A novel phylogeny-based generic classification for Chenopodium sensu lato, and a tribal rearrangement of Chenopodioideae (Chenopodiaceae)

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A novel phylogeny-based generic classification for *Chenopodium* sensu lato, and a tribal rearrangement of *Chenopodioideae (Chenopodiaceae)*

Abstract

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Molecular phylogenetic analysis of the subfamily *Chenopodioideae* of the goosefoot family *(Chenopodiaceae)*, with the addition of *matK/trnK* sequences to an existing *trnL-F* data set, indicates that *Chenopodium* as traditionally recognised consists of six independent lineages. One of these, the *Dysphania-Teloxys* clade, had already been recognised previously as a separate tribe *Dysphanieae.* Of the five others, *Chenopodium* is here re-defined in a narrow sense so as to be monophyletic. The *C. polyspermum, C. rubrum* and *C. murale* clades are successive sisters of a lineage constituted by *Atripliceae* s.str. plus *Chenopodium* s.str. Consequently, the long forgotten genera *Lipandra* (for *C. polyspermum)* and *Oxybasis* (for *C. rubrum* and relatives) are revived, and the new genus *Chenopodiastrum* (for *C. murale* and relatives) is published. The afore-mentioned five clades, taken together, are a monophylum corresponding to an enlarged tribe *Atripliceae* (a name that has priority over *Chenopodieae*). Last, the Linnaean genus *Blitum* (for *C. capitatum* and relatives), enlarged to include *C. bonus-henricus,* is the sister group of *Spinacia* in the tribe *Anserineae* (a name that has priority over *Spinacieae*). The aromatic species of *Dysphania*, the related genus *Teloxys,* as well as *Cyclocoma* and *Suckleya* form the enlarged tribe *Dysphanieae*. Building upon phylogenetic results, the present study provides a modern classification for a globally distributed group of plants that had suffered a complex taxonomic history due to divergent interpretation of single morphological characters for more than two hundred years. The seven genera among which the species traditionally assigned to *Chenopodium* are now distributed are defined morphologically and keyed out; for four of them *(Blitum, Chenopodiastrum, Lipandra, Oxybasis)* the component species and subspecies are enumerated and the necessary nomenclatural transfers are effected.

Additional key words: *Caryophyllales,* phylogenetic classification, non-coding chloroplast DNA, nrITS, *Blitum, Chenopodiastrum, Lipandra, Oxybasis*

Introduction

Chenopodium L. has been considered as one of the largest genera in the *Chenopodiaceae* Vent., with an estimated number of about 150 species (Kühn 1993). The history of its classification is complex and over time various generic and infrageneric taxa were recognised by different authors. Providing one of the most comprehensive treatments of the group, Aellen (1960–61) for example divided the genus in no less than 13 sections. Several modern treatments of *Chenopodium* recognised three subgenera, viz. *C.* subg. *Ambrosia* A. J. Scott, subg. *Chenopodium* and subg. *Blitum* (L.) Hiitonen (e.g. Uotila 2001b, Clemants & Mosyakin 2003). The presence of glandular hairs and aromatic secondary compounds in the species of *C.* subg. *Ambrosia* led Carolin (1983) and Mosyakin & Clemants (2002) to recognise a separate genus *Dysphania* R. Br., as they believed these characters to indi-

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cate the existence of a lineage independent from the rest of *Chenopodium*. However, many of the morphological characters in *Chenopodium* s.lat. are rather homoplastic. This was also the cause for strongly differing concepts of genera and infrageneric entities that were based on divergent interpretations of single morphological characters.

In "Species Plantarum" Linnaeus (1753) described *Blitum* L. and *Chenopodium* as two different genera based on the number of stamens, one in *Blitum* (class *Monandria*) and five in *Chenopodium* (class *Pentandria*). While *Blitum* was accepted as a distinct genus by Meyer (1829), Moquin-Tandon (1849), Schur (1866) and Scott (1978), other authors included it in *Chenopodium* s.lat., first as a section (Ambrosi 1857) and then as a subgenus (Hiitonen 1933). Currently, *C.* subg. *Blitum* is widely accepted, containing five sections: *C.* sect. *Blitum* (L.) Benth. & Hook. f., *C.* sect. *Pseudoblitum* (Gren. & Godr.) Syme, *C.* sect. *Glauca* (Standl.) Ignatov, *C.* sect. *Agathophytum* (T. Nees) Benth. & Hook. f. and *C.* sect. *Degenia* Aellen (Mosyakin & Clemants 1996; Judd & Ferguson 1999; Mosyakin 2002).

More recently, molecular phylogenetic analyses of *Chenopodium* s.lat. and the *Chenopodioideae* Burnett have revolutionised our understanding of this group of plants. These studies recover for *Chenopodioideae* the tribes *Atripliceae* Duby, *Chenopodieae* Dumort. and *Axyrideae* G. Kadereit & Sukhor. (Kadereit & al. 2003; Kadereit & al. 2010). Moreover, the results have clearly shown that *Chenopodium* as widely treated during the past decades is not monophyletic. First hints were obtained from the analysis of relationships in the *Chenopodiaceae-Amaranthaceae* alliance, which pointed to at least three independent lineages of *Chenopodium* s.lat. within the *Chenopodioideae* (Kadereit & al. 2003; Müller & Borsch 2005). The incremented taxon sampling of *Chenopodium* s.lat. then allowed Fuentes-Bazan & al. (2012) to resolve five individual lineages based on sequence data of the plastid region *trnL-F* and the nuclear ITS region. While all five lineages as such gained good support, their position within *Chenopodioideae* remained partly unclear. The most diverse of these lineages, which includes *C. album* L., the type of the generic name (Mosyakin & Clemants 1996), is referred to as *Chenopodium* s.str. It includes also the members of the former Australian genera *Einadia* Raf. and *Rhagodia* R. Br. (Wilson 1983), which could be unambiguously shown as derivatives of *Chenopodium* s.str. (Fuentes-Bazan & al. 2012). Another lineage corroborates the pre-cladistic view (Mosyakin & Clemants 1996) that the aromatic species of *C.* subg. *Ambrosia* form a distinct group, and hence support their transfer to the separate genus *Dysphania* R. Br. (Kadereit & al. 2010; Zacharias & Baldwin 2010; Fuentes-Bazan & al. 2012).

The classification of the remaining three lineages of *Chenopodium* s.lat. within the *Chenopodioideae* remains to be revised, both at the generic and species level. These lineages are: (1) the sister clade of *Spinacia* L. enclosed in the clade of the *Anserineae* Dumort., which comprises a large share of the species previously assigned to *C.* subg. *Blitum;* (2) a lineage composed of *C. rubrum* L. and relatives, thus encompassing another part of the species previously so classified (e.g. *C. glaucum* L.*, C. rubrum*); (3) a lineage constituted by *C. murale* L. and some other species of *C.* subg. *Chenopodium* (e.g. *C. coronopus* Moq., *C. hybridum* L.). Whereas *Chenopodium* s.str. was shown as sister to *Atripliceae, Blitum* to belong to the *Anserineae* and the aromatic group as *Dysphania* to a separate tribe *Dysphanieae* Pax, the positions of the *C. murale* lineage and *C. rubrum* lineage within *Chenopodioideae* were not yet clear (see Fuentes-Bazan & al. 2012) and *C. polyspermum* L. was unassessed. Adding further characters from the *matK/trnK* region allows to test the relationships shown in the tree based on *trnL-F* (Fuentes-Bazan & al. 2012).

In this sense, the objectives of the present paper are: (i) to assess the position of the *Chenopodium rubrum* and *C. murale* lineages within *Chenopodioideae* using a combined data set of *trnL-F* and *matK/trnK* plastid regions, (ii) to establish the position of *C. polyspermum* within *Chenopodioideae* and (iii) to discuss, based on the phylogenetic reconstruction, the taxonomic status of the genera and tribes within the subfamily and to elaborate the correct formal taxonomy for the revealed lineages.

Material and methods

Taxon sampling — Species of *Chenopodium* s.str., the *C. rubrum* clade, the *C. murale* clade and also of the tribes *Atripliceae, Axyrideae, Dysphanieae* and *Anserineae* were sampled, following Fuentes-Bazan & al. (2012). The new sample added in this study is *C. polyspermum*. Representatives from *Betoideae* Ulbr. (*Beta* L. and *Hablitzia* M. Bieb.) and *Salicornioideae* Ulbr. (*Allenrolfea* Kuntze) were used as outgroups based on the tree of Müller & Borsch (2005). All samples and their vouchers are listed in Appendix 1.

DNA isolation, amplification and sequencing — Genomic DNA of the new samples was isolated from silica gel dried leaf tissue using the modified CTAB method (Borsch & al. 2003), or, in most cases, was already available from the study of Fuentes-Bazan & al. (2012). The nuclear ITS region and the plastid *trnL-F* region were amplified and sequenced following the methodology described in Fuentes-Bazan & al. (2012). The *matK/trnK* region was amplified and sequenced in two overlapping halves, or in four overlapping halves for herbarium specimens and other difficult samples, using internal primers and protocols as described by Müller & Borsch (2005).

Alignment and coding of length mutational events — Sequences were edited and aligned manually using PhyDE (Phylogenetic Data Editor) version 0.995 (Müller J. & al. 2007), following the rules outlined in Löhne &

Borsch (2005). Regions of uncertain homology (mutational hotspots) were excluded from the analysis (Borsch & al. 2003; Müller & Borsch 2005). The *trnL-F* and *matK/trnK* data sets were combined for phylogenetic analysis. Indels were coded with the Simple Indel Coding method (Simmons & Ochoterena 2000) using the program SeqState 1.40 (Müller 2005a).

Phylogenetic analyses — Maximum Parsimony (MP) analyses were carried out using the Parsimony Ratchet (Nixon 1999) as implemented in the software PRAP (Müller 2004) in combination with PAUP* version 4.0b10 (Swofford 1998). Ratchet settings were 200 ratchet iterations with 25 % of the positions randomly upweighted (weight = 2) during each replicate and 10 random addition cycles. PRAP generated command files 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. In order to evaluate the confidence into individual branches of the topology, Jackknife (JK) support was calculated 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 (Müller 2005b).

Bayesian inference (BI) was done with MrBayes 3.1 (Huelsenbeck & Ronquist 2001). The best nucleotide substitution model for the combined data set of *trnL-F-matK/trnK* was GTR+G based on the AIC criteria calculated by JModeltest 0.1 (Posada 2008). A binary (restriction site) model was assumed for the coded indels. All analyses were implemented 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 200 000, and a majority consensus tree was computed with the remaining trees.

Results

PCR amplification of the complete *trnL-F* region (*trnL* gene including group I intron and spacer) was successful for all samples except *Chenopodium polyspermum,* although specific *Amaranthaceae*-*Chenopodiaceae* primers were used in two overlapping halves. For the latter species, products could only be obtained for the *trnL* intron but not for the *trnL-F* spacer. For *matK/trnK* the amplification was successful. The tree reconstruction was done with a combined data set including the intron of *trnL* of *C. polyspermum* (Fig. 1).

The combined *trnL-F* and *matK/trnK* data set — The aligned combined data set, without the areas classified as "hotspots" (HS), comprised 3772 characters, including 822 characters that were parsimony informative. In the *trnL-F* region seven HS were excluded (Fuentes-Bazan & al. 2012) and in the *matK/trnK* region three HS were excluded. The statistics of the regions including and excluding HS are in Appendix 2. One inversion was found in the *trnL* intron in *Krascheninnikovia* Gueldenst. (Fuentes-Bazan & al. 2012). The final matrix, including coded indels, comprised 3992 characters, of which 948 characters were parsimony informative. The MP search resulted in 128 shortest trees (L=2415, CI=0.720, RI=0.918 and RC= 0.661). The resulting strict consensus tree for MP was identical in topology with the Bayesian (BI) majority-rule consensus tree (Fig. 1).

The nuclear ITS data set — For the ITS data set of *Chenopodium* s.lat. the sequence lengths varied for ITS1 from 148 to 171 nt and for ITS2 from188 to 205 nt without hotspots. Only one hotspot of about 65 nt in length was detected in ITS1 and two hotspots of 6 and 26 nt in length, respectively, were found in ITS2. Including the indels coded for the ITS data set, the matrix had 668 characters in total and of all characters 39 % were parsimony informative. Parsimony analyses with indels coded resulted in 93 shortest trees (L=764, CI=0.552, RI=0.849, RC=0.469) for the ITS data set. The tree topology recovered by both MP and Bayesian analyses was identical (Fig. 2).

Phylogenetic relationships — Both tree inference methods (MP and BI) recovered eight major lineages within *Chenopodioideae* based on the combined plastid data set (Fig. 1). *Chenopodium* s.str. is highly supported as monophyletic by the plastid data set (100 % JK/1 PP) and well supported by the nuclear data set (87 % JK/ 0.95 PP).

The *Atripliceae* s.str. (100 % JK/1 PP), represented by *Atriplex* L. and *Microgynoecium* Hook. f., is supported as the sister clade to *Chenopodium* s.str. by both genomic compartments (Fig. 1 and 2).

The sister clade to *Atripliceae* s.str. plus *Chenopodium* s.str., based on the combined plastid data set, is the *C. murale* clade (100 % JK/1 PP, = *Chenopodiastrum* in Fig. 1 and 2), which includes the closely related *C. murale* and *C. coronopus* (100 % JK/1 PP) and their sister clade with *C. hybridum* L. and *C. badachschanicum* Tzvelev (100 % JK/1 PP, Fig. 1).

The sister clade to all the previous clades is the *Chenopodium rubrum* clade (100 % JK/1 PP, = *Oxybasis* in Fig. 1 and 2), encompassing the closely related *C. rubrum* and *C. glaucum* (91 % JK/ 1 PP), *C. urbicum* as their sister (100 % JK/1 PP) and *C. chenopodioides* as the sister to all three (100 % JK/ 1 PP, Fig. 1).

The samples of *Chenopodium polyspermum* constitute an own, highly supported lineage, based on the plastid regions (99 % JK, = *Lipandra* Fig. 1 and 2), sister to the monophyletic group composed by the *C. rubrum,* the *C. murale, Atripliceae* s.str. and *Chenopodium* s.str. clades. Based on the ITS data set all the described clades are supported but show a position inconsistent with that based on the plastid regions (Fig. 2).

The tribe *Anserineae* (100 % JK/1 PP) is highly supported based on the plastid data set and well supported based on the nuclear ITS data set (75 % JK/0.89 PP, Fig. 2), encompassing two defined sister lineages: the *Spinacia* lineage (100 % JK/1 PP with both reconstructions) with *S. oleracea* L., *S. tetrandra* Steven ex M. Bieb. and *S. turkestanica* Iljin.; and a lineage of *Chenopodium capitatum* (L.) Ambrosi, *Monolepis nuttalliana* (Schult.) Greene and *C. foliosum* Asch. (100 % JK/ 1 PP), *C. californicum* (S. Watson) S. Watson (100 % JK/ 1 PP) and *C. bonus-henricus* L. (= *Blitum* in Fig. 1 and 2). These two subclades are supported by the nuclear data set but their internal relationships are not recovered (Fig. 2).

The tribe *Dysphanieae* is highly supported by both reconstructions (100 % JK/1 PP), encompassing *Dysphania* and *Teloxys* Moq. In spite of the increased number of characters in the combined data set, *Dysphanieae* are still showing an unresolved position within *Chenopodioideae* (compare Fig. 1 and 2).

Finally, the tribe *Axyrideae* (100 % JK/1 PP), represented by *Axyris* L.*,* *Ceratocarpus* Buxb. ex L. and *Krascheninnikovia,* is highly supported based on both data sets. Its position within *Chenopodioideae,* however, is inconsistently resolved in the trees based on cp DNA an nuclear ITS.

Discussion

Phylogenetic position of the lineages of *Chenopodium* s.lat. in the *Chenopodioideae*

Based on the combined data set of *trnL-F* and *matK/trnK,* the phylogenetic reconstruction recovers six highly supported lineages of *Chenopodium* s.lat. within subfamily *Chenopodioideae*. The delimitation of *Chenopodium* s.str. as monophyletic is again highly supported as is its sister group relationship with the tribe *Atripliceae* s.str. At the next successive deeper nodes the *Chenopodium murale* and *C. rubrum* clades branch off, with maximam or near maximum (95 % JK) support (*Chenopodiastrum* and *Oxybasis* in Fig. 1), confirming the previous *trnL-F* tree (Fuentes-Bazan & al. 2012).

A new, isolated lineage of *Chenopodium polyspermum* as sister to all previously mentioned clades is found with cp DNA (*Lipandra* in Fig. 1) but lacks convincing support with ITS (inconsistent topology, see Fig. 2). Nevertheless, the isolated position of *C. polyspermum* within the *Atripliceae* s.lat. is indicated by both genomic compartments in agreement with the deviating morphology reported by Uotila (2001b).

Moreover, in the present study the new resolved phylogeny supports the view that the tribe *Atripliceae* in the sense of Kadereit & al. (2010) should be extended in order to accommodate the four different *Chenopodium* s.lat. lineages described above (see Taxonomic treatment). The alternative scenario of creating three additional, small tribes in order to classify monophyletic entities, appears inferior.

While the tribes *Dysphanieae* and *Anserineae* are well supported as such, their relative position becomes even less well defined when more chloroplast characters are sampled (Fig. 1). The *trnL-F* tree of Fuentes-Bazan & al. (2012) had shown the *Dysphanieae* as second and the *Anserineae* as third branch in *Chenopodioideae*. The tribe *Dysphanieae* is also recovered in the phylogenetic reconstruction of Kadereit & al (2010), a formal circumscription, however, was not suggested. Based on Kadereit & al. (2010), Fuentes-Bazan & al. (2012) and the present study, the close relationship of *Dysphania, Cycloloma* Moq., *Suckleya* A. Gray and *Teloxys* is evident as implemented in our circumscription of the tribe *Dysphanieae* (see Taxonomic treatment).

Within *Anserineae,* the already well supported sister relationship of *Spinacia* to the lineage of *Chenopodium capitatum, Monolepis nuttalliana, C. foliosum* and relatives is once more confirmed by *matK/trnK* data in this study (= *Blitum* in Fig. 1 and 2). In this sense the present study redefines the tribe *Anserineae* (see Taxonomic treatment). Modern treatments recognise three species of *Spinacia,* all of which were sampled already by Fuentes-Bazan & al. (2012) and again in this study (Fig. 1): *S. oleracea, S. tetrandra* and *S. turkestanica* (Iljin 1936; Kühn 1993; Shults 2003). *Spinacia* can be easily separated from its sister lineage by monoecy, and, as pointed out by Flores-Olvera & al. (2011), by the pistillate flowers being enclosed by two opposite accrescent perianth segments. Species of *Chenopodium* s.lat. mostly have three or five herbaceous or fleshy but not accrescent perianth segments. In addition, *Spinacia* has a chromosome base number of 6 (Schmitz-Linneweber & al. 2001) that appears to be reduced from a base number of 9 found in other *Chenopodioideae* (Fuentes-Bazan & al. 2012).

While the crown groups of the *Chenopodium capitatum* clade, the *C. rubrum* clade, the *C. murale* clade and the *C. polyspermum* clade as being independent from the *Chenopodium* s.str. clade have been established by phylogenetic analyses in Fuentes-Bazan & al. (2012) and in this study, their internal relationships and classification remain to be evaluated. We will discuss clade by clade in the following.

Internal relationships and taxonomy of the different clades of *Chenopodium* sensu lato

The lineage of *Chenopodium capitatum* and relatives

Phylogeny. — Molecular phylogenetic analyses of plastid and nuclear ITS sequences provided evidence for the relationship of *Chenopodium capitatum* (≡ *Blitum capitatum*) and *C. foliosum* (= *B. virgatum*), which taken together constituted the genus *Blitum* (Fig. 1 and 2) in its original Linnaean circumscription. Moreover, phylogenetic reconstruction shows that *Monolepis nuttalliana*

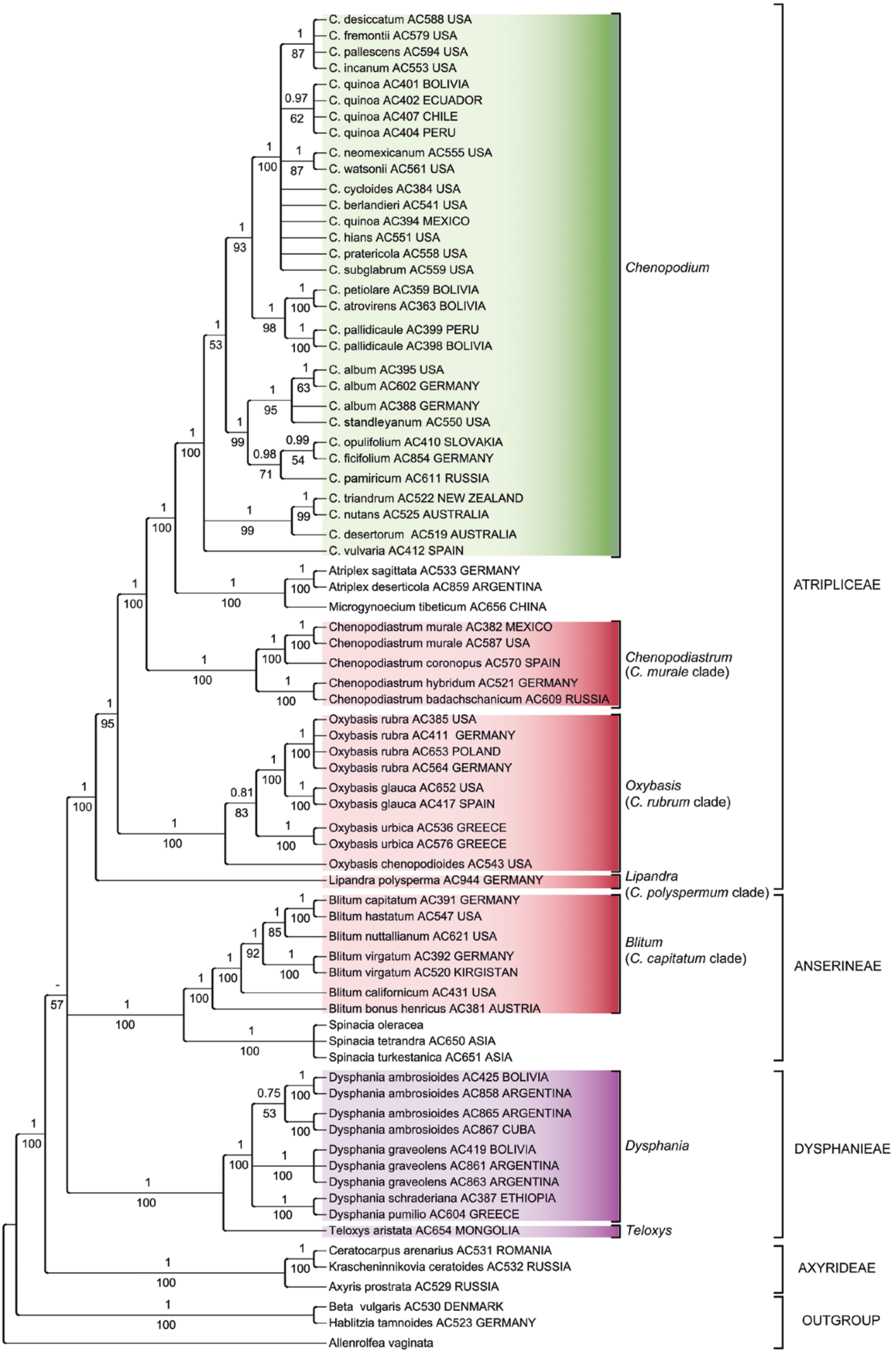

Fig. 1. Strict consensus tree based on the *trnL-F* and *matK/trnK* data sets. – Jackknife values (JK) are given below and Bayesian posterior probabilities (PP) for the respective nodes above branches. All clades that were previously classified under the generic name *Chenopodium* s.lat. are highlighted with colours (green = *Chenopodium* s.str; red = genera recognised newly in this study; violet = *Dysphania* and *Teloxys* as recognised by recent previous studies).

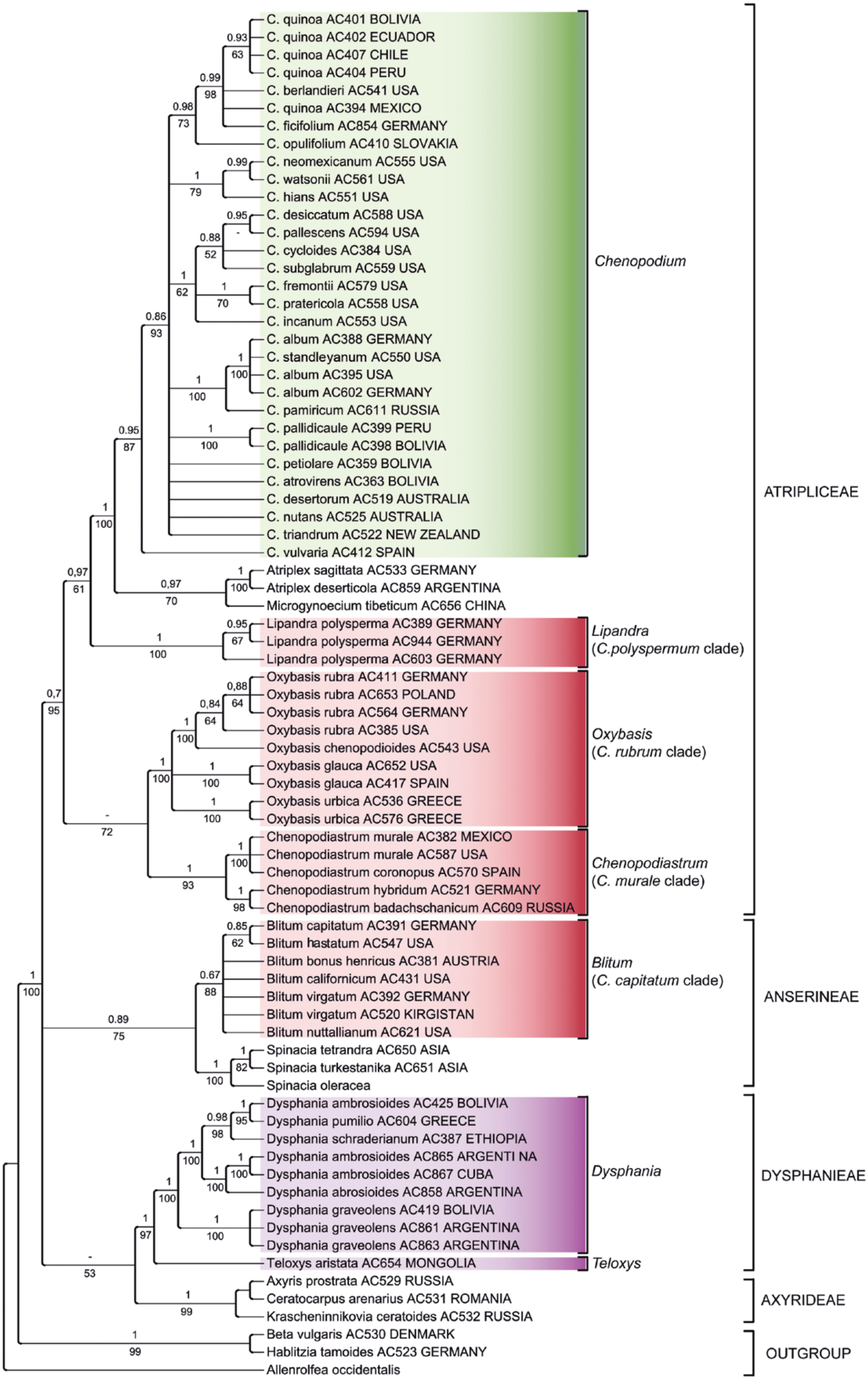

Fig. 2. Strict consensus tree based on the ITS data set. – Jackknife values (JK) are given below and Bayesian posterior probabilities (PP) for the respective nodes above branches. All clades that were previously classified under the generic name *Chenopodium* s.lat. are highlighted with colours (green = *Chenopodium* s.str; red = genera recognised newly in this study; violet = *Dysphania* and *Teloxys* as recognised by recent previous studies).

(≡ *Blitum nuttallianum* Schult.) belongs to the same clade and, based on plastid data, appears to be close to *C. capitatum*. The addition of *matK/trnK* sequence data to the *trnL-F* matrix analysed in Fuentes-Bazan & al. (2012) further increased statistical support for a clade of these three species (Fig. 1), with *C. californicum* and *C. bonus-henricus* being successive sisters. The ITS trees, however, are largely unresolved and do not allow much insight into species relationships within the clade. Based on the phylogenetic analysis of *rbcL* sequences by Kadereit & al. (2003), the monotypic genus *Scleroblitum* Ulbr. is also part of the same clade (resolved as sister to *C. foliosum*). Its sole species in fact was originally described as *Blitum atriplicinum* by Mueller (1855).

On the other hand, our phylogenetic data indicate that other species originally described as members of the genus *Blitum,* such as *B. chenopodioides* (≡ *Chenopodium chenopodioides*), belong to the clade of *C. rubrum* rather than to the *C. capitatum* clade discussed here. The same holds true for several species described as *Chenopodium* but later transferred to *Blitum*, e.g. *C. rubrum* and *C. glaucum*.

Morphological characters. — The original delimitation of *Blitum* was based on low stamen number, vertical seeds and fleshy perianths forming succulent berry-like glomerules in fruit. Other species with vertical seeds but non-fleshy perianth in fruit and more stamens were later included, which considerably added heterogeneity to the genus. This led to description of a small segregate genus, *Scleroblitum,* with peculiar fruits, and to reinstating the genus *Monolepis*. At present, the *Chenopodium capitatum* clade is in floral characters and life form the most variable among the newly recognised lineages of *Chenopodium* s.lat. The numbers of perianth segments and stamens vary from (0–)1–3 in *Monolepis*, to 2–3 in *Blitum,* to 4 in *Scleroblitum* and to 4–5 in *C. bonus-henricus*. Perianth segments are usually connate at least near the base, often up to the middle, and they usually change in fruit stage. The plants vary from sturdy perennials to reduced annuals.

The taxonomic valuation of the fleshy perianth decreased when species with less succulent fruits but nevertheless closely related to species with fleshy perianth were described. The not-fleshy perianth is persistent and becomes in fruit more or less hardened in species that grow on higher mountains. This is the case in *Chenopodium exsuccum, C. litwinowii, C. korshinskyi* and *C. foliosum* subsp. *montanum*, which are related to *C. foliosum,* and in *C. hastatum,* which is related to *C. capitatum*. However, a tendency to a fleshy or in some other way changing perianth is still an important character for the differentiation between *Blitum* and similar genera.

The lineage of *Chenopodium rubrum* and relatives

Phylogeny. — The combined data set of *trnL-F* and *matK/trnK* in this study resolves a well-supported *Chenopodium rubrum* clade and also the internal relationships among its species. *C. rubrum* is sister to *C. glaucum*. Successive sisters to these two species are *C. urbicum* and *C. chenopodioides* (all taxa annotated as *Oxybasis* in Fig. 1, see also Taxonomic treatment, below), the latter being the morphologically most differentiated species of the whole clade. The nuclear data set of ITS supported the *C. rubrum* clade as different from the other lineages of *Chenopodium* s.lat.; the internal relationships of the species are, however, unresolved (Fig. 2).

Morphological characters. — The inclusion of several species both in the *Chenopodium capitatum* and *C. rubrum* clades tells about the morphological similarity of these clades, but also of their heterogeneity. Typical features for both clades are varying numbers of 1–3(–5) stamens, mostly vertical seeds and more or less glabrous surfaces (sometimes not so on the lower surface of leaves). Compared with the *C. capitatum* clade, plants of the *C. rubrum* clade are mostly clearly dimorphic: the terminal flowers are 5-merous and have horizontal seeds, the lateral flowers are 3-merous and have vertical seeds. In the *C. capitatum* clade flowers are not dimorphic and have usually less than 5 perianth segments and stamens, and the seeds are vertical. Perianth segments in the *C. rubrum* clade are dry to somewhat fleshy, but unchanged in fruit, whereas in the *C. capitatum* clade the perianth segments usually become succulent or hardened in fruit. All species in the *C. rubrum* clade are to some extent of an appearance that is intermediate between *Blitum* and *Chenopodium,* and hence the name "*Pseudoblitum"* was commonly accepted and used.

While all species of the *Chenopodium rubrum* clade have dimorphic flowers, hermaphroditic terminal ones and pistillate lateral flowers, the proportion varies considerably: 3-merous flowers with vertical seeds are numerous in *C. chenopodioides* and *C. rubrum,* quite few in *C. glaucum* and rare in *C. urbicum*. Terminal flowers are 5-merous, as is usual in *Chenopodium* s.str. and in the *C. murale* and *C. polyspermum* clades. Perianth segments of lateral flowers are connate to various degree, usually below the middle but in *C. chenopodioides* and *C. macrospermum* almost up to the apex. These species differ to some extent from the others also in other characters, such as the habit (lower branches subopposite, long), and their placement in a section of their own is well understood. On the other hand, *C. glaucum* and *C. macrospermum* differ from the other species in the clade and from other groups by sharing leaf blades that are glabrous above and very densely covered by vesicular hairs below.

Rarity of flowers with vertical seeds in *Chenopodium urbicum* and the shape and surface characters of seeds similar to, e.g. *C. album,* apparently caused the misplacement of *C. urbicum* with *C. album* and related species. The affinity of *C. urbicum* to *C.* sect. *Pseudoblitum* can be seen also in its missing vesicular hairs and pure to yellowish green colour. Perhaps, indications of some similarity of *C. rubrum, C. chenopodioides, C. urbicum* and even *C. glaucum* are quite frequent misidentifications between them.

The lineage of *Chenopodium murale* and relatives

Phylogeny. — The phylogenetic reconstruction of both plastid and nuclear regions resolved that *Chenopodium murale* is sister to *C. coronopus* and sister to these two species are *C. hybridum* and *C. badachschanicum* (under *Chenopodiastrum* in Fig. 1 and 2). *C. badachschanicum* is a Central Asiatic species, related to *C. hybridum* as supported by the present study and morphology (Uotila 1997, 2001a), even though its affinity with *C. hybridum* was not discussed by Tzvelev (1960).

Morphological characters. — Species and species groups of this clade are quite characteristic and different, even to the degree that it is quite easy to recognise them individually, but difficult to characterise the whole clade. *Chenopodium coronopus* is small in size, richly branched with long branches already from the base, the leaves have a small, deeply incised triangular-ovate blade with long, narrow lobes and a narrowly cuneate base; the sparse inflorescence is formed of small glomerules on main stem and short branches. Its diffuse branching habit and deeply lobed small leaves resemble superficially *Dysphania botrys* and related species. *C. murale* is a small to medium sized plant with quite short and few branches; leaves are rhombic-ovate with irregular large teeth; the dense inflorescence is formed of small glomerules terminal on main stem and lateral short branches. *C. hybridum, C. badachschanicum* and the related North American *C. simplex* have a quite sparingly branched angular stem, the leaves are large, with few lobe-like large teeth and often a somewhat cordate base; the inflorescence is mostly ebracteate and lax. All are green to olive green (not greyish), often glabrescent, the inflorescence is formed of small glomerules, usually with only few flowers, the perianth segments are more or less prominently keeled at the apex and have a strong midrib visible inside, all seeds are horizontal, with the margin sharply acute *(C. murale* and *C. coronopus)* to fairly acute *(C. badachschanicum* and *C. simplex)* or obtuse *(C. hybridum)*. The seed surface is clearly pitted in *C. coronopus, C. murale* and *C. hybridum,* but smoother in the others species.

The lineage of *Chenopodium polyspermum*

Phylogeny. — The newly resolved lineage of *Chenopodium polyspermum* is supported by both phylogenetic reconstructions based on the combined plastid data set and the nuclear data set (= *Lipandra* in Fig. 1 and 2). The position of *C. polyspermum* is inconsistent, because based on the nuclear region it is resolved as the next sister to the *Chenopodium* s.str. plus *Atriplex* clades (Fig. 2), whereas based on the combined plastid regions it is the next sister to the *Chenopodium* s.str., *Atriplex, C. murale* plus *C. rubrum* clades, but without support (Fig. 1). The results clearly support, however, the separate position of *C. polyspermum.*

Morphological characters. — In its combination of morphological characters, *Chenopodium polyspermum* is unique in *Chenopodium* s.lat. (Uotila 2001b). The leaves are thin, practically glabrous, the inflorescence is formed of diffusely branched lateral cymes (resembling some *Dysphania* species), the perianth segments are strongly spreading in fruit (rarely so in *Chenopodium* s.lat.), the seeds are brownish with a unique surface ornamentation of small pits and radial sinuous furrows, and the pollen deviates from other *Chenopodium* species in having a low pore number and fairly large pores (Uotila 1974).

Taxonomic treatment

Based on our current understanding of phylogenetic relationships, we propose a revised classification for the *Chenopodioideae* that recognises monophyletic entities at the tribal and generic levels for the former *Chenopodium* s.lat. , has been consulted. The four currently recognised tribes are *Atripliceae* (newly circumscribed here), *Anserineae* (a name with priority over *Spinacieae* (see Reveal 2011+)), *Dysphanieae* (formally circumscribed here) and *Axyrideae* (as established by Kadereit & al. 2010, not treated here in detail).

In the present treatment we provide a synopsis of species that belong to the genera that have been segregated from the former, polyphyletic *Chenopodium* s.lat. including their tribal affiliation. A revised generic description is also provided for *Chenopodium* s.str., including *Einadia* and *Rhagodia,* which were recently merged with it, as well as for *Dysphania* and *Teloxys,* which are recognised as distinct lineages (Kadereit & al. 2010; Fuentes-Bazan 2012). Additionally, a key to the respective genera is provided.

Key to the seven genera among which the species of the former *Chenopodium* s. lat. are distributed

1. Plants aromatic, leaves and perianth with stalked glandular hairs and/or subsessile glands . . . . *Dysphania*
– Plants non-aromatic (but sometimes foetid), vesicular hairy (farinose) or glabrous 2
2. Inflorescences in dichasial or monochasial loose cymes; plants glabrous or glabrescent 3
– Inflorescences spicately or paniculately arranged dense glomerules with few to many flowers; plants farinose at least when young or glabrous 4
3. Leaves linear to linear-oblong or linear-lanceolate; dichasia with sterile, often spinose ultimate branches . . . . *Teloxys*
– Leaves ovate to elliptic; dichasia without sterile ultimate branches . . . . *Lipandra*
4. Stems unbranched or sparingly branched; basal

leaves often forming a rosette; perianth often changed to succulent or hardened in fruit, sometimes reduced to one lobe; stigmas 2–4; seeds vertical . . . *Blitum*
– Stem usually branched; basal leaves not in a rosette; perianth unchanged in fruit, not reduced; stigmas 2(–3), seeds vertical and/or horizontal 5
5. Flowers often dimorphic, in lateral flowers perianth segments 3(–5), seeds mostly vertical or sometimes horizontal; stamens 1–3 . . . . *Oxybasis*
– Flowers not dimorphic, perianth segments 5, seeds exclusively horizontal; stamens almost always 6
6. Young stems and leaves densely covered with vesicular globose trichomes becoming cup-shaped when dry and mostly persistent at maturity; perianth segments without prominent midvein visible inside; seeds smooth or striate and somewhat rugulose, sometimes pitted . . . . *Chenopodium*
– Young stems and leaves with vesicular trichomes becoming totally collapsed when dry, mostly caducous or rarely present at maturity; perianth segments with prominent midvein visible inside; seeds distinctly pitted to sometimes rugulose or almost smooth . . . . *Chenopodiastrum*

Chenopodioideae Burnett, Outlines Bot.: 591, 1091, 1142. 1835.
= *Blitoideae* Raf., Fl. Tellur. 3: 45. 1837.

Tribe 1. *Atripliceae* Duby, Bot. Gall. 1: 394. 1828.
= *Chenopodieae* Dumort., Anal. Fam. Pl.: 17. 1829, **syn. nov.**

The tribe *Atripliceae* was redefined by Kadereit & al. (2010) to include the genera *Archiatriplex* G. L. Chu, *Atriplex* L., *Exomis* Fenzl ex Moq., *Extriplex* E. H. Zacharias, *Grayia* Hook. & Arn., *Holmbergia* Hicken, *Manochlamys* Aellen, *Microgynoecium* Hook. f., *Proatriplex* (W. A. Weber) Stutz & G. L. Chu and *Stutzia* E. H. Zacharias. Because the *Chenopodieae* as previously defined are paraphyletic to *Atripliceae,* we extend the circumscription of the *Atripliceae* to also include the genera *Chenopodium* (treated in the following at genus level), *Chenopodiastrum, Oxybasis* and *Lipandra* (the latter three treated in the following with all species). In this new definition the *Atripliceae* are monophyletic.

Chenopodium L., Sp. Pl.: 218. 1753 ≡ *Vulvaria* Bubani, Fl. Pyren. 1: 174. 1897, nom. illeg. – Type (designated by Hitchcock in Prop. Brit. Bot.: 137. 1929; see Note below): *C. album* L.
= *Rhagodia* R. Br., Prodr. Fl. Nov. Holland.: 408. 1810. – Type (designated by Ulbrich in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 16c: 480. 1934): *R. billardierei* R. Br., nom. illeg. (*Chenopodium baccatum* Labill., *R. baccata* (Labill.) Moq.).
= *Einadia* Raf., Fl. Tellur. 4: 121. 1838. – Type: *E. linifolia* (R. Br.) Raf. (*Rhagodia linifolia* R. Br., *Chenopodium linifolium* (R. Br.) Roem. & Schult.).
= *Chenopodium* sect. *Leprophyllum* Dumort., Fl. Belg.: 21. 1827. – Type (designated by Scott in Bot. Jahrb. Syst. 100: 217. 1978): *C. album* L.
= *Chenopodium* sect. *Chenopodiastrum* Moq. in Candolle, Prodr. 13(2): 61. 1849. – Type (designated by Scott in Bot. Jahrb. Syst. 100: 217. 1978): *C. album* L.

Note. — Britton & Brown (1913) designated *Chenopodium rubrum* as the type of *Chenopodium*. This choice is now declared to be supersedable, as it was made following the “largely mechanical method of selection” provided for in the American Code of Botanical Nomenclature. Indeed, Britton & Brown’s work is the prime (“voted” and therefore binding) example mentioned in the International Code of Botanical Nomenclature (McNeill & al. 2006: Art. 10, Ex. 7) of a publication with supersedable type designations. It is currently widely accepted, even though a few recent authors, e.g. Scott (1978) and Wilson (1983), dissent, that Hitchcock’s (1929) choice of *C. album* effectively supersedes Britton & Brown’s type designation (see e.g. Jarvis 2007), which anyway many considered unfortunate and even arbitrary (e.g. Scott 1978; Uotila 1993). As foretold earlier (e.g. Uotila 1993; Clemants & Mosyakin 2003), the type choice is now critically important when *Chenopodium* in the wide sense is split into several genera.

The problem is that it is not always clear whether type designations made by other authors who followed but implicitly, if obviously, the “American Code” are also supersedable. Such doubt concerns, among others, the work of Standley (1916), the next author after Britton & Brown to designate a type for *Chenopodium,* who again opted for *C. rubrum.* In view of such doubts, the recent XVIII International Botanical Congress in Melbourne decided to appoint a special committee to examine the question and present proposals to solve it to the next following IBC (McNeill & al. 2011). In the event that the conclusion were to allow Standley’s designation to stand, it would be imperative to propose the conservation of *Chenopodium* with its currently accepted type.

Annual or perennial, nonaromatic (but sometimes foetid) herbs, shrubs or small trees, young stems and leaves often densely farinose, i.e. covered with vesicular globose trichomes, which later collapse forming a cup shaped structure mostly persistent; monoecious or (rarely) dioecious. *Stems* erect or ascending, prostrate or scrambling, branched, branches alternate or the lowermost ones sometimes subopposite. *Leaves* alternate or opposite, petiolate; *blade* thin to thickish, sometimes somewhat fleshy, linear to trullate, rhombic or triangular-hastate; *margins* entire to dentate or lobed. *Inflorescence* terminal and lateral, ebracteate or with bract-like leaves, with flowers in compact or loose glomerules arranged spicately or paniculately, sometimes in part single. *Flowers* in monoecious plants dimorphic, bisexual or pistillate; *perianth* sometimes coloured but mostly otherwise unchanged in fruit, segments (4–)5, connate near the base or close to the middle, usually with membranous margins and roundish to keeled back, in fruit somewhat closing or spreading; *stamens* almost always 5; *stigmas* 2. *Fruit* with membranous or sometimes succulent pericarp, firmly adherent to or ± easily removable from the seed. *Seeds* horizontal, depressed-globular to lenticular, margin rounded to subacute, testa black, almost smooth to finely striate, rugulose or variously pitted.

Chenopodiastrum S. Fuentes, Uotila & Borsch, **gen. nov.** ≡ *Chenopodium* subsect. *Undata* Aellen & Iljin ex Mosyakin & Clemants in Novon 6: 400. 2006. – Type: *C. murale* (L.) S. Fuentes, Uotila & Borsch (*Chenopodium murale* L.).

= *Chenopodium* [unranked] *Hybrida* Standl. in N. Amer. Fl. 21: 13. 1916 ≡ *Chenopodium* sect. *Grossefoveata* Aellen & Iljin ex Mosyakin in Ukrayins'k Bot. Zhurn. 50(5): 75. 1993. – Type: *C. hybridum* L.

Annual, non-aromatic herbs, young stems and leaves glabrescent, with vesicular trichomes, which later totally collapse when dry and are mostly caducous. *Stems* erect, branched. *Leaves* alternate, petiolate; *blade* thickish triangular, ovate, rhombic-ovate to lanceolate; *margin* irregularly dentate to lobed, or pinnatifid with narrow dentate lobes. *Inflorescence* axillary and terminal, largely leafy to leafless, with flowers in small dense glomerules arranged spicately or paniculately. *Flowers* bisexual or pistillate; *perianth segments* 5, basally connate, with strong midrib visible inside and prominent keel near the apex, enclosing the fruit or spreading in fruit; *stamens* 5; *stigmas* 2. *Fruits* with membraneous pericarp, usually firmly adherent to the seed. *Seeds* horizontal, lenticular, round in outline, margin acute to fairly obtuse, testa black, often prominently pitted, sometimes rugulose or almost smooth.

1. *Chenopodiastrum murale* (L.) S. Fuentes, Uotila & Borsch, **comb. nov.** ≡ *Chenopodium murale* L., Sp. Pl.: 219. 1753. – Lectotype (designated by Brenan in Fl. Trop. E. Africa, Chenopodiaceae: 7. 1954): Herb. Linn. 313.6 (LINN).

2. *Chenopodiastrum coronopus* (Moq.) S. Fuentes, Uotila & Borsch, **comb. nov.** ≡ *Chenopodium coronopus* Moq. in Candolle, Prodr. 13(2): 76. 1849. – Lectotype(designated by León & al. in Vieraea 11: 70. 1982): La Isletta de Gde Canaria, 11.3.1846, *Bourgeau* (FI-W 155641; isolectotype: P 83265).

3. *Chenopodiastrum hybridum* (L.) S. Fuentes, Uotila & Borsch, **comb. nov.** ≡ *Chenopodium hybridum* L., Sp. Pl.: 219. 1753. – Lectotype (designated by Larsen, Fl. Cambodge, Laos, Vietnam 24: 95. 1989): Herb. Linn. 313.11 (LINN).

4. *Chenopodiastrum badachschanicum* (Tzvelev) S. Fuentes, Uotila & Borsch, **comb. nov.** ≡ *Chenopodium badachschanicum* Tzvelev in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 20: 434. 1960. – Holotype: Tajikistan, Pamir occidentalis, in declivitate lapidoso paullo ruderata in valle fl. Murgab 3–4 km infra ostium fl. Pschart occidentalis, alt. c. 3300 m, 16.6.1958, *N. Tzvelev* (LE!).

5. *Chenopodiastrum simplex* (Torrey) S. Fuentes, Uotila & Borsch, **comb. nov.** ≡ *Chenopodium hybridum* var. *simplex* Torrey in Ann. Lyceum Nat. Hist. New York 2: 239. 1828 ≡ *Chenopodium simplex* (Torrey) Raf. in Atlantic J. 1: 146. 1832. – Holotype: Eng. Cant. [engineer cantonment near Council Bluffs], [1820], *Dr James* (NY).

= *Chenopodium gigantospermum* Aellen in Repert. Spec. Nov. Regni Veg. 26: 144. 1929. – Lectotype (designated by Bassett & Crompton in Canad. J. Bot. 60: 600. 1982; see comment in Dorn 1988): Canada, British Columbia, Vernon, 9.7.1889, *J. Macoun* (US 102537).

Lipandra Moq., Chenopod. Mongr. Enum.: 19. 1840 (May) ≡ *Oligandra* Less. in Linnaea 9: 199. 1835 [non Less. 1832] ≡ *Gandriloa* Steud., Nomencl. Bot., ed. 2, 1: 662. Nov. 1840, nom. illeg. ≡ *Oliganthera* Endl., Gen. Pl., Suppl. 1: 1377. 1841, nom. illeg. – Type: *L. atriplicoides* (Less.) Moq. (*Oligandra atriplicoides* Less., *Gandriloa atriplicoides* (Less.) Steud.).

= *Chenopodium* [unranked] *Polysperma* Standl. in N. Amer. Fl. 21:13. 1916 ≡ *Chenopodium* subsect. *Polysperma* (Standl.) Kowal ex Mosyakin & Clemants in Novon 6: 400. 1996. – Type: *C. polyspermum* L.

Annual, non-aromatic herbs, glabrous. *Stems* erect to ascending or prostrate, branched, lower branches subopposite, long. *Leaves* alternate, petiolate; *blade* thin, ovate-elliptic; *margin* entire. *Inflorescence* leafy and bracteate, composed of large, loose axillary dichasia or sometimes more condensed glomerules arranged spicately. *Flowers* bisexual or pistillate; *perianth* unchanged in fruit, segments (4–)5, free near to the base, with membranous margins, not-keeled, spreading in fruit; *stamens* 1–3(–5); *stigmas* 2. *Fruits* with membranous pericarp, free. *Seeds* horizontal, compressed-globose, round in outline, margin fairly obtuse, testa brown to blackish, undulately striate.

1. *Lipandra polysperma* (L.) S. Fuentes, Uotila & Borsch, **comb. nov.** ≡ *Chenopodium polyspermum* L., Sp. Pl.: 220. 1753 ≡ *Vulvaria polysperma* (L.) Bubani, Fl. Pyren. 1: 175. 1897. – Lectotype (designated by Larsen, Fl. Cambodge, Laos, Vietnam 24: 95. 1989): Herb. Linn. 313.19 (LINN).

= *Oligandra atriplicoides* Less. in Linnaea 9: 199. 1835 ≡ *Lipandra atriplicoides* (Less.) Moq., Chenop. Monogr. Enum: 19. 1840. – Type: [Russia, Chelyabinsk Oblast] Troitsk, *Lessing* (LE!).

Note. — *Chenopodium polyspermum* was described by Linnaeus (1753), and since then it has not been transferred to any other genus, except for Crantz (1766), who included it in *Atriplex*. But Lessing (1834) described a new genus *Oligandra* with one species, *O. atriplicoides,* which was said to resemble much *C. polyspermum*. However, Lessing did not remember that two years earlier he described *Oligandra* as a genus of a Brasilian *Asteraceae*. Three authors realised almost simultaneously that the younger name was illegitimate and gave each a substitute names for it: *Lipandra* Moq., *Gandriloa* Steud. and *Oligantha* Endl. Moquin-Tandon (1840) was the earliest of them, and his name *Lipandra* became the name of the genus. He supposed that the genus may belong to *Chenopodium,* and Meyer (1843) was the first to identify the taxon as *C. polyspermum*. So, recognising of *C. polyspermum* at generic level was soon forgotten and the species was still regarded as a *Chenopodium*.

Oxybasis Kar. & Kir. in Bull. Soc. Imp. Naturalistes Moscou 1841: 738. 1841. – Type: *O. minutiflora* Kar. & Kir.

= *Chenopodium* subg. *Pseudoblitum* Gren. & Godr., Fl. France 3: 22. 1855 ≡ *Blitum* subg. *Pseudoblitum* (Gren. & Godr.) Schur, Enum. Pl. Transsilv.: 571. 1866 ≡ *Chenopodium* sect. *Pseudoblitum* (Gren. & Godr.) Syme in Sowerby, Engl. Bot., ed. 3, 8: 20. 1868. – Type (designated by Mosyakin in Ukrayins'k. Bot. Zhurn. 50(6): 74. 1993): *C. rubrum* L. (*Blitum rubrum* (L.) Rchb.).

= *Chenopodium* [unranked] *Rubra* Standl. in N. Amer. Fl. 21: 29. 1916. – Type: *C. rubrum* L.

= *Chenopodium* [unranked] *Glauca* Standl. in N. Amer. Fl. 21: 28. 1916 ≡ *Chenopodium* subsect. *Glauca* (Standl.) A. J. Scott in Bot. Jahrb. Syst. 100: 216. 1978 ≡ *Chenopodium* sect. *Glauca* (Standl.) Ignatov, Sosud. Rast. Sovet. Dal'nego Vostoka 3: 22. 1988. – Type: *C. glaucum* L.

= *Chenopodium* [unranked] *Urbica* Standl., N. Amer. Fl. 21: 11. 1916 ≡ *Chenopodium* sect. *Urbica* (Standl.) Mosyakin in Ukrayins'k. Bot. Zhurn. 59: 700. 2002. – Type: *C. urbicum* L.

= *Chenopodium* sect. *Degenia* Aellen in Magyar Bot. Lapok 25: 56. 1927. – Lectotype (designated by Wilson in Fl. Australia 4: 137. 1983): *C. macrospermum* Hook. f.

Notes. — Karelin & Kirilov (1841) described from the present-day Kazakhstan a new genus *Oxybasis* with the single species *O. minutiflora* Kar. & Kir., and placed it in the tribe *Atripliceae* s.str. While *Oxybasis* is the oldest generic name for the *Chenopodium rubrum* clade, and thus has to be accepted, their species is not distinct from *Blitum chenopodioides* (≡ *Chenopodium chenopodioides,* ≡ *Oxybasis chenopodioides*) described by Linnaeus in 1753 as pointed out by Iljin & Aellen (1936).

Chenopodium gubanovii Sukh. was recently described by Sukhorukov (1999), who pointed out that the species belongs to *C.* sect. *Pseudoblitum*. However, molecular analysis is needed to confirm its placement in *Oxybasis:* glabrous plants, sparingly branched stem, 2–4 almost free perianth segments somewhat enlargening in fruit and vertical seeds might refer also to *Blitum*.

Annual, non-aromatic herbs, more or less glabrous, sometimes leaves densely farinose below. *Stems* erect to ascending or prostrate, branched, lower branches sometimes subopposite. *Leaves* alternate, petiolate; *blade* thickish, somewhat fleshy, triangular to narrowly triangular, hastate or rhombic or lanceolate; *margin* entire to dentate. *Inflorescence* axillary and terminal, usually largely leafy or bracteate, sometimes ebracteate, flowers in compact glomerules arranged spicately or sometimes paniculately. *Flowers* usually dimorphic. *Terminal flowers* bisexual; *perianth segments* 3–5, free to major part; *stamens* 1(–5); *stigmas* 2(–3). *Lateral flowers* usually female, *perianth segments* 3(–4), variously connate; *stamens* 0–1; *stigmas* 2. *Fruit* with membranous pericarp, free or loosely attached to seed. *Seeds* horizontal in terminal flowers, vertical or horizontal in lateral flowers, oval to orbicular in outline, margin rounded, testa brownish to black, almost smooth to finely reticulate or minutely pitted.

1. *Oxybasis rubra* (L.) S. Fuentes, Uotila & Borsch, **comb. nov.** ≡ *Chenopodium rubrum* L., Sp. Pl.: 218. 1753 ≡ *Blitum rubrum* (L.) Rchb., Fl. Germ. Excurs.: 582. 1832 ≡ *Orthosporum rubrum* (L.) T. Nees, Gen. Fl. Germ., fasc. 7: ad t. 6 (or t. [127]; or vol. [1]; t. 57). 1835. – Lectotype (designated by Uotila in Ann. Bot. Fenn. 30: 190. 1993): Herb. Linn. 313.5 (LINN).

2. *Oxybasis glauca* (L.) S. Fuentes, Uotila & Borsch, **comb. nov.** ≡ *Chenopodium glaucum* L., Sp. Pl.: 220. 1753. – Lectotype (designated by Uotila in Ann. Bot. Fenn. 30: 190. 1993): Herb. Linn. 313.17 (LINN).

3. *Oxybasis urbica* (L.) S. Fuentes, Uotila & Borsch, **comb. nov.** ≡ *Chenopodium urbicum* L., Sp. Pl.: 218. 1753. – Lectotype (designated by Uotila in Ann. Bot. Fenn. 30: 190. 1993): Herb. Linn. 313.2 (LINN).

4. *Oxybasis macrosperma* (Hook. f.) S. Fuentes, Uotila & Borsch, **comb. nov.** ≡ *Chenopodium macrospermum* Hook. f., Bot. Antarct. Voy. 1 (Fl. Antarct.): 341. 1846. – Lectotype (designated here): Falkland Islands, 1839–43, *J. D. Hooker* (K 583178; isolectotypes: BM 993193, P 606443).

= *Chenopodium halophilum* Phil. in Anales Univ. Chile 1861: 67. 1861 ≡ *Chenopodium macrospermum* subsp. *halophilum* (Phil.) Aellen in Repert. Spec. Nov. Regni. Veg. 26: 42. 1929. – Lectotype not designated.

5. *Oxybasis chenopodioides* (L.) S. Fuentes, Uotila & Borsch, **comb. nov.** ≡ *Blitum chenopodioides* L., Mant. Pl. Altera: 170. 1771 ≡ *Chenopodium chenopodioides* (L.)

Aellen in Anon. (ed.), Ostenia: 98. 1933. – Neotype (designated by Uotila in Ann. Bot. Fenn. 38: 96. 2001): [Russia, Daghestan] in fossis Kislar, *C. Steven* (H 1037202).

= *Chenopodium botryodes* Sm. in Sowerby, Engl. Bot.: ad t. 2247. 1811. – Type not designated.

= *Oxybasis minutiflora* Kar. & Kir. in Bull. Soc. Imp. Naturalistes Moscou 1841: 738. 1841. – Lectotype (collection at LE designated by Gubanov & al., Naucn. Nasledie Karelin & Kirilova: 21. 1998; specimen designated here): [Kazakhstan] in salsis non procul a Semipalatinsk trans fl. Irtysh rarissime, 1840, *Karelin & Kiriloff 1020* (LE!). — *Note:* In LE there are two sheets of *O. minutiflora* with identical label information, except for that one of the sheets was possessed by Fischer and the other by Ledebour. The second step in the type designation is proposed here to restrict the choice to the specimen from herb. Fischer; the sheet form herb. Ledebour and two other sheets with more incomplete labels are isolectotypes.

– *Chenopodium crassifolium* auct., non Hornem., Hort. Bot. Hafn.: 254. 1813.

Note. — While most species are morphologically distinct entities, the circumscription of *Oxybasis chenopodioides* has varied. The neotypification of *Chenopodium chenopodioides* by Uotila (2001c) clarified the interpretation by Aellen (1933) of the original description of the species, and the commonly used younger names *C. botryodes* and *C. crassifolium* fell in synonymy. Earlier views by Moquin-Tandon (1849) and Syme (1868), who treated it as an infraspecific race of *C. rubrum,* are not only rejected by the molecular results (Fuentes Bazan & al. 2012; this study) but also morphology. Aellen (1927, 1960–61) pointed out the connate, sac-like perianth of the lateral flowers, and described a new section, *C.* sect. *Degenia,* for *C. crassifolium* and the related *C. macrospermum.* Clemants & Mosyakin (2003) also accepted *C. chenopodioides* (as a member of sect. *Pseudoblitum* in *C.* subg. *Blitum*).

Tribe 2. *Anserineae* Dumort., Fl. Belg.: 20. 1827.

= *Spinacieae* Moq., Chenop. Monogr. Enum.: 5, 48. 1840

Anserineae Dumort. is the oldest available name at tribal rank for the *Spinacia* clade in the revised circumscription by Fuentes Bazan & al. 2012. This tribe includes the two genera *Blitum* (= *Anserina*) and *Spinacia.*

Blitum L., Sp. Pl.: 4. 1753 ≡ *Morocarpus* Boehmer in Ludwig, Def. Gen. Pl., ed. 3: 385. 1760, nom. illeg. ≡ *Chenopodium* sect. *Blitum* (L.) Benth. & Hook f., Gen. Pl. 3(1): 52. 1880 ≡ *Chenopodium* sect. *Eublitum* Aellen in Verh. Naturf. Ges. Basel 41: 103. 1930 ≡ *Chenopodium* subg. *Blitum* (L.) Hiitonen, Suom. Kasvio: 307. 1933. – Type (designated by Britton & Brown, Ill. Fl. N. U.S. 2: 15. 1913; confirmed by Hitchcock in Prop. Brit. Bot.: 115. 1929): *B. capitatum* L. (*Morocarpus capitatus* (L.) Scop., *Chenopodium capitatum* (L.) Ambrosi).

= *Anserina* Dumort., Fl. Belg.: 21. 1827 ≡ *Agathophytum* Moq. in Ann. Sci. Nat., Bot., ser. 2, 1: 291. 1834, nom. illeg. ≡ *Orthosporum* subg. *Agathophytum* T. Nees, Gen. Fl. Germ., fasc. 7: ad t. 6 (or t. [127]; or vol. [1]; t. 57). 1835 ≡ *Chenopodium* sect. *Agathophytum* (T. Nees) Benth. & Hook. f., Gen. Pl. 3: 52. 1880. – Type: *Anserina bonus-henricus* (L.) Dumort. (*Chenopodium bonus-henricus* L., *Blitum bonus-henricus* (L.) Rchb., *Agathophytum bonus-henricus* (L.) Moq.).

= *Monolepis* Schrad., Index Seminum Hort. Acad. Gotting. 1830: 4. 1830. – Type: *M. trifida* (Trevir.) Schrad. (*Chenopodium trifidum* Trevir.) [= *Blitum nuttallianum* Schult.].

= *Scleroblitum* Ulbr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 16c: 495. 1934 ≡ *Chenopodium* sect. *Atriplicina* Aellen in Verh. Naturf. Ges. Basel 41: 99. 1930. – Type: *S. atriplicinum* (F. Muell.) Ulbr. (*Blitum atriplicinum* F. Muell., *Chenopodium atriplicinum* (F. Muell.) F. Muell.).

= *Chenopodium* [unranked] *Californica* Standl. in N. Amer. Fl. 21: 30. 1916. – Type: *C. californicum* (S. Wats.) S. Wats. (*Blitum californicum* S. Wats.).

Notes. — The oldest generic name within the *Chenopodium capitatum* clade is *Blitum.* However, since the second half of the 19th century the inclusion of *Blitum* into *Chenopodium* became gradually accepted. Most of the treatments since the 20th century in fact have merged *Blitum* with *Chenopodium* (e.g. Aellen 1929; Iljin & Aellen 1936; Aellen & Just 1943; Aellen 1960–61; Grubov 1966; Brenan & Akeroyd 1993; Tzvelev 1996; Uotila 1997, 2001a, b; Clemants & Mosyakin 2003). However, some authors continued to accept the separate genus *Blitum,* such as Meyer (1829), Schur (1866), Watson (1874), Britton & Brown (1913), Standley (1916), Scott (1978) and Greuter & al. (1984). Whereas Linnaeus (1753) just included two species, *B. capitatum* and *B. virgatum,* that are characterised by more or less succulent glomerules (concept adopted, e.g. by Scott 1978), most authors defined the genus more widely. For example, Meyer (1829) used a much wider concept not only including species that we now consider to belong to the genus (e.g. *B. bonus henricus, B. nutallianum*) but also *B. pumilio* C. A. Mey. (now *Dysphania*) and *B. rubrum* (now *Oxybasis*).

Aellen (1930) pointed out some unique morphological features for the Australian *Blitum atriplicinum,* which was originally described in *B.* sect. *Orthosporum* by Mueller (1855) and placed it in the monotypic *Chenopodium* sect. *Atriplicina.* Ulbrich (1934) published for this species the monotypic genus *Scleroblitum,* a classification widely used in the following (e.g. Kühn 1993; Kadereit & al. 2003). To the contrary, Scott (1978) thought that *C.* sect. *Atriplicina* belongs to *C.* subg. *Ambrosia* (now *Dysphania*), what was opposed by Mosyakin & Clemants (2002), who considered *C.* sect. *Atriplicina* to belong to *C.* subg. *Blitum.*

Monolepis pusilla S. Watson, Botany (Fortieth Parallel): 289. 1871 ≡ *Micromonolepis pusilla* (S. Watson) Ulbr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 16c: 500. 1934, is excluded; it does not seem to be closely related to *Monolepis* (Kadereit & al. 2010).

Annual or perennial, non-aromatic herbs, glabrous or sometimes with stipitate vesicular hairs and sticky when young. *Stems* erect or ascending to prostrate, several from the base, unbranched or sparingly branched mostly with few secondary branches only. *Leaves* alternate, petiolate, the basal ones often long-petiolate and forming a rosette; *blade* thin or thickish and somewhat succulent, triangular to triangular-hastate or triangular-lanceolate, or spathulate; *margins* entire to dentate. *Inflorescence* of spicately arranged compact glomerules, ebracteate or axillary with small, leaf-like bracts. *Flowers* bisexual or pistillate; *perianth segments* (1–)3–5, connate only at base or close to the middle, herbaceous, often becoming succulent or dry and hard in fruit, not keeled; sometimes perianth absent; *stamens* 1–5; *stigmas* 2–4. *Fruit* with membranous pericarp, usually adherent to the seed. *Seeds* vertical, broadly ovate to orbicular in outline, margin slightly acute to rounded or truncate, testa dark brown to black, dull, almost smooth or slightly striate, rugulose or reticulate.

1. ***Blitum capitatum*** L., Sp. Pl.: 4. 1753 ≡ *Chenopodium capitatum* (L.) Ambrosi, Fl. Tirolo Mer. 2: 180. 1857. – Lectotype (designated by Jonsell & Jarvis in Regnum Veg. 127: 25. 1993): Herb. Linn. 14.1 (LINN).

2. ***Blitum hastatum*** Rydb. in Bull. Torrey Bot. Club 1901: 273. 1901 [non *Chenopodium hastatum* Phil. 1860] ≡ *Chenopodium overi* Aellen in Repert. Spec. Nov. Regni Veg. 26: 159. 1929. – Type: Wyoming, Buffalo, 4000–5000', 9.1900*, F. Tweedy 3295* (NY 324302).

= *Chenopodium capitatum* var. *parvicapitatum* Welsh in Great Basin Naturalist 44: 199. 1984. – Holotype: USA, Utah, Beaver County, Fish Lake Forest, Tushar Mountains, Indiana Creek, c. 12 mi due NE of Beaver, 2288 m, 28.6.1978, *S. L. Welsh & al. 17148* (BRY).

3. ***Blitum nuttallianum*** Schult., Mant. 1: 65. 1822 ≡ *Blitum chenopodioides* Nutt., Gen. N. Amer. Pl. 1: 4. 1818 [non L. 1771] ≡ *Monolepis chenopodioides* Moq. in Candolle, Prodr. 13(2): 85. 1849, nom. illeg. ≡ *M. nuttalliana* (Schult.) Greene, Fl. Francisc.: 168. 1891. – Described from the banks of the Missouri river; type not designated.

= *Chenopodium trifidum* Trev., Ind. Sem. Hort. Bot. Vratislav. 1829 [n.v.] ≡ *Monolepis trifida* (Trev.) Schrad., Ind. Sem. Hort. Goett: 4. 1830. – Lectotype (designated here): "*C. trifidum* Trev., m[isit] Trevianus" [later added:] "*M. trifida* Schrad." [both, manu Ledebour] in herb. Ledebour (LE!).

4. ***Blitum spathulatum*** (A. Gray) S. Fuentes, Uotila & Borsch, **comb. nov.** ≡ *Monolepis spathulata* A. Gray in Proc. Amer. Acad. Arts 7: 389. 1868. – Holotype: California, Mono Pass, 1866, *Bolander* (GH 37208; isotype: MO 1958277, NY 324359 & 1085538-40, US 1085539).

5. ***Blitum asiaticum*** (Fisch. & C. A. Mey) S. Fuentes, Uotila & Borsch, **comb. nov.** ≡ *Monolepis asiatica* Fisch. & C. A. Mey. in Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg 2: 131. 1843. – Lectotype (designated here): [Russia, Sakha Republic], "Nizhne-Kolymsk, *Sharypov* 1834" [= southern side of Kolyma River, 20.7.1834, *Sharypov 94*] (LE!). — *Note:* The type material in LE includes collections from two different places from the Kolyma river in 1834 and from the Anya river in 1829. Only plants from Kolyma river are with certainty from "prope oppidulum Nischne-Kolymsk" as given in the protologue. However, the specimen with the original label by the collector has been mounted on the same sheet with a specimen from the Anya river, and it is not definitely sure, which plants belong to *Sharypov 94*. The type material includes two evident duplicates with identical labels copied later: "*M. asiatica* F. & Mey., Nischne-Kolymsk, *Sharypov 1834*" and with very similar fragments as a part of the material on the mixed sheet; the other part corresponds well with other plants from the Anya river. To be sure of which specimens belong to the collection from the Kolyma river, the lower specimen on the sheet has been designated as the lectotype.

6. ***Blitum virgatum*** L., Sp. Pl.: 4. 1753 ≡ *Morocarpum foliosum* Moench, Methodus: 342. 1794, nom. illeg. ≡ *Chenopodium virgatum* (L.) Ambrosi, Fl. Tirolo Mer. 2: 179. 1857 [non Thunb. 1815] ≡ *Chenopodium foliosum* Asch., Fl. Brandenburg 1: 572. 1864. – Lectotype (designated by Jafri & Rateeb in Jafri & El-Gadi, Fl. Libya 58: 11. 1978): Herb Linn. 14.2 (LINN).

7. ***Blitum virgatum*** subsp. ***montanum*** (Uotila) S. Fuentes, Uotila & Borsch, **comb. nov.** ≡ *Chenopodium foliosum* subsp. *montanum* Uotila in Ann. Bot. Fenn. 30: 190. 1993. – Holotype: Iran, Gorgan, in declivibus borealibus montium Shahvar supra Hadjilang, in pasquis argillaceis l. d. Osta-Maidan, 3200 m, 26.–27.7.1948, *K. H. Rechinger & F. Rechinger 6046* (W; isotypes: E, G).

8. ***Blitum litwinowii*** (Paulsen) S. Fuentes, Uotila & Borsch, **comb. nov.** ≡ *Monolepis litwinowii* Paulsen in Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1903: 187. 1903 ≡ *Chenopodium litwinowii* (Paulsen) Uotila in Ann. Bot. Fenn. 30: 190. 1993. – Holotype: Pamir, in siccis prope fl. Müscol, 4300 m, 2.7.1898, *O. Paulsen 667* (C).

9. ***Blitum korshinskyi*** Litv. in Trudy Bot. Muz. Imp. Akad. Nauk 7: 76. 1910 ≡ *Chenopodium korshinskyi* (Litv.) Minkw. in Fedtschenko, Rastitel'n. Turkestana:

332. 1915. – Lectotype (designated here): [Tajikistan] Darwas, Buchara, in fissuris rupium inter Doschtak & Kergowat, 14.6.1897, *S. Korshinsky Iter Turkestanicum 1559* (LE). — *Note:* In LE there are three sheets with identical looking plants and identical labels except for the Iter Turkestanicum numbers *(1559, 1560* and *1566).* These numbers, however, are herbarium numbers, not collector's numbers, so No. *1560* and *1566* are isolectotypes.

10. *Blitum petiolare* Link, Enum. Hort. Berol. Alt. 1: 8. 1821. – Neotype (designated here): "*Blitum petiolare* Link!, Hort. bot. Br.", ex Museo botanico Berolinensi (LE!). — *Note:* Link (1821) described the third species of *Blitum* based on plants cultivated in Berlin. The plants probably originated from Portugal, which Johann Centurius Hoffmann Graf von Hoffmannsegg and Johann Heinrich Friedrich Link visited 1797–1801; later, in 1815, Link became professor of natural history, curator of the herbarium and director of the Botanic Garden Berlin. The description matches well with the plant known during last decades as *Chenopodium exsuccum* (see Uotila 1979). No specimen of *B. petiolare* with certainty from Link has been found in the herbarium in Berlin (B) or many other European herbaria studied. But it has been grown in the nineteenth century in several European botanical gardens, and the specimens collected are mostly named correctly. The correctly named, old but undated good specimen at LE, received from Berlin, is designated as the neotype of *Blitum petiolare*.

= *Blitum exsuccum* C. Loscos in Loscos, Trat. Pl. Aragón, Supl. 5–8: 106. 1886 ≡ *Chenopodium exsuccum* (C. Loscos) Uotila in Ann. Bot. Fenn. 16: 237. 1979. – Described from Spain, Aragón, Castelserás; type not designated.

11. *Blitum californicum* S. Watson in Proc. Amer. Acad. Arts 9: 101. 1874 ≡ *Chenopodium californicum* (S. Watson) S. Watson in Brewer & Watson, Bot. California 2: 48. 1880. – Described from California (10 syntypes mentioned); type not designated; one syntype (without locality, "Fremont's 2nd Exped.", NY 8484) could serve as lectotype if none of the others is available.

12. *Blitum bonus-henricus* (L.) Rchb., Fl. Germ. Excurs.: 582. 1832 ≡ *Chenopodium bonus-henricus* L., Sp. Pl.: 218. 1753 ≡ *Anserina bonus-henricus* (L.) Dumort., Fl. Belg.: 21. 1827 ≡ *Agathophyton bonus-henricus* (L.) Moq. in Ann. Sci. Nat., Bot., ser. 2: 291. 1834 ≡ *Orthosporum bonus-henricus* (L.) T. Nees, Gen. Fl. Germ., fasc. 7: ad t. 6 (or t. [127]; or vol. [1]; t. 57). 1835. – Lectotype (designated by Jonsell & Jarvis in Nordic J. Bot. 14: 155. 1994): Herb. Linn. 313.1 (LINN).

13. *Blitum atriplicinum* F. Muell. in Trans. & Proc. Victorian Inst. Advancem. Sci. 1: 133. 1855 ≡ *Chenopodium atriplicinum* (F. Muell.) F. Muell., Fragm. 7: 11. 1869 ≡ *Scleroblitum atriplicinum* (F. Muell.) Ulbr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 16c: 496. 1934. – Lectotype (designated by Wilson in Fl. Australia 4:197. 1983): Cudnaka, 10.1850, *F. Mueller* (MEL).

Tribe 3. *Dysphanieae* Pax in Engler & Prantl, Nat. Pflanzenfam. 3, 1b: 69, 92. 1889.

The tribe *Dysphanieae,* orginally described by Pax (1889), was previously supported by Kadereit & al. (2010) and Fuentes-Bazan & al. (2012), albeit in a new extended circumscription including *Cycloloma, Dysphania, Suckleya* and *Teloxys*. The additional results in this srudy also are in line. In the following, we treat *Dysphania* and *Teloxys* at genus level (without listing their species), because they formerly belonged to *Chenopodium* s.lat.

Dysphania R. Br., Prodr. Fl. Nov. Holland.: 411. 1810. – Type: *D. littoralis* R. Br.

= *Chenopodium* [unranked] *Orthosporum* R. Br., Prodr. Fl. Nov. Holland.: 407. 1810 ≡ *Blitum* [unranked] *Orthosporum* (R. Br.) C. A. Mey. in Ledebour, Fl. Altaic. 1: 11. 1829 ≡ *Orthosporum* (R. Br.) T. Nees, Gen. Fl. Germ., fasc. 7: ad t. 6 (or t. [127]; or vol. [1]; t. 57). 1835. – Type (designated by Scott in Bot. Jahrb. Syst. 100: 214. 1978): *C. pumilio* R. Br. (*Dysphania pumilio* (R. Br.) Mosyakin & Clemants).

= *Chenopodium* [unranked] *Botryoides* C. A. Mey. in Ledebour, Fl. Altaic. 1: 410. 1829 ≡ *Chenopodium* [unranked] *Botrys* Rchb., Fl. Germ. Excurs.: 580. 1832 ≡ *Chenopodium* sect. *Botrys* (Rchb.) W. D. J. Koch, Syn. Fl. Germ. Helv.: 607. 1837 ≡ *Ambrina* sect. *Botryois* Moq., Chenop. Monogr. Enum: 36. 1840, nom. illeg. ≡ *Vulvaria* sect. *Botrys* (Rchb.) Bubani, Fl. Pyren. 1: 177. 1897 ≡ *Botrys* (Rchb.) Nieuwl., Amer. Midl. Naturalist 3: 274. 1914 [non Fourr. 1869] ≡ *Chenopodium* subsect. *Botrys* (Rchb.) Aellen & Iljin in Komarov, Fl. URSS 6: 46. 1936 ≡ *Neobotrydium* Moldenke in Amer. Midl. Naturalist 35: 330. 1946 ≡ *Chenopodium* sect. *Botryoides* (C. A. Mey.) A. J. Scott in Bot. Jahrb. Syst. 100: 212. 1978. – Type: *C. botrys* L. (*Ambrina botrys* (L.) Moq., *Vulvaria botrys* (L.) Bubani, *Neobotrydium botrys* (L.) Moldenke, *Dysphania botrys* (L.) Mosyakin & Clemants).

= *Roubieva* Moq. in Ann. Sci. Nat., Bot., ser. 2, 1: 292. 1834 ≡ *Ambrina* Spach, Hist. Nat. Vég. Phan. 5: 295. 1836, nom. illeg. ≡ *Chenopodium* sect. *Roubieva* (Moq.) Volkens in Engler & Prantl, Nat. Pflanzenfam. 3, 1a: 61. 1893. – Type: *R. multifida* (L.) Moq. (*C. multifidum* L., *Ambrina pinnatisecta* Spach, nom. illeg., *Dysphania multifida* (L.) Mosyakin & Clemants).

= *Botrydium* Spach, Hist. Nat. Vég. Phan. 5: 298. 1836 [non Wallr. 1815]. – Type (designated by Scott in Bot. Jahrb. Syst. 100: 212. 1978): *B. aromaticum* Spach, nom. illeg. (*Chenopodium botrys* L., *Botrydium botrys* (L.) Small, *Dysphania botrys* (L.) Mosyakin & Clemants).

= *Ambrina* Moq., Chenopod. Monogr. Enum.: 36. 1840 [non Spach 1836] ≡ *Ambrina* sect. *Adenois* Moq., Chenopod. Monogr. Enum.: 39. 1840 ≡ *Chenopodium* sect. *Ambrina* Benth. & Hook f., Gen. Pl. 3: 51. 1880 ≡ *Chenopodium* [unranked] *Ambrosioidia* Standl. in N. Amer. Fl. 21: 26. 1916 ≡ *Chenopodium* subg. *Ambrosia* A. J. Scott in Bot. Jahrb. Syst. 100: 211. 1978. – Type (designated by Scott in Bot. Jahrb. Syst. 100: 213. 1978): *A. ambrosioides* (L.) Spach (*Chenopodium ambrosioides* L., *Dysphania ambrosioides* (L.) Mosyakin & Clemants).

= *Chenopodium* [unranked] *Carinata* Standl. in N. Amer. Fl. 21: 27. 1916. – Type: *C. carinatum* R. Br. (*Dysphania carinata* (R. Br.) Mosyakin & Clemants).

= *Chenopodium* [unranked] *Incisa* Standl. in N. Amer. Fl. 21: 25. 1916. – Type: *C. graveolens* Willd. 1809 [non Lag. & Rodr. 1802] (*Dysphania graveolens* Mosyakin & Clemants).

= *Meiomeria* Standl. in N. Amer. Fl. 21: 7. 1916 ≡ *Chenopodium* sect. *Meiomeria* (Standl.) A. J. Scott in Bot. Jahrb. Syst. 100: 211. 1978. – Type: *M. stellata* (S. Watson) Standl. (*Chenopodium stellatum* S. Watson, *Dysphania stellata* (S. Watson) Mosyakin & Clemants).

= *Chenopodium* sect. *Tetrasepala* Aellen in Bot. Jahrb. Syst. 63: 490. 1930 ≡ *Dysphania* sect. *Tetrasepalae* (Aellen) A. J. Scott in Bot. Jahrb. Syst. 100: 218. 1978. – Type (designated by Scott in Bot. Jahrb. Syst. 100: 218. 1978): *C. inflatum* Aellen (*Dysphania inflata* (Aellen) A. J. Scott).

= *Chenopodium* sect. *Margaritaria* Brenan in Kew Bull. 11: 166. 1956. – Type: *C. congolanum* (Hauman) Brenan (*Chenopodium glaucum* var. *congolanum* Hauman, *Dysphania congolana* (Hauman) Mosyakin & Clemants).

= *Chenopodium* sect. *Nigrescentia* Aellen in Acta Bot. Acad. Sci. Hung. 19: 3. 1973 – Type: *C. burkartii* (Aellen) Vorosch. (*Chenopodium ambrosioides* subsp. *burkartii* Aellen, *Dysphania burkartii* (Aellen) Mosyakin & Clemants).

= *Dysphania* sect. *Caudatae* A. J. Scott in Bot. Jahrb. Syst. 100: 218. 1978. – Type: *D. plantaginella* F. Muell. (*Chenopodium plantaginella* (F. Muell.) Aellen).

Annual or short-lived perennial, aromatic herbs, with glandular hairs and subsessile glands. *Stems* erect ascending, decumbent or prostrate, branched. *Leaves* alternate, petiolate; *blade* fairly thin, lanceolate, oblanceolate, ovate or elliptic, often pinnately lobed; *margin* entire, dentate or serrate. *Inflorescence* terminal and axillary, ebracteate, of loose, compound ebracteate cymes, or glomerules arranged spicately and often subtended by reduced leaf-like bracts. *Flowers* bisexual or rarely unisexual; *perianth segments* 1–5, mostly free near to the base and later loosely covering the fruit, or fused to form a sac surrounding the fruit, sometimes becoming whitish but otherwise unchanged; margins membranous or herbaceous, back roundish to keeled (rarely cristate); *stamens* 1–5; *stigmas* 1–3. *Fruit* with membranous, non-adherent pericarp. *Seeds* horizontal or vertical; subglobose to lenticular, ovoid, margin obtuse to truncate, testa reddish brown or black, smooth to rugose or reticulate

Teloxys Moq. in Ann. Sci. Nat., Bot., ser. 2, 1: 289. 1834 ≡ *Chenopodium* sect. *Teloxys* (Moq.) Beck in Reichenbach, Icon. Fl. Germ. Helv. 24: 116. 1908 ≡ *Chenopodium* [unranked] *Aristata* Standl. in N. Amer. Fl. 21: 25. 1916 ≡ *Chenopodium* subsect. *Teloxys* (Moq.) Aellen & Iljin in Komarov, Fl. URSS 6: 47. 1936. – Type: *T. aristata* (L.) Moq. (*C. aristatum* L., *Dysphania aristata* (L.) Mosyakin & Clemants).

Annual, non-aromatic herbs, almost glabrous. *Stems* erect, richly branched. *Leaves* alternate, petiolate, sometimes with scattered inflated hairs especially on petiole; *blade* linear to oblong-linear, gradually tapering to the petiole, margin more or less entire. *Infloresence* axillary from near the base and terminal, composed of dichasial or monochasial cymes with single flowers in axils of dichotomes, ultimate branches often transformed into spines. *Flowers* bisexual; perianth often later reddening, otherwise unchanged, *perianth segments* 5, broadly membraneous, herbaceous only in the middle, free almost to the base, more or less spreading in fruit; *stamens* 5; *stigmas* 2. *Fruit* with membraneous pericarp, adherent to the seed. *Seeds* horizontal, lenticular to subglobose, margin rimmed, testa smooth.

Tribe 4. *Axyrideae* G. Kadereit & Sukhor. in Amer. J. Bot. 97: 1682. 2010 ≡ *Axyridinae* Heklau inTaxon 57: 572. 2008.

= *Eurotiinae* Moq. in Candolle, Prodr. 13(2): 44, 119. 1849, nom. illeg.

The tribe comprises the three genera, *Axyris* L., *Ceratocarpus* L. and *Krascheninnikovia* Gueldenst. (Kadereit & al. 2010) and is corroborated in this circumscription in the present study.

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Note. — Fuentes-Bazan & al. (2011) transferred *Rhagodia crassifolia* to *Chenopodium* but their new combination *C. crassifolium* is illegitimate because of an earlier homonym. Therefore a new name is provided here:
Chenopodium wilsonii S. Fuentes, Borsch & Uotila, **nom. nov.** ≡ *Rhagodia crassifolia* R. Br., Prodr. Fl. Nov. Holland.: 408. 1810 ≡ *Chenopodium crassifolium* (R. Br.) S. Fuentes & Borsch in Molec. Phylogenet. Evol. 62: 372. 2011, nom. illeg. [non. Hornem. 1813]. – Eponymy: The name honours Paul G. Wilson, the author of the *Chenopodiaceae* of Flora of Australia.

Appendix 1. Sampling

Plants obtained from silica gel and herbarium specimens, the field or garden origin are first in the list, followed by the country, collector and collection number, the herbarium abbreviation in parentheses, the project code (ACXX). Finally the accession numbers of the regions are listed: the *trnL-F*, *trnk/matK* and ITS accessions. The *trnL-F* accessions (except for AC858, AC859, AC861, AC863, AC865, AC867) and ITS accessions (except for AC858, AC859, AC861, AC863, AC865, AC867, AC425 are from Fuentes-Bazan & al. (2012) and the *trnK/matK* accessions of the outgroup are from Müller & Borsch (2005). The rest of sequences were generated in the present study. In case that the samples were cultivate accessions number of GRIN are present (USA ARS GRIN refers to USDA, ARS, National Genetic Resources Program. Germplasm Resources Information Network - (GRIN). [Online Database] National Germplasm Resources Laboratory, Beltsville, Maryland) or accession numbers of the Bonaiscal Garden Berlin and the Botanical garden Bonn are write as Berlin Bot. Gard and Bonn Bot. Gard. respectively.

Outgroups: ***Beta vulgaris*** subsp. ***maritima*** (L.) Thell., Denmark, Jylland, *Cubr 39900* (B), AC530, HE577473, AY514832.1, HE577334. ***Hablitzia tamnoides*** M. Bieb., Germany, Berlin Bot Gard No: 16611 *S. Fuentes 018* (B), AC523, HE577474, AY514825.1, HE577335. ***Allenrolfea vaginata*** Kuntze, Germany, Bonn, Bot Gard No: 2488, AC017, HE577472, AY514828.1 AY181875.1.

Ingroup: ***Atripliceae: Atriplex*** **clade:** ***Atriplex deserticola*** Phil., Argentina, *Z. Noaga F O 12057* (B), AC859 HE855680, HE855638, HE855671. ***A. sagittata*** Borkh., Germany, Berlin Bot. Gard. No: 063119110, *S. Fuentes 021* (B), AC533 HE577499, HE855637, HE577359. ***Microgynoecium tibeticum*** Hook. f., China, *B. Dickoré 4284* (B), AC656, HE577503, HE855639, HE577363. — ***Chenopodium*** **s.str.:** ***C. album*** L., Germany, Bonn, *S. Fuentes 001* (B), AC388, HE577557, HE855644, HE577419. ***C. album*** L., USA, ARS GRIN PI608030 [USA], *S. Fuentes 007* (B), AC395, HE577568, HE855664, HE577430. ***C. album*** L., Germany, Usedom, *Weber* (B), AC602, HE577559, HE855665, HE577421. ***C. atrovirens*** Rydb., Bolivia, *S. G. Beck 11328* (B, KAS, LPB), AC363, HE577586, HE855642, HE577450. ***C. berlandieri*** Moq. USA, Nevada, *J. C. Beatley 11698* (NY), AC541, HE577561, HE855645, HE577423. ***C. cycloides*** A. Nelson, USA, *T. Borsch, Müller & Pratt 3452* (B), AC384, HE577598, HE855643, HE577459. ***C. desertorum*** subsp. ***anidiophyllum*** (Aellen) P.G. Wilson, Australia, *C. Michaell & J. Risler 1773* (B, NT), AC519, HE577555, HE855660, HE577417. ***C. desiccatum*** A. Nelson, USA, Missouri, *B. Summers & Harris 9813*

(MO), AC588, HE577550, HE855646, HE577412. ***C. ficifolium*** Sm., Germany, Berlin, *R. & E. Willing 12.260 D* (B), AC854, HE577606, HE855666, HE577466. ***C. fremontii*** S. Watson, USA, California, *G. Schoolcraft 2206* (UC), AC579, HE577546, HE855647, HE577408. ***C. standleyanum*** Aellen, USA, Kansas, *C. A. Morse 10855* (NY), AC550, HE577551, HE855657, HE577413. ***C. hians*** Standl., USA, Wyoming, *S. Stephens 70636* (NY), AC551, HE577610, HE855658, HE577470. ***C. pamiricum*** Iljin, Russia, *L. Martins 2490* (B), AC611, HE577608, HE855667, HE577468. ***C. incanum*** (S. Watson) A. Heller, USA, *R. D. Worthington 17439* (NY), AC553, HE577548, HE855659, HE577410. ***C. neomexicanum*** Standl., USA, *R. D. Worthington 13394* (NY), AC555, HE577611, HE855656, HE577471. ***C. nutans*** (R. Br.), Australia, S. Fuentes & Borsch, Berlin Bot. Gard. No: 187199, *S. Fuentes 019* (B), AC525, HE577553, HE855662, HE577415. ***C. opulifolium*** Schrad. ex W. D. J. Koch & Ziz, Slovakia, *T. Borsch 3899* (B), AC410, HE577595, HE855663, HE577455. ***C. pallescens*** Standl., USA, *G. Yatskievych 03-93* (MO), AC594, HE577547, HE855655, HE577409. ***C. pallidicaule*** Aellen, Bolivia, USA ARS GRIN PI478406, No Voucher, AC398, HE577574, HE855654, HE577439. ***C. pallidicaule*** Aellen, Peru, USA ARS GRIN PI510525, No Voucher, AC399, HE577573, HE855653, HE577438. ***C. petiolare*** Kunth, Bolivia, R. de Michel 2873 (B, KAS, LPB), AC359, HE577588, HE855641, HE577434. ***C. praterícola*** Rydb., USA, *K. H. Dueholm 10922* (B, LPB), AC558, HE577562, HE855668, HE577424. ***C. quinoa*** Willd., Bolivia, USA ARS GRIN Ames 13214, *S. Fuentes 013* (B), AC401, HE577580, HE855649, HE577445. ***C. quinoa*** Willd., Ecuador, USA ARS GRIN Ames 13228, *S. Fuentes 017* (B), AC402, HE577576, HE855650, HE577441. ***C. quinoa*** Willd., Peru, USA ARS GRIN PI510551, *S. Fuentes 009* (B), AC404, HE577579, HE855652, HE577444. ***C. quinoa*** Willd., Chile, USA ARS GRIN PI614880, *S. Fuentes 010* (B), AC407 HE577582, HE855651, HE577447. ***C. berlandieri*** subsp. ***nuttalliae*** (Saff.) H. Dan. Wilson & Heiser, Mexico, USA ARS GRIN PI568155, *S. Fuentes 016* (B), AC394, HE577571, HE855648, HE577433. ***C. subglabrum*** (S. Watson) A. Nelson, USA, Wyoming, *R. D. Dorn 5434* (NY), AC559, HE577605, HE855669, HE577465. ***C. triandrum*** G. Forst., New Zealand, *P. Hein 12560* (B, CHR), AC522, HE577554, HE855661, HE577416. ***C. vulvaria*** L., Spain, *T. Borsch 3918* (B), AC412, HE577591, HE855640, HE577407. ***C. watsonii*** A. Nelson, USA, *D. H. Goldman 2095* (NY), AC561, HE577602, HE855670, HE577462. — ***Chenopodium polyspermum*** **clade (=** ***Lipandra*****):** ***C. polyspermum*** L. Germany, *S. Fuentes 002* (B), AC389, not generated, not generated, HE855677. ***C. polyspermum*** L. Germany, *P. Hein 12483* (B), AC603, not generated, not generated, HE855678. ***C. polyspermum*** L. Germany, *T. Borsch s/n* (B), AC944, HE855686, HE855631, HE855679. — ***Chenopodium murale*** **clade (=** ***Chenopodiastrum*****):** ***C. murale*** L., Mexico, *T. Borsch & H. Flores Olvera 3871* (B, MEXU), AC382, HE577541, HE855632, HE577401. ***C. murale*** L., USA, *G. Gust & L. Nyle 476* (MO), AC587, HE577545, HE855633, HE577405. ***C. hybridum*** L. Germany, *R. & E. Willing 20.856 D* (B), AC521, HE577529, HE855634, HE577389. ***C. badachschanicum*** Tzvelev, Russia, *L. Martins 2329* (B), AC609, HE577528, HE855635, HE577413. ***C. coronopus*** Moq. Spain, Canary Islands, *Royl 6823* (B), AC570, HE577543, HE855636, HE577403. — ***Chenopodium rubrum*** **clade (=** ***Oxybasis*****):** ***C. chenopodioides*** (L.) Aellen, USA, Montana, *P. C. Lesica 5792* (NY), AC543, HE577519, HE855622, HE577379. ***C. glaucum*** L.,USA, USA ARS GRIN PI612859, *S. Fuentes 184* (B), AC652, HE577526, HE855627, HE577386. ***C. glaucum*** L., Spain, *T. Borsch 3931* (B), AC417, HE577527, HE855628, HE577387. ***C. rubrum*** L., Germany, *T. Borsch* [08.07] (B), AC411, HE577520, HE855624, HE577380. ***C. rubrum*** L. Germany, *E. Willing 10.931D* (B), AC564, HE577522, HE855626, HE577382. ***C. rubrum*** L., Poland, USA ARS GRIN Ames 23860, *S. Fuentes 182* (B), AC653, HE577521, HE855625, HE577381. ***C. rubrum*** L., USA, *T. Borsch 3448* (B), AC385, HE577525, HE855623, HE577385. ***C. urbicum*** L. Greece, Fthiotis, *R. & E. Willing 146.1979* (B), AC576, HE577524, HE855630, HE577384. ***C. urbicum*** L., Greece, Berlin Bot. Gard. No: 269400010, *S. Fuentes 026* (B), AC536, HE577523, HE855629, HE577383.

Anserineae: Chenopodium capitatum **clade (=** ***Blitum*****):** ***C. bonus-henricus*** L., Austria, *T. Borsch 3821* (B), AC381, HE577512, HE855613, HE577372. ***C. californicum*** (S. Watson) S. Watson., USA, California, *P. Davis & D. Lightowless 66504* (B), AC431, HE577516, HE855616, HE577376. ***C. capitatum*** (L.) Ambrosi, Germany, Bonn Bot. Gart. No: 19116, *S. Fuentes 004* (B), AC391, HE577513, HE855614, HE577373. ***C. capitatum*** (L.) Ambrosi, USA, *K. Moon & al. 1993* (NY), AC547, HE577514, HE855615, HE577374. ***C. foliosum*** Asch., Germany, Bonn Bot Gart No: 19117, *S. Fuentes 003* (B), AC392, HE577517, HE855617, HE577377. ***C. foliosum*** Asch., Kirgizstan, *Cubr 42389* (B), AC520, HE577518, HE855618, HE577378. ***Monolepis nuttalliana*** (Schult.) Greene, USA, *R. C. Holmgren 317* (B), AC621, HE577515, HE855621, HE577375. — ***Spinacia: S. oleracea*** L., AJ400848.1, AJ400848.1, EU606218.1. ***S. tetrandra*** Steven ex M. Bieb., Asia, USA ARS GRIN Ames 23664, *S. Fuentes 180* (B), AC650, HE577482, HE855619, HE577345. ***S. turkestanica*** Iljin, Asia, USA ARS GRIN Ames 23666, *S. Fuentes 181* (B), AC651 HE577483, HE855620, HE577346.

Dysphanieae: Dysphania ambrosioides (L.) Mosyakin & Clemants Bolivia, *S. G. Beck 31178* (B, LPB), AC425 HE577493, HE855605, HE577353. ***D. ambrosioides*** (L.) Mosyakin & Clemants, Argentina, *Z Noaga F O 11806* (B), AC858, HE855681, HE855607, HE855672. ***D. ambrosioides*** (L.) Mosyakin & Clemants, Argentina, *Z Noaga F O 11603* (B), AC865, HE855682, HE855610, HE855673. ***D. ambrosioides*** (L.) Mosyakin & Clemants, Cuba, *T. Borsch & al. 4397* (B), AC867, HE855683, HE855611, HE855674. ***D. graveolens*** Mosyakin & Clemants, Argentina, *Z Noaga F O 11911* (B), AC861, HE855684, HE855608, HE855675. ***D. graveolens*** Mosyakin & Clemants, Argentina, *Z Noaga F O 11913* (B), AC863, HE855685, HE855609, HE855676. ***D. graveolens*** Mosyakin & Clemants, Bolivia, *E. Thomas 258* (B, LPB), AC419, HE577495, HE855604, HE577355. ***D. pumilio*** (R. Br.) Mosyakin & Clemants, Greece, *R. & E. Willing 85.571* (B), AC604, HE577485, HE855606, HE577342. ***D. schraderianum*** (Schult.) Mosyakin & Clemants, Ethiopia, *M. Wondafrash 2255* (B, ETH), AC387, HE577490, HE855603, HE577349. — ***Teloxys aristata*** (L.) Moq., Mongolia, USA ARS GRIN Ames 25314, *S. Fuentes 183* (B), AC654, HE577481, HE855612, HE577341.

Axyrideae: Axyris prostrata L., Russia, *E. v. Raab-Straube 020232a* (B), AC529, HE577509, HE855600, HE577369. — ***Ceratocarpus arenarius*** L., Romania, Navodari, *A. Romanovsch* (B), AC531, HE577504, HE855601, HE577364. — ***Krascheninnikovia ceratoides*** (L.) Gueldenst., Russia, *R. Hand 1536* (B), AC532, HE577507, HE855602, HE577367.

Appendix 2. Sequence statistics of individual regions and the combined plastid data set for *Chenopodium* s.l.

	***trnL* intron**	***trnL* 3' exon**	***trnL-F* sapcer**	***trnK* 5' intron**	***matK***	***trnK* 3' intron**	**combined**
Dataset with hotspots							
Length range	304–630	50	164–386	672–750	1493–1536	195–229	
Mean length (SD)	531(73)	50	358(25)	706(12)	1525(6)	210(7)	
% GC	31.8	30.3	44	31.3	32.3	33	
Inversions	1	0	0	0	0	0	
Dataset without hotspots							
Length range	295–538	50	159–369	651–722	1493–1536	178–212	3053–3347
Mean length (SD)	478(54)	50	347(24)	680(11)	1525(6)	197(7)	3277(6)
% variable characters	24.7	2	42.3	28.9	33.1	41.3	32.1
% informative characters	16.3	2	27.2	19.8	23.4	25.6	21.8
Number of coded indels	63	0	74	44	6	30	217