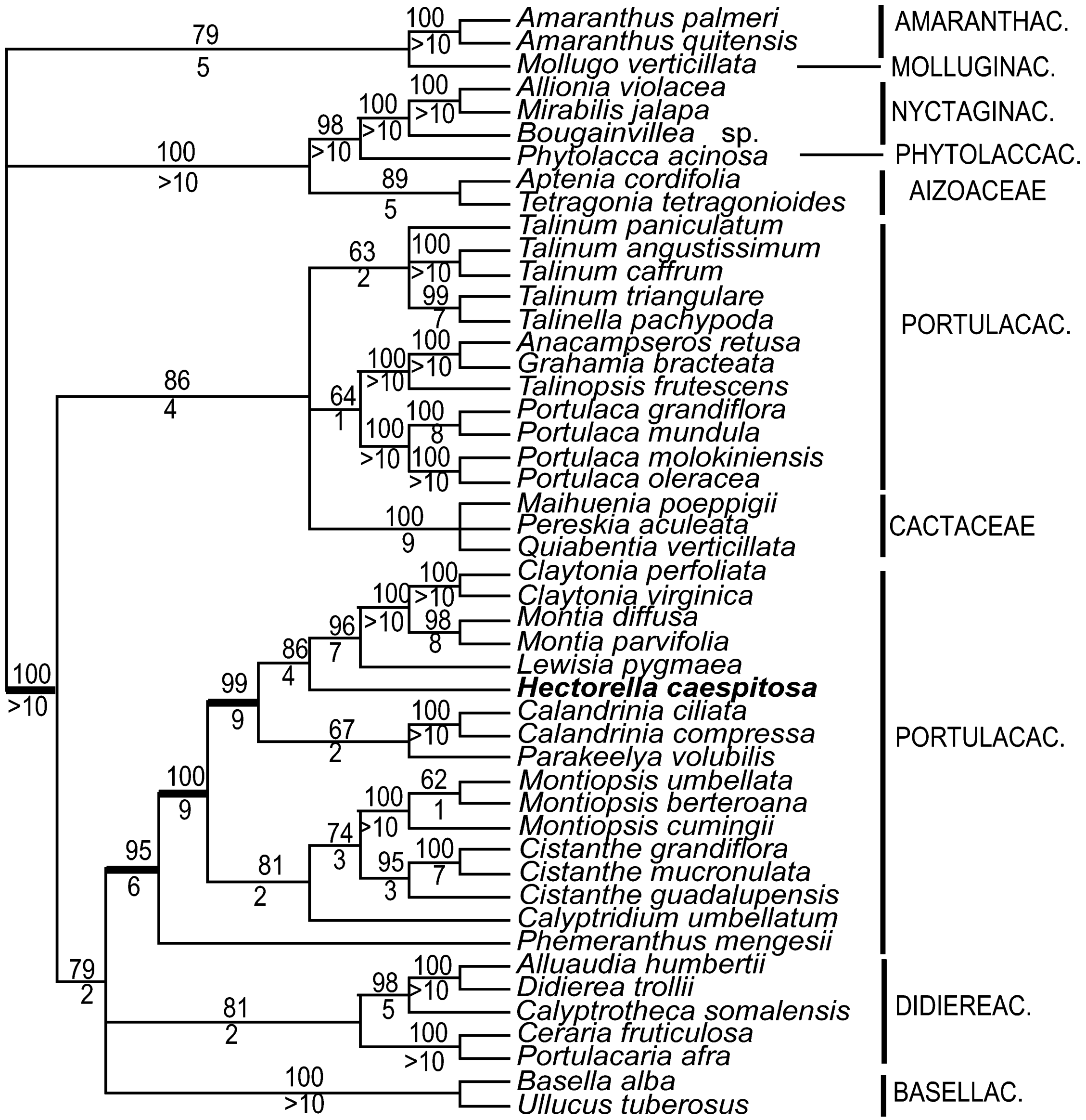

FIG. 1. *ndhF* maximum parsimony (MP) analysis, strict consensus of 33 most parsimonious trees, with MP bootstrap percentages above branches, decay indices below branches. Length (L) = 1958; restriction index (RI) = 0.708; rescaled consistency index (RC) = 0.419; consistency index (CI) excluding uninformative characters = 0.525. Thickened branches represent well-supported clades (>95% bootstrap support) that confirm the placement of *Hectorella* within Portulacaceae.

prising *Hectorella* and *Claytonia* was one of the best-supported clades on the tree (97% MP bootstrap). Both ML and Bayesian analyses also supported *Hectorella* as sister to *Claytonia*. Maximum likelihood searches resulted in a single tree with a $-\ln L = 5678.66$. This tree placed the included representatives of Basellaceae (*Anredera*, *Basella*) in a clade with *Mollugo*; that clade was sister to a clade containing the remaining representatives of the portulacaceous alliance, including *Hectorella*. However, the relationship of *Mollugo* to Basellaceae was not supported by likelihood bootstrap analysis. By contrast, the Bayesian consensus tree placed *Mollugo* and *Limeum* in an unresolved polytomy at the base of the clade containing the portulacaceous families plus Nyctaginaceae, Phytolaccaceae, Sarcobataceae and Aizoaceae.

DISCUSSION

The three chloroplast DNA data sets examined all supported the placement of *Hectorella* within Portulacaceae; in addition, both *matK* and *ndhF* indicated that

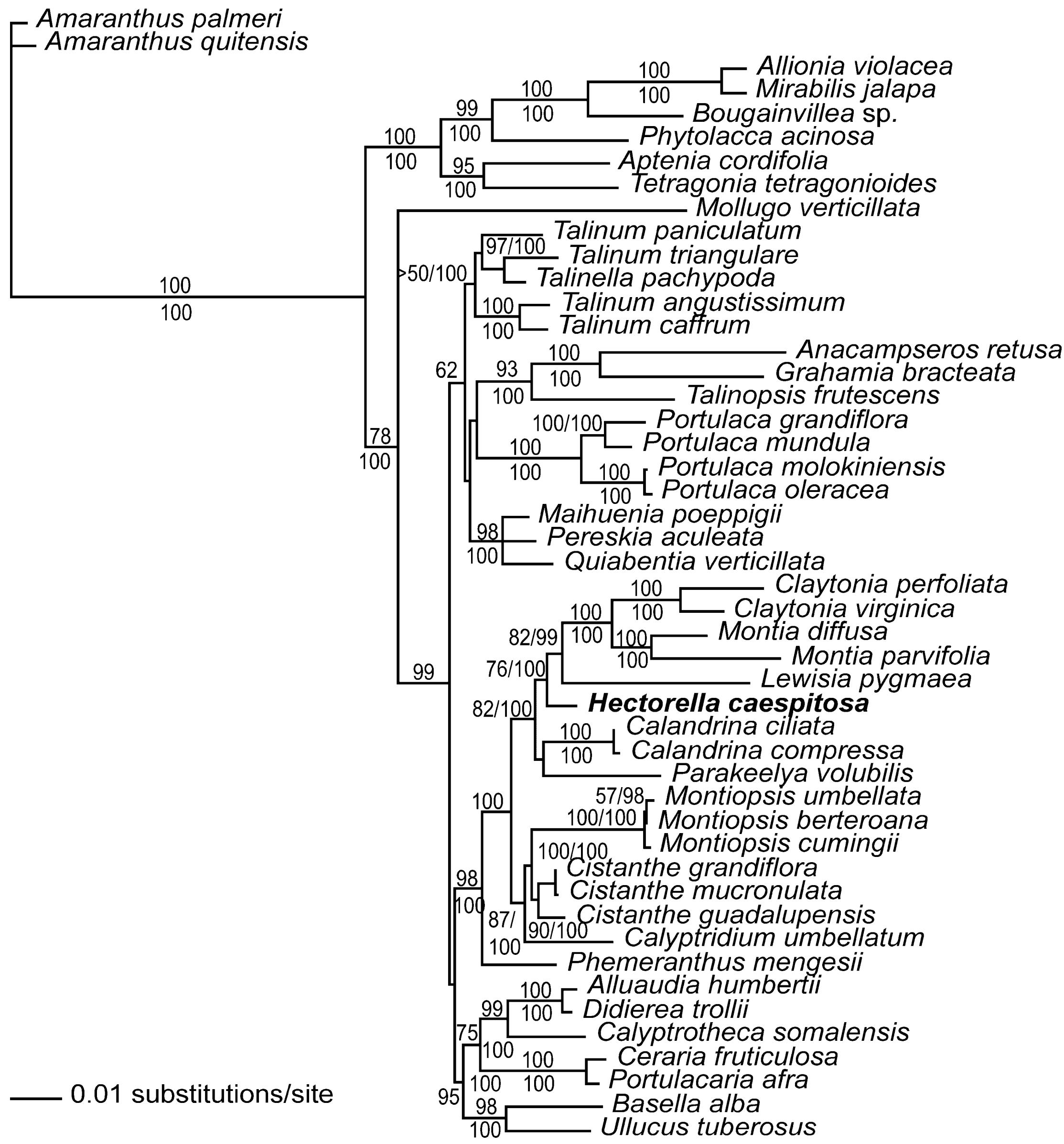

FIG. 2. *ndhF* phylogram inferred under maximum likelihood (ML), identical in topology to Bayesian consensus phylogram. Values above branches indicate ML bootstrap percentages; values under branches indicate posterior probabilities.

Hectorella belongs to the clade of ''western American'' Portulacaceae (sensu Hershkovitz 1993), and is sister to a group of primarily North American genera comprising *Montia*, *Claytonia*, and *Lewisia*. It seems clear, therefore, that continued recognition of Hectorellaceae is unwarranted. Phylogenies based on ITS (Hershkovitz and Zimmer 1997), *ndhF* (Applequist and Wallace 2001), and *matK* (Cuenoud et al. 2002) have shown somewhat incongruent results with regard to relationships among members of the portulacaceous alliance, probably because the critical basal branches are short in all phylogenies. Available data from *matK* (Cuenoud et al. 2002; cf. Fig. 3A) leave relationships among major lineages of Portulacaceae poorly resolved, but taxon sampling has been limited. The addition of *Hectorella* slightly altered the topology of the *ndhF* cladograms: without it, *Parakeelya volubilis* was weakly supported as sister to the *Lewisia*-Montieae clade (Applequist and Wallace 2001), whereas after it was added, *Parakeelya* was weakly supported as sister to *Calandrinia* sensu stricto (Figs. 1, 2).

Morphological similarities between *Hectorella* and its apparent closest relatives may be found. In *Montia* and *Claytonia*, as in *Hectorella*, the stamens are usually

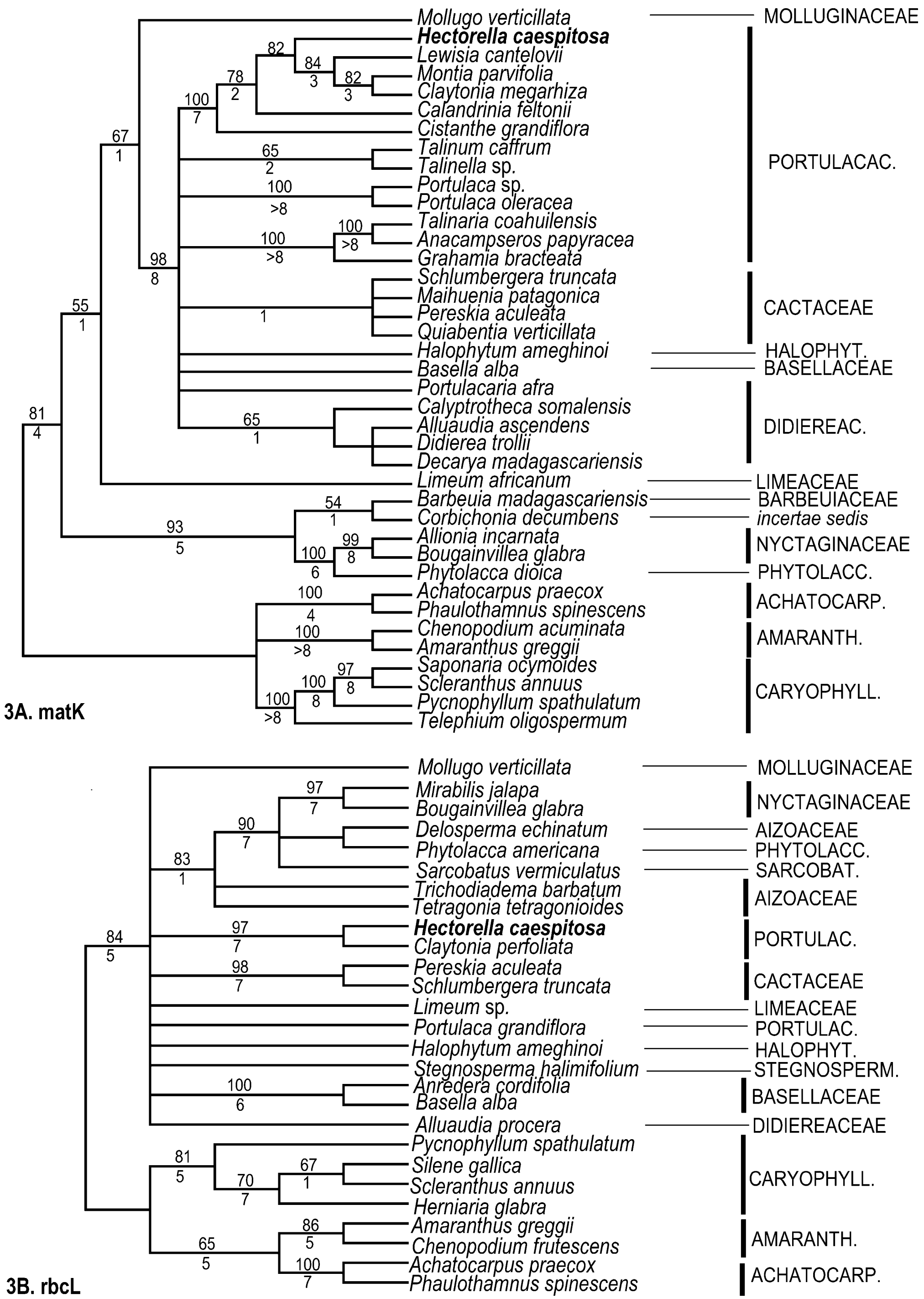

FIG. 3. Strict consensus trees from *matK* and *rbcL* maximum parsimony analyses (uninformative characters excluded), with MP bootstrap percentages above branches, decay indices below branches: 3A, *matK,* consensus of 176 most parsimonious trees. L = 790; RI = 0.636; RC = 0.320; CI = 0.504. 3B, *rbcL,* consensus of 69 most parsimonious trees. L = 514; RI = 0.574; RC = 0.259; CI = 0.451. Abbreviations as in Fig. 1.

five or fewer in number and the seeds are few. There are few obvious shared characters with *Lewisia*, an atypical genus with numerous apparently autapomorphic features. However, Carlquist (1997) observed particular anatomical similarities between the wood of *Hectorella* and that of *Lewisia*, including high vessel densities, very narrow vessels, secondary xylem cylinders at least sometimes broken into segments, and vessels with helical thickenings and sometimes secondary wall interconnections between helices.

The portulacaceous cohort are primarily New World in distribution; molecular data (e.g., Applequist and Wallace 2001) provide some support for the hypothesis that South America or the southern portion of North America is the group's place of origin. Taxa native to the southern Pacific therefore represent later dispersals; direct contact was possible between South America and Australia, via Antarctica, longer than between any other Gondwanan continents (Raven and Axelrod 1974). Several independent dispersals have occurred. Indigenous members of Montieae include the widely distributed *Montia fontana*, which extends into Antarctica (Hooker 1847), and the New Zealand and Australian endemic *Claytonia australasica* Hook. f. (Hooker 1864; Cheeseman 1906); Heenan (1999) has recently described from within the latter several new species, placed within the occasionally recognized segregate genus *Neopaxia*, endemic to New Zealand. Other Portulacaceae native to the southern Pacific region include the distinctive *Anacampseros australiana* J. M. Black, plus probably at least one and possibly two yet undescribed Australian species of *Anacampseros* (Forster 1987; Applequist et al., unpubl. data; J. West, pers. comm.), several endemic species of *Portulaca*, and a cohesive group of Australian species, formerly placed within *Calandrinia*, that were segregated by Hershkovitz (1998) as *Parakeelya*. Montieae and *Parakeelya* belong to the clade that was termed ''western American'' by Hershkovitz (1993), and the nearest relatives of *Anacampseros*, as well as early-diverging lineages within that genus, are South American or Central American. The molecular data indicate that *Hectorella* represents yet another independent dispersal of the western American Portulacaceae to the southern Pacific.

It is necessary to provide a tribal placement for *Hectorella* and *Lyallia* within Portulacaceae (as presently defined; rearrangement of this family will be necessary if a strictly monophyletic classification is to be attained). None of the modern tribal classifications (McNeill 1974; Carolin 1987, 1993; Nyananyo 1990) is phylogenetic in nature, as all include at least one tribe that is demonstrably polyphyletic. Nyananyo's (1990) classification is the only one to place *Hectorella* within a tribe, Calyptrideae, and while he is to be commended for recognizing the kinship of *Hectorella* to the western American Portulacaceae, a tribe including *Calyptridium* and *Hectorella* would be polyphyletic according to the present molecular data. Other tribes recognized by Nyananyo include Montieae (*Montia* and *Claytonia*), Lewiseae (*Lewisia*), and Calandrineae (including *Calandrinia* and segregate genera *Parakeelya*, *Cistanthe*, and *Montiopsis*, therefore paraphyletic). Collaborative discussions on an improved classification of Portulacaceae and related families have begun; the placement of *Hectorella* within the Western American Portulacaceae conveniently provides an existing family name, Hectorellaceae, to be applied to those taxa in the event that Portulacaceae should be subdivided. *Hectorella* and *Lyallia* cannot be placed into any existing tribe of Portulacaceae without causing paraphyly or polyphyly; the only monophyletic options for classification are to lump them into a single tribe with *Lewisia* and the present Montieae, two distinct groups that have never before been placed in the same tribe, or to create a new tribe. We therefore recognize the tribe Hectorelleae:

Hectorelleae Appleq., Nepokr. & W. L. Wagner, trib. nov.—TYPE GENUS: *Hectorella* Hook. f., Handb. New Zealand Fl. 27 (1864).

Based on Hectorellaceae Philipson & Skipworth, Trans. Roy Soc. New Zealand, Bot. 1:31 (1961).

Hectorelleae are characterized by a densely caespitose habit with thick, coriaceous, densely imbricate, spirally arranged leaves, axillary flowers, and stamens that are alternate with the petals (rather than opposite as in most Portulacaceae) and frequently one fewer in number. Flowers may be bisexual or unisexual; the gynoecium is 2-carpellate (Skipworth 1961; Nyananyo and Heywood 1987; Philipson 1993) and the fruit is a 1-loculed, one- to few-seeded capsule that disintegrates rather than releasing seeds through valves as in most Portulacaceae (Allan 1961; Philipson 1993).

Hectorelleae comprise two monotypic genera: *Hectorella*, endemic to New Zealand, and *Lyallia*, endemic to the Kerguélen Islands of Antarctica. There is little doubt that these taxa are sister to one another; Nyananyo and Heywood (1987) placed both in a single genus (*Lyallia*) based on such shared features as their habit, floral position, stamen position and number relative to petal number, and fruit type, as well as their 3-colpate pollen and typical black reniform seeds (the latter characters being plesiomorphic and common within Portulacaceae). However, there are also several significant differences: *Hectorella* has mostly unisexual flowers with 5(–6) petals and 4–5(–6) stamens, whereas flowers of *Lyallia* are hermaphroditic and have 4 petals and 3 stamens (Allan 1961; Skipworth 1961; Nyananyo and Heywood 1987; Philipson 1993; Lourteig 1994). These reproductive characters seem sufficient to justify the maintenance of two genera.

ACKNOWLEDGEMENTS. The authors thank S. Downie, K. A. Ford, M. Timana, and W. R. Sykes for plant and DNA samples, C. L. McCracken for lab assistance, E. A. Kellogg for access to lab facilities, and P. Herendeen, J. Smith, and two anonymous reviewers for helpful comments. Primers designated 455F, 816F, and 854R were designed by C. L. McCracken; primers 955F and 1352R were designed by J. Skog and L. Prince respectively.

LITERATURE CITED

ALLAN, H. H. 1961. *Flora of New Zealand,* vol. 1. Wellington: R. E. Owen.

ANGIOSPERM PHYLOGENY GROUP. 1998. An ordinal classification for the families of flowering plants. *Annals of the Missouri Botanical Garden* 85: 531–553.

———. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG 2. *Botanical Journal of the Linnean Society* 141: 399–436.

APPLEQUIST, W. L. and D. B. PRATT. 2005. The Malagasy endemic *Dendroportulaca* (Portulacaceae) is referable to *Deeringia* (Amaranthaceae): molecular and morphological evidence. *Taxon* 54: 681–687.

——— and R. S. WALLACE. 2001. Phylogeny of the portulacaceous cohort based on *ndhF* sequence data. *Systematic Botany* 26: 406–419.

——— and ———. 2003. Expanded circumscription of Didiereaceae and its division into three subfamilies. *Adansonia, sér. 3* 25: 13–16.

BEHNKE, H.-D. 1975. *Hectorella caespitosa*: ultrastructural evidence against its inclusion into *Caryophyllaceae*. *Plant Systematics and Evolution* 124: 31–34.

BENTHAM, G. 1862. Notes on Caryophylleae, Portulaceae, and some allied orders. *Journal of the Proceedings of the Linnean Society: Botany* 6: 55–77.

BREMER, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* 42: 795–803.

CARLQUIST, S. 1997 [publ. 1998]. Wood anatomy of Portulacaceae and Hectorellaceae: ecological, habital, and systematic implications. *Aliso* 16: 137–153.

CAROLIN, R. 1987. A review of the family Portulacaceae. *Australian Journal of Botany* 35: 383–412.

———. 1993. Portulacaceae. Pp. 544–555 in *The families and genera of vascular plants, vol. 2,* eds. K. Kubitzki, J. G. Rohwer, and V. Bittrich. Berlin: Springer-Verlag.

CHEESEMAN, T. F. 1906. *Manual of the New Zealand flora.* Wellington: John Mackay.

CLEMENT, J. S. and T. J. MABRY. 1996. Pigment evolution in the Caryophyllales: a systematic overview. *Botanica Acta* 109: 360–367.

CONTI, E., A. FISCHBACH, and K. J. SYTSMA. 1993. Tribal relationships in Onagraceae: implications from *rbcL* sequence data. *Annals of the Missouri Botanical Garden* 80: 672–685.

CRONQUIST, A. 1981. *An integrated system of classification of flowering plants.* New York: Columbia University Press.

CUENOUD, P., V. SAVOLAINEN, L. W. CHATROU, M. POWELL, R. J. GRAYER, and M. W. CHASE. 2002. Molecular phylogenetics of Caryophyllales based on nuclear 18S rDNA and plastid *rbcL, atpB* and *matK* DNA sequences. *American Journal of Botany* 89: 132–144.

DALHGREN, R. 1975. A system of classification of the angiosperms to be used to demonstrate the distribution of characters. *Botaniska Notiser* 128: 119–147.

DIELS, L. 1897. Vegetations-Biologie von Neu-Seeland. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 22: 201–300.

DONOGHUE, M. J., R. J. OLMSTEAD, J. F. SMITH, and J. D. PALMER. 1992. Phylogenetic relationships of Dipsacales based on *rbcL* sequences. *Annals of the Missouri Botanical Garden* 79: 333–345.

FELSENSTEIN, J. 1981. Evolutionary trees from DNA sequences: a maximum likelihood approach. *Journal of Molecular Evolution* 37: 368–376.

———. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.

FORSTER, P. 1987. Notes on *Ancampseros australiana* J. M. Black (Portulacaceae). *Anacampseros (Australian National Cactus and Succulent Journal)* 3: 48–55.

GOLDMAN, N. 1993. Statistical tests of models of DNA substitution. *Journal of Molecular Evolution* 36: 182–198.

GRAY, A. 1876. Botany. Pp. 20–30 in *Contributions to the natural history of Kerguélen Island, made in connection with the United States Transit of Venus Expedition, 1874–75, vol. 2,* ed. J. H. Kidder. *Bulletin of the U. S. National Museum* 1(3).

HARMS, H. 1934. Reihe Centrospermae. Pp. 1–6 in *Die natürlichen Pflanzenfamilien, 2nd ed., vol. 16c,* eds. A. Engler and K. Prantl. Leipzig: W. Engelmann.

HEENAN, P. B. 1999. A taxonomic revision of *Neopaxia* O. Nilss. (Portulacaceae) in New Zealand. *New Zealand Journal of Botany* 37: 213–234.

HERSHKOVITZ, M. A. 1993. Revised circumscriptions and subgeneric taxonomies of *Calandrinia* and *Montiopsis* (Portulacaceae) with notes on phylogeny of the portulacaceous alliance. *Annals of the Missouri Botanical Garden* 80: 333–365.

———. 1998. *Parakeelya*: a new genus segregated from *Calandrinia* (Portulacaceae). *Phytologia* 84: 98–106.

——— and E. A. ZIMMER. 1997. On the evolutionary origins of the cacti. *Taxon* 46: 217–242.

HOOKER, J. D. 1847. *The botany of the Antarctic voyage of J. M. S. Discovery ship Erebus and Terror, in the years 1839–1843, vol. 1, Flora Antarctica, part 2.* London: Reeve and Co.

———. 1864. *Handbook of the New Zealand flora, vol. 1.* London: Reeve and Co.

HOOT, S. B., S. MAGALLÓN, and P. R. CRANE. 1999. Phylogeny of basal eudicots based on three molecular data sets: *atpB, rbcL,* and 18S nuclear ribosomal DNA sequences. *Annals of the Missouri Botanical Garden* 86: 1–32.

HUELSENBECK, J. P. and F. RONQUIST. 2001. MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755.

JOHNSON, L. A. and D. E. SOLTIS. 1994. *matK* DNA sequences and phylogenetic reconstruction in Saxifragaceae s. str. *Systematic Botany* 19: 143–156.

KADEREIT, G., T. BORSCH, K. WEISING, and H. FREITAG. 2003. Phylogeny of Amaranthaceae and Chenopodiaceae and the evolution of C4 photosynthesis. *International Journal of Plant Sciences* 164: 959–986.

LEVIN, R. A., W. L. WAGNER, P. HOCH, M. NEPOKROEFF, J. C. PIRES, E. A. ZIMMER, and K. J. SYTSMA. 2003. Family-level relationships of Onagraceae based on chloroplast *rbcL* and *ndhF* data. *American Journal of Botany* 90: 107–115.

LOURTEIG, A. 1994. *Lyallia kerguelensis* Hook. f. and its artificial propagation. Pp. 321–327 in *Caryophyllales: evolution and systematics,* eds. H.-D. Behnke and T. H. Mabry. Berlin: Springer-Verlag.

MABRY, T. J., P. NEUMAN, and W. R. PHILIPSON. 1978. *Hectorella*: a member of the betalain-suborder *Chenopodiineae* of the order *Centrospermae*. *Plant Systematics and Evolution* 130: 163–165.

MANHART, J. R. and J. H. RETTIG. 1994. Gene sequence data. Pp. 235–246 in *Caryophyllales: evolution and systematics,* eds. H.-D. Behnke and T. H. Mabry. Berlin: Springer-Verlag.

MANOS, P. S. and K. P. STEELE. 1997. Phylogenetic analyses of "higher" Hamamelidae based on plastid sequence data. *American Journal of Botany* 84: 1407–1419.

MCNEILL, J. 1974. Synopsis of a revised classification of the Portulacaceae. *Taxon* 23: 725–728.

MEIMBERG, H., P. DITTRICH, G. BRINGMANN, J. SCHLAUER, and G. HEUBL. 2000. Molecular phylogeny of Caryophyllidae s.l.

based on *matK* sequences with special emphasis on carnivorous taxa. *Plant Biology* 2: 218–228.

MÜLLER, K. and T. BORSCH. 2005. Phylogenetics of Amaranthaceae based on *matK/trnK* sequence data—evidence from parsimony, likelihood, and Bayesian analyses. *Annals of the Missouri Botanical Garden* 92: 66–102.

NYANANYO, B. L. 1990. Tribal and generic relationship in the Portulacaceae (Centrospermae). *Feddes Repertorium* 101: 237–241.

——— and V. H. HEYWOOD. 1987. A new combination in *Lyallia* (Portulacaceae). *Taxon* 36: 640–641.

NYFFELER, R. 2002. Phylogenetic relationships in the cactus family (Cactaceae) based on evidence from *trnK/matK* and *trnL-trnF* sequences. *American Journal of Botany* 89: 312–326.

OLMSTEAD, R. G., H. J. MICHAELS, K. M. SCOTT, and J. D. PALMER. 1993. A parsimony analysis of the Asteridae and identification of their major lineages inferred from DNA sequences of *rbcL*. *Annals of the Missouri Botanical Garden* 80: 700–722.

PAX, F. 1889a. Caryophyllaceae. Pp. 61–94 in *Die natürlichen Pflanzenfamilien, 1. Aufl., vol. III/1b,* eds. A. Engler and K. Prantl. Leipzig: W. Engelmann.

———. 1889b. Portulacaceae. Pp. 51–60 in *Die natürlichen Pflanzenfamilien, 1. Aufl., vol. III/1b,* eds. A. Engler and K. Prantl. Leipzig: W. Engelmann.

——— and K. HOFFMANN. 1934. Caryophyllaceae. Pp. 275–364 in *Die natürlichen Pflanzenfamilien, 2. Aufl, vol. 16c,* eds. A. Engler and K. Prantl. Leipzig: W. Engelmann.

PHILIPSON, W. R. 1993. Hectorellaceae. Pp. 331–334 in *The families and genera of vascular plants, vol. 2,* eds. K. Kubitzki, J. G. Rohwer, and V. Bittrich. Berlin: Springer-Verlag.

——— and J. P. SKIPWORTH. 1961. Hectorellaceae: a new family of dicotyledons. *Transactions of the Royal Society of New Zealand: Botany* 1: 31.

POSADA, D. and K. A. CRANDALL. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14: 817–818.

RAVEN, P. H. and D. I. AXELROD. 1974. Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Garden* 61: 539–673.

RETTIG, J. H., H. D. WILSON, and J. R. MANHART. 1992. Phylogeny of the Caryophyllales—gene sequence data. *Taxon* 41: 201–209.

RODMAN, J. E. 1990. Centrospermae revisited, part I. *Taxon* 39: 383–393.

———, M. K. OLIVER, R. R. NAKAMURA, J. U. MCCLAMMER JR., and A. H. BLEDSOE. 1984. A taxonomic analysis and revised classification of Centrospermae. *Systematic Botany* 9: 297–323.

SAVOLAINEN, V., M. W. CHASE, S. B. HOOT, C. M. MORTON, D. E. SOLTIS, C. BAYER, M. F. FAY, A. Y. DE BRUIJN, S. SULLIVAN, and Y. L. QIU. 2000a. Phylogenetics of flowering plants based on combined analysis of plastid *atpB* and *rbcL* gene sequences. *Systematic Biology* 49: 306–362.

———, M. F. FAY, D. C. ALBACH, A. BACKLUND, M. VAN DER BANK, K. M. CAMERON, S. A. JOHNSON, M. D. LLEDO, J. C. PINTAUD, M. POWELL, M. C. SHEAHAN, D. E. SOLTIS, P. S. SOLTIS, P. WESTON, W. M. WHITTEN, K. J. WURDACK, and M. W. CHASE. 2000b. Phylogeny of the eudicots: a nearly complete familial analysis based on *rbcL* gene sequences. *Kew Bulletin* 55: 257–309.

SKIPWORTH, J. P. 1961. The taxonomic position of *Hectorella caespitosa* Hook. f. *Transactions of the Royal Society of New Zealand* 1: 17–30.

SOLTIS, D. E., P. S. SOLTIS, P. K. ENDRESS, and M. W. CHASE. 2005. *Phylogeny and evolution of angiosperms.* Sunderland: Sinauer Associates.

STEELE, K. P. and R. VILGALYS. 1994. Phylogenetic analyses of Polemoniaceae using nucleotide sequences of the plastid gene *matK*. *Systematic Botany* 19: 126–142.

SULLIVAN, J., J. A. MARKERT, and C. W. KILPATRICK. 1997. Phylogeography and molecular systematics of the *Peromyscus aztecus* group (Rodentia: Muridae) inferred using parsimony and likelihood. *Systematic Biology* 46: 426–440.

SWOFFORD, D. L. 2001. *PAUP*. Phylogenetic analysis using parsimony (*and other methods).* Version 4. Sunderland: Sinauer Associates.

TAKHTAJAN, A. 1973. *Evolution und Ausbreitung der Blütenpflanzen.* Jena-Stuttgart: G. Fischer.

THORNE, R. F. 1976. A phylogenetic classification of the angiosperms. *Evolutionary Biology* 9: 35–106.

YANG, Z., N. GOLDMAN, and A. FRIDAY. 1995. Maximum likelihood trees from DNA sequences. *Journal of Molecular Evolution* 39: 315–329.

APPENDIX 1

Taxa included in phylogenetic analyses, with accession data or source of previously published sequence and GenBank accession numbers.

Taxa included in *ndhF* analysis (all but *Hectorella* from Applequist and Wallace 2001). **Aizoaceae**: *Aptenia cordifolia* Schwant., AF194824. *Tetragonia tetragonioides* (Pall.) Kuntze, AF194829. **Amaranthaceae**: *Amaranthus palmeri* S. Wats., AF194821. *Amaranthus quitensis* HBK, AF194822. **Basellaceae**: *Basella alba* L., AF194834. *Ullucus tuberosus* Lozano, AF194865. **Cactaceae**: *Maihuenia poeppigii* (Otto ex Pfeiff.) F. A. C. Weber ex K. Schum., AF206714. *Pereskia aculeata* (Plum.) Mill, AF194852. *Quiabentia verticillata* (Vaup.) Vaup., AF194858. **Didiereaceae**: *Alluaudia humbertii* Choux, AF194832. *Calyptrotheca somalensis* Gilg, AF194839. *Ceraria fruticulosa* Pearson & Stephens, AF 194841. *Didierea trollii* Capuron & Rauh, AF194845. *Portulacaria afra* Jacq., AF194857. **Hectorellaceae**: *Hectorella caespitosa* Hook. f., New Zealand, Fiordland (Southland L.D.), Lake Wapiti, *K. A. Ford 117/98* (CHR), DQ093963 **Molluginaceae**: *Mollugo verticillata* L., AF194827. **Nyctaginaceae**: *Allionia violacea* Loefl., AF194823. *Bougainvillea* sp., AF194825. *Mirabilis jalapa* L., AF194826. **Phytolaccaceae**: *Phytolacca acinosa* Roxb., AF194828. **Portulacaceae**: *Anacampseros retusa* Poelln., AF194833. *Calandrinia ciliata* (Ruíz & Pav.) DC. var. *menziesii* (Hook.) Macbr., AF194835. *Calandrinia compressa* Schrad., AF194836. *Calyptridium umbellatum* (Torr.) Greene, AF194840. *Cistanthe guadalupensis* (Dudley) Carolin ex Hershk., AF194860. *Claytonia perfoliata* Donn ex Willd., AF194831. *Claytonia virginica* L., AF194856. *Grahamia bracteata* Gill. ex Hook., AF194846. *Lewisia pygmaea* (A. Gray) B. L. Robinson, AF194847. *Montia diffusa* (Nutt.) Greene, AF194848. *Montia parvifolia* (Moc. ex DC.) Greene, AF194851. *Montiopsis berteroana* (Phil.) D. I. Ford, AF194849. *Montiopsis cumingii* (Hook. & Arnott) D. I. Ford, AF194850. *Parakeelya volubilis* (Benth.) Hershk., AF194838. *Phemeranthus mengesii* (Wolf) Kiger, AF194861. *Portulaca grandiflora* Hook., AF194853. *Portulaca molokiniensis* Hobdy, AF194854. *Portulaca mundula* I. M. Johnst., AF194855. *Portulaca oleracea* L., AF194867. *Talinella pachypoda* Eggli, AF194862. *Talinopsis frutescens* A. Gray, AF194863. *Talinum angustissimum* (A. Gray) Woot. & Standl., AF194866. *Talinum caffrum* (Thunb.) Ecklon & Zeyh., AF194859. *Talinum paniculatum* (Jacq.) Gaertn., AF194830. *Talinum triangulare* (Jacq.) Willd., AF206713.

Taxa included in *matK* analysis (from Cuenoud et al., 2002, except where otherwise noted). **Achatocarpaceae**: *Achatocarpus praecox* Griseb., Müller and Borsch 2005, AY514845. *Phaulothamnus spinescens* A. Gray, AY042630. **Amaranthaceae**: *Amaranthus greggii* S. Watson, Müller and Borsch 2005, AY514808. *Chenopodium acuminatum* Willd., Müller and Borsch 2005, AY514836. **Barbeuiaceae**: *Barbeuia madagascariensis* Steud., AY042552. **Basellaceae**: *Basella alba* L., AY042553. **Cactaceae**: *Maihuenia patagonica* Britton & Rose, Nyffeler 2002, AY015281. *Quiabentia verticillata* (Vaup.) Vaup., AY042641. *Schlumbergera truncata* (Haw.) Moran, Nyffeler 2002, AY015343. *Pereskia aculeata* (Plum.) Mill. AY042626. **Caryophyllaceae**: *Scleranthus annuus* L., *W. L. Wagner 6862* (US), DQ267196. *Pycnophyllum spathulatum* Mattf., *Timana s.n.* (TEX), DQ267198. *Saponaria ocymoides* L., AY042651. *Telephium oligospermum* Steud. ex Boiss., AY042664. **Didiereaceae**: *Alluaudia ascendens* Drake, AY042541. *Calyptrotheca somalensis* Gilg, AY042563. *Decaryia madagascariensis* Choux AY042574. *Didierea trollii* Capuron & Rauh, AY042576. *Portulacaria afra* Jacq., AY042637. **Halophytaceae**: *Halophytum ameghinoi* Speg., AY042599. **Hectorellaceae**: *Hectorella caespitosa* Hook. f., New Zealand, Fiordland (Southland L.D.), Lake Wapiti, *K. A. Ford 117/98* (CHR), DQ267197. **Limeaceae**: *Limeum africanum* L., AY042608. **Molluginaceae**: *Mollugo verticillata* L., *S. Downie 1062* (ILL), DQ267195. **Nyctaginaceae**: *Allionia incarnata* L., AY042540. *Bougainvillea glabra* Choisy, AY042560. **Phytolaccaceae**: *Phytolacca dioica* L., AY042631. **Portulacaceae**: *Anacampseros papyracea* E. Mey. ex Sond., AY042545. *Calandrinia feltonii* Skottsb., AY042562. *Cistanthe grandiflora* (Lindl.) Carolin ex Hershk., AY042568. *Claytonia megarhiza* (A. Gray) Perry ex S. Watson, AY042569. *Grahamia bracteata* Gill. ex Hook., Nyffeler 2002, AY015273. *Lewisia cantelovii* Howell, AY042607. *Montia parvifolia* (Moc. ex DC.) Greene AY042616. *Portulaca* sp., AY042636. *Portulaca oleracea* L., Meimberg et al. 2000, AF204867. *Talinaria coahuilensis* (S. Watson) P. Wilson, AY042661. *Talinum caffrum* (Thunb.) Ecklon & Zeyh., AY042662. *Talinella* sp., Müller and Borsch 2005, AY514859. **incertae sedis**: *Corbichonia decumbens* Scop., AY042572.

Taxa included in *rbcL* analysis. **Achatocarpaceae**: *Achatocarpus praecox* Griseb., Kadereit et al., 2003, AY270142. *Phaulothamnus spinescens* A. Gray, Manhart and Rettig 1994, M97887. **Aizoaceae**: *Delosperma echinatum* Schwantes, Savolainen et al. 2000a, AJ235778. *Trichodiadema barbatum* Schwantes, Cuenoud et al. 2002, AY046587. *Tetragonia tetragonioides* (Pall.) Kuntze, Clement and Mabry 1996, AF132094. **Amaranthaceae**: *Amaranthus greggii* S. Watson, Kadereit et al. 2003, AY270055. *Chenopodium frutescens* C. A. Mey., Kadereit et al. 2003, AY270082. **Basellaceae**: *Anredera cordifolia* (Ten.) Steenis, Kadereit et al. 2003, AY270147. *Basella alba* L., Rettig et al., 1992, M62564. **Cactaceae**: *Pereskia aculeata* (Plum.) Mill., Manhart and Rettig 1994, M97888. *Schlumbergera truncata* (Haw.) Moran, Rettig et al. 1992, M83543. **Caryophyllaceae**: *Herniaria glabra* L., Clement and Mabry 1996, AF132091. *Pycnophyllum spathulatum* Mattf., *Timana s.n.* (TEX), DQ267194. *Silene gallica* L., Rettig et al. 1992, M83544. *Scleranthus annuus* L., Kadereit et al. 2003, AY270145. **Didiereaceae**: *Alluaudia procera* Drake, Rettig et al. 1992, M62563. **Halophytaceae**: *Halophytum ameghinoi* Speg., Savolainen et al. 2002b, HAM403024. **Hectorellaceae**: *Hectorella caespitosa* Hook. f., New Zealand, Fiordland (Southland L.D.), Lake Wapiti, *K. A. Ford 117/98* (CHR), DQ267193. **Limeaceae**: *Limeum* sp., Hoot et al. 1999, AF093727. **Molluginaceae**: *Mollugo verticillata* L., Rettig et al. 1992, M62566. **Nyctaginaceae**: *Bougainvillea glabra* Choisy, Manhart and Rettig 1994, M88340. *Mirabilis jalapa* L., Rettig et al., 1992, M62565. **Phytolaccaceae**: *Phytolacca americana* L., Rettig et al. 1992, M62567. **Portulacaceae**: *Claytonia perfoliata* Donn ex Willd., Clement and Mabry 1996, AF132093. *Portulaca grandiflora* Hook., Rettig et al. 1992, M62568. **Sarcobataceae**: *Sarcobatus vermiculatus* (Hook.) Torr., Clement and Mabry 1996, AF132088. **Stegnospermataceae**: *Stegnosperma halimifolium* Benth., Rettig et al. 1992, M62571.