

Revision and tribal placement of the Argentinean genus *Parodiodoxa* (Brassicaceae)

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Abstract *Parodiodoxa* is a monotypic genus of Brassicaceae endemic to northwestern Argentina. It is poorly known and until now remained the only South American genus of the family that had not been assigned to a particular tribe. Sequence data from the nuclear ribosomal ITS region and the chloroplast *trnL* intron/*trnL*-F spacer region were used in this study to determine the systematic position of *Parodiodoxa*. For this purpose, taxa were sampled both at the tribal and generic levels. Results from tribal-level sampling support the inclusion of *Parodiodoxa* in the tribe Thelypodieae, whereas those at the generic level reveal a relationship to *Weberbaueria* (*W. rosulans* and *W. herzogii*). Topologies within the Thelypodieae were poorly resolved, in agreement with previous studies. Morphological characteristics of *Parodiodoxa* are also discussed in relation to other genera of the tribe.

Keywords Brassicaceae · ITS · *Parodiodoxa* · Thelypodieae · *trnL*-F · *Weberbaueria*

Introduction

Brassicaceae (Cruciferae) is a well-defined family distributed worldwide and includes approximately 320 genera and 3,660 species currently assigned to 49 tribes (Al-Shehbaz 2012a). Most species grow in temperate

areas, with the highest diversity in the Irano–Turanian region, Mediterranean area, and western North America (Al-Shehbaz 1984; Appel and Al-Shehbaz 2003; Warwick et al. 2006). The family is also well represented in southern South America, especially Argentina and Chile, where approximately 71 genera and 301 species grow (Al-Shehbaz 2008). Argentina has 59 genera and 222 species, of which 103 species are native and 57 are endemic (Al-Shehbaz 2012b).

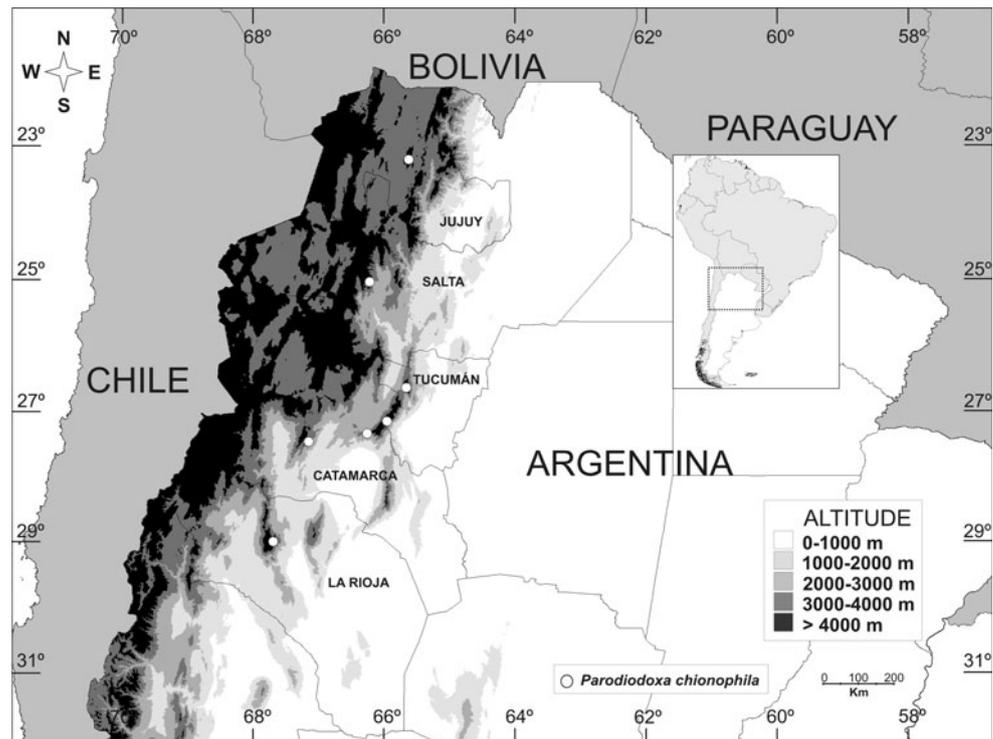
Since the pioneering molecular phylogenetic analyses on the Brassicaceae (Zunk et al. 1993, 1996; Price et al. 1994), numerous studies (Bailey et al. 2006; Warwick et al. 2006, 2007, 2008, 2009, 2010, 2011; Al-Shehbaz and Warwick 2007; Koch et al. 2007; Beilstein et al. 2006, 2008; German and Al-Shehbaz 2008; Warwick and Hall 2008; Koch and Al-Shehbaz 2009; Franzke et al. 2009; German et al. 2009; Khosravi et al. 2009; Couvreur et al. 2010) have included the phylogenetic position of approximately 94 % of the family genera and placed them in 49 monophyletic tribes (Warwick et al. 2010; Al-Shehbaz 2012a).

Spegazzini (1898) described *Thlaspi chionophilum* Speg., but Schulz (1929) placed it in the new monotypic genus *Parodiodoxa* O.E. Schulz, on the basis of critical comparison with other species of *Thlaspi*. *Parodiodoxa chionophila* (Speg.) O.E. Schulz is a highly restricted Argentinean endemic of Catamarca, Jujuy, La Rioja, Salta, and Tucumán provinces (Fig. 1). The morphological features of *Parodiodoxa* remained poorly known until recently (Al-Shehbaz 2012b), and because of the lack of molecular studies it remained the only South American endemic that has not yet been assigned to a tribe (Al-Shehbaz 2012a). *Parodiodoxa chionophila* grows on rocky soil protected by boulders and tussocks at high elevations of 3,500–5,100 m (Ancibor 1984).

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Fig. 1 Geographical distribution of *Parodiodoxa chionophila* (Speg.) O.E. Schulz in Argentina (open dots)



The objectives of this study were to determine the tribal placement of *Parodiodoxa*, by use of the nuclear ribosomal ITS and chloroplast *trnL*-F sequences, and critical evaluation of its morphology.

Materials and methods

Taxon sampling

Herbarium samples of *Parodiodoxa chionophila* from BAA, CORD, LIL, LP, and SI were studied. Sequences of the nuclear ribosomal ITS (ITS1-5.8S-ITS2) and chloroplast region *trnL* intron/*trnL*-F spacer were obtained from one collection, *Barboza* et al. 2566 (CORD); the ITS and *trnL*-F Genbank numbers are JX971121 and JX971122, respectively. Molecular analysis was conducted to determine the tribal affiliation of *Parodiodoxa* within the Brassicaceae, and the generic-level relationship within the tribe Thelypodieae. In analysis at the tribal level, 95 ITS and 88 *trnL*-F sequences of Brassicaceae, representing 45 and 34 tribes, respectively, were downloaded from Genbank (<http://www.ncbi.nlm.nih.gov/genbank/>). *Cleome lutea* Hook. (ITS) and *C. spinosa* Jacq. (*trnL*-F) were used as outgroup because Cleomaceae is widely recognized as sister family to the Brassicaceae (Hall et al. 2002).

The analysis within Thelypodieae included 43 ITS and *trnL*-F sequences representing ca. 96 % of the genera currently assigned to tribes (Al-Shehbaz 2012a). Two

species each of the tribes Brassicaceae, Isatidaceae, and Sisymbriaceae were selected as the outgroup. All Genbank accession numbers are listed in the Appendix.

DNA extraction, amplification, and sequencing

Total DNA was isolated from leaves of *Barboza* et al. 2566 (CORD) by use of the modified (CTAB) procedure of Doyle and Doyle (1987). The ITS region was PCR-amplified by using the ITS4 and ITS5 primers of Baldwin (1992) whereas the *trnL*-F region was amplified by using primers C of Taberlet et al. (1991) and *F_{dw}* (5'CAG-TCCTCTGCTCTACCAGC3'). PCR reactions were performed in 25 μ L final volumes with 50–100 ng template DNA, 0.2 μ M of each primer, 25 μ M dNTP, 5 mM MgCl₂, 1 \times buffer, and 1.5 U Taq polymerase provided by Invitrogen Life Technologies. PCR amplifications were set at: (ITS) a first period of denaturation at 94 $^{\circ}$ C for 5 min, followed by 35 cycles of denaturation at 94 $^{\circ}$ C for 30 s, annealing at 50 $^{\circ}$ C for 60 s, and extension at 72 $^{\circ}$ C for 90 s, with a final extension at 72 $^{\circ}$ C for 7 min; (*trnL*-F) a first period of denaturation at 94 $^{\circ}$ C for 3 min, followed by 35 cycles of denaturation at 94 $^{\circ}$ C for 30 s, annealing at 48 $^{\circ}$ C for 60 s, and extension at 72 $^{\circ}$ C for 90 s, with a final extension at 72 $^{\circ}$ C for 10 min. Cleaning of PCR products and sequencing reactions were performed by MacroGen (Seoul, Korea). Sequences were assembled and edited by use of the software Chromas Pro v1.41 (Technelysium, South Brisbane, Australia).

Sequence alignment and phylogenetic analyses

Alignments were generated with MAFFT v9.03b (Kato et al. 2009), using the “L-INS-i” algorithm and the default settings. Brassicaceae and Thelypodieae datasets from *ITS* and *trnL-F* were analyzed by using the maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) approaches. The *ITS* and *trnL-F* datasets of the tribe Thelypodieae were also analyzed by using the incongruence-length difference test by Farris et al. (1995) in PAUP v4.0b10 (Swofford 2003) (“HomPart” command) and 1,000 replications. Both datasets were combined because they were not significantly incongruent ($p = 0.481$).

Gaps were treated as missing data. For MP analysis, tree searches were generated by use of the software TNT v1.1 (Goloboff et al. 2008) using heuristic searches with 1,000 random addition sequences, tree bisection and reconnection, branch swapping (TBR), and holding 10 trees per replicate. Generated trees were then submitted to a new round of TBR branch swapping to completion. Support values for nodes were estimated by Jackknife (JK) analysis (Farris et al. 1996) with 2,000 replicates of 10 random addition sequences, holding four trees per replicate and using the default removal probability (0.36). Maximum likelihood analysis was conducted using RAxML v7.2.6 (Stamatakis 2006). The models of nucleotide substitution were selected by use of the Akaike information criterion (AIC) implemented in jModeltest v0.1.1 (Posada 2008): SYM + G (*ITS* “Brassicaceae” and “Thelypodieae”), TVM + G (*trnL-F* “Brassicaceae”), TIM1 + G (*trnL-F* “Thelypodieae”). The algorithm implemented in RAxML was used to conduct nonparametric bootstrap (BS) analysis and searches for the best-scoring ML tree in a single run (Stamatakis et al. 2008). We executed 1,000 rapid bootstrap inferences and thereafter a thorough ML search under the GTRMIX model. Bayesian analyses were conducted using MrBayes v3.2 (Ronquist et al. 2012). Models were set in MrBayes as $nst = 6$, $rates = \text{gamma}$ with rate matrix parameters, state frequencies, gamma shape parameter, and proportion of invariable sites unlinked across partitions. The priors on state frequencies, rates, and shape of the gamma distribution were estimated automatically from the data, assuming no prior knowledge about their values (uniform Dirichlet prior). Two simultaneous analyses, starting from different random trees and with four Markov Monte Carlo chains were run for 8 million generations and sampled every 1,000 generations to ensure independence of the successive samples. The first 2,000 trees (25 % of total trees) were discarded as burn-in. The convergence and the effective sample size (ESS) of each replicate were checked using Tracer v. 1.5 (Rambaut and Drummond 2007). The remaining samples of each run were combined, and the majority-rule consensus tree from 12,000 trees was calculated.

Results

The *ITS* and *trnL-F* sequences of *Parodiodoxa chionophila* were 600 and 659 pb long, respectively. The *ITS* alignment for the Brassicaceae dataset included 96 taxa and was 712 bp long, of which 340 (48 %) were parsimony-informative. The MP analysis resulted in 81 most parsimonious trees, and together the ML and BI analyses recovered similar topologies with the same strongly supported clades. All *ITS* topologies recovered *P. chionophila* within tribe Thelypodieae (Fig. 2) (JK 99 %, BS 91 %, PP 1). This tribe was included in a clade together with tribes Brassicaceae, Isatidae, and Sisymbrieae (JK and BS < 50 %; PP 0.8).

The *trnL-F* dataset included 89 taxa and was 1,406 bp long, of which 292 (20 %) were parsimony-informative. The MP analysis recovered more than 10,000 most parsimonious trees, and ML and BI topologies showed *Parodiodoxa chionophila* in a clade together with several Thelypodieae species of the genera *Romanschulzia* O.E. Schulz, *Streptanthus* Nutt., *Thelypodium* Endl., and *Warea* Nutt. (JK and BS < 50 %; PP 0.62) (Fig. 3). These and other Thelypodieae genera were included in a clade together with tribes Brassicaceae, Isatidae, and Sisymbrieae (JK 58 %; BS 67 %; PP 0.99). The monophyly of Thelypodieae could not be resolved as members of the tribe were recovered in a polytomy.

When *Parodiodoxa chionophila* was analyzed using the Thelypodieae dataset, the *ITS* alignment was 573 bp long, of which 113 (20 %) were parsimony-informative, whereas the *trnL-F* dataset was 784 bp long, of which only 31 (4 %) were parsimony-informative. MP analysis for both regions resulted in more than 10,000 MPT; these, together with the ML and BI topologies, were poorly resolved (data not shown). Because the *ITS* and *trnL-F* were not significantly incongruent (see “Materials and methods”), the two datasets were concatenated. Trees obtained from MP, ML, and BI analysis were similar and showed *P. chionophila* included within the Thelypodieae in a clade (Fig. 4) (JK and BS < 50 %; PP 0.76) together with *Weberbaueria herzogii* (O.E. Schulz) Al-Shehbaz and *W. rosulans* (O.E. Schulz) Al-Shehbaz. The monophyly of Thelypodieae was well supported (JK 87 %, BS 88 %, PP 0.97), whereas the relationships within the tribe were poorly resolved.

Discussion

All this analysis placed the Argentinean genus *Parodiodoxa* in tribe Thelypodieae. Although the monophyly of this tribe with the chloroplast region *trnL* intron/*trnL-F* spacer was not resolved, the nuclear ribosomal ITS1-5.8S-ITS2 strongly supported the inclusion of *P. chionophila* in this tribe. The Thelypodieae include 26 genera and 244 species all of which genera except for the monotypic *Pringlea* T.

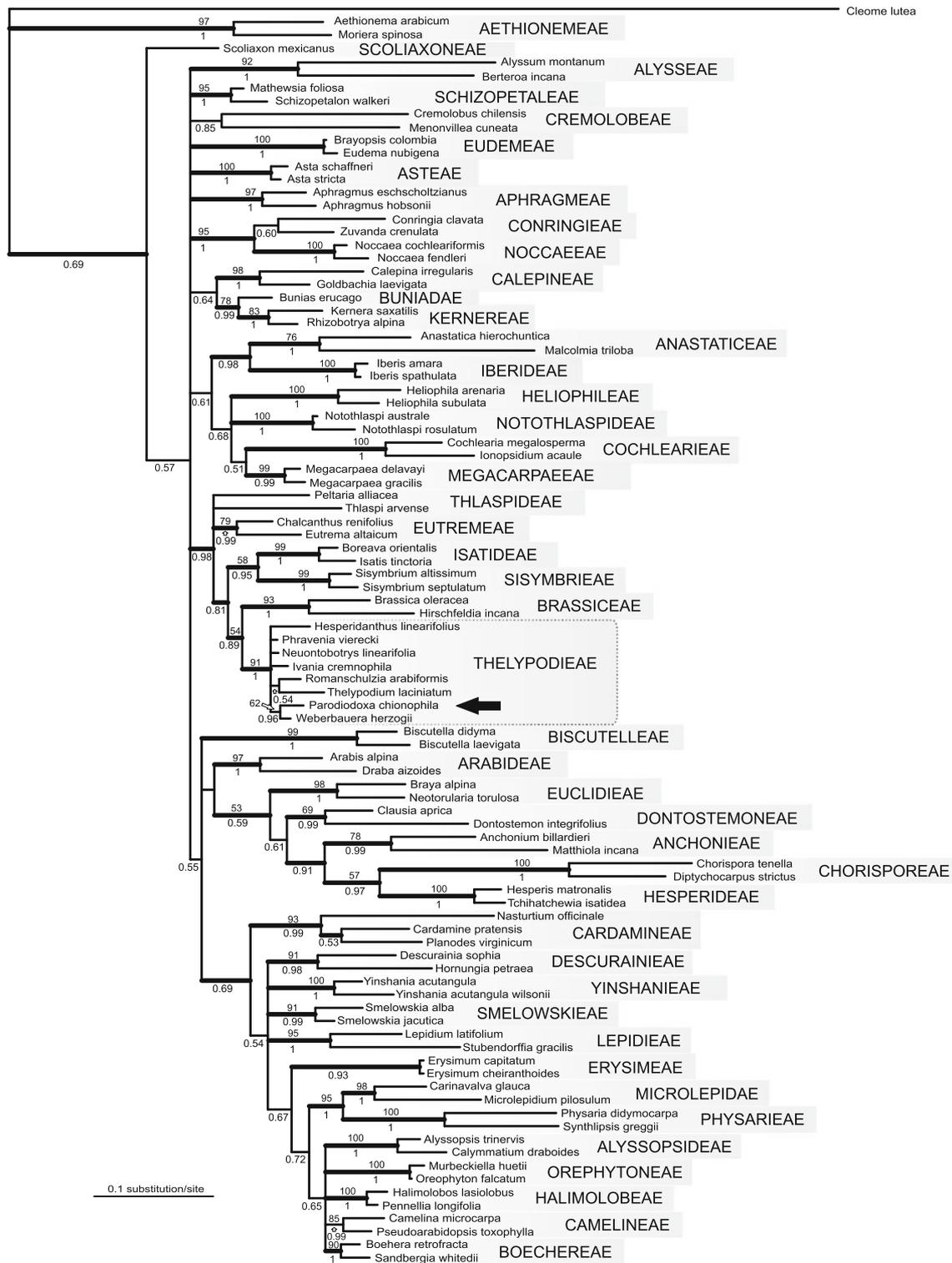


Fig. 2 Bayesian 50 % majority-rule consensus tree from 12,000 trees obtained in the Bayesian analysis with ITS sequences at the tribal level within Brassicaceae. Tribes are indicated to the *right*. Values above and below branches correspond to maximum likelihood

bootstrap/Bayesian posterior probability, respectively. Thick branches indicate internal branches present in the maximum parsimony strict consensus tree. The black arrow indicates the position of *Parodiodoxa chionophila*

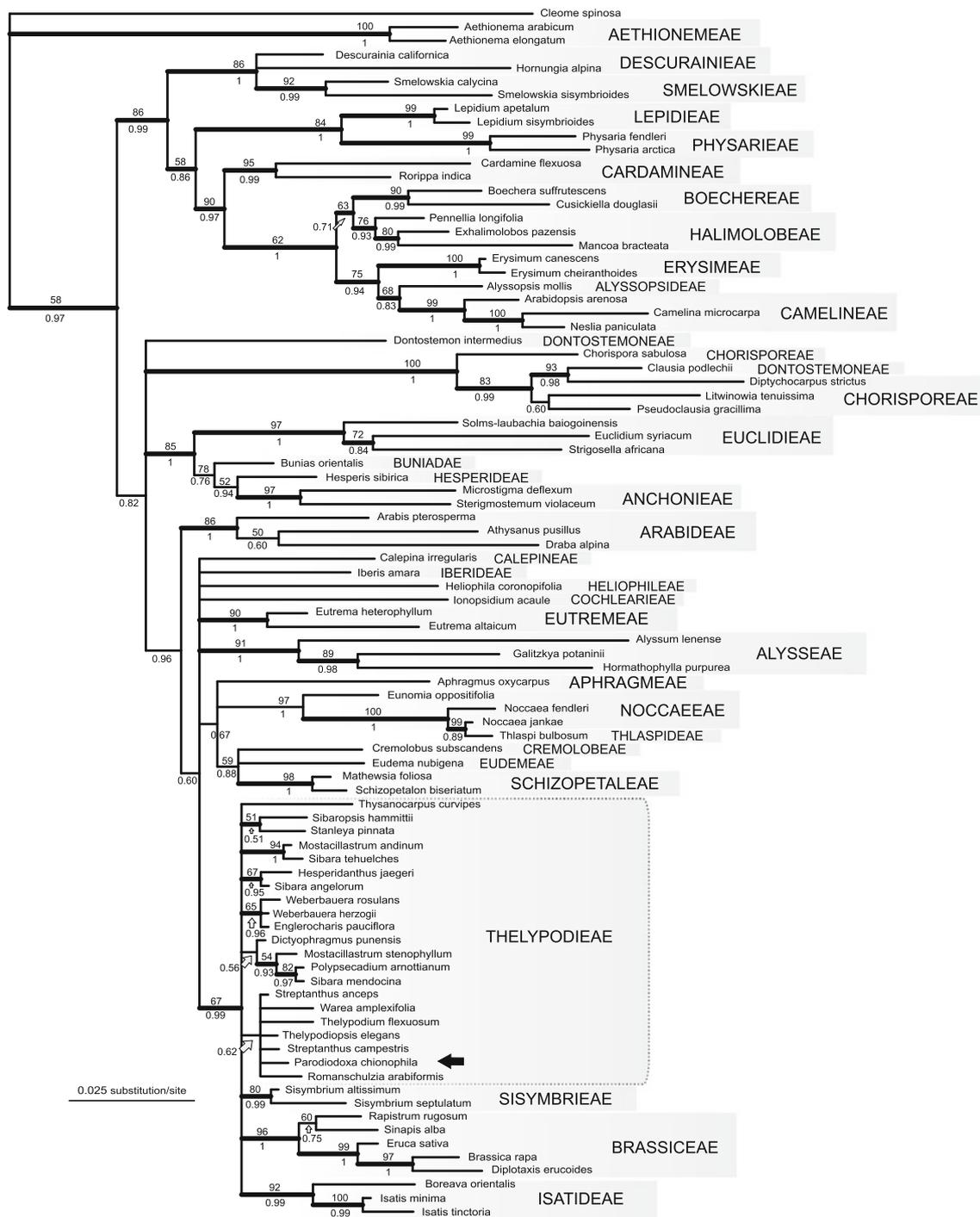


Fig. 3 Bayesian 50 % majority-rule consensus tree from 12,000 trees obtained in the Bayesian analysis with *trnL-F* sequences at the tribal level within Brassicaceae. Tribes are indicated to the right. Values above and below branches correspond to maximum likelihood

bootstrap/Bayesian posterior probability, respectively. Thick branches indicate internal branches present in the maximum parsimony strict consensus tree. The black arrow indicates position of *Parodiodoxa chionophila*

Anderson ex Hook. f. (South Indian Ocean islands) are distributed in North and South America (Al-Shehbaz 2012a). Monophyly of the tribe has been widely demonstrated in previous work (Warwick et al. 2009, 2010, 2011; Alexander et al. 2010; Bartish et al. 2012). However,

phylogenetic relationships within this tribe are still unclear, mainly because of the lack of resolution in using traditional DNA regions (e.g., ITS, *ndhF*, *trnL-F*) (Warwick et al. 2009, 2011; Alexander et al. 2010; Bartish et al. 2012). Although these molecular data are exceptionally useful in

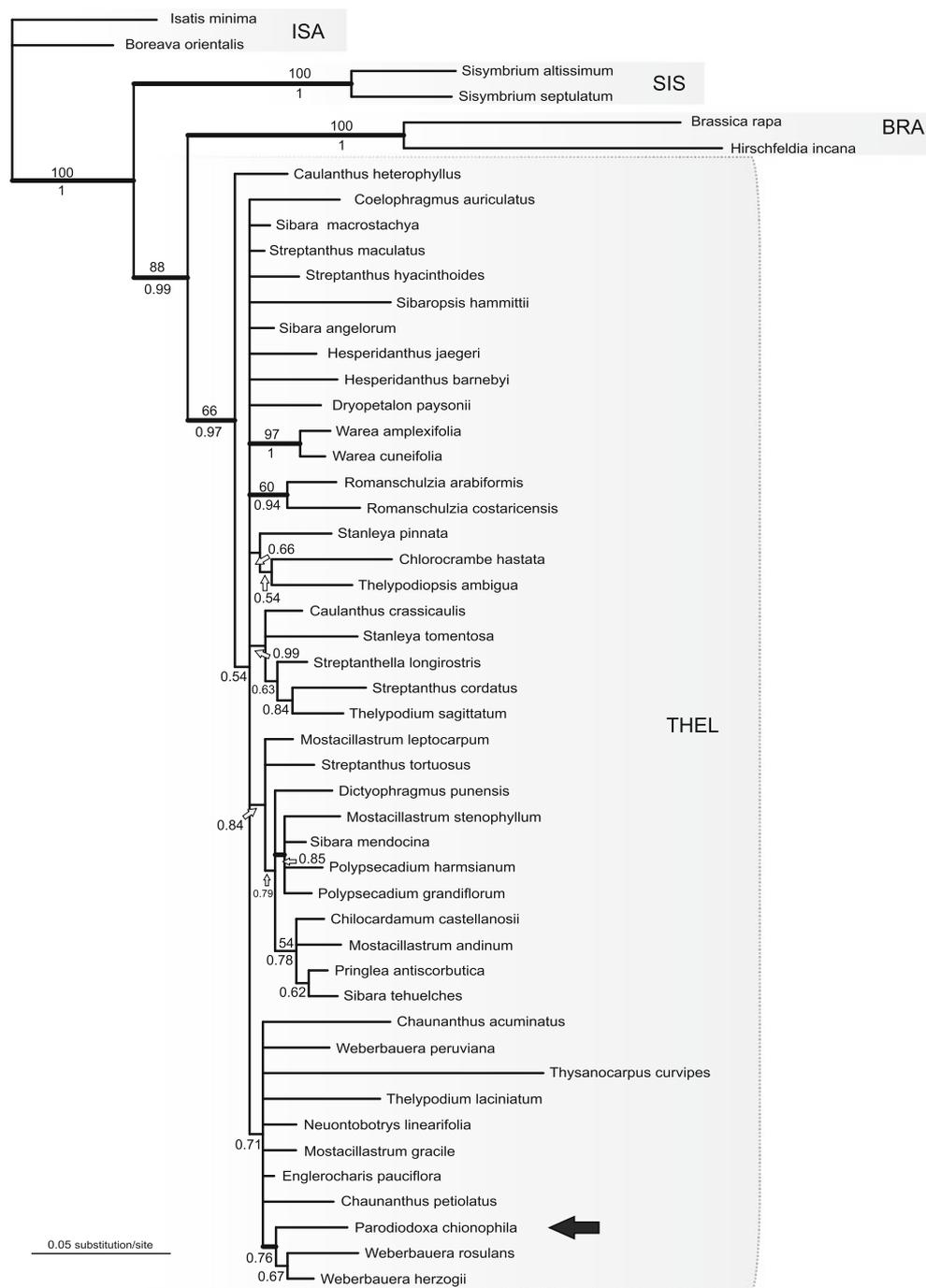


Fig. 4 Bayesian 50 % majority-rule consensus tree from 12,000 trees obtained in the Bayesian analysis with the combined dataset ITS + *trnL-F* at the generic level within Thelypodieae. Tribes are indicated to the right: *ISA* Isatideae, *SIS* Sisymbrieae, *BRA* Brassiceae, *THEL* Thelypodieae. Values above and below branches

correspond to maximum likelihood bootstrap/Bayesian posterior probability, respectively. Thick branches indicate internal branches present in the maximum parsimony strict consensus tree. The black arrow indicates the position of *Parodiodoxa chionophila*

assigning genera to tribes, they are not helpful in delimiting genera in the Thelypodieae (Al-Shehbaz 2012c). This situation seems to be mainly because the tribe is rather young in age and that the molecular markers studied have not had enough time to diverge (Al-Shehbaz 2012c). High

diversification rates have been postulated for different Andean plant groups (Linder 2008) for example *Gentianella* (von Hagen and Kadereit 2001), Valerianaceae (Bell and Donoghue 2005) and *Lupinus* (Hughes and Eastwood 2006); it is therefore likely that a similar situation is

occurring in the Thelypodieae. Additionally, although chromosome numbers are little known in members of the tribe Thelypodieae, especially the South American species, several counts indicate that they are highly variable in the tribe, with the main haploid numbers (n) 7, 11, 12, 13, 14, 28 (Warwick and Al-Shehbaz 2006). This chromosome number variability suggests that events of polyploidization (autopolyploidization and/or hybridization and allopolyploidization) could have accelerated the diversification and therefore facilitated adaptative radiation in Thelypodieae. Hybridization and allopolyploidization are common phenomena in the Brassicaceae and were crucial in the genetic diversification and the species radiation of the family (Marhold and Lihová 2006; Franzke et al. 2010).

The Thelypodieae are represented in Argentina by 11 genera and 47 native species: *Chilocardamum* O.E. Schulz (4 spp.), *Dictyophragmus* O.E. Schulz (1 sp.), *Mostacillastrum* O.E. Schulz (12 spp.), *Neuontobotrys* O.E. Schulz (6 spp.), *Parodiodoxa* O.E. Schulz (1 sp.), *Petroravenia* Al-Shehbaz (3 spp.), *Phlebolobium* O.E. Schulz (1 sp.), *Polypsecadium* O.E. Schulz (6 spp.), *Sarcodraba* Gilg & Muschl. (4 spp.), *Sibara* Greene (2 spp.), *Weberbaueria* Gilg & Muschl. (7 spp.) (Al-Shehbaz 2012b). Of these, *Chilocardamum*, *Parodiodoxa*, and *Phlebolobium* are endemic to Argentina.

Parodiodoxa is easily distinguished from other genera of the Thelypodieae by having a stout, woody caudex, long-petiolate, rosulate, entire basal leaves, rarely with a few cauline leaves as bracts, and strongly angustiseptate, and oblong to elliptic fruits with 10–24 ovules. Except for the Patagonian *Sarcodraba dusenii* (O.E. Schulz) Al-Shehbaz and Californian *Streptanthus californicus* (S. Watson) Greene, angustiseptate fruits are not known elsewhere in the tribe. The former species has non-rosulate, usually dentate leaves and multibranched caudex whereas *S. californicus* has siliques, strongly two-lobed stigmas, and staminal filaments of three unequal lengths. Other taxa of Thelypodieae, for example *Chilocardamum*, *Weberbaueria*, and *Sarcodraba subterranea* O.E. Schulz, have rosulate basal leaves; however, these genera have siliques, and *Weberbaueria* usually also has well-developed cauline leaves. The presence of silicles is uncommon within the Thelypodieae; this character can also be found in *Petroravenia*, *Pringlea*, and *Thysanocarpus* Hook. *Petroravenia* differs by having well-developed cauline leaves with simple and branched trichomes (vs. cauline leaves and trichomes absent in *Parodiodoxa*). *Pringlea* is easily distinguished by its bracteate and densely flowered racemes and equal stamens (vs. ebracteate 5–12 flowered racemes and tetradynamous stamens in *Parodiodoxa*). Finally, *Thysanocarpus* differs by containing annual plants with well-developed cauline leaves and indehiscent 1-seeded silicles (vs. perennials with dehiscent 10–24-seeded silicles in *Parodiodoxa*). This study showed that

Parodiodoxa is sister to *Weberbaueria*, however this genus is clearly differentiated from *Parodiodoxa* by its well-developed cauline leaves and terete, oblong to linear, siliques. The great diversity in vegetative and floral characters, together with the variation in chromosome numbers and lack of resolution in the molecular phylogenies, suggests rapid radiation of the tribe Thelypodieae (Warwick et al. 2009). Future molecular analysis using both traditional DNA regions, together with new fast-evolving regions, would probably reveal the phylogenetic relationship and morphological evolution among genera of the Thelypodieae.

Parodiodoxa is a genus poorly known taxonomically; except for brief generic (Schulz 1929) and species (Spegazzini 1898) descriptions, hardly anything else is known. Therefore, detailed descriptions and distribution are provided herein.

Taxonomic treatment

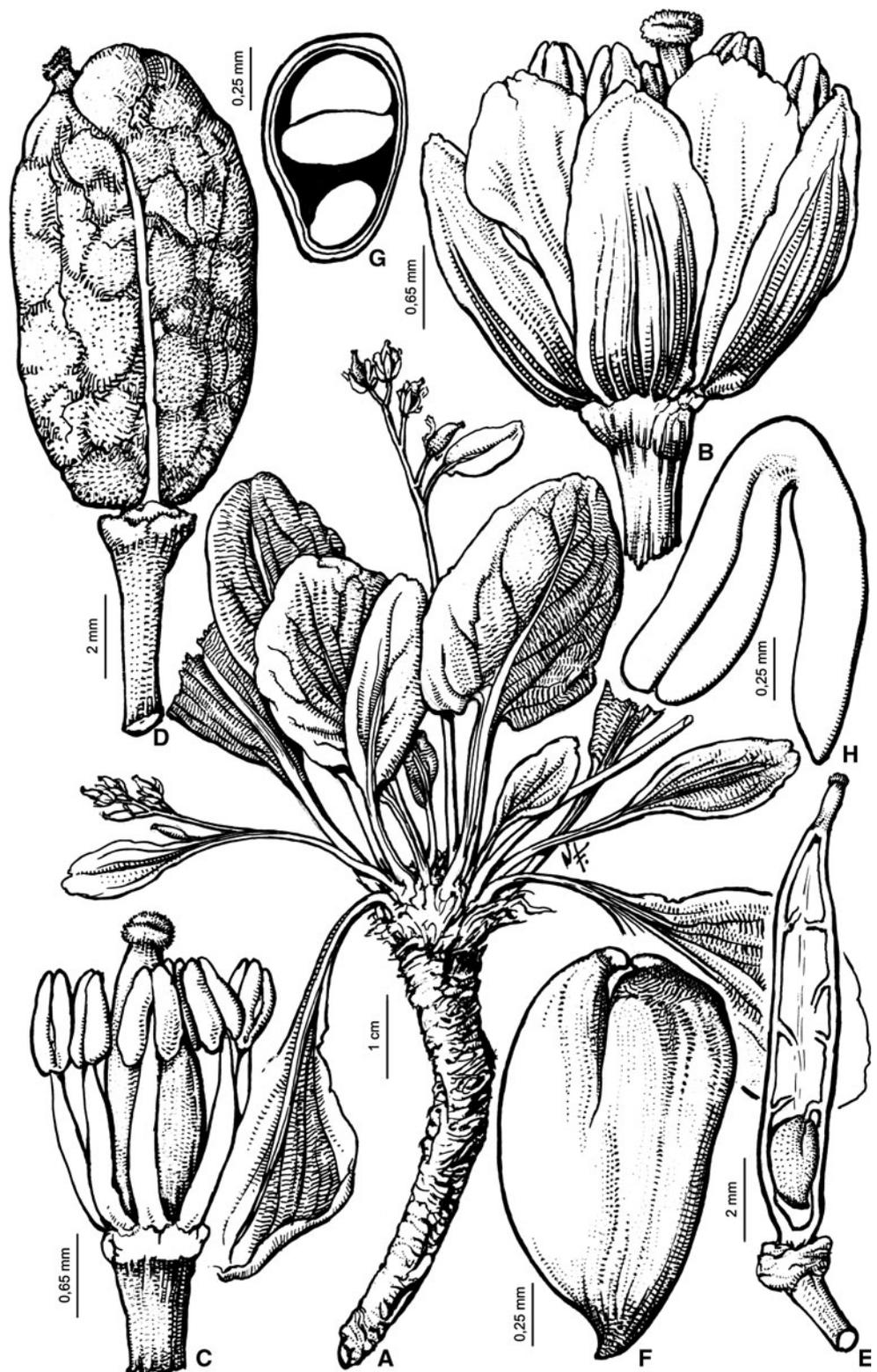
Parodiodoxa O.E. Schulz, Notizbl. Bot. Gart. Berlin-Dahlem 10: 781. 1929. Type: *Parodiodoxa chionophila* (Speg.) O.E. Schulz (= *Thlaspi chionophilum* Speg.).

Perennial herbs, with simple or few-branched caudex. Trichomes absent. Multicellular glands absent. Stems erect to ascending, simple. Basal leaves long petiolate, rosulate, simple, entire; cauline leaves absent, occasionally a few present as bracts, petiolate, not auriculate at base, entire. Racemes few to several flowered, ebracteate or lowermost flowers bracteate, corymbose, elongated in fruit; rachis straight; fruiting pedicels ascending to divaricate, persistent. Sepals ovate, free, often persistent at fruit maturity, suberect, equal, base of lateral pair not saccate. Petals white fading to pale lavender or violet, erect at base with flaring blade, longer than sepals; blade obovate to spatulate, apex obtuse; claw slightly differentiated from blade, shorter than sepals, glabrous, unappendaged, entire. Stamens 6, slightly exserted, erect, slightly tetradynamous; filaments wingless, unappendaged, glabrous, free; anthers ovate, not apiculate. Nectar glands confluent, subtending bases of all stamens; median nectaries present. Ovules 10–24 per ovary; placentation parietal. Fruits dehiscent, capsular silicles, oblong to elliptic, strongly angustiseptate, not inflated, unsegmented; valves papery, midvein distinct, lateral veins obscure, glabrous, keeled, smooth, wingless, unappendaged; gynophore to 2 mm long; replum rounded, visible; septum complete, membranous, veinless; style to 3 mm long, slender, persistent; stigma capitate, entire, unappendaged. Seeds uniseriate, wingless, oblong, plump, seed coat not mucilaginous when wetted; cotyledons incumbent.

Monotypic genus, endemic to northwestern Argentina.

Parodiodoxa chionophila (Speg.) O.E. Schulz, Notizbl. Bot. Gart. Berlin-Dahlem 10: 783. 1929. *Thlaspi*

Fig. 5 *Parodiodoxa chionophila* (Speg.) O.E. Schulz. *a* Habit. *b* Flower. *c* Flower only with the androecium and gynoecium. *d* Fruit and fruiting pedicel. *e* Replum and funicles. *f* Seed, lateral view. *g* Seed, cross section view showing the incumbent disposition of cotyledons. *h* Embryo, lateral view



chionophilum Speg., *Comun. Mus. Nac. Buenos Aires* 1: 48. 1898. Type: Argentina, Salta, Cerro de Cachi, Jan 1897, C. Spegazzini 10457 (holotype, LP!).

Herbs, perennial, glabrous throughout; caudex stout, woody to 1.5 cm in diam. Stems several from caudex, decumbent, 3–20 cm long, leafless or occasionally

1–4-leaved. Basal leaves rosulate, glabrous; petiole 2–6(–9) cm long; leaf blade obovate, spatulate, or oblanceolate, 2–7.5(–11) × 1–3.5(–5) cm, base cuneate, margin entire, repand, or obtusely and sparsely dentate, apex obtuse to rounded; cauline leaves much smaller, short petiolate, much reduced in size upward. Racemes 5–12-flowered; rachis straight; fruiting pedicels divaricate to ascending, straight, 4–7(–10) mm long. Sepals oblong to ovate, glabrous, 2.5–4 × 1–2.5 mm; petals spatulate to obovate, 3.5–5.5 × 1.5–2.5 mm, attenuate at base, obtuse at apex; filaments 2–4 mm long; anthers 0.7–1 mm long. Fruits angustiseptate, oblong to obovate, glabrous, (6–)8–13(–17) × 4–8(–10) mm; septum complete; gynophore 0.3–2 mm long; style slender to stout, (0.5–)1–3 mm long. Seeds oblong, 1.5–2 × 0.8–1.2 mm Fig. 5.

Geographic distribution and habitat Argentina (Catarmarca, Jujuy, La Rioja, Salta and Tucumán); it grows in open, rocky soils between 3,500 and 5,100 m elevation.

Additional material examined CATAMARCA. Dpto. Ambato, Sierra de Ambato, cerca de la Cumbre del Cerro Manchado, *Hunziker 20859* (BAA, BACP). Dpto. Andalgalá, Capellitas, Cerro Yutuyaco, *Sparre 9821* (LIL). Dpto. Belén, Faldeo S de las Cumbres de las Bayas, *Sleumer* and *Voorst 2628* (BAA). JUJUY. Dpto. Humahuaca, Mina Aguilar, cerro arriba del Molino, *Sleumer 3367* (BAA, P). LA RIOJA. Dpto. Famatina, bajando de la Mina la Mejicana, camino al campamento, *Barboza et al. 2566* (CORD). SALTA. Dpto. Cachi, Nevado de Cachi, *Bravo and Bravo s.n.* (LIL 535285). TUCUMÁN. Dpto. Chicligasta, Nevado del Aconquija, Circo del Cochuna, cerca refugio G.A.C., *Halloy s.n.* (LIL 585287). Dpto. Tañi del Valle, Cumbres Calchaquies, Cerro Negrito, *Sparre et al. 9660* (BAA).

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Appendix

Taxa and GenBank accession numbers for the ITS and *trnL-F* sequences used in the phylogenetic analyses (*ITS*, *trnL-F*). All sequences were downloaded from GenBank, except those corresponding to *Parodiodoxa chionophila*, which were generated for this study.

Cleomaceae. *Cleome lutea* Hook. (AF137588, –); *Cleome spinosa* Jacq. (–, DQ649093). Brassicaceae. Tribe Aethionemeae. *Aethionema arabicum* Andr. ex DC.

(AY254539, DQ180218); *Aethionema elongatum* Boiss. (–, DQ180216); *Moriera spinosa* Boiss. (GQ424545, –). Tribe Alysseae. *Alyssum lenense* Adams (–, FN677633); *Alyssum montanum* L. (AY237938, –); *Berteroa incana* (L.) DC. (EF514632, –); *Galitzkya potaninii* (Maxim.) V.V. Botschantz. (–, FN677635); *Hormathophylla purpurea* (Lag. and Rodr.) P. Küpfer (–, FN677738). Tribe Alyssopsidae. *Alyssopsis mollis* O.E. Schulz (–, FJ188227); *Alyssopsis trinervis* Botsch. and Seifulin (GQ497846, –); *Calymmatium draboides* O.E. Schulz (GQ497854, –). Tribe Anastaticae. *Anastatica hierochuntica* L. (GQ424524, –); *Malcolmia triloba* Spreng. (DQ357561, –). Tribe Anchonieae. *Anchonium billardieri* DC. (DQ357512, –); *Matthiola incana* (L.) W.T. Aiton (AJ628339, –); *Microstigma deflexum* Juz. (–, FN677641); *Sterigmostemum violaceum* (Botsch.) H.L. Yang (–, FN677640). Tribe Aphragmeae. *Aphragmus eschscholtzianus* Andr. ex DC. (DQ165334, –); *Aphragmus hobsonii* (H. Pearson) Al-Shehbaz and Warwick (DQ165357, –); *Aphragmus oxycarpus* (Hook. f. and Thomson) Jafri (–, DQ518350). Tribe Arabideae. *Arabis alpina* L. (AF137559, EF449508); *Athysanus pusillus* (Hook.) Greene (–, GU246241); *Draba aizoides* L. (AF146512, –); *Draba alpina* L. (–, DQ467004). Tribe Asteae. *Asta schaffneri* (S. Watson) O.E. Schulz (HQ541168, –); *Asta stricta* Rollins (HQ541171, –). Tribe Biscutelleae. *Biscutella didynima* L. (DQ452058, –); *Biscutella laevigata* L. (DQ452056, –). Tribe Boechereae. *Boechera retrofacta* (Graham) Á. Löve and D. Löve (AF183105, –); *Boechera suffrutescens* (S. Watson) Dorn (–, DQ013046); *Cusickiella douglasii* (A. Gray) Rollins (–, AF307557); *Sandbergia whitedii* (Piper) Greene (AJ628295, –). Tribe Brassiceae. *Brassica oleracea* L. (AY722423, –); *Brassica rapa* L. (JN564039, GQ268033); *Diplotaxis eruroides* (L.) DC. (–, AY751763); *Eruca sativa* Lam. (–, AY751765); *Hirschfeldia incana* (L.) Lagr.-Fossat (AY722470, EU620407); *Rapistrum rugosum* (L.) All. (–, AY751769); *Sinapsis alba* L. (–, JQ041854). Tribe Buniadae. *Bunias erucago* L. (GQ497885, –); *Bunias orientalis* L. (–, FN677645). Tribe Calepineae. *Calepina irregularis* (Asso) Thell. (DQ249822, AY751760); *Goldbachia laevigata* (M. Bieb.) DC. (DQ357545, –). Tribe Camelinae. *Arabidopsis arenosa* (L.) Lawalrée (–, GQ386472); *Camelina microcarpa* (AF137574, DQ821412); *Neslia paniculata* (L.) Desv. (–, DQ310518); *Pseudoarabidopsis toxophylla* (M. Bieb.) Al-Shehbaz, O’Kane and R.A. Price (AF137558, –). Tribe Cardamineae. *Cardamine flexuosa* With. (–, AB247985); *Cardamine pratensis* L. (AY245995 and AY246025, –); *Nasturtium officinale* W.T. Aiton (AY254531, –); *Planodes virginicum* (L.) Greene (GQ424554, –); *Rorippa indica* (L.) Hiern (–, EF426788). Tribe Chorisporeae. *Chorispora sabulosa* Cambess. (–, FN677724);

- Chorispora tenella* (Pall.) DC. (DQ357526, –); *Diptychocarpus strictus* (Fisch. ex M. Bieb.) Trautv. (DQ357534, FN677717); *Litwinowia tenuissima* (Pall.) Woronow ex Pavlov (–, FN677714); *Pseudoclausia gracillima* A.N. Vassiljeva (–, FN677652). Tribe Cochlearieae. *Cochlearia megalosperma* Vogt (AF336208, –); *Ionopsidium acaule* (Desf.) DC. Ex Rchb. (AF336210 and AF336211, HQ268714). Tribe Conringieae. *Conringia clavata* Boiss. (AY722505, –); *Zuvanda crenulata* Askerova (DQ357606, –). Tribe Cremolobaeae. *Cremolobus chilensis* (Lag. ex DC.) DC. (GQ424530, –); *Cremolobus subscandens* Kuntze (–, EU620348); *Menonvillea cuneata* (Gillies and Hook.) Rollins (GQ497868, –). Tribe Descurainieae. *Descurania californica* (A. Gray) O.E. Schulz (–, GU246239); *Descurania sophia* (L.) Webb ex Prantl (DQ418727, –); *Hornungia alpina* (Sievers) O. Appel (–, DQ310515); *Hornungia petraea* Rchb. (AJ628293 and AJ628294, –). Tribe Dontostemoneae. *Clausia aprica* (Stephan) Korn.-Trotzky (DQ357529, –); *Clausia podlechii* Dvořák (–, FN677719); *Dontostemon integrifolius* (L.) C.A. Mey. (DQ357536, –); *Dontostemon intermedius* Vorosch. (–, FN677644). Tribe Erysimeae. *Erysimum canescens* Roth (–, EU170623); *Erysimum capitatum* (Douglas ex Hook.) Greene (DQ357540, –); *Erysimum cheiranthoides* L. (DQ005989, EU170622). Tribe Euclidieae. *Braya alpina* Sternb. and Hoppe (AY353095, –); *Euclidium syriacum* (L.) W.T. Aiton (–, EF426780); *Neotorularia torulosa* (Desf.) Hedge and J. Léonard (AY353164, –); *Solms-laubachia baiogoinensis* (K.C. Kuan and C.H. An) J.P. Yue, Al-Shehbaz and H. Sun (–, DQ523315); *Strigosella africana* (L.) Botsch. (–, EU170625). Tribe Eudemeae. *Brayopsis colombiana* Al-Shehbaz (EU620283, –); *Eudema nubigena* Bonpl. (EU620297, EU620354). Tribe Eutremeae. *Chalcanthus renifolius* (Boiss.) Boiss. (GQ424528, –); *Eutrema altaicum* (C.A. Mey.) Al-Shehbaz and Warwick (DQ165364, DQ649087); *Eutrema heterophyllum* (W.W. Sm.) H. Hara (–, DQ649086). Tribe Halimolobaeae. *Exhalimolobos pazensis* (Rusby) Al-Shehbaz and C.D. Bailey (–, AF307547); *Halimolobos lasiobolus* O.E. Schulz (–, AF307647); *Mancoa bracteata* (S. Watson) Rollins (–, AF307556); *Pennellia longifolia* (Benth.) Rollins (AF307627, AF307549). Tribe Heliophileae. *Heliophila arenaria* Sond. (AJ863600, –); *Heliophila coronopifolia* L. (–, DQ518369); *Heliophila subulata* Burch. and DC. (AJ863580 and AJ864835, –). Tribe Hesperideae. *Hesperis matronalis* L. (DQ357547, –); *Hesperis sibirica* L. (–, FN677642); *Tchihatchewia isatidea* Boiss. (GQ497882, –). Tribe Iberideae. *Iberis amara* L. (AJ440311, AY122455); *Iberis spathulata* Bergeret (AJ440312, –). Tribe Isatideae. *Boreava orientalis* Jaub. and Spach (DQ249859, –); *Isatis minima* Bunge (GQ131320, DQ821409); *Isatis tinctoria* L. (DQ249851, DQ518370). Tribe Kernereae. *Kernera saxatilis* (L.) Rchb. (AF401118 and AF401119, –); *Rhizobotrya alpina* Tausch (AJ440315, –). Tribe Lepidieae. *Lepidium apetalum* Willd. (–, DQ821406); *Lepidium latifolium* L. (AJ582447 and AJ582521, –); *Lepidium sisymbrioides* Hook. f. (–, DQ997056); *Stubendorffia gracilis* Botsch. and Vved. (DQ780944 and DQ780945, –). Tribe Megacarpaeae. *Megacarpaea delavayi* Franch. (AJ628325 and AJ628326, –); *Megacarpaea gracilis* Lipsky (AJ628327 and AJ628328, –). Tribe Microlepidae. *Carinavalva glauca* Ising (GQ424527, –); *Microlepidium pilosulum* F. Mull. (GQ497869, –). Tribe Noccaeae. *Eunomia oppositifolia* DC. (–, AY122456); *Noccaea cochleariformis* (DC.) Á. Löve and D. Löve (DQ249838, –); *Noccaea fendleri* (A. Gray) Holub (AY154824, AY154786); *Noccaea jankae* (A. Kern.) F.K. Mey. (–, AY154796). Tribe Notothlaspidiae. *Notothlaspi australe* Hook. f. (AF100689, –); *Notothlaspi rosulatum* Hook. f. (AF100690, –). Tribe Oreophytoneae. *Murbeckiella huetii* Rothm. (GQ424546, –); *Oreophyton falcatum* O.E. Schulz (GQ424549, –). Tribe Physarieae. *Physaria arctica* (Wormsk. ex Hornem.) O’Kane and Al-Shehbaz (–, GQ245072); *Physaria didymocarpa* (Hook.) A. Gray (AF137583, –); *Physaria fendleri* (A. Gray) O’Kane and Al-Shehbaz (–, AF055266); *Synthlipsis greggii* A. Gray (AF137590, –). Tribe Schizopetaleae. *Mathewsia foliosa* Hook. and Arn. (DQ357563, EU620360); *Schizopetalon biseriatum* Phil. (–, EU620375); *Schizopetalon walkeri* Sims (EU620315, –). Tribe Scoliaxoneae. *Scoliaxon mexicanum* (S. Watson) Payson (HQ541174, –); *Sisymbrium altissimum* L. (AF531560, AY958545); *Sisymbrium septulatum* DC. (AF531600, AY958565). Tribe Smelowskieae. *Smelowskia alba* (Pall.) Regel (AY230562, –); *Smelowskia calycina* (Stephan) C.A. Mey. (–, JF298538); *Smelowskia jacutica* (Botsch. and Karav.) Al-Shehbaz and Warwick (AY230646, –); *Smelowskia sisymbrioides* (Regel and Herder) Lipsky ex Paulsen (–, JF298539). Tribe Thelypodieae. *Caulanthus crassicaulis* (Torr.) S. Watson (EU620252 and EU620341); *Caulanthus heterophyllum* (Nutt.) Payson (EU620267, –); *Chaunanthus acuminatus* (Rollins) R.A. Price and Al-Shehbaz (EU620344, EU620344); *Chaunanthus petiolatus* (Hemsl.) O.E. Schulz (EU620289, EU620345); *Chilocardamum castellanosii* (O.E. Schulz) Al-Shehbaz (AY958592, AY958548); *Chlorocrambe hastata* (S. Watson) Rydb. (EU620254 and EU620269, EU620346); *Coelophragmus auriculatus* (A. Gray) O.E. Schulz (AF531598, EU620347); *Dictyophragmus punensis* (Romanczuk) Al-Shehbaz (EU620294, EU620349); *Dryopetalon paysonii* (Rollins) Al-Shehbaz (EU620270 and EU620255, EU620350); *Englerocharis pauciflora* Al-Shehbaz (EU620295, EU620351); *Hesperidanthus barnebyi* (S.L. Welsh and N.D. Atwood) Al-Shehbaz (EU620271 and EU620256, EU620356);

- Hesperidanthus jaegeri* (Rollins) Al-Shehbaz (GQ424569, EU620357); *Hesperidanthus linearifolius* (A. Gray) Rydb. (AF531612, –); *Ivania cremnophila* (I.M. Johnst.) O.E. Schulz (HQ541176, –); *Mostacillastrum andinum* (Phil.) Al-Shehbaz (AF531649., EU620363); *Mostacillastrum gracile* (Wedd.) Al-Shehbaz (EU620304, AY958553); *Mostacillastrum leptocarpum* (Hook. and Arn.) Al-Shehbaz (AF531632, AY958556); *Mostacillastrum stenophyllum* (Gilles ex Hook. and Arn.) O.E. Schulz (EU620305, EU620364); *Neuontobotrys linearifolia* (Kuntze) Al-Shehbaz (EU620306, EU620367); *Parodiodoxa chionophila* (Speg.) O.E. Schulz (JX971121, JX971122); *Phravenia vierecki* (O.E. Schulz) Al-Shehbaz and S.I. Warwick (HQ541181, –); *Polypsecadium arnottianum* (Gillies ex Hook. and Arn.) Al-Shehbaz (–, EU620369); *Polypsecadium grandiflorum* Romanczuk and Boelcke (EU620309, EU620370); *Polypsecadium harmsianum* (Muschl.) O.E. Schulz (EU620310, EU620371); *Pringlea antiscorbutica* R. Br. ex Hook. f. (AF531619, AY533521); *Romanschulzia arabiformis* (DC.) Rollins (AF531635, AY958538); *Romanschulzia costaricensis* (Standl.) Rollins (AF531636, AY958539); *Sibara angelorum* (S. Watson) Greene (EU620317, EU620379); *Sibara macrostachya* (O.E. Schulz) Al-Shehbaz (EU620337, EU620403); *Sibara mendocina* (Boelcke) Al-Shehbaz (EU620338, EU620404); *Sibara tehuelches* (Speg.) Al-Shehbaz (EU620311, EU620374); *Sibaropsis hammitii* S. Boyd and T.S. Ross (EU620318, EU620380); *Stanleya pinnata* (Pursh) Britton (EU620319, EU620381); *Stanleya tomentosa* Parry (EU620273 and EU620258, EU620382); *Streptanthella longirostris* (S. Watson) Rydb. (EU620320, EU620383); *Streptanthus anceps* (Payson) Hoover (–, JF827264); *Streptanthus campestris* S. Watson (–, AY958571); *Streptanthus cordatus* Nutt. (EU620322, EU620384); *Streptanthus hyacinthoides* Hook. (EU620276 and EU620261, EU620385); *Streptanthus maculatus* Nutt. (EU620326, EU620386); *Streptanthus tortuosus* Kellogg (EU620277 and EU620262, EU620387); *Thelypodopsis ambigua* (S. Watson) Al-Shehbaz (EU620278 and EU620263, EU620389); *Thelypodopsis elegans* (M.E. Jones) Rydb. (–, EU620391); *Thelypodium flexuosum* B.L. Rob. (–, AY958582); *Thelypodium laciniatum* (Hook.) Endl. (EU620328, EU620392); *Thelypodium sagittatum* (Nutt.) Endl. (EU620279 and EU620264, EU620393); *Thysanocarpus curvipes* Hook. (EU620330, GU246194); *Warea amplexifolia* (Nutt.) Nutt. (EU620280 and EU620265, EU620397); *Warea cuneifolia* (Muhl. ex Nutt.) Nutt. (EU620281 and EU620266, EU620398); *Weberbaueria peruviana* (DC.) Al-Shehbaz (EU620336, EU620402); *Weberbaueria rosulans* (O.E. Schulz) Al-Shehbaz (EU620284, EU620340); *Weberbaueria herzogii* (EU620334, EU620400). Tribe Thlaspidaceae. *Peltaria alliacea* Jacq. (DQ249855, –). *Thlaspi arvense* L. (AF336152S1 and AF336152S2, –); *Thlaspi bulbosum* Boiss. (–, AY154798). Tribe Yinshaniceae. *Yinshania acutangula* (O.E. Schulz) Y.H. Zhang (AH007969, –); *Yinshania acutangula* subsp. *wilsonii* (O.E. Schulz) Al-Shehbaz, G. Yang, L.L. Lu and T.Y. Cheo (AH007968, –).

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