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Towards a species level tree of the globally diverse genus *Chenopodium* (Chenopodiaceae)

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ABSTRACT

Chenopodium is a large and morphologically variable genus of annual and perennial herbs with an almost global distribution. All subgenera and most sections of *Chenopodium* were sampled along with other genera of Chenopodieae, Atripliceae and Axyrideae across the subfamily Chenopodioideae (Chenopodiaceae), totalling to 140 taxa. Using Maximum parsimony and Bayesian analyses of the non-coding *trnL-F* (cpDNA) and nuclear ITS regions, we provide a comprehensive picture of relationships of *Chenopodium* sensu lato. The genus as broadly classified is highly paraphyletic within Chenopodioideae, consisting of five major clades. Compared to previous studies, the tribe *Dysphanieae* with three genera *Dysphania*, *Teloxys* and *Suckleya* (comprising the aromatic species of *Chenopodium* s.l.) is now shown to form one of the early branches in the tree of Chenopodioideae. We further recognize the tribe *Spinacieae* to include *Spinacia*, several species of *Chenopodium*, and the genera *Monolepis* and *Scleroblitum*. The *Chenopodium rubrum* and the *Ch. murale*-clades were newly discovered as distinct major lineages but their relationships within Chenopodioideae will need further evaluation. Based on our results, we suggest the delimitation of *Chenopodium* to include *Einadia* and *Rhagodia* because these are part of the crown group composed of species of subg. *Chenopodium* that appear sister to the *Atripliceae*. The tetraploid crops such as *Ch. berlandieri* subsp. *nuttalliae* and *Ch. quinoa* also belong to *Chenopodium* sensu stricto. Trees derived from *trnL-F* and ITS were incongruent within this shallow crown group clade. Possible biological causes are discussed, including allopolyploidization.

1. Introduction

The genus *Chenopodium* sensu lato has been estimated to comprise some 150 species (Kühn, 1993). Most of them are annual herbs growing in arid or semi arid regions, and also on salt-rich soils. Compared to other plants of dry environments they lack typical adaptations to such ecological conditions, such as the Kranz type leaf anatomy and the C_4 photosynthetic pathway – both frequent in other Chenopodiaceae (Carolin et al., 1975; Jacobs, 2001) – and succulence. Morphologically, *Chenopodium* shows great variability in leaf shape and indumentum, floral structures, inflorescence architecture, and seed morphology (Aellen and Just, 1943; Kühn, 1993; Clemants and Mosyakin, 2003). While a large number of different species and intraspecific taxa have been described, the latest most comprehensive synopsis dates back from around 60 years ago (Aellen and Just, 1943), despite the fact that several species are economically important either as crops (e.g., *Chenopodium berlandieri* Moq. subsp. *nuttalliae* (Saff.) H.D. Wilson and Heiser, 1979 ["Huauzontle"]; *Ch. pallidicaule* Aellen ["Cañihua"]; and *Ch. quinoa* Willd. ["Quinoa"]) or weeds (*Ch. ambrosioides* L.; *Ch. murale* L.; Wiersema and León, 1999). An integrative approach to a modern systematic treatment is therefore needed.

Chenopodium belongs to the subfamily Chenopodioideae, within the goosefoot family Chenopodiaceae (Caryophyllales). Chenopodiaceae contain approximately 100 genera and 1700 species, mainly distributed in temperate and subtropical regions of both hemispheres (Aellen, 1960; Kühn, 1993; Welsh et al., 2003). Results of recent molecular phylogenetic analyses (e.g., Kadereit et al., 2003) are in line with earlier classification systems with regard to this placement of *Chenopodium* (see Kühn, 1993). Although phylogenetic relationships of major lineages within Chenopodiaceae still remain poorly understood, the subfamily Chenopodioideae is considered to be monophyletic, based on sequence data of chloroplast *rbcL* (Kadereit et al., 2003) and *matK*/*trnK* (Müller and Borsch, 2005).

While ongoing multigene analysis confirms the monophyly of the Chenopodioideae (Borsch et al., unpubl. data) all phylogenetic studies hitherto carried out, indicate that *Chenopodium* is polyphyletic. Species of *Chenopodium* were found in three different clades within the Chenopodioideae. These clades were initially named

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Chenopodieae I–III (Kadereit et al., 2003; Müller and Borsch, 2005) and constitute the subfamily Chenopodioideae together with the tribe *Atripliceae*. Recent progress has been made in elucidating the evolutionary history of the *Atripliceae* based on DNA sequence data (Kadereit et al., 2010; Zacharias and Baldwin, 2010), in the context of which a distinct status of *Axyrideae* and *Dysphanieae* (both formerly Chenopodieae III) was also recognized. Nevertheless, taxon sampling and tree resolution remain insufficient for a reliable circumscription of *Chenopodium*. The aromatic species are the only group of *Chenopodium* species that have been better characterized phylogenetically. The first *rbcL* tree of Kadereit et al. (2003) revealed relationships between *Dysphania glomulifera* and other aromatic taxa within Chenopodieae III, but these lacked statistical support. More recently Kadereit et al. (2010) included four aromatic species of *Chenopodium* along with *Cycloloma*, *Suckleya* and *Teloxys*, providing greater confidence for a clade for which the tribal name *Dysphanieae* was resurrected.

The complex taxonomic history of *Chenopodium* is summarized in Table 1, and shows over time large differences in the number of sections (between 2 and 13) and subsections that were recognized (Moquin-Tandon, 1849; Bentham and Hooker, 1880; Ulbrich, 1934; Aellen and Just, 1943; Aellen, 1960; Scott, 1978a; Wilson, 1983; Mosyakin and Clemants, 1996; Judd and Ferguson, 1999; Clemants and Mosyakin, 2003). The most comprehensive treatments remain those of Aellen and Just (1943) and Aellen (1960), upon which the morphology-based classification system of Mosyakin and Clemants (1996, 2002) is largely based. Compared to the previous classification system, these authors recognized the subg. *Blitum* within *Chenopodium*, and the distinct genus *Dysphania* (Table 1). Mosyakin and Clemants (2002, 2008) pointed out that *Dysphania* is the oldest name for this group and consequently re-classified the subgenus *Ambrosia* with all its sections under the generic name *Dysphania*. Although there is now even increased phylogenetic support for the aromatic species to be a distinct group (Kadereit et al., 2010), the majority of aromatic species has never been included into any molecular phylogenetic analysis.

Chromosome counts in different species of *Chenopodium* show a great extent of valences, from diploid ($2n = 2x = 18$) to hexaploid ($2n = 6x = 54$; e.g. Aellen and Just, 1943; Uotila, 1973; Rahiminejad and Gornall, 2004; Bhargava et al., 2006). Based on these counts, a base number for *Chenopodium* of $x = 9$ was suggested (Aellen and Just, 1943; Bhargava et al., 2006). However $2n = 2x = 16$ chromosomes were reported for *Ch. ambrosioides* (Uotila, 1973; Palomino et al., 1990), while *Spinacia oleracea* was reported to deviate by $2n = 2x = 12$ chromosomes (Ellis and Janick, 1960). Karyological data were also not conclusive in improving the overall classification of *Chenopodium* or in understanding relationships within the Chenopodioideae.

The degree of polyploidization encountered in *Chenopodium* has been associated with hybridization processes (Rahiminejad and Gornall, 2004; Bhargava et al., 2006). Hybrid speciation has been suggested to play an important role in *Chenopodium*, largely based on morphological observations, chromosome counts, hybridization experiments, allozyme and flavonoid analyses, (Wilson, 1988; Wilson and Manhart, 1993; Uotila, 2001; Rahiminejad and Gornall, 2004; Bhargava et al., 2006). The well-known and economically important species *Ch. quinoa* ($2n = 4x = 36$) and *Ch. berlandieri* subsp. *nuttalliae* ($2n = 4x = 36$) are both tetraploids of putative allopolyploid origin (Wilson and Manhart, 1993). Another case of morphologically allied species is the so-called *Chenopodium album* complex, members of which are reported as diploid, tetraploid or hexaploid but so far no hybrid origin has been shown. For the origin of polyploidy in *Chenopodium album*, endopolyploidy was reported and autopolyploidy may also be involved (Kolano et al., 2008).

Understanding the origin and evolution of these crop plants as of all other polyploids requires a species level phylogenetic framework of *Chenopodium* using organellar and nuclear genomic partitions in order to detect putative parental taxa. Currently there is no phylogenetic framework at all for *Chenopodium* taking into account the extensive taxonomic, morphological, and biogeographic diversity within the group. This study aims to clarify the phylogeny of *Chenopodium* based on both cpDNA (*trnL-F*) and nrDNA (ITS), using extensive sampling within the genus and broad sampling across other genera of Chenopodioideae, and also to examine whether distinct subclades possess certain chromosome numbers as synapomorphies and how ploidy levels are distributed in the group.

2. Materials and methods

2.1. Taxon sampling

All three subgenera, and nine from 13 sections of *Chenopodium* sensu lato, were sampled, overall representing c. 50% of the species. The sampling followed the most comprehensive treatments of Aellen (1960), Table 2. Missing samples include only sect. *Thellungia* (1 sp. in Patagonia), sect. *Polygnoidea* (about 5 spp. in Australia), sect. *Tetrasepala* (1 sp. in Australia) that clearly belongs to *Dysphania* (Scott, 1978a), and sect. *Auricoma* that was covered by the *rbcL* analysis of Kadereit et al. (2003) and shows close affinity to both *Ch. desertorum* and the Australian genera *Einadia* and *Rhagodia*. The inclusion of the last two sections will therefore only be relevant at species level within the respective subclades. We tried to represent species from various parts of the world within these infrageneric entities, covering pronounced morphological differences between species as much as possible. Also, several individuals from very widespread species (e.g., occurring on different continents) were sampled in order to get an idea if such morphology-based taxa correlate with molecular lineages.

We further sampled potentially close relatives of *Chenopodium* within the Chenopodioideae: genera of the Chenopodieae I (*Einadia* and *Rhagodia*; not included in Kadereit et al. (2003)), the Chenopodieae II (*Monolepis, Spinacia*), the genus *Suckleya* (in *Atripliceae* sensu Kühn, 1993; but in *Dysphanieae* according to Kadereit et al., 2010), along with representatives of the tribes *Atripliceae* (*Atriplex*, *Grayia*, *Microgynoecium* and *Stutzia*) and *Axyrideae* (*Axyris*, *Ceratocarpus*, *Krascheninnikovia*). Several taxa from Betoideae (*Beta* and *Hablitzia*) and Salsoloideae tribe *Camphorosmeae* (*Bassia*) (Table 2) were used as outgroups based on the tree of Müller and Borsch (2005).

2.2. DNA isolation, amplification and sequencing

Genomic DNA was isolated from silica gel dried leaf tissue and herbarium specimens, using either a modified CTAB method (Borsch et al., 2003) or the Nucleo Spin Plant II extraction kit (Macherey Nagel, Düren, Germany). The quantity and quality of each DNA sample were measured by NanoDrop spectrophotometer (ND-1000, PeqLab, Erlangen, Germany).

The *trnL-F* region was amplified and sequenced using the forward primer trnTAC2 (5′-CATTTTTCGGTATAGTAABCC-3′), specifically designed for the Amaranthaceae–Chenopodiaceae clade (this study) and the standard reverse primer trnTf (5′-ATTTGAACTGGTGACAC GAG-3′; Taberlet et al., 1991). For some samples the standard forward primer trnTc (5′-CGAAATCGGTAGACGCTACG-3′; Taberlet et al., 1991) was used for both amplification and sequencing. The internal sequencing primers used were: trnL-460F (5′-GAGA ATAAAGATAGAGTCC-3′; Worberg et al., 2007) and trnTd (5′-GGGGATAGAGGGACTTGAAC-3′; Taberlet et al., 1991). The ITS region was amplified and sequenced with a specific Amaranthaceae–Chenopodiaceae forward primer designed in this study:

Table 1
Historical overview on classification systems in *Chenopodium* L.

Moquin-Tandon (1849)	Bentham and Hooker (1880)/ Volkens (1893)	Ulbrich (1934)	Aellen and Just (1943)	Aellen (1960)	Aellen (1978a)	P.G. Wilson (1983)	Mosyakin and Clemants (1996)
Chenopodium L.							
					Subg. Ambrosia	**Subg. Ambrosida**	
Sect. *Botryois*	Sect. *Botrydium*	Sect. *Botryoides*	Sect. *Botryoides*	Sect. *Botryoides*	Sect. *Botryoides*		
			Subsect. *Botrys*	Subsect. *Botrys* **(3)**	Subsect. *Botrys*		
			Subsect. *Teloxys*	Subsect. *Teloxys* **(3)**	Subsect. *Teloxys*		
	Sect. *Ambrina*	Sect. *Ambrina*	Sect. *Ambrina*	Sect. *Ambrina* **(4)**	Sect. *Ambrina*	Sect. *Ambrina*	
	Sect. *Orthosporum*	Sect. *Orthosporum*	Sect. *Orthosporum*	Sect. *Orthosporum* **(4)**	Sect. *Orthosporum*	Sect. *Orthosporum*	
							Subg. Blitum
	Sect. *Blitum*						Sect.*Blitum*
	Sect. *Pseudoblitum*	Sect. *Pseudoblitum*	Sect. *Pseudoblitum*	Sect. *Pseudoblitum*			
				Subsect. *Viridia* **(4)**			
				Subsect. *Glauca* **(2)**			
		Sect. *Eublitum*	Sect. *Eublitum*	Sect. *Eublitum*			
				Subsect. *Capitata* **(2)**			Subsect. *Capitata*
				Subsect. *Foliosa* **(2)**			Subsect. *Foliosa*
					Subg. Chenopodium	**Subg. Chenopodium**	**Subg. Chenopodium**
	Sect. *Agathophyton*	Sect. *Agathophyton*	Sect. *Agathophyton*	Sect. *Agathophyton* **(2)**	Sect. *Agathophyton*[a]		
		Sect. *Degenia*	Sect. *Degenia*	Sect. *Degenia* **(1)**	Sect. *Degenia*	Sect. *Degenia*[a]	
						Sect. *Desertorum* **(1)**	
	Sect. *Rhagodioides*	Sect. *Rhagodioides*			Sect. *Rhagodioides*	Sect. *Rhagodiodes*	
		Sect. *Roubieva*	Sect. *Roubieva*	Sect. *Roubieva* **(1)**	Sect. *Roubieva*		
		Sect. *Thellungia*	Sect. *Thellungia*	Sect. *Thellungia*	Sect. *Thellungia*		
		Sect. *Skottsbergia*			Sect. *Skottsbergia*		
		Sect. *Tetrasepala*		Sect. *Tetrasepala*			
				Sect. *Auricoma*	Sect. *Auricoma*	Sect. *Auricoma*	
Sect. *Chenopodiastrum*	Sect. *Chenopodiastrum*	Sect. *Euchenopodium*	Sect. *Chenopodia*	Sect. *Chenopodium*	Sect. *Chenopodium*	Sect. *Chenopodium*	Sect. *Chenopodium*
					Subsect. *Chenopodium*		Subsect. *Chenopodium*
					Subsect. *Glauca*[a]		
					Sect. *Leprophyllum*	Sect. *Leprophylum*	
			Subsect. *Undata*	Subsect. *Undata* **(14)**			Subsect. *Undata*
							Subsect. *Leptophylla*
							Subsect. *Urbica*
							Subsect. *Fremontiana*
							Subsect. *Favosa*
							Subsect. *Standleyana*
				Subsect. *Polysperma*			Subsect. *Polysperma*
					Sect. *Atriplicina*		
					Sect. *Margaritaria*		
					Sect. *Meiomeria*		
			Subsect. *Lejosperma*	Subsect. *Lejosperma* **(43)**			
			Subsect. *Cellulata*	Subsect. *Cellulata* **(21)**			
				Ser. *Foveasa*			
				Ser. *Cicatricosa*			Subsect. *Cicraticosa*
				Subsect. *Acuminata*			
				Subsect. *Grossefoveata* **(4)**			Sect. *Grossefoveata*
				Sect. *Polygonoidea*	Sect. *Polygonoidea*		

[a] Indicates sections which have been placed in different subgenera by the authors. Numbers in parentheses indicate the respective number of taxa sampled here with respect to the classification of Aellen (1960).

AC-ITS5 (5′-GGAAGGAGAAGTCGWAACARGG-3′), and the universal reverse primer ITS4 (5′-TCCTCCGCTTATTGATATGC-3′; White et al., 1990).

PCR amplification was performed using the following reaction mix: 1.5 mM $MgCl_2$, 1X PeqLab Taq Buffer S (including $MgCl_2$), 0.25 mM each dNTP, 0.8 pmol primer, 0.03 U/ul Taq polymerase (PeqLab, Erlangen Germany) and 0.8 ng/ul DNA template. For difficult templates (e.g. DNA isolated from herbarium material), betaine was added to a final concentration of 1 M. The PCR was performed in a T3 Thermocycler (Biometra, Göttingen, Germany) or a Mastercycler (Eppendorf, Hamburg, Germany). The PCR program used for the chloroplast region *trnL-F* was: 30 cycles of denaturation (60 s at 94 °C), annealing (60 s at 52 °C), extension (120 s at 72 °C) and a final extension step (15 min at 72 °C). The PCR program for the ITS region was: 35 cycles of denaturation (60 s at 97 °C), annealing (60 s at 48 °C), extension (45 s at 72 °C) and a final extension step (7 min at 72 °C). Primer dimers and secondary banding patterns were separated from the requested bands using a 1.5% NEEO agarose gel (Carl Roth, Germany) running for 3 h at 100 volts. Gel extraction was performed using the AveGene Gel/PCR DNA Fragments Extraction Kit (AveGene life science Corporation). The quality and quantity of the purified PCR product were measured with a NanoDrop spectrophotometer. Cycle sequencing, fragment purification, and direct automated sequencing was performed by Macrogen Inc. (Seoul, South Korea).

2.3. Alignment and coding of length mutational events

Sequences were edited and aligned manually using PhyDE (Phylogenetic Data Editor) version 0.995 (Müller et al., 2007), following the rules outlined in Löhne and Borsch (2005). Regions of uncertain homology (mutational hotspots) were excluded from the analysis (see Appendices A, B and D). Hypothesized microstructural mutations that explain the length variability patterns of sequences in the aligned partition are listed in Appendices A and B, as suggested by Borsch et al. (2007), Morrison (2009) and Ochoterena (2009). The inversions were re-inverted and coded as mutational event in the indel matrix following Löhne and Borsch (2005). Indels were then coded automatically using the Simple Indel Coding method (Simmons and Ochoterena, 2000) as implemented in SeqState 1.40 (Müller, 2005a). The alignments are available in TreeBase (Submission 11780).

2.4. Phylogenetic analyses

Maximum Parsimony (MP) analyses were performed using the Parsimony Ratchet (Nixon, 1999) using the software PRAP (Müller, 2004) in combination with PAUP* v. 4.0b10 (Swofford, 1998). Ratchet settings were 200 ratchet iterations with 25% of the positions randomly up weighted (weight = 2) during each replicate and 10 random addition cycles.

The command files generated with PRAP were then run in PAUP, using the heuristic search with the following parameters: all characters have equal weight, gaps are treated as "missing", TBR branch swapping, initial swapping on 1 tree already in memory, Maxtrees set to 100 (auto increased by 100) and branches collapsed actively if branch length is zero. The Jackknife (JK) support for branches was also performed in PAUP with 10,000 replicates, using a TBR branch swapping algorithm with 36.788% of characters deleted and one tree held during each replicate, following Müller (2005b).

Bayesian inference (BI) was carried out using MrBayes 3.1 (Huelsenbeck and Ronquist, 2001). Optimal nucleotide substitution models for the respective *trnL–F* (GTR + G) and ITS (GTR + G + I) data sets were chosen following the Akaike Information criterion (AIC) in Modeltest 3.7 (Posada and Crandall, 1998). A binary (restriction site) model was implemented for the coded indels. All analyses were performed with four independent runs of Markov Chains Monte Carlo (MCMC) each with four parallel chains. Each chain was performed for 1 million generations, saving one random tree every 100th generation. The burn in was set to 100,000, and a majority consensus tree was computed with the remaining trees.

To test for congruence between the respective data sets, we ran the Incongruence Length Difference (ILD) test (Farris et al., 1994), implemented in PAUP* as the Partition Homogeneity Test, and using the following parameters: 10,000 replicates with 50 Random Addition Searches, holding only two trees each step and saving no more than 5 trees. The test was conducted for (i) the complete data set (140 taxa), (ii) a reduced data set including only diploid taxa, and (iii) for each of the well-supported major clades.

3. Results

3.1. The non-coding trnL–F chloroplast region

Sequence lengths varied from 304–643 nt in the intron and 137–386 nt in the spacer. The aligned data set comprised 1240 characters including 345 (27%) that were parsimony informative. Seven areas classified as "hotspots" (HS) sensu Borsch et al. (2003) were excluded from the analyses (Appendix D). One inversion was found in the *trnL* intron in all samples of *Kraschenninnikovia* (Appendix A). The final matrix, including coded indels, comprised 1402 characters of which 461 (33%) were parsimony informative. The MP search resulted in 307 shortest trees (L = 1027, CI = 0.702, a RI = 0.933 and a RC = 0.655). The resulting strict consensus tree was identical in topology with the Bayesian majority-rule consensus tree (see Fig. 1).

3.2. The nuclear ITS region

Sequence lengths varied from 149–174 nt in ITS1 and 188–205 nt in ITS2. Both spacers were surprisingly well aligned except some sequence parts excluded as mutational hotspots (Appendix D). The hotspot in ITS1 was on average 60 nt in length and the two hotspots in ITS2 were 6 and 19 nt in length, respectively. Hypothesized microstructural mutations are listed in Appendix B. Of all characters, 35% were parsimony informative, after indels were coded as binary characters and added to the matrix (687 characters in total), the percentage of parsimony informative characters increased to 39%. Parsimony analyses of the ITS region resulted in 1633 shortest trees (L = 939, CI = 0.502, RI = 0.890, RC = 0.446) with indels coded. Both MP and Bayesian analyses gave consensus trees with identical topology (Fig. 2).

3.3. Phylogenetic relationships

MP and Bayesian analyses of the respective *trnL-F* and ITS data sets depict seven strongly supported clades (clades 1–7; Figs. 1 and 2), encompassing both the *Chenopodieae* (clades 2–5, 7) and the *Atripliceae* sensu stricto (clade 6). Clade 1 contains *Axyris*, *Ceratocarpus* and *Kraschenninnikovia* (maximum support in all trees) and either appears sister to the remaining Chenopodioideae (*trnL-F*; Fig. 1) or is inconsistently resolved among the early branching lineages of the Chenopodioideae (ITS). The genus *Chenopodium* itself is highly paraphyletic to nearly all other genera of the subfamily and its species are distributed in five different well defined lineages (clades 2–5 and 7; Figs. 1 and 2). Clade 2 (*trnL-F* 100% JK/1 PP, ITS 98% JK/1 PP) encompasses *Ch. ambrosioides* and a number of other aromatic species as well as the monotypic genus *Suckleya*. Clade 3 receives high support with *trnL-F* (99% JK /1 PP) but only moderate support in the ITS tree (67% JK/1 PP). It comprises *Chenopodium bonus-henricus* and relatives and *Monolepis* in one subclade and all spe-

Table 2
Samples included in this study.

Taxon	Field/Garden origin	Voucher	Code	*trn*L-F Acc.	ITS Acc.
	Subfamily Chenopodioideae				
Tribe Atripliceae C. A. Meyer					
Atriplex hortensis L.	Estonia, Tallin	Gawe 41350 (B)	AC516	HE577500	HE577360
Atriplex patula L.	Germany, Brandenburg	R. & E. Willing 20.836 (B)	AC605	HE577498	HE577358
Atriplex sagittata Borkh.	Berlin Bot. Gard. No: 063119110 [Germany]	S. Fuentes 021 (B)	AC533	HE577499	HE577359
Atriplex nitens Schkuhr	Germany, Brandenburg	R. & E. Willing 10.701 D (B)	AC573	HE577501	HE577361
Stutzia dioica (Nutt.) E.H. Zacharias	USA	L. Welp 6269 (NY)	AC351	HE577502	HE577362
Grayia spinosa (Hook.) Moq.	USA ARS GRIN W626763 [USA, California]	S. Fuentes 177 (B)	AC625	HE577496	HE577356
Grayia brandegeei A. Gray	USA ARS GRIN W630044 [USA, Colorado]	S. Fuentes 179 (B)	AC627	HE577497	HE577357
Microgynoecium tibeticum Hook. f.	China	B. Dickoré 4284 (B)	AC656	HE577503	HE577363
Tribe Axyrideae G. Kadereit & Sukhorukov					
Axyris amaranthoides L.	Russia	L. Martins 2346 (B)	AC647	HE577510	HE577370
Axyris hybrida L.	Russia	L. Martins 2417 (B)	AC648	HE577511	HE577371
Axyris prostrata L.	Russia	E. v. Raab-Straube 020232a (B)	AC529	HE577509	HE577369
Ceratocarpus arenarius L.	Romania, Navodari	A. Romanovsch (B)	AC531	HE577504	HE577364
Ceratocarpus arenarius L.	Russia	L. Martins 2447 (B)	AC649	HE577505	HE577365
Krascheninnikovia ceratoides (L.) Gueldenst.	Russia	L. Martins 2500 (B)	AC608	HE577506	HE577366
Krascheninnikovia ceratoides (L.) Gueldenst.	Russia	R. Hand 1536 (B)	AC532	HE577507	HE577367
Krascheninnikovia lanata (Pursch) A. Meeuse & A. Smit	USA ARS GRIN W629970 [USA, Colorado]	S. Fuentes 178 (B)	AC626	HE577508	HE577368
Tribe Dysphanieae Pax					
Suckleya suckleyana (Torr.) Rydb.	USA	R. Darn 5373 (NY)	AC350	HE577484	HE577347
sect. Ambrina (Spach.) Hook					
Chenopodium ambrosioides L.	Bolivia, Beni	I. Guareco 420 (B, LPB)	AC420	HE577492	HE577352
Chenopodium ambrosioides L.	Bolivia, La Paz	S. G. Beck 31178 (B, LPB)	AC425	HE577493	HE577353
Chenopodium ambrosioides L.	Berlin Bot. Gard. No: 10095019310 [Italy]	S. Fuentes 024 (B)	AC527	HE577491	HE577351
Chenopodium ambrosioides L. [=*Dysphania ambrosioides* (L.) Mosyakin & Clemants]	Ethiopia	M. Wondafrash 2223 (B, ETH)	AC386	HE577488	HE577350
sect. Botryoides C. A. Meyer					
subsect. Botrys (Koch) Aellen et Iljin					
Chenopodium schraderianum Schult.	Ethiopia	M. Wondafrash 2255 (B, ETH)	AC387	HE577490	HE577349
Chenopodium graveolens Willd. [=*Dysphania graveolens* (Wlld.) Mosyakin & Clemants]	Bolivia	E. Thomas 258 (B, LPB)	AC419	HE577495	HE577355
subsect. Teloxys (Moq.) Aellen et Iljin					
Chenopodium aristatum L.	Berlin Bot. Gard. No: 309669170 [Germany]	S. Fuentes 025 (B)	AC528	HE577480	HE577340
Chenopodium aristatum L.	Russia	L. Martins 2377 (B)	AC610	HE577479	HE577339
Chenopodium aristatum L. [=*Teloxys aristata* (L.) Moq.]	USA ARS GRIN Ames 25314 [Mongolia]	S. Fuentes 183 (B)	AC654	HE577481	HE577341
sect. Orthosporum R. Br.					
Chenopodium melanocarpum (J.M. Black) J.M. Black. [=*Dysphania melanocarpa* (J.M. Black) Mosyakin & Clemants]	Australia	C.R. Michael & J. Risles 1921 (B)	AC429	HE577487	HE577344
Chenopodium pumilio R. Br.	Germany	T. Borsch (B)	AC524	HE577486	HE577343
Chenopodium pumilio R. Br.	Greece	R. & E. Willing 85.571 (B)	AC604	HE577485	HE577342
Chenopodium pumilio R. Br. [=*Dysphania pumilio* (R. Br.) Mosyakin & Clemants]	Mexico	T. Borsch (B)	AC615	HE577489	HE577348
Tribe Chenopodieae					
Einadia nutans (R. Br.) A. J. Scott.	Berlin Bot. Gard. No: 187199 [Australia]	S. Fuentes 019 (B)	AC525	HE577553	HE577415
Monolepis nuttalliana (Schult.) Greene	USA, Utha	R. C. Holmgren 317 (B)	AC621	HE577515	HE577375
Rhagodia triandra (G.Forst.) Aellen	New Zealand	P. Hein 12560 (B, CHR)	AC522	HE577554	HE577416
Chenopodium L.					
Subgen. Ambrosida					
sect. Botryoides C. A. Meyer					
subsect. Botrys (Koch) Aellen et Iljin					
Chenopodium coronopus Moq.	Spain, La Palma	Royl 6823 (B)	AC570	HE577543	HE577403
Subgen. Blitum					
sect. Degenia Aellen					
Chenopodium chenopodioides (L.) Aellen	USA, Montana	P. C. Lesica 5792 (NY)	AC543	HE577519	HE577379
sect. Pseudoblitum Hook					
subsect. Glaucum Aellen					
Chenopodium glaucum L.	USA ARS GRIN PI612859 [USA]	S. Fuentes 184 (B)	AC652	HE577526	HE577386
Chenopodium glaucum L.	Spain	T. Borsch 3931 (B)	AC417	HE577527	HE577387

(*continued on next page*)

Table 2 (*continued*)

Taxon	Field/Garden origin	Voucher	Code	*trn*L-F Acc.	ITS Acc.
subsect. Viride Aellen					
Chenopodium rubrum L.	Germany, North See	T. Borsch [08.07] (B)	AC411	HE577520	HE577380
Chenopodium rubrum L.	Germany	E. Willing 10.931D (B)	AC564	HE577522	HE577382
Chenopodium rubrum L.	USA ARS GRIN Ames 23860 [Poland]	S. Fuentes 182 (B)	AC653	HE577521	HE577381
Chenopodium rubrum L.	USA	T. Borsch 3448 (B)	AC385	HE577525	HE577385
Subgen. Chenopodium sect. Chenopodium Aellen subsect. Cellulata Aellen					
Chenopodium berlandieri Moq.	USA, Nevada	J. C. Beatley 11698 (NY)	AC541	HE577561	HE577423
Chenopodium berlandieri Moq.	USA, Colorado	G. Rink 2527 (NY)	AC599	HE577567	HE577429
Chenopodium berlandieri var. *boscianum* (Moq.) Wahl	USA, Lousiana	D. M. Ferguson 1072 (NY)	AC545	HE577564	HE577426
Chenopodium berlandieri subsp. *nuttalliae* (Saff.) H.Dan. Wilson & Heiser	Mexico	T. Borsch & H. Flores Olvera (B, MEXU)	AC616	HE577565	HE577427
Chenopodium berlandieri var. *zschackei* (Murr) Murr ex Graebn.	USA, Colorado	C. C. Freeman 16479 (NY)	AC542	HE577563	HE577425
Chenopodium berlandieri var. *zschackei* (Murr) Murr ex Graebn.	USA, Wyoming	A. J. Roderick 2286 (NY)	AC600	HE577569	HE577431
Chenopodium ficifolium Sm.	Germany, Berlin	R. & E. Willing 12.260 D (B)	AC854	HE577606	HE577466
Chenopodium quinoa Willd.	USA ARS GRIN Ames 13214 [Bolivia]	S. Fuentes 013 (B)	AC401	HE577580	HE577445
Chenopodium quinoa Willd.	USA ARS GRIN Ames 13228 [Ecuador]	S. Fuentes 017 (B)	AC402	HE577576	HE577441
Chenopodium quinoa Willd.	USA ARS GRIN PI568155 [Mexico]	S. Fuentes 015 (B)	AC403	HE577581	HE577446
Chenopodium quinoa Willd.	USA ARS GRIN PI510551 [Peru]	S. Fuentes 009 (B)	AC404	HE577579	HE577444
Chenopodium quinoa Willd.	USA ARS GRIN PI587173 [Argentina]	S. Fuentes 012 (B)	AC405	HE577577	HE577442
Chenopodium quinoa Willd.	USA ARS GRIN PI596498 [Peru]	S. Fuentes 008 (B)	AC406	HE577578	HE577443
Chenopodium quinoa Willd.	USA ARS GRIN PI614880 [Chile]	S. Fuentes 010 (B)	AC407	HE577582	HE577447
Chenopodium quinoa Willd.	USA ARS GRIN PI614914 [Bolivia]	S. Fuentes 011 (B)	AC408	HE577583	HE577448
Chenopodium quinoa Willd.	USA ARS GRIN PI568155 [Mexico]	S. Fuentes 016 (B)	AC394	HE577571	HE577433
Chenopodium neomexicanum Standl.	USA, New Mexico	R.D. Worthington 13394 (NY)	AC555	HE577611	HE577471
Chenopodium neomexicanum Standl.	USA, Arizona	S. Fuentes 172 (B)	AC598	HE577601	HE577461
Chenopodium pallescens Standl.	USA, Missouri	G. Yatskievych 03–93 (MO)	AC594	HE577547	HE577409
Chenopodium pallescens Standl.	USA, Illinois	T.G. Lammers 10336 (NY)	AC557	HE577604	HE577464
Chenopodium watsonii A. Nelson	USA, Arizona	D.H. Goldman 2095 (NY)	AC561	HE577602	HE577462
subsect. Grossefoveata Aellen					
Chenopodium hybridum L.	Germany	T. Borsch 3897 (B)	AC380	HE577530	HE577390
Chenopodium hybridum L.	Russia, Altay Republic	L. Martins 2329 (B)	AC609	HE577528	HE577388
Chenopodium hybridum L.	Germany, Brandenburg	R. & E. Willing 20.856 D (B)	AC521	HE577529	HE577389
Chenopodium gigantospermum var. *standleyanum* Aellen	USA, Kansas	C.A. Morse 10855 (NY)	AC550	HE577551	HE577413
subsect. Lejosperma Aellen					
Chenopodium album L.	Greece, Messinia	R. & E. Willing 122.544 (B)	AC571	HE577558	HE577420
Chenopodium album L.	Germany, Usedom	Weber (B)	AC602	HE577559	HE577421
Chenopodium album L.	Russia, Altay Republic	E. v. Raab-Straube 020350 (B)	AC575	HE577609	HE577469
Chenopodium album L.	Germany, Bonn	S. Fuentes 001 (B)	AC388	HE577557	HE577419
Chenopodium album L.	Spain	T. Borsch 3921 (B)	AC414	HE577592	HE577453
Chenopodium album L.	USA ARS GRIN PI608030 [USA]	S. Fuentes 007 (B)	AC395	HE577568	HE577430
Chenopodium album L.	USA ARS GRIN Ames 27372 [USA]	S. Fuentes 006 (B)	AC396	HE577570	HE577432
Chenopodium album L.	Spain	T. Borsch 3921 (B)	AC427	HE577593	HE577456
Chenopodium album L.	Russia, Altay Republic	L. Martins 2423 (B)	AC614	HE577552	HE577414
Chenopodium album L.	USA, Arizona	H.D. Hammond 11926 (MO)	AC591	HE577596	HE577457
Chenopodium album L.	USA, Wisconsin	N.J. Holmberg 1976 (MO)	AC590	HE577556	HE577418
Chenopodium atrovirens Rydb.	Bolivia, La Paz	S.G. Beck 11328 (B, KAS, LPB)	AC363	HE577586	HE577450
Chenopodium atrovirens Rydb.	Bolivia, La Paz	S.G. Beck 8377 (B, LPB)	AC421	HE577587	HE577452
Chenopodium atrovirens Rydb.	USA, Utha	M. Madsen 40772 (MO)	AC586	HE577584	HE577449
Chenopodium atrovirens Rydb.	USA, Colorado	T.G. Lammers et al. 11321 (NY)	AC540	HE577585	HE577451
Chenopodium cycloides A. Nelson	USA	T. Borsch, Müller and Pratt 3452 (B)	AC384	HE577598	HE577459
Chenopodium cycloides A. Nelson	USA, Kansas	C.C. Freeman 2549 (NY)	AC544	HE577599	HE577460
Chenopodium desiccatum A. Nelson	USA, Missouri	B. Summers & Harris 9813 (MO)	AC588	HE577550	HE577412
Chenopodium fremontii S. Watson	USA, California	G. Schoolcraft 2206 (UC)	AC579	HE577546	HE577408
Chenopodium fremontii S. Watson	USA. Utha	S. Fuentes 185 (B)	AC597	HE577572	HE577436
Chenopodium giganteum D. Don	Bonn Bot. Gart. No: 21397 [India]	S. Fuentes 014 (B)	AC428	HE577597	HE577458
Chenopodium hians Standl.	USA, Wyoming	S. Stephens 70636 (NY)	AC551	HE577610	HE577470
Chenopodium incanum (S. Watson) A. Heller	USA, New Mexico	R. D. Worthington 17439 (NY)	AC553	HE577548	HE577410
Chenopodium iljinii Golosk.	Russia, Altay Republic	L. Martins 2490 (B)	AC611	HE577608	HE577468
Chenopodium iljinii Golosk.	Russia, Altay Republic	L. Martins 2424 (B)	AC613	HE577607	HE577467
Chenopodium leptophyllum (Moq.) Nutt. ex S. Watson	USA, Montana	P.C. Lesica 8846 (NY)	AC554	HE577566	HE577428
Chenopodium nevadense Standl.	USA, Nevada	A. Tiehm 13320 (NY)	AC556	HE577549	HE577411
Chenopodium opulifolium Schrad. ex W.D.J. Koch & Ziz	Slovakia	T. Borsch 3899 (B)	AC410	HE577595	HE577455
Chenopodium opulifolium Schrad. ex W.D.J. Koch & Ziz	Spain	T. Borsch 3926 (B)	AC416	HE577594	HE577454
Chenopodium pallidicaule Aellen	USA ARS GRIN PI478406 [Bolivia]	No Voucher	AC398	HE577574	HE577439

Table 2 (*continued*)

Taxon	Field/Garden origin	Voucher	Code	*trn*L-F Acc.	ITS Acc.
Chenopodium pallidicaule Aellen	USA ARS GRIN PI510525 [Peru]	No Voucher	AC399	HE577573	HE577438
Chenopodium pallidicaule Aellen	USA ARS GRIN PI 510530 [Peru]	No Voucher	AC400	HE577575	HE577440
Chenopodium pallidicaule Aellen	Bolivia, Tarija	S. G. Beck 31939 (B, LPB)	AC426	HE577600	HE577437
Chenopodium pratericola Rydb.	USA, Wyoming	K. H. Dueholm 10922 (B, LPB)	AC558	HE577562	HE577424
Chenopodium petiolare Kunth	Bolivia, Oruro	R. de Michel 2873 (B, KAS, LPB)	AC359	HE577588	HE577434
Chenopodium petiolare Kunth	Bolivia, La Paz	S. G. Beck 22972 (B, LPB)	AC423	HE577589	HE577435
Chenopodium standleyanum Aellen	USA, Missouri	A. E. Brant & R. Jefferson 4450 (MO)	AC595	HE577560	HE577422
Chenopodium standleyanum Aellen	USA, Missouri	N. J. Holmberg 554 (MO)	AC596	HE577603	HE577463
Chenopodium subglabrum (S. Watson) A. Nelson	USA, Wyoming	R. D. Dorn 5434 (NY)	AC559	HE577605	HE577465
Chenopodium urbicum L.	Greece, Fthiotis	R. & E. Willing 146.1979 (B)	AC576	HE577524	HE577384
Chenopodium urbicum L.	Berlin Bot. Gard. No: 269400010 [Greece]	S. Fuentes 026 (B)	AC536	HE577523	HE577383
Chenopodium vulvaria L.	Spain	T. Borsch 3918 (B)	AC412	HE577591	HE577407
Chenopodium vulvaria L.	Greece, Evrytania	R. & E. Willing 148.759 (B)	AC562	HE577590	HE577406
subsect. Undata Aellen					
Chenopodium murale L.	Bolivia, La Paz	S. G. Beck 22970 (B, KAS, LPB)	AC360	HE577538	HE577398
Chenopodium murale L.	Chile	T. Borsch 3097 (B)	AC383	HE577539	HE577400
Chenopodium murale L.	USA ARS GRIN Ames 26140 [USA]	S. Fuentes 005 (B)	AC397	HE577534	HE577394
Chenopodium murale L.	Spain	T. Borsch 3919 (B)	AC413	HE577535	HE577395
Chenopodium murale L.	Spain	T. Borsch 3924 (B)	AC415	HE577536	HE577396
Chenopodium murale L.	Bolivia, La Paz	S. G. Beck 145PG94 (B, LPB)	AC424	HE577537	HE577397
Chenopodium murale L.	Slovakia	T. Borsch 3915 (B)	AC409	HE577533	HE577391
Chenopodium murale L.	Greece, Korinthias	R. & E. Willing 143.462 (B)	AC430	HE577540	HE577399
Chenopodium murale L	Mexico, Ixtapan	T. Borsch & H. Flores Olvera 3871 (B, MEXU)	AC382	HE577541	HE577401
Chenopodium murale L.	USA, California	C. Dietrich et al. 32 (MO)	AC589	HE577531	HE577392
Chenopodium murale L.	Greece, Evvia	R. & E. Willing 145.733 (B)	AC566	HE577532	HE577393
Chenopodium murale L.	Greece	R. & E. Willing 145.592 (B)	AC565	HE577542	HE577402
Chenopodium murale L.	USA, California	T. Ross 4084 (UC)	AC581	HE577544	HE577404
Chenopodium murale L.	USA, California	G. Gust & L. Nyle 476 (MO)	AC587	HE577545	HE577405
sect. Desertorum Wilson					
Chenopodium desertorum subsp. *anidiophyllum* (Aellen) P.G. Wilson	Australia	C. Michaell & J. Risler 1773 (B, NT)	AC519	HE577555	HE577417
sect. Roubieva Rouy					
Chenopodium multifidum L. [=*Dysphania multifida* (L.) Mosyakin & Clemants]	Greece, Florina	R. & E. Willing 85631 (B)	AC574	HE577494	HE577354
Tribe Spinaceae Moq. (this study)					
sect. Agathophyton Hook					
Chenopodium bonus-henricus L.	Austria	T. Borsch 3821 (B)	AC381	HE577512	HE577372
Chenopodium californicum (S. Watson) S. Watson.	USA, California	P. Davis & D. Lightowless 66504 (B)	AC431	HE577516	HE577376
sect. Eublitum (Moq.) Aellen					
subsect. Capitata Kowal ex Mosyakin and Clemants					
Chenopodium capitatum (L.) Ambrosi	Bonn Bot. Gart. No: 19116	S. Fuentes 004 (B)	AC391	HE577513	HE577373
Chenopodium capitatum var. *parvicapitatum* S.L. Welsh	USA, Utha	K. Moon et al. 1993 (NY)	AC547	HE577514	HE577374
Spinacia oleracea L.				AJ400848.1	
Spinacia oleracea L.					EU606218.1
Spinacia tetrandra Steven ex M. Bieb.	USA ARS GRIN Ames 23664 [Asia]	S. Fuentes 180 (B)	AC650	HE577482	HE577345
Spinacia turkestanica Iljin	USA ARS GRIN Ames 23666 [Asia]	S. Fuentes 181 (B)	AC651	HE577483	HE577346
subsect. Foliosa Kowal ex Mosyakin and Clemants					
Chenopodium foliosum Asch.	Bonn Bot Gart No: 19117 [Germany]	S. Fuentes 003 (B)	AC392	HE577517	HE577377
Chenopodium foliosum Asch.	Kirgistan, Central Asia	Cubr 42389 (B)	AC520	HE577518	HE577378
OUTGROUPS					
Subfamily Betoideae Ulbr.					
Beta vulgaris subsp. *maritima* (L.) Thell.	Denmark, Jylland	Cubr 39900 (B)	AC530	HE577473	HE577334
Hablitzia tamnoides M. Bieb.	Germany, Bonn Bot. Gard No: 03609–90	No Voucher	AC018	HE577475	-
Hablitzia tamnoides M. Bieb.	Germany, Berlin Bot Gard No: 16611	S. Fuentes 018 (B)	AC523	HE577474	HE577335
Hablitzia tamnoides M. Bieb.					AY858590.1
Subfamily Camphorosmoideae Luerss.					
Bassia laniflora (S.G. Gmel.) A.J. Scott	Germany, Berlin Bot Gard No: 17809970	S. Fuentes 022 (B)	AC534	HE577476	HE577336
Bassia scoparia (L.) A.J. Scott	Russia	L. Martins 2295 (B)	AC607	HE577477	HE577337
Bassia prostrata (L.) A.J. Scott	Russia	L. Martins 2429 (B)	AC606	HE577478	HE577338

(*continued on next page*)

Table 2 (*continued*)

Taxon	Field/Garden origin	Voucher	Code	*trn*L-F Acc.	ITS Acc.
Subfamily Salicornideae Ulbr.					
Allenrolfea vaginata Kuntze	Germany, Bonn Bot Gard No: 2488		AC017	HE577472	-
Allenrolfea occidentalis Kuntze					AY181875.1

Note: The circumscription of subfamilies in Chenopodiacae follows the tree annotations in Kadereit et al. (2003); within Chenopodioideae the tribes Atripliceae, Axyrideae and Dysphanieae are recognized based on Kadereit et al. (2010); Spinacieae are listed as resurrected here; remaining genera are included into Chenopodieae (Kühn, 1993) using the infrageneric classification of *Chenopodium* by Aellen (1960) except the members of Dysphanieae and Wilson (1983) for sect. *Desertorum* of *Chenopodium*. USA ARS GRIN refers to USDA, ARS, National Genetic Resources Program. *Germplasm Resources Information Network* - (GRIN). [Online Database] National Germplasm Resources Laboratory, Beltsville, Maryland.

cies of *Spinacia* in another. The monophyly of *Spinacia* (*trnL-F* 100% JK/1 PP, ITS 100% JK/1 PP) is supported here for the first time. Clade 4 (*trnL-F* 100% JK/1 PP, ITS 100% JK/1 PP) is composed of *Ch. rubrum* and a number of other species (*Ch. rubrum* clade) and clade 5 (*trnL-F* 100% JK/1 PP, ITS 83% JK/1 PP) contains *Chenopodium murale*, *Ch. hybridum* and relatives (*Ch. murale* clade). Finally, clade 7 (*trnL-F* 100% JK/1 PP, ITS 88% JK/1 PP) embraces most of the other *Chenopodium* species, along with the genera *Einadia* and *Rhagodia*. The remaining clades 1 and 6 only include taxa from the former *Atripliceae* sensu lato. While clade 6 (*trnL-F* 97% JK/1 PP, ITS 50% JK/0.65 PP) encompasses *Atriplex*, *Stutzia*, *Grayia* and *Microgynoecium*, the maximally supported clade 1 consists of *Axyris*, *Ceratocarpus* and *Krascheninnikovia*.

3.4. Phylogenetic incongruence

The ILD test showed strong incongruence between the respective partitions of the data sets, even in the absence of polyploid taxa ($P < 0.001$). When clades were compared separately, topological incongruence was also detected within clades 2, 3, 4 and 7 ($P < 0.001$), but not for clades 1, 5, and 6 ($P = 1$, excluding *Microgynoecium* due to its unclear phylogenetic position). The position of the three first branching lineages in Chenopodioideae differs between ITS and *trnL-F*. In the ITS tree, deep nodes are unsupported in MP and only clade 1 as third branching is supported by a PP of 1. Clade 4 and 5 are resolved either as sister lineages (ITS 82% JK/0.91 PP) or in a grade (*trnL-F*). Within clade 7, resolution is poor but individual samples (e.g. *Ch. ficifolium*) are inferred incongruently in the chloroplast and nuclear trees.

4. Discussion

This study is based on the most extensive sampling of *Chenopodium* species to date. By using the highly variable non-coding *trnL-F* (cpDNA) and ITS (nrDNA) regions, we provide the first comprehensive phylogeny of this controverted large genus. Overall, we support the highly paraphyletic status of *Chenopodium*, as suggested by Kadereit et al. (2003) and Müller and Borsch (2005), and reveal new well-supported lineages, resolved with high confidence (Figs. 1 and 2). Because of this paraphyly, our results also affect the picture of the subfamily Chenopodioideae. Whereas the studies by Kadereit et al. (2003, 2010) suggested three of the five lineages of *Chenopodium* s.l. (Chenopodieae I, II, III; Chenopodieae III were already called *Dysphanieae* in Kadereit et al., 2010), our results offer further support and resolution of these lineages and identify two novel major clades (*Ch. murale* and relatives, *Ch. rubrum* and relatives) out of the Chenopodieae I. Our data also provide statistical support for the Chenopodieae II, which we recognize as *Spinacieae*.

4.1. Congruence of data partitions

Different combinations on the ILD test reveal some topological incongruence between the respective data partitions, as exemplified by the respective positions of clades 1, 2 and 3 (*Ayridae*, *Dysphanieae*, *Spinacieae*; Figs. 1 and 2) or the position of *Ch. opulifolium* within clade 7. In the first example incongruence is soft (no statistic confidence in deviating topologies) whereas it is hard (well supported nodes differ) in the second case. Causes for incongruence are manifold, and can be either of non-biological (e.g. insufficient taxon sampling, long-branch attraction, etc.) or biological (e.g. incomplete linage sorting, orthology/paralogy conflation, or hybridization) origin (Wendel and Doyle, 1998; Sanderson et al., 2000).

On the one hand, the extent of our current taxon sampling (more than 135 taxa representing the diversity of *Chenopodium* sensu lato) and the similar topologies obtained from both MP and Bayesian analyses of the respective markers allow us to reject with confidence most analytical causes of topological incongruence. Indeed, it has been recently demonstrated that an increase of taxon sampling in a Bayesian context tends to decrease the risk of erroneous topologies due to long-branch attraction (Van der Niet and Linder, 2008). Furthermore, incomplete lineage sorting of the ITS alleles can be excluded as a cause of topological conflict due to the absence of polymorphic sites in all direct sequences investigated. Yet, this lack of ITS polymorphism does not allow us to identify potential additive polymorphic sites, which would support past hybridization events (Nieto Feliner et al., 2001; Mansion et al., 2005; Guggisberg et al., 2009).

We are aware that we cannot clearly discriminate between orthology/paralogy conflation and reticulation patterns in the absence of extensive cloning of the ITS region, especially in clades with low interspecific resolution (e.g. clade 7, Figs. 1 and 2). A more detailed study, taking into account the current limitations of our current molecular data set, and using non-molecular evidence based on caryology, morphology, and phytochemistry is underway.

Overall, we feel that it is more appropriate to individually discuss evolutionary and taxonomic implications of trees inferred from organellar and nuclear genomic compartments, especially when sources of potential incongruence remain unclear. Furthermore, such an approach allows us to compare the phylogenetic utility of the respective data partitions.

4.2. Phylogenetic utility of the trnL-F and ITS regions

The use of non-coding and rapidly evolving genomic regions from the chloroplast genome in angiosperm phylogenetics has been accelerating during recent years. Following initial proposals (e.g. Taberlet et al., 1991), it has been demonstrated that not only the percentage of variable sites, and thus the quantity of information, but also the quality of phylogenetic signal of non-coding regions outperforms more conserved coding genes such as *rbcL* (Borsch et al., 2003; Müller et al., 2006). One of the major insights is that chloroplast DNA mutational dynamics follows certain principles across genomic regions and taxa (see Borsch and Quandt, 2009 for a summary). As a consequence, motif based alignment allows more precise homology statements (Morrison, 2009; Ochoterena, 2009), although, on the other hand mutational hot-

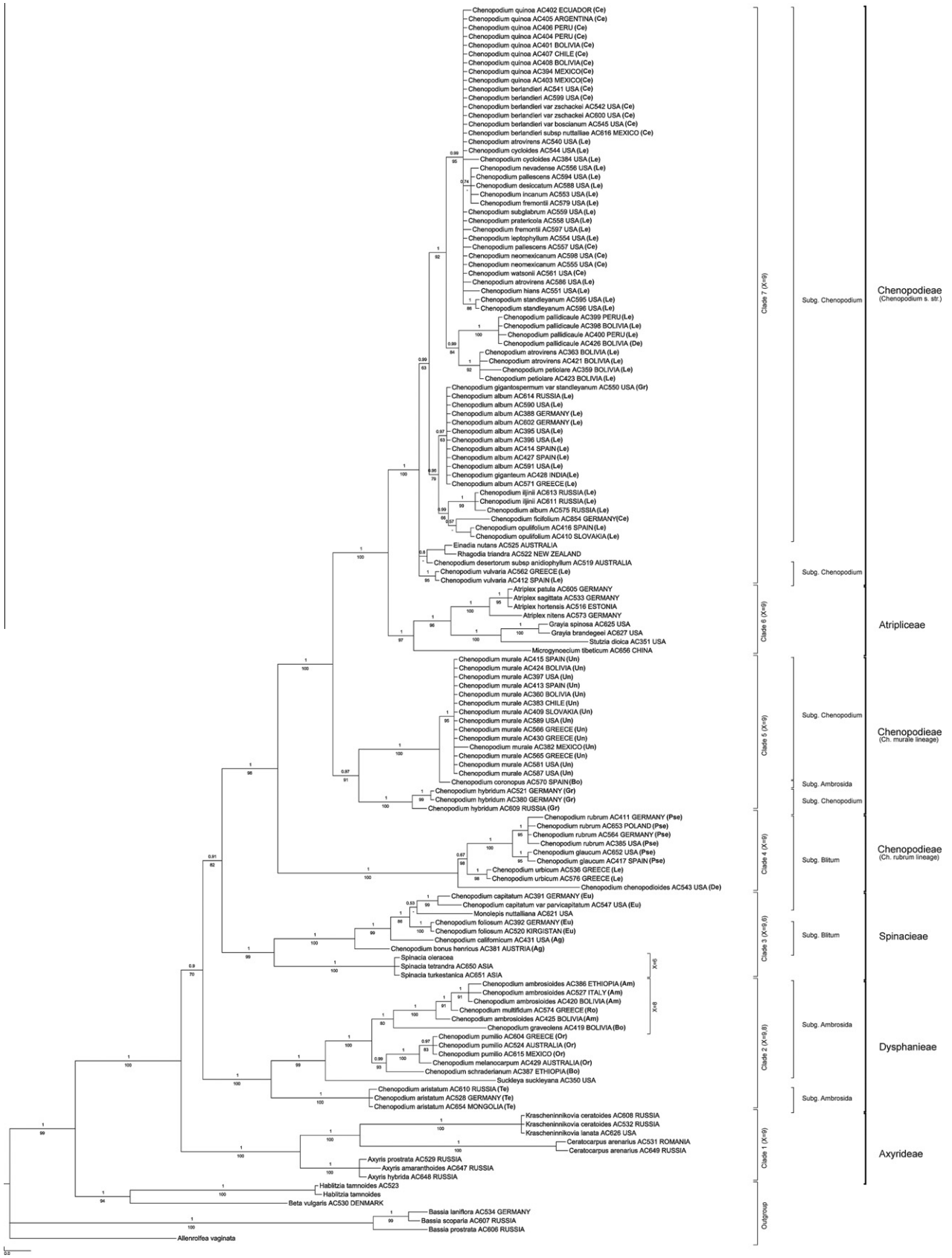

Fig. 1. Bayesian majority rule tree based on the sequence dataset of *trnL-F* including coded indels. Bayesian posterior probabilities (pp) are given above and Jackknife (JK) values below branches. The abbreviations following species names in parentheses refer to the sections and subsections proposed for *Chenopodium* by Aellen (1960); (Ag) = Sect. *Agathophyton*, (Am) = sect. *Ambrina*, (Bo) = sect. *Botryoides*; the sect. *Chenopodium* is represented by (Ce) = subsect. *Cellulata*, (Gr) = subsect. *Grossefoveata*, (Le) = subsect. *Lejosperma*, and (Un) = subsect. *Undata*; further sections are (De) = sect. *Degenia*, (Eu) = sect. *Eublitum*, (Or) = sect. *Orthosporum*, (Pse) = sect. *Pseudoblitum*, and (Ro) = sect. *Roubieva*. The second column of clade annotations refers to the accepted subgenera of *Chenopodium* (Judd and Ferguson, 1999), and the third column to tribe names accepted in this study as explained in Fig. 2.

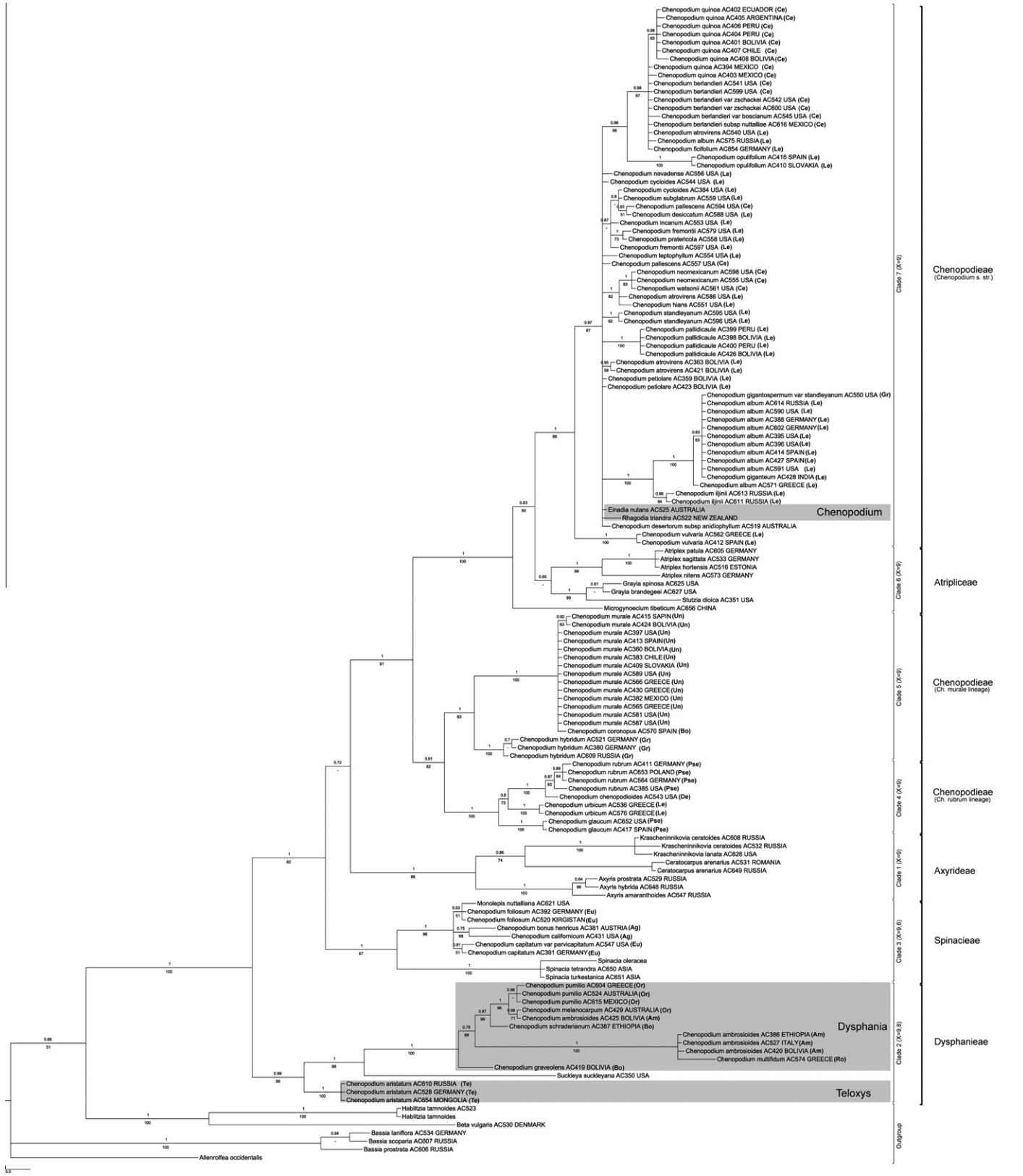

Fig. 2. Bayesian majority rule tree based on the sequence dataset of nrITS including coded indels. Bayesian posterior probabilities (pp) are given above and Jackknife (JK) values below branches. Boxes in gray mark the genera *Dysphania* and *Teloxys* from the *Dysphanieae* that are now accepted as genera distinct from the former *Chenopodium* sensu lato, and the representatives of the former genera *Einadia* and *Rhagodia* that are included into *Chenopodium* s.str. (clade 7) in this study. The second column refers to tribe names *Spinacieae* (newly resolved in this study), *Atripliceaea*, *Axyrideae* and *Dysphanieae* (sensu Kadereit et al. (2010) and Zacharias and Baldwin (2010); supported in this study); and for *Chenopodieae* the newly *Chenopodium* s.str, *Ch. murale* lineage and *Ch. rubrum* linegae found in this study.

spots of unclear homology have to be excluded even in data sets representing species level diversity within genera. This study provides a further example for this (seven mutational hotspots in the *trnL-F* region of *Chenopodium* s.l.). The current *trnL-F* data set is one of the largest so far generated for a family of Caryophyllales. Previous workers used the *trnL-F* region, due to its high variability compared to other chloroplast markers in *Suaeda*, *Salicornia* and allies, or *Beta* and allies (Kapralov et al., 2006; Murakeözy et al., 2007; Hohmann et al., 2006). The first molecular analysis of the Amaranthaceae–Chenopodiaceae alliance by Kadereit et al. (2003) was based on sequences of the *rbcL* gene, but the resulting trees were largely unresolved at deeper nodes and lacked statistical support in many parts. A subsequent analysis by Müller and Borsch (2005) used *trnK/matK* plastid data, and generated a much improved phylogenetic hypothesis for Amaranthaceae and Chenopodiaceae. Remarkably, the *trnL-F* region (composed of the *trnL* gene with its group I intron and the *trnL–trnF* intergentic spacer; e.g. Quandt et al., 2004) is about half the size of *matK/trnK* and yields the so far best resolved and supported tree of a major Chenopodiaceae lineage. This is paralleled by *trnL-F* trees from the speciose subfamily Gomphrenoideae of the Amaranthaceae (Sánchez del Pino et al., 2009), suggesting that *trnL-F* should be employed as a standard marker in Amaranthaceae–Chenopodiaceae.

The nuclear, biparentally inherited internal transcribed spacer region (ITS1, 5.8S, ITS2) yields trees that essentially show the same seven major lineages. Only some nodes, especially at deeper parts of the tree, are weakly supported and inconsistently resolved (see Clades 1, 2 and 3, Fig. 2). This pattern may be explained because ITS evolves differently to chloroplast regions. Motifs for microstructural changes are less evident. In fact, most mutations (see indel character list; Appendix B) appear to be mostly deletions or insertions of single nucleotides. Occurring repeatedly at greater distances, this may obscure sequence divergence caused by substitutions, leading to less robust homology assessments, in addition to potential effects of concerted evolution of many ITS copies (see Álvarez and Wendel, 2003; Nieto Feliner and Rosselló, 2007). Some parts of the ITS tree are clearly incongruent (see Fig. 2) to the chloroplast tree. This suggests reticulate patterns which could be explained by patterns of speciation. The deep topological differences are rather inconsistent (low support) and this can be explained by intrinsic patterns of molecular evolution.

4.3. Paraphyly of Chenopodium L.

Both MP and Bayesian analyses based on DNA markers of different genomic compartments (cp- and nrDNA) support the paraphyly of the genus as currently described, and further the inclusion of all the investigated species of *Chenopodium* into five different clades (Figs. 1 and 2). For clarity, the name *Chenopodium* is used throughout for all species it has been applied to over time (Figs. 1 and 2).

A clade containing aromatic species of *Chenopodium* (clade 2, see below "*Dysphanieae*"), is highly supported (Figs. 1 and 2), and is either resolved as a first or second diverging lineage of *Chenopodium* s.l., depending on whether ITS or *trnL-F* are analysed. It comprises *Ch. ambrosioides*, *Ch. graveolens*, *Ch. melanocarpum*, *Ch. multifidum*, *Ch. pumilio*, *Ch. schraderianum*, and *Ch. aristatum*, which all share the presence of specialized aromatic glandular hairs ("type 8"; Carolin, 1983; Bonzani et al., 2003), as well as *Suckleya suckleyana* which has inflated unicellular trichomes (Chu et al., 1991). Our data support the previous proposal by Carolin (1983) and Mosyakin and Clemants (1996) to separate aromatic chenopods with glandular hairs under the generic name *Dysphania* (including *Teloxys* in this genus) from the remaining ones (possessing bladder or sub-stellate hairs), and denote the importance of hair types as characters for the systematics of Chenopodioideae. Within the aromatic clade, *Suckleya suckleyana*, previously placed in the *Atripliceae* sensu lato (Kühn, 1993), is resolved with high confidence (99% JK/1 PP) as sister group to all other species of aromatic *Chenopodium* except *Ch. aristatum* (= *Teloxys aristata*).

Our results corroborate a recent tree based on *rbcL* (Kadereit et al., 2010) and also find *Suckleya* in a position sister to a number of *Dysphania* species, clearly apart of the *Atripliceae* clade. *Suckleya* shares ebracteolate flowers with the aromatic chenopods, but differs by being monoecious and by its female perianth which becomes winged when mature (Chu et al., 1991). It is thus justified to maintain it as a separate genus distinct from the other aromatic species of *Chenopodium* (= *Dysphania spp.*). To confirm the presence of glandular trichomes as a putative synapomorphy for clade 2, it will be necessary to revisit the fine structure of *Suckleya* trichomes and to confirm their glandular nature. Nevertheless, available data (Chu et al., 1991) show that the inflated unicellular trichomes of *Suckleya* appear to be similar to the Type I trichomes found in other aromatic species of *Chenopodium* (= *Dysphania spp.*; Bonzani et al., 2003). The three samples representing geographically different populations of *Ch. aristatum* appear as sister group (100% JK/ 1 PP) to the remainder of the species in clade 2. This species also differs morphologically by having dichasial inflorescences (Moquin-Tandon, 1840; Weber, 1985) and bristle-tipped terminal inflorescence branches (Mosyakin and Clemants, 2002, 2008) that would support its recognition as a distinct genus *Teloxys*. It should be noted that this circumscription of *Teloxys* corresponds to the concept of the genus held by Ulbrich (1934) or of subsect. *Teloxys* (of *Dysphania* sect. *Dysphania*) proposed by Mosyakin and Clemants (2002), respectively.

Clade 3 is strongly supported by *trnL-F* (Fig. 1; 99% JK/1 PP) to comprise several *Chenopodium spp.*, *Monolepis* and *Spinacia* but has only moderate support in the ITS tree (67% JK, Fig. 2). It corresponds to "Chenopodieae II" sensu Kadereit et al. (2003, 2010) that, however, was not recovered with statistic confidence in their previously published *rbcL* tree. "Chenopodieae II" as depicted here (Figs. 1 and 2) lacks clear morphological synapomorphies except the presence of dense, head-like glomerules on terminal or axillary branches. Within this clade, a *Spinacia* lineage is highly supported by both DNA markers (100 JK, Figs. 1 and 2) as sister to the remaining taxa, and comprises all *Spinacia* species described so far (Kühn, 1993; Welsh et al., 2003). The *Spinacia* subclade is further characterized by the presence of unisexual flowers without perianth, not found in the sister lineage comprising *Ch. capitatum*, *Ch. californicum*, *Ch. bonus-henricus*, *Ch. foliosum* and *Monolepis nuttalliana*. The latter all have bisexual flowers and a differentiated perianth. Our data strongly refute a previous hypothesis of a sister group relationship between *Spinacia oleracea* and *Monolepis nuttaliana* that was found based on *rbcL* sequences (Kadereit et al., 2003), but agree with the recently suggested exclusion of *Spinacia* from *Atripliceae* (Kadereit et al., 2010).

The *Chenopodium rubrum* clade (Clade 4; Figs. 1 and 2) is newly resolved here based on both *trnL-F* and ITS with maximum confidence. It encompasses *Chenopodium chenopodioides*, *Ch. glaucum*, *Ch. rubrum* and *Ch. urbicum*. Whereas chloroplast sequences suggest its placement in a grade branching after the Chenopodieae II (=Spinacieae; see Fig. 1), nuclear ITS data provide some evidence for the clade being sister to a *Ch. murale* clade (Clade 4; Fig. 2). Based on the available morphological data, morphological synapomorphies for this clade are not clear at this point. Flowers with 3–4 perianth segments are shared by *Ch. rubrum* and *Ch. glaucum*, whereas flowers of *Ch. chenopodioides* consistently present only three segments, and those of *Ch. urbicum* have five segments. Moreover, a reddish seed coat is shared by *Ch. rubrum*, *Ch. glaucum* and *Ch. urbicum*, whereas *Ch. chenopodioides* has seeds with a black coat. Inflorescences with subglobose glomerules are present in all these taxa and seem to be a

synapomorphy. Nevertheless, this character is homoplastic within Chenopodioideae (Iljin, 1936; Aellen, 1960; Welsh et al., 2003). Looking at the sectional level within *Chenopodium*, (based on Aellen and Just, 1943 and Aellen, 1960) this clade is composed of members of section *Pseudoblitum* (*Ch. rubrum* and *Ch. glaucum*) that is morphologically similar to section *Degenia* (Aellen and Just, 1943), here represented by *Ch. chenopodioides*. Our data confirm this, although the type species of the latter section, *Ch. macrospermum*, remains to be included in a molecular analysis. *Chenopodium urbicum* of section *Chenopodia* subsection *Lejosperma* is also part of this clade (Aellen and Just, 1943). This means that smooth or nearly smooth seeds and an indistinctly ridged or slightly pitted testa must have evolved twice, once in *Ch. urbicum* and second in the ancestor of the remaining, largely North American species of subsect. *Lejosperma*, which thus is clearly polyphyletic.

As currently depicted, the *Chenopodium rubrum* clade comprises annual herbs with triangular, narrowly triangular, rhombic or lanceolate leaf blades, and sinuate, dentate or serrate leaf margins. The inflorescences are composed of subglobose glomerules. The flowers have 3–5 tepals, and uniseriate trichomes are only found on axillary (flower or leaf) buds. The seeds have a rounded margin and are smooth or rugulate.

The *Chenopodium murale* clade (Clade 5; 91% JK with *trnL-F* and 83% JK with ITS; Fig. 1) contains three species (*Ch. murale*, *Ch. coronopus* and *Ch. hybridum*), all characterized by rounded, compressed and rugose seeds (Iljin, 1936). This feature, not present in all other species sampled so far, seems to be a synapormorphy for clade 5. The *Chenopodium murale* clade is further divided into two well-supported subclades (each 100% JK *trnL-F* and ITS; Figs. 1 and 2): one containing all accessions of *Ch. hybridum*, the other all accessions of *Ch. murale* and *Ch. coronopus*. Morphologically, *Ch. hybridum* differs from the two latter species by having seeds without conspicuously flattened margins (Iljin, 1936). The *Chenopodium murale* clade corresponds to the subsection *Unduata* as formally recognized by Mosyakin and Clemants (1996). The description of this subsection was based on *Ch. murale* as type species (Mosyakin and Clemants, 1996).

The large clade shown at the top of Figs. 1 and 2 (clade 7) is the clade of *Chenopodium* s.str., and corresponds to the "Chenopodieae I" of Kadereit et al. (2003), but excluding *Microgynoecium*. It is sister to the phylogenetically defined *Atripliceae* (Kadereit et al., 2010; clade 6). The position of *Microgynoecium* was inferred with only weak support as sister to the remaining Chenopodieae I using *rbcL*. There is now increasing evidence that it rather belongs to the *Atripliceae* (Fig. 1; see below). The large *Chenopodium* s.str. clade (clade 7) encloses most species of *Chenopodium* sampled in this study (>40%), including *Chenopodium album*, which is the type species of *Chenopodium* (Mosyakin and Clemants, 1996), along with the genera *Einadia* and *Rhagodia* (Figs. 1 and 2). Overall, the phylogenetic relationships within this core *Chenopodium* clade are not well resolved. There is also some difficulty in finding morphological synapomorphies for the entire clade. Nevertheless, some characters seem diagnostic to particular subclades. *Chenopodium vulvaria* is characterized by a particular fetid odour due to its trimethylamine compounds (Croemwell, 1950). It forms an isolated lineage (100% JK/1 PP) in both the ITS and *trnL-F* trees. *Einadia* and *Rhagodia*, which differ from *Chenopodium* by their perennial habit and fleshy fruits (Wilson, 1983), form a well-supported lineage in the *trnL-F* tree, which also includes the Australian *Ch. desertorum* (92% JK/1 PP). The chloroplast tree (Fig. 1) further depicts three major subclades, one comprising the polyploid *Ch. album* and relatives (the "*Ch. album* complex"), then a lineage of South American diploid species (*Ch. atrovirens*, *Ch. pallidicaule* and *Ch. petiolare*), and the biggest one with the allotetraploid *Ch. quinoa*, and *Ch. berlandieri* together with numerous North American diploid species. Nonetheless, resolution within this major *Chenopodium* clade in the ITS tree is even worse than in the chloroplast tree (Fig. 2).

4.4. Circumscription and phylogenetic position of the tribes Atripliceae and Axyrideae

Within the *Atripliceae* and the *Axyrideae*, our analyses reveal two highly supported lineages of *Chenopodium* sensu lato that have been recognized at tribal levels (Heklau and Röser, 2008; Kadereit et al., 2010; clades 1 and 6, respectively). The *Axyrideae* might be sister to all remaining Chenopodioideae (Fig. 1; chloroplast data), also found by Kadereit et al. (2010), or constitute a third branch (ITS data; Fig. 2). As indicated before, additional nuclear data are needed to test this hypothesis. The *Atripliceae* are congruently inferred to be nested within *Chenopodium* sensu lato. Looking at a refined tribal classification within Chenopodioideae, they are also nested within Chenopodieae.

The *Atripliceae* clade including *Microgynoecium* receives high support (97% JK/ 1 PP) based on *trnL-F* sequence data. The position of *Microgynoecium tibeticum* as sister to all remaining taxa of *Atripliceae* (96% JK/1 PP *trnL-F*; Fig. 1) is also depicted here. This is congruent to the *atpB-rbcL* topology in Kadereit et al. (2010), albeit the tree shown in the latter study lacks significant posterior probabilities for the respective nodes. However, our nuclear ITS tree, the position of *Microgynoecium* is inconsistently resolved as sister to the remaining Atripliceae plus the *Chenopodium* s.str. clade (50% JK/0.83 PP; Fig. 2). The BEAST summary tree based on ITS of Kadereit et al. (2010) depicts *Microgynoecium* in yet another position, as sister to the *Archiatriplex* clade, but again lacking statistical confidence. The broad scale analysis of Caryophyllales using *petD* intron sequences (Schäferhoff et al., 2009) also indicates a close affinity of *Microgynoecium* to the *Atripliceae*, although their taxon sampling of Chenopodiaceae is low. The flowers of *Microgynoecium* are similar to *Archiatriplex* (Flores Olvera and Davis, 2001), a fact supporting close affinities between these two taxa. Pollen morphology of *Microgynoecium* rather stands out from most other taxa of *Atripliceae*. Together with *Manochlamys*, the genus *Archiatriplex* has very large pollen grains but a high pore number with few ektexinous bodies (Flores Olvera et al., 2006). Overall, our results do not support a relationship between *Axyris* and *Microgynoecium*, as suggested by Flores Olvera and Davis (2001), based on flower morphology. Instead, *Microgynoecium* most likely belongs to the *Atripliceae*, although the nuclear-based phylogenies require further testing through additional genomic regions. Internally, the *Atripliceae* are composed of two major lineages: one encompassing *Atriplex*, the other *Grayia brandegeei*, *G. spinosa* and *Stutzia dioica* (Figs. 1 and 2). This corresponds to the *Atriplex* clade and the *Archiatriplex* clade in line with the denser sampled analyses of the *Atripliceae* by Kadereit et al. (2010) and Zacharias and Baldwin (2010). *Grayia* and *Stutzia* share morphological features, such as the presence of carnose leaves, characteristic inflorescences in glomerules and with non-foliose bracts, and fruits with short bracteoles of less than half the length of the leaves (Flores Olvera and Davis, 2001; Flores Olvera et al., 2006; Kadereit et al., 2010).

The *Axyrideae* appear as an isolated lineage and include *Axyris*, *Ceratocarpus*, and *Krascheninnikovia*. The genera *Ceratocarpus* and *Krascheninnikovia* are characterized by the presence of sub-stellate dendroid hairs and form a strongly supported subclade, which is sister to *Axyris* (*trnL-F* 100% JK/1 PP; ITS 74% JK/0.86 PP), the latter having sub-stellate branched hairs (Kühn, 1993; Flores Olvera and Davis, 2001; Welsh et al., 2003; Zhu et al., 2003; Heklau and Röser, 2008). Their close relationship was also suggested based on pollen morphology because these three genera share the highest density of microspines (Flores Olvera et al., 2006). Our results support the monophyly and relationships of *Axyris*, *Ceratocarpus*, and

Kraschenninnikovia as reported by Heklau and Röser (2008) and Kadereit et al. (2010). However, considering the branching sequence of major clades of the Chenopodioideae, which are all recognized at tribal level, the subtribe *Axyridinae* should also be classified as an own tribe as suggested by Kadereit et al. (2010).

4.5. Chromosome evolution in Chenopodioideae

Differences in chromosome numbers have long been known in *Chenopodium* and relatives, but so far no attempt has been made to study chromosome evolution in a phylogenetic context (Appendix C). In addition to genome duplications that result in higher ploidy level, as reported from *Atriplex* (Kühn, 1993; Welsh et al., 2003) and *Chenopodium* s.str. (this study), dysploid changes in chromosome number were anticipated (Aellen and Just, 1943). The base chromosome numbers in angiosperms can either correlate with lineages (Schneeweiss et al., 2004; Hidalgo et al., 2007; Blöch et al., 2009) or evolve independently (e.g., Baldwin and Wessa, 2000; Ellison et al., 2006). Chenopodioideae provide another case for lineage specific dysploid chromosome number changes, as suggested by our results. Whereas a base number of $x = 9$ can be unambiguously inferred for Chenopodioideae, thus corroborating earlier ideas of Turner (1994), our tree topology suggests independent dysploid chromosome loss in two derived lineages. One is found in the subclade of *Ch. ambrosioides*, *Ch. multifidum* and *Ch. graveolens* ($x = 8$; IPCN 1986–2003; Fig. 1). Also, the *Spinacia* subclade is characterized by the unusual chromosome number of $x = 6$, that only can be explained by a reduction from $x = 9$ (Fig. 1). Polyploidy, on the other hand, seems to be less characteristic for lineages. It rather seems to occur within some lineages, such as the *Atripliceae* and *Chenopodium* s.str. (clade 7), where speciation may be triggered by polyploid formation. For *Chenopodium*, further analysis of clade 7 will be needed to unravel putative events of reticulation and allopolyploid speciation. Additional chloroplast markers are necessary to improve tree resolution and sequences of low copy nuclear genes are needed for testing the ITS topology.

4.6. Towards a new tribal and generic classification of Chenopodioideae

Our results support the subdivision of *Chenopodium* into five separate, well-supported clades (Figs. 1 and 2) within Chenopodioideae. These clades themselves are paraphyletic to other genera. The necessary taxonomic changes should be oriented at a compromise to conserve traditional use of generic names and to implement new molecular results that allow classifying only monophyletic groups. Keeping a large genus *Chenopodium* (Aellen and Just, 1943; Aellen, 1960; Kühn, 1993; Judd and Ferguson, 1999; Welsh et al., 2003) would dramatically underestimate the morphological diversity in this group. It would also result in the inclusion of well-known genera, such as *Atriplex* or *Spinacia*, in *Chenopodium*. Giving a new name for each clade found by molecular data without any other evidence, would add to the current taxonomic confusion in the group.

In this study, we found that the highly paraphyletic genus *Chenopodium* comprises five lineages which could be recognized at generic level (corresponding to clades 2, 3, 4, 5 and 7; Fig. 2). However, the situation is complex and further work, including a larger taxon sampling, are needed before the genus can finally be re-classified. For some clades, the situation is clearer. e.g. *Dysphania* should be accepted as a genus for the most diverse sublineage of clade 2 (see Figs. 1 and 2), following the suggestion of Kadereit et al. (2010). The same applies to the genus *Teloxys* (see above) which so far is only sometimes accepted in more recent treatments. All names for the respective genera are already available. Another clear situation exists for the well supported clade of *Chenopodium* sensu stricto (clade 7) that also contains the type species of the genus, *Ch. album* L. (lectotypified by Mosyakin and Clemants, 1996). As a consequence of this study, *Einadia* Raf. and *Rhagodia* R. Br. should be included in *Chenopodium* L. (the necessary new names are provided below). The subtribe *Rhagodiinae*, proposed by Scott (1978b) to subdivide the *Chenopodieae*, can therefore not be upheld. Its diagnostic features, such as a succulent pericarp and predominantly unisexual flowers (Scott, 1978b), now rather appear as homoplastic derived states that arose independently in several lineages of the subfamily Chenopodioideae. *Holmbergia*, which was also included in *Rhagodiinae* by Scott (1978b) based on its spongy and inflated berries, was shown to belong to the *Archiatriplex* clade of *Atripliceae* by Kadereit et al. (2010) and Zacharias and Baldwin (2010).

Within Chenopodioideae, two additional major clades deserve recognition at tribal level. One are the *Dysphanieae* (Fig. 2). Based on molecular markers and morphological characters (trichomes), the monophyly and isolated position of *Dysphania*, *Suckleya*, and *Teloxys* is evident (Clade 2, Figs. 1 and 2). This tribe *Dysphanieae* was already proposed by Pax (1889) but to accommodate the three Australian species of *Dysphania* within Caryophyllaceae–Alsinoideae. Pax thereby had followed the view of Bentham (1870) who placed *Dysphania* rather as an isolated genus in Chenopodiaceae than a somewhat abnormal genus of Illecebraceae (based on *Illecebrum*, a member of Caryophyllaceae–Alsinoideae–Paronychieae; Pax, 1889). Almost half a century later, Pax (1927) created an own family Dysphaniaceae for the genus *Dysphania*, which was based on the valvate perianth and pedicelled perianth parts. He considered Dysphaniaceae to be intermediate between Chenopodiaceae and Caryophyllaceae, a view upheld in the second edition of the Natürlichen Pflanzenfamilien (Pax and Hoffmann, 1934). Aellen (1960) included *Dysphania* in *Chenopodium* as an own section. Eckardt (1967) corroborated this view by his comparative anatomical study, in which he found the floral architecture and gynoecium of *Dysphania* to strongly differ from Illecebraceae. Scott (1978a), however, classified an own subg. *Ambrosia* of *Chenopodium*, based on *Ch. ambrosioides* as type species, but on the other hand kept *Dysphania* as a separate genus. As indicated above, our phylogenetic data finally show that all the aromatic species that were shuffled in these pre-cladistic classification systems, in fact belong to a single clade that is best named *Dysphania*. On a higher level, *Dyphania*, *Suckleya* and *Teloxis* compose the *Dysphanieae*. In line with this, and recent molecular findings by Kadereit et al. (2010), our results also support the inclusion of the subtribe *Suckleyinae* in *Dysphanieae* and not in *Chenopodieae* as originally proposed by Chu et al. (1991).

The other lineage that should be recognized at tribal level are the *Spinacieae* (clade 3). The tribe *Spinacieae* was originally described by Moquin-Tandon (1840) and included *Atriplex* along with a number of further genera. The earlier published *Atripliceae* (Meyer, 1829) were then used by most other authors in a circumscription that included *Spinacia*.

In this study, we newly define *Spinaceae* as different from *Atripliceae* and to include the genera *Monolepis* and *Spinacia*, along with a group of *Chenopodium* species related to *Chenopodium capitatum* and *Ch. foliosum* (Figs. 1,2) and *Scleroblitum* (not sampled here but closely related to *Ch. foliosum* based on *rbcL*; Kadereit et al., 2003). However, relationships within *Spinacieae* require further study. An issue will be to test, by inclusion of more taxa and sequence characters, if the respective *Chenopodium* species within this larger clade are monophyletic. Such a monophyletic assemblage would then correspond to the Linnaean genus *Blitum* (*Blitum capitatum* = *Ch. capitatum*; lectotypified by Mosyakin and Clemants, 1996).

Even with these realignments, the tribe *Chenopodieae* remains paraphyletic to the *Atripliceae*. Right now, our trees depict two clades which are composed of *Chenopodium rubrum* and relatives (clade 4,

Figs. 1 and 2), and of *Chenopodium murale* and relatives (clade 5; Figs. 1 and 2), with unclear relationships to each other. Further characters, both molecular and morphological, are needed to resolve this part of the Chenopodieae and to move towards a stable generic classification. Finally, phylogenetic classification will either require establishing one or two additional tribes or merging *Atripliceae* and *Chenopodieae*.

In summary, our study showed that the current delimitations of *Chenopodium* need to be redefined. We suggest, based on our phylogenetic reconstruction, that the clade 7 (Figs. 1 and 2) may best represent the monophyletic *Chenopodium* s.str.

5. Taxonomic conclusions

For several species of the genera *Einadia* and *Rhagodia*, no names under *Chenopodium* exist. These are validated in the following treatment. However, names under *Chenopodium* do already exist for a number of species that so far have been treated under *Einadia* and *Rhagodia* (Wilson, 1983). These are: *Chenopodium allanii* Aellen; *Chenopodium baccatum* Labill.; *Chenopodium polygonoides* (Murr.) Aellen; *Chenopodium preissii* (Moq.) Diels; *Chenopodium triandrum* G. Forster; *Chenopodium trigonon* Roem. et Schult.; *Chenopodium ulicinum* Gand.

(1) *Chenopodium nutans* (R. Br.) S. Fuentes & Borsch, **comb. nov.**
Basionym: *Rhagodia nutans* R. Br., Prodr. Fl. Nov. Holland. 408. 1810.
≡*Einadia nutans* (R. Br.) A. J. Scott, Feddes Repert. 89: 3. 1978.

(1a) *Chenopodium nutans* (R. Br.) S. Fuentes & Borsch subsp. *nutans.*

(1b) *Chenopodium nutans* subsp. *oxycarpa* (Gauba) S. Fuentes & Borsch, **comb. nov.**
Basionym: *Einadia nutans* subsp. *oxycarpa* (Gauba) Paul G. Wilson, Nuytsia 4(2): 203. 1983.
≡*Rhagodia nutans* var. *oxycarpa* Gauba, Vict. Nat. 65: 167. 1948.

(1c) *Chenopodium nutans* subsp. *linifolia* (R. Br.) S. Fuentes & Borsch, **comb. nov.**
Basionym: *Einadia nutans* subsp. *linifolia* (R. Br.) Paul G. Wilson, Nuytsia 4(2): 204. 1983.
≡*Rhagodia linifolia* R. Br., Prodr. Fl. Nov. Holland. 408. 1810. ≡*Einadia linifolia* (R. Br.) Raf. Fl. Tellur. 4: 121. 1838; Ulbrich in Engler et Pratl. Nat. Pflanzenfam. ed. 2, 16c: 558. 1934 pro. syn. sub *Suaeda linifolia* Pall. ≡*Einadia nutans* var. *linifolia* (R. Br.) A. J. Scott, Feddes Repert. 89: 4. 1978.

(1d) *Chenopodium nutans* subsp. *eremaea* (Paul G. Wilson) S. Fuentes & Borsch, **comb. nov.**
Basionym: *Einadia nutans* subsp. *eremaea* Paul G. Wilson, Nuytsia 4: 204. 1983.

(2) Infraspecific taxa of *Chenopodium trigonon* Roem. et Schult., Syst. Veg. 6: 275. 1820.

(2a) *Chenopodium trigonon* subsp. *stellulatum* (Benth.) S. Fuentes & Borsch, **comb. nov.**
Basionym: *Einadia trigonos* subsp. *stellulata* (Benth.) Paul G. Wilson, Nuytsia 4(2): 208. 1983. ≡*Chenopodium triangulare* var. *stellulatum* Benth. Fl. Austral. 5: 161.1870. ≡*Ch. stellulatum* (Benth.) Aellen, Verh. Naturf. Ges. Basel 41: 93. 1931. nom. illeg., nonAellen, 1928.

(2b) *Chenopodium trigonon* subsp. *leiocarpa* (Paul G. Wilson) S. Fuentes & Borsch, **comb. nov.**
Basionym: *Einadia trigonos* subsp. *leiocarpa* Paul G. Wilson, Nuytsia 4(2): 209. 1983.

(3) *Chenopodium hastata* (R. Br.) S. Fuentes & Borsch, **comb. nov.**
Basionym: *Rhagodia hastata* R. Br., Prodr. Fl. Nov. Holland. 408. 1810. ≡*Einadia hastata* (R. Br.) A.J. Scott, Feddes Repert. 89: 4 (1978).

(4) Infraspecific taxa of *Chenopodium baccatum* Labill.

(4a) *Chenopodium baccatum* subsp. *dioicum* (Nees) S. Fuentes & Borsch, **comb. nov.**
Basionym: *Rhagodia baccata* subsp. *dioica* (Nees) Paul G. Wilson, Nuytsia 4(2): 225. 1983. ≡*Rhagodia dioica* Nees, Pl. Preiss. 1: 636. 1845.

(5) *Chenopodium candolleanum* (Moq.) S. Fuentes & Borsch, **comb. nov.**
Basionym: *Rhagodia candolleana* Moq., Chenop. Monogr. Enum. 10. 1840. ≡*Rhagodia baccata* var. *candolleana* (Moq.) Moq., Prod. (DC.) 13(2): 50 (1849).

(5a) *Chenopodium candolleanum* (Moq.) S. Fuentes & Borsch, subsp. *candolleanum.*

(5b) *Chenopodium candolleanum* subsp. *argenteum* (Paul G. Wilson) S. Fuentes & Borsch, **comb. nov.**
Basionym: *Rhagodia candolleana* subsp. *argentea* Paul G. Wilson, Nuytsia 4(2): 215. 1983.

(6) *Chenopodium crassifolium* (R. Br.) S. Fuentes & Borsch, **comb. nov.**
Basionym: *Rhagodia crassifolia* R. Br., Prodr. Fl. Nov. Holland.: 408. 1810.

(7) *Chenopodium acicularis* (Paul G. Wilson) S. Fuentes & Borsch, **comb. nov.**
Basionym: *Rhagodia acicularis* Paul G. Wilson, Nuytsia 4(1): 51. 1982.

(8) Infraspecific taxa of *Chenopodium preissii* (Moq.) Diels.

(8a) *Chenopodium preissii* subsp. *obovatum* (Moq.) S. Fuentes & Borsch, **comb. nov.**
Basionym: *Rhagodia preisii* subsp. *obovata* (Moq.) Paul G. Wilson, Nuytsia 4(2): 222. 1983. ≡*Rhagodia obovata* Moq., Chenop. Monogr. Enum.: 10 (1840).

(9) *Chenopodium latifolium* (Benth.) S. Fuentes & Borsch, **comb. nov.**
Basionym: *Rhagodia latifolia* (Benth.) Paul G. Wilson, Nuytsia 4(2): 228. 1983. ≡*Rhagodia crassifolia* var. *latifolia* Benth., Fl. Austral. 5: 155. 1870.

(9a) *Chenopodium latifolium* subsp. *rectum* (Paul G. Wilson) S. Fuentes & Borsch, **comb. nov.**
Basionym: *Rhagodia latifolia* subsp. *recta* Paul G. Wilson, Nuytsia 4(2): 228. 1983.

(10) *Chenopodium drummondii* (Moq.) S. Fuentes & Borsch, **comb. nov.**
Basionym: *Rhagodia drummondii* Moq., Prod. (DC.) 13(2): 52. 1849.

(11) *Chenopodium spinescens* (R. Br.) S. Fuentes & Borsch, **comb. nov.**
Basionym: *Rhagodia spinescens* R. Br., Prodr. Fl. Nov. Holland.: 408. 1810.

(12) *Chenopodium eremaea* (Paul G. Wilson) S. Fuentes & Borsch, **comb. nov.**
Basionym: *Rhagodia eremaea* Paul G. Wilson, Nuytsia 4(2): 232. 1983.

(13) *Chenopodium parabolicum* (R. Br.) S. Fuentes & Borsch, **comb. nov.**
Basionym: *Rhagodia parabolica* R. Br., Prodr. Fl. Nov. Holland.: 408. 1810.

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Appendices A–D. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2011.10.006.

References

Aellen, P., 1960. Chenopodiaceae. In: Rechinger, K.H., Hegis Illustrierte Flora von Mitteleuropa. Band 3. 2 Auflage. Berlin and Hamburg, pp. 533–762.

Aellen, P., Just, T., 1943. Key and synopsis of the American species of the genus *Chenopodium*L. Am. Midl. Nat. 30, 47–76.

Álvarez, I., Wendel, J.F., 2003. Ribosomal ITS sequences and plant phylogenetic inference. Mol. Phylogenet. Evol. 29, 417–434.

Baldwin, B.G., Wessa, B.L., 2000. Origin and relationships of the tarweed-silversword lineage (Compositae-Madiinae). Am. J. Bot. 87, 1890–1908.

Bentham, G., 1870. Fl. austral, vol. 5. Loveed Reeved Co., London.

Bentham, G., Hooker, J.D., 1880. Chenopodiaceae. In: Genera Plantarum ad exemplaria imprimis in herbariis Kewensibus. Vol. 3, pp. 43–78.

Bhargava, A., Shukla, S., Ohri, D., 2006. Karyotypic studies on some cultivated and wild species of *Chenopodium* (Chenopodiaceae). Genet. Resour. Crop Evol. 53, 1309–1320.

Blöch, C., Weiss-Schneeweiss, H., Schneeweiss, G.M., Barfuss, M.H.J., Rebernig, C.A., Villaseñor, J.L., Stuessy, T.F., 2009. Molecular phylogenetic analyses of nuclear and plastid DNA sequences support dysploid and polyploid chromosome number changes and reticulate evolution in the diversification of *Melampodium* (Millerieae, Asteraceae). Mol. Phylogenet. Evol. 53, 220–233.

Bonzani, N.E., Barboza, G.E., Bugatti, M.A., Ariza Espinar, L., 2003. Morpho-histological studies in the aromatic species of *Chenopodium* from Argentina. Fitoterapia 74, 207–225.

Borsch, T., Quandt, D., 2009. Mutational dynamics and phylogenetic utility of non-coding chloroplast DNA. Plant Syst. Evol. 282, 169–199.

Borsch, T., Hilu, K.W., Quandt, D., Wilde, V., Neinhuis, C., Barthlott, W., 2003. Non-coding plastid *trnT–trnF* sequences reveal a well resolved phylogeny of basal angiosperms. J. Evol. Biol. 16, 558–576.

Borsch, T., Hilu, K.W., Wiersema, J.H., Löhne, C., Barthlott, W., Wilde, V., 2007. Phylogeny of *Nymphaea* (Nymphaeaceae): evidence from substitutions and microstructural changes in the chloroplast *trnT–trnF* region. Int. J. Plant Sci. 168, 639–671.

Carolin, R.C., 1983. The trichomes of the Chenopodiaceae and Amaranthaceae. Bot. Jahrb. Syst. 103, 451–466.

Carolin, R.C., Jacobs, S.W.L., Maret, V., 1975. Leaf structure in chenopodiaceae. Bot. Jahrb. Syst. 95, 226–255.

Chu, G.L., Stutz, H.C., Sanderson, S.C., 1991. Morphology and taxonomic position of *Suckleya suckleyana* (Chenopodiaceae). Am. J. Bot. 78, 63–68.

Clemants, S.E., Mosyakin, S.L., 2003. Chenopodium. In: Welsh, L.S., Cro mpton, W.C., Clemants, S.E. (Eds.), Flora of North America: Magnoliophyta: Caryophyllidae, vol. 4. Oxford University Press, New York, pp. 275–300 (part 1).

Croemwell, B.T., 1950. The micro-estimation and origin of trimethylamine in *Chenopodium vulvaria* L. Biochem. J. 46, 578–582.

Eckardt, T., 1967. Vergleich von *Dysphania* mit *Chenopodium* und mit Illecebraceae. Bauhinia 3, 327–344.

Ellis, J.R., Janick, J., 1960. The chromosomes of *Spinacia oleracea*. Amer. J. Bot. 47, 210–214.

Ellison, N.W., Liston, A., Steiner, J.J., Williams, W.M., Tayler, N.L., 2006. Molecular phylogenetics of the clover genus (*Trifolium*-Leguminoseae). Mol. Phylogenet. Evol. 39, 688–705.

Farris, J.S., Källersjö, M., Kluge, A.G., Bult, C., 1994. Testing significance of incongruence. Cladistics 10, 315–319.

Flores Olvera, H., Davis, J.I., 2001. A cladistic analysis of *Atripliceae* (Chenopodiaceae) based on morphological data. J. Torrey Bot. Soc. 128, 297–319.

Flores Olvera, H., Fuentes-Soriano, S., Hernández, E.M., 2006. Pollen morphology and systematics of *Atripliceae* (Chenopodiaceae). Grana 45, 175–194.

Guggisberg, A., Mansion, G., Conti, E., 2009. Disentangling reticulate evolution in an Arctic–Alpine polyploid complex. Syst. Biol. 58, 55–73.

Heklau, H., Röser, M., 2008. Delineation, taxonomy and phylogenetic relationships of the genus *Krascheninnikovia* (Amaranthaceae subtribe *Axyridinae*). Taxon 57, 563–576.

Hidalgo, O., Garcia-Jaca, N., Garnatje, T., Susanna, A., Siljak-Yakovlev, S., 2007. Karyological evolution in *Rhaponticum* Vaill. (Asteraceae, Cardueae) and related genera. Bot. J. Linn. Soc. 153, 193–201.

Hohmann, S., Kadereit, J., Kadereit, G., 2006. Understanding Mediterranean-Californian disjunctions: molecular evidence from Chenopodiaceae-Betoideae. Taxon 55, 67–78.

Huelsenbeck, J.P., Ronquist, F., 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17, 754–755.

Iljin, M., 1936. Chenopodiaceae. In: Komarov, V.L. (Ed.), Flora SSSR 6. Moscow & Leningrad, pp. 2–354.

Jacobs, S.W.L., 2001. Review of leaf anatomy and ultrastructure in the Chenopodiaceae (Caryophyllales). J. Torrey Bot. Soc. 128, 236–253.

Judd, W.S., Ferguson, I.K., 1999. The genera Chenopodiaceae in the Southeastern United States. Harv. Pap. Bot. 4, 365–416.

Kadereit, G., Borsch, T., Weising, K., Freitag, H., 2003. Phylogeny of Amaranthaceae and Chenopodiaceae and the evolution of C4 photosynthesis. Int. J. Plant Sci. 164, 959–986.

Kadereit, G., Mavrodiev, E.V., Zacharias, E.H., Sukhorukov, A.P., 2010. Molecular phylogeny of *Atripliceae* (Chenopodioideae, Chenopodiaceae): implications for systematics, biogeography, flower and fruit evolution, and the origin of C4 photosynthesis. Am. J. Bot. 97, 1664–1687.

Kapralov, M.V., Akhani, H., Voznesenskaya, E.V., Edwards, G., Franceschi, V., Roalson, E.H., 2006. Phylogenetic relationships in the Salicornioideae/Suaedoideae/Salsoloideae s.l. (Chenopodiaceae) clade and a clarification of the phylogenetic position of *Bienertia* and *Alexandra* using multiple DNA sequence data sets. Syst. Bot. 31, 571–585.

Kolano, B., Siwińska, D., Maluszyńska, J., 2008. Comparative cytogenetic analysis of diploid and hexaploid *Chenopodium album* agg. Acta Soc. Bot. Polon. 4, 293–298.

Kühn, U., 1993. Chenopodiaceae. In: Kubitzki, K. (Ed.), The families and genera of vascular plants, vol. 2. Springer, Hamburg, pp. 253–281.

Löhne, C., Borsch, T., 2005. Molecular evolution and phylogenetic utility of the *petD* group II intron: a case study in basal angiosperms. Mol. Biol. Evol. 22, 317–332.

Mansion, G., Zeltner, L., Bretagnolle, F., 2005. Phylogenetic patterns and polyploid evolution within the Mediterranean genus *Centaurium* (Gentianaceae-*Chironieae*). Taxon 54, 931–950.

Meyer, C.A., 1829. Chenopodeae [Chenopodiaceae]. In: Ledebour, C.F., Flora, G. (Eds.), Altaica, vol. 1. Reimer, Berlin, pp. 370–418.

Moquin-Tandon, A., 1840. Chenopodearum Monographica Enumerato. Parisiis, Tolosae.

Moquin-Tandon, A., 1849. Salsolaceae. In: Candolle, A.P. de (Ed.) Prodromus systematics naturalis, vol. 13. sect 2., Parisiis, pp. 43–230.

Morrison, D., 2009. A framework for phylogenetic sequence alignment. Plant Syst. Evol. 282, 127–149.

Mosyakin, S.L., Clemants, S.E., 1996. New infrageneric taxa and combinations in *Chenopodium* L. (Chenopodiaceae). Novon 6, 398–403.

Mosyakin, S.L., Clemants, S.E., 2002. New nomenclatural combinations in *Dysphania* R. Br. (Chenopodiaceae): taxa occurring in North America. Ukr. Bot. Zhurn. 59, 380–385.

Mosyakin, S.L., Clemants, S.E., 2008. Further transfers of glandular-pubescent species from *Chenopodium* subg. *Ambrosida* to *Dysphania* (Chenopodiaceae). J. Bot. Res. Inst. Texas 2, 425–431.

Müller, K.F., 2004. PRAP–computation of Bremer support for large data sets. Mol. Phylogenet. Evol. 31, 780–782.

Müller, K.F., 2005a. SeqState-primer design and sequence statistics for phylogenetic DNA data sets. Appl. Bioinf. 4, 65–69.

Müller, K.F., 2005b. The efficiency of different search strategies in estimating parsimony jackknife, bootstrap, and Bremer support. BMC Evol. Biol. 5, 58.

Müller, K.F., Borsch, T., 2005. Phylogenetics of Amaranthaceae based on *matK/trnK* sequence data: evidence from parsimony, likelihood, and Bayesian analyses. Ann. Mol. Bot. Gard. 92, 66–102.

Müller, K.F., Borsch, T., Hilu, K.W., 2006. Phylogenetic utility of rapidly evolving DNA at high taxonomical levels: Contrasting *matK*, *trnT-F*, and *rbcL* in basal angiosperms. Mol. Phylogenet. Evol. 41, 99–117.

Müller, J., Müller, K.F., Neinhuis, C., Quandt, D., 2007. PhyDE-Phylogenetic Data Editor. http://www.phyde.de.

Murakeözy, E., Aïnouche, A., Meudec, A., Deslandes, E., Poupart, N., 2007. Phylogenetic relationships and genetic diversity of the *Salicornieae*

(Chenopodiaceae) native to the Atlantic coasts of France. Plant Syst. Evol. 264, 217–237.
Nieto Feliner, G., Rosselló, J.A., 2007. Better the devil you know? Guidelines for insightful utilization of nrDNA ITS in species-level evolutionary studies in plants. Mol. Phylogenet. Evol. 44, 911–919.
Nieto Feliner, G., Fuertes Aguilar, J., Rosselló, J.A., 2001. Can extensive reticulation and concerted evolution result in a cladistic structured molecular data set? Cladistics 17, 301–312.
Nixon, K.C., 1999. The parsimony ratchet, a new method for rapid parsimony analysis. Cladistics 15, 407–414.
Ochoterena, H., 2009. Homology in coding and non-coding DNA sequences: a parsimony perspective. Plant Syst. Evol. 282, 151–168.
Palomino, G.H., Segura, M.D., Bye, R., Mercado, P.R., 1990. Cytogenetic distinction between *Teloxys* and *Chenopodium* (Chenopodiaceae). Southwest Nat. 35, 351–353.
Pax, F., 1889. Caryophyllaceae. In: Engler, A., Prantl, K. (Eds.), Die Natürlichen Pflanzenfamilien, vol. 3, Teil 1. Abteilung B. Wilhelm Engelmann, Leipzig, pp. 61–94.
Pax, F., 1927. Zur Phylogenie der Caryophyllaceae. Bot. Jahrb. Syst. 61, 223–241.
Pax, F., Hoffmann, K., 1934. Dysphaniaceae. In: Engler, A., Prantl, K. (Eds.), Die Natürlichen Pflanzenfamilien ed. 2, vol. 16c. Wilhelm Engelmann, Leipzig, pp. 272–274.
Posada, D., Crandall, K., 1998. MODELTEST: testing the model of DNA substitution. Bioinformatics 14, 817–818.
Quandt, D., Müller, K.F., Stech, M., Frahm, J.P., Frey, W., Hilu, K.W., Borsch, T., 2004. Molecular evolution of the chloroplast *trnL-F* region in land plants. Monogr. Syst. Bot. Missouri Bot. Gard. 98, 13–37.
Rahiminejad, M.R., Gornall, R.J., 2004. Flavonoid evidence for allopolyploidy in the *Chenopodium album* aggregate (Amaranthaceae). Plant Syst. Evol. 246, 77–87.
Sánchez del Pino, I., Borsch, T., Motley, T.J., 2009. *TrnL-F* and *rpl*16 sequence data and dense taxon sampling reveal monophyly of unilocular anthered Gomphrenoideae (Amaranthaceae) and an improved picture of their internal relationships. Syst. Bot. 34, 57–67.
Sanderson, M.J., Wojciechowski, M.F., Hu, J.M., Khan, T.S., Brady, S.G., 2000. Error, bias, and long-branch attraction in data for two chloroplast photosystem genes in seed plants. Mol. Biol. Evol. 17, 782–797.
Schäferhoff, B., Müller, K.F., Borsch, T., 2009. Caryophyllales phylogenetics: disentangling Phytolaccaceae and Molluginacea and description of Microteaceae as a new isolated family. Willdenowia 39, 209–228.
Schneeweiss, G.M., Palomeque, T., Colwell, A.E., Weiss-Schneeweiss, H., 2004. Chromosome numbers and karyotype evolution in holoparasitic *Orobanche* (Orobanchaceae) and related genera. Am. J. Bot. 91, 439–448.
Scott, A.J., 1978a. A review of the classification of *Chenopodium* L. And related genera (Chenopodiaceae). Bot. Jahrb. Syst. 100, 205–220.
Scott, A.J., 1978b. *Rhagodiinae*: a new subtribe in the Chenopodiaceae. Feddes Repert. 89, 1–12.
Simmons, M.P., Ochoterena, H., 2000. Gaps as characters in sequence-based phylogenetic analyses. Syst. Biol. 49, 369–381.
Swofford, D.L., 1998. PAUP* Phylogenetic Analysis Using Parsimony (*and other methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.
Taberlet, P., Gielly, L., Pautou, G., Bouvet, J., 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. Plant Mol. Biol. 17, 1105–1109.
Turner, B.L., 1994. Chromosome numbers and their phyletic interpretation. In: Behnke, H.D., Mabry, T.J. (Eds.), Caryophyllales evolution and systematics. Springer-Verlag, Berlin, pp. 27–43.
Ulbrich, E., 1934. Chenopodiaceae. In: Engler, A., Prantl, K. (Eds.) Die Natürlichen Pflanzenfamilien, vol. 2, band 16c.Wilhelm Engelmann, Leipzig, pp. 379–584.
Uotila, P., 1973. Chromosome counts on *Chenopodium* L. SE Europe and SW Asia. Ann. Bot. Fenn. 10, 337–340.
Uotila, P., 2001. Taxonomic and nomenclatural notes on *Chenopodium* (Chenopodiaceae) for Flora Nordica. Ann. Bot. Fenn. 38, 95–97.
Van der Niet, T., Linder, H.P., 2008. Dealing with incongruence in the quest for the species tree: a case study from the orchid genus *Satyrium*. Mol. Phylogenet. Evol. 47, 154–174.
Weber, W.A., 1985. The genus *Teloxys* (Chenopodiaceae). Phytologia 58, 477–478.
Welsh, L.S., Crompton, W.C., Clemants, S.E., 2003. Chenopodiaceae. In: Flora of North America: Magnoliophyta: Caryophyllidae Part 1, vol. 4. Oxford University Press, New York, pp. 258–404.
Wendel, J.F., Doyle, J.J., 1998. Phylogenetic incongruence. Window into genome history and molecular evolution. In: Soltis, D.E., Soltis, P.S., Doyle, J.J. (Eds.), Molecular systematics of plants II: DNA sequencing. Kluwer Academic Publishers, London, pp. 265–296.
White, T.J., Bruns, T., Lee, S., Taylor, J., 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis, M.A., Gelfand, D.H., Shinsky, J.J., White, T.J. (Eds.), PCR protocols: a guide to methods and applications. Academic Press, San Diego, pp. 315–322.
Wiersema, J.H., León, B., 1999. World economic plants: a standard reference. CRC Press, Boca Raton.
Wilson, P.G., 1983. A taxonomic revision of the tribe *Chenopodieae* (Chenopodiaceae) in Australia. Nutsya 4, 135–162.
Wilson, H.D., 1988. Quinoa biosystematics I: domesticated populations. Econ. Bot. 42, 461–477.
Wilson, H.D., Heiser Jr., C.B., 1979. The origin and evolutionary relationships of 'Huauzontle' (*Chenopodium nuttalliae* Safford), domesticated Chenopod of Mexico. Am. J. Bot. 66, 198–206.
Wilson, H.D., Manhart, J., 1993. Crop/weed gene flow: *Chenopodium quinoa* Willd. And *C. berlandieri* Moq. Theor. Appl. Genet. 86, 642–648.
Worberg, A., Quandt, D., Barniske, A.M., Löhne, C., Hilu, K.W., Borsch, T., 2007. Phylogeny of basal eudicots: insights from non-coding and rapidly evolving DNA. Org. Divers. Evol. 7, 55–77.
Zacharias, E.H., Baldwin, B.H., 2010. A molecular phylogeny of North American *Atripliceae* (Chenopodiaceae), with implications for floral and photosynthetic pathway evolution. Syst. Bot. 35, 839–857.
Zhu, G., Mosyakin, S.L., Clemants, S.E., 2003. Chenopodiaceae. In: Zhengyi, W., Raven, P.H., Deyuan, H. (Eds.), Flora of China, vol. 5. Science Press and Missouri Botanical garden Press, New York, pp. 351–414.