

**MOLECULAR PHYLOGENY OF ATRIPLICEAE
(CHENOPODIOIDEAE, CHENOPODIACEAE): IMPLICATIONS FOR
SYSTEMATICS, BIOGEOGRAPHY, FLOWER AND FRUIT EVOLUTION,
AND THE ORIGIN OF C₄ PHOTOSYNTHESIS¹**

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- *Premise of the study:* Atripliceae (Chenopodiaceae), including *Atriplex* (300 spp.) as the largest genus of the family, are an ecologically important group of steppes and semideserts worldwide. Relationships in Atripliceae are poorly understood due to obscure and potentially convergent morphological characters.
- *Methods:* Using sequence variation of two chloroplast markers (*rbcL* gene, *atpB-rbcL* spacer) and one nrDNA marker (ITS) analyzed with BEAST, we investigated the systematics and biogeography of Atripliceae. We surveyed flower morphology and fruit anatomy to study the evolution of flowers and fruits in the tribe.
- *Key results:* Female flowers with persistent foliar cover (the diagnostic character of traditional Atripliceae) evolved three times in Chenopodioideae, in Atripliceae s.s., Axyrideae, and *Spinacia*. Atripliceae s.s. started to diversify during the Early Miocene in Eurasia, separating into the *Archiatriples* and the *Atriplex* clades. The former consists of eight species-poor, disjunct, and morphologically heterogeneous genera and is likely a relictual lineage. The *Atriplex* clade comprises the majority of species and evolved one C₄ lineage 14.1–10.5 Ma, which diversified rapidly worldwide. The C₄ *Atriplex* entered North America during the Middle/Late Miocene and spread to South America subsequently. Australia was colonized by two C₄ lineages both arriving during the Late Miocene. One of them diversified rapidly, giving rise to most Australian *Atriplex* species.
- *Conclusions:* Atripliceae s.s. comprise *Archiatriples*, *Atriplex*, *Exomis*, *Extriplex*, *Grayia*, *Halimione*, *Holmbergia*, *Mano-chlamys*, *Proatriplex*, and *Stutzia*. *Microgynoecium* is included based on morphology but only weak molecular support. *Axyris*, *Krascheninnikovia*, and *Ceratocarpus* (here described as Axyrideae) and *Spinacia* are excluded from Atripliceae.

Key words: *Archiatriples*; *Atriplex*; *Cremnophyton*; *Exomis*; *Extriplex*; *Grayia*; *Halimione*; *Holmbergia*; *Microgynoecium*; *Stutzia*.

The Atripliceae traditionally belong to subf. Chenopodioideae and comprise c. 330 species in 12 genera according to the most recent comprehensive treatment by Kühn et al. (1993) (Table 1). The tribe is distributed worldwide in subtropical and temperate regions and consists of annual or perennial herbs, subshrubs or shrubs found in steppes, deserts, and coastal or ruderal habitats (Table 1). Many species can tolerate saline conditions and several species are dominant elements of arid communities worldwide, e.g., shadscale (*Atriplex confertifolia*) in

the Great Basin (Sanderson et al., 1990), zampa (*A. lampa*) in northwestern Patagonia (Busso and Bonvissuto, 2009), bladder saltbush (*A. vesicaria*) in western New South Wales and northern and eastern regions of South Australia (Groves, 1994), Oldman saltbush (*A. nummularia*) in southeastern Australia (Anderson, 1967; Leigh, 1994), and *A. cana* formations in Eurasian semideserts (Korovin, 1934; Bykov, 1965).

After Meyer (1829), who included four genera in the tribe Atripliceae (Table 2), characteristic flower morphology has been considered as the key diagnostic character for this tribe. In the majority of species, all flowers are unisexual (a few species also show some bisexual flowers), and the female flowers lack a perigon but have two subtending, paired bracteoles (hereafter referred to as bracts, after Urmi-König, 1981) that enclose the ovary. These bracts are either tightly attached to but free from each other or connate to various degrees along their margins. In fruit the bracts are persistent and variously modified. Often they develop structures that likely enhance fruit dispersal. These typical female flowers with a foliar cover have been viewed by most authors as a syndrome that characterizes a natural group (Standley, 1916; Ulbrich, 1934; Aellen, 1979; Kühn et al., 1993; Judd and Ferguson, 1999). The tribe has often been subdivided into two subtribes, Atriplicinae and Eurotiinae, according to differences in pubescence (e.g., Moquin-Tandon, 1849;

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TABLE 1. Genera of Atripliceae and Chenopodieae and information about species number, distribution, life form and representatives in this study.

Taxon	Species number, distribution and life form	Number of sampled species for data set A (<i>rbcL</i>), B (<i>atpB-rbcL</i> spacer), C (ITS)
Chenopodieae		
<i>Baolia</i> H. W. Kung & G. L. Chu	1 sp., China, annual	no material available
<i>Chenopodium</i> L.	c. 100 spp., worldwide, annual or perennial herbs, subshrubs, shrubs or small trees	A = 9, B = 11, C = 1 (see Appendix 1 for list of sampled species)
<i>Cycloloma</i> Moq.	1 sp., west and central North America, annual	A = 1, B = 1 (<i>C. atriplicifolium</i>)
<i>Dysphania</i> R. Br.	c. 32 spp., worldwide, annual or short-lived perennial herbs* ¹	A = 4, B = 4 (<i>D. ambrosioides</i> , <i>D. botrys</i> , <i>D. cristata</i> , <i>D. glomulifera</i>)
<i>Einadia</i> Raf.	6 spp., Australia, New Zealand, herbaceous or weakly woody perennials	A = 1, B = 1 (<i>E. nutans</i>)
<i>Holmbergia</i> Hicken	1 sp., Paraguay, Uruguay, Argentina, climbing shrub	B = 1, C = 2 (<i>H. tweedii</i>)
<i>Micromonolepis</i> Ulbr.	1 sp., western North America, annual	A = 1, B = 1 (<i>M. pusilla</i>)
<i>Monolepis</i> Schrad.	5 spp., northern Siberia, western North America, South America, annuals	A = 1, B = 1 (<i>M. nutalliana</i>)
<i>Rhagodia</i> R. Br.	11 spp., Australia, shrubs	A = 1, B = 2 (<i>R. drumondii</i> , <i>R. parabolica</i>)
<i>Scleroblitum</i> Ulbr.	1 sp., Australia, annual	A = 1 (<i>S. atriplicinum</i>)
<i>Teloxys</i> Moq.* ¹	1 sp., Central Asia, annual* ¹	A = 1, B = 1 (<i>T. aristata</i>)
Atripliceae		
<i>Archiatrilex</i> G. L. Chu	1 sp., China, annual	A = 1, B = 1, C = 1 (<i>A. nanpinensis</i>)
<i>Atriplex</i> L. (incl.: <i>Blackiella</i> * ² Aellen, <i>Haloxanthium</i> Ulbr., <i>Morrisiella</i> * ² Aellen, <i>Neopreissia</i> Ulbr., <i>Obione</i> Gaertner, <i>Pachypharynx</i> * ² Aellen, <i>Senniella</i> * ² Aellen, <i>Theleophyton</i> (Hook. f.) Moq., <i>Axyris</i> L., <i>Ceratocarpus</i> L., <i>Cremnophyton</i> Brullo & Pavone, <i>Exomis</i> Fenzl ex Moq., <i>Extriplex</i> E. H. Zacharias)	~300 spp., worldwide, annual or perennial herbs, subshrubs or shrubs	A = 19, B = 55, C = 92 (see Appendix 1 for list of sampled species)
<i>Grayia</i> Hook. & Arn. (incl. <i>Zuckia</i> Standl.)	6 spp., Central Asia, Himalaya, west China, annuals	A = 1, B = 1 (<i>A. prostrata</i>)
<i>Halimione</i> Aellen	2 spp., East Europe, West Asia, annuals	A = 1 (<i>C. arenarius</i>)
<i>Krascheninnikovia</i> Gueldenst.	1 sp., Malta and Gozo, shrub	A = 1, B = 2, C = 1 (<i>C. lanfrancoi</i>)
<i>Manochlamys</i> * ³ Aellen	1 sp., South to West Africa, shrub	A = 1, B = 1, C = 1 (<i>E. microphylla</i>)
<i>Microgynoecium</i> Hook. f.	1 sp., western North America, annual or perennial herbs	A = 2, B = 2, C = 2 (<i>E. joaquinana</i> , <i>E. californica</i>)
<i>Proatrilex</i> (W. A. Weber) Stutz & G. L. Chu	2 spp., western North America, shrubs	A = 2, B = 4, C = 5 (<i>G. spinosa</i> , <i>G. brandegeei</i>)
<i>Spinacia</i> L.	3 spp., Europe, W Asia, annuals and shrubs	A = 2, B = 2, C = 4 (<i>H. pedunculata</i> , <i>H. verrucifera</i> , <i>H. portulacoides</i>)
<i>Stutzia</i> E. H. Zacharias (<i>Endolepis</i> Torrey, nom. illeg.)	8 spp.* ⁴ , Europe, Asia, North America, subshrubs or shrubs	A = 1, B = 2 (<i>K. ceratoides</i>)
<i>Suckleya</i> A. Gray	1 sp., South Africa, shrub	A = 1, B = 1, C = 1 (<i>M. albicans</i>)
	1 sp., Tibet, Sikkim, annual	A = 1, B = 1, C = 1 (<i>M. tibeticum</i>)
	1 sp., western North America, annual	C = 2 (<i>P. pleiantha</i>)
	3 spp., North Africa, West Asia, annual or biennial herbs	A = 1, B = 1 (<i>S. oleracea</i>)
	2 spp., western North America, annual	A = 2, B = 2, C = 3 (<i>S. dioica</i> , <i>S. covillei</i>)
	1 sp., western North America, annual	A = 1 (<i>S. suckleyana</i>)

*¹ Mosyakin and Clemants (2002) and Clemants and Mosyakin (2003) expanded the circumscription of *Dysphania* comprising all glandular taxa of *Chenopodium* subg. *Ambrosia* A. J. Scott (species previously also classified as *Roubieva* Moq., *Teloxys* Moq., *Neobotrydium* Moldenke). *² Aellen (1937/1938). Aellen (1938a). *³ Aellen (1939b). *⁴ According to Heklau and Röser (2008) only one polymorphic species with two subspecies.

Volkens, 1893; Ulbrich, 1934). The circumscription of Atripliceae in earlier important treatments is summarized in Table 2. Some authors, however, included the Atripliceae into a broadly circumscribed Chenopodieae (e.g., Blackwell, 1977; Williams and Ford-Lloyd, 1974; Wilson, 1984), the species of which generally have bisexual flowers with 4–5 small tepals that are persistent but not modified in fruits.

The core genus of the tribe is *Atriplex*, which comprises 91% of the species of the tribe in its present circumscription (Table 1; Kühn et al., 1993). Most of the genera that had been classified under Atripliceae had been in or excluded from the genus at various times by different authors. Exceptions are the Central Asian monotypic genera *Archiatrilex* and *Microgynoecium*, several genera traditionally assigned to Eurotiinae (nom. illeg., now as subtribe. Axyridinae Heklau [Heklau and Röser, 2008]),

viz., *Axyris*, *Ceratocarpus*, and *Krascheninnikovia*, and the often overlooked genus *Cremnophyton*. *Endolepis* Torrey (nom. illeg.), *Exomis* Fenzl, *Obione* Gaertn., *Halimione* Aellen, *Blackiella* Aellen, *Haloxanthium* Ulbr., *Morrisiella* Aellen, *Neopreissia* Ulbr., *Pachypharynx* Aellen, *Senniella* Aellen, *Theleophyton* Moq., *Manochlamys* Aellen, *Proatrilex* (W. A. Weber) Stutz & G. L. Chu, and *Grayia* Hook. and Arn. had all been considered as congeneric with *Atriplex* at some stage (Tables 1, 2). In several cases, a particular morphology of the fruiting bracts was considered an important character for delimitation at the genus level. Two examples of this are the Australian genera *Neopreissia* and *Senniella*. *Neopreissia* was separated from *Atriplex* on the basis of its thick and hard fruiting bracts with a turbinate stipe at the base (Ulbrich, 1934), and *Senniella* was excluded from *Atriplex* on the basis of its united and spongy fruiting

TABLE 2. Classifications of Atripliceae

Meyer (1829)	Moquin-Tandon (1840)	Moquin-Tandon (1849)	Volken (1893)	Ulbrich (1934)	Kühn et al. (1993)	Falkovitsh and Kovalev (2007)
Tribe Atripliceae	Tribe Spinaciae	Tribe Spinaciae Subtribe Atripliceae [=Atriplicinae]	Tribe Atripliceae Subtribe Atriplicinae	Tribe Atripliceae Subtribe Atriplicinae	Tribe Atripliceae	Subfam. Atriplicioideae Tribe Atripliceae
<i>Atriplex</i>	<i>Atriplex</i> <i>Obione</i> <i>Exomis</i> <i>Spinacia</i>	<i>Atriplex</i> <i>Obione</i> <i>Theleophyton</i> <i>Exomis</i> <i>Spinacia</i> <i>Oxybasis</i> (> <i>Chenopodium</i>) <i>Axyris</i>	<i>Atriplex</i> (<i>Endolepis</i> ³) (incl. in <i>Atriplex</i>) (incl. in <i>Atriplex</i>) <i>Exomis</i> <i>Spinacia</i> <i>Microgynoecium</i> <i>Suckleya</i>	<i>Atriplex</i> <i>Obione</i> <i>Theleophyton</i> <i>Exomis</i> <i>Spinacia</i> <i>Microgynoecium</i> <i>Suckleya</i> <i>Endolepis</i> ³ <i>Rumic astrum</i> (>Portulacaceae) <i>Neopreissia</i> <i>Haloxanthium</i> <i>Zuckia</i>	<i>Atriplex</i> (incl. in <i>Atriplex</i>) (incl. in <i>Atriplex</i>) <i>Exomis</i> <i>Spinacia</i> <i>Microgynoecium</i> <i>Suckleya</i> <i>Endolepis</i> ³ (incl. in <i>Atriplex</i>) (incl. in <i>Atriplex</i>) <i>Zuckia</i>	<i>Atriplex</i> (incl. in <i>Atriplex</i>) (incl. in <i>Atriplex</i>) <i>Exomis</i> <i>Spinacia</i> <i>Microgynoecium</i> incl. in Chenopodioideae <i>Endolepis</i> ³ (incl. in <i>Atriplex</i>) (incl. in <i>Atriplex</i>) <i>Zuckia</i> Tribe Eurotieae <i>Ceratocarpus</i> <i>Krascheninnikovia</i> <i>Grayia</i> Chenopodioideae <i>Axyris</i> <i>Archiatriples</i> ⁴ <i>Proatriplex</i> ⁴ <i>Senniella</i> ⁴ <i>Halimione</i> ⁴ <i>Cremnophyton</i> ⁴ <i>Manochlamys</i> ⁴
<i>Ceratocarpus</i> <i>Diotis</i> ¹	<i>Ceratocarpus</i> <i>Eurotia</i> ²	Subtribe Eurotieae <i>Ceratocarpus</i> <i>Eurotia</i> ² <i>Grayia</i>	Subtribe Eurotiinae <i>Ceratocarpus</i> <i>Eurotia</i> ² <i>Grayia</i>	Subtrib. Eurotiinae <i>Ceratocarpus</i> <i>Eurotia</i> ² <i>Grayia</i>	<i>Ceratocarpus</i> <i>Krascheninnikovia</i> <i>Grayia</i>	
<i>Axyris</i>	<i>Axyris</i> <i>Acnida</i> (>Amaranthaceae s.s.)		<i>Axyris</i>	<i>Axyris</i>	<i>Axyris</i> <i>Archiatriples</i> (not mentioned) (incl. in <i>Atriplex</i>) (incl. in <i>Atriplex</i>) (not mentioned) (incl. in <i>Exomis</i>)	

¹ nom illeg. (incl. *Krascheninnikovia* p.p., *Halimione* p.p.); ² nom. illeg. later corrected to *Krascheninnikovia* Gueldenst.; ³ nom. illeg. later corrected to *Stutzia* E. H. Zacharias; ⁴ classified in Atripliceae by Falkovitsh and Kovalev (2007). **Note:** The genera *Blackiella*, *Morrisiella* and *Pachypharynx* described by Aellen (1938b) were not accepted by Kühn et al. (1993) and Falkovitsh and Kovalev (2007) but included in *Atriplex*.

bracts (Aellen, 1937/1938). Because *Atriplex* is a rather polymorphic genus with fruiting bract morphology that has many transitional character states, the delimitation from its satellite genera has always been problematic [e.g., *Senniella* and *Neopreissia* were included in *Atriplex* by Wilson (1984)]. Early in the taxonomic history of *Atriplex*, the genus *Obione* Gaertn. was separated on the basis of *O. muricata* Gaertn. (= *A. sibirica* L.; Gaertner, 1791). In contrast to other *Atriplex* species already described at that time, *Obione muricata* has concrescent and sclerified bracts in the female flowers and an embryo with the radicle pointing upward. Many authors agreed with this segregation although at different taxonomic levels (i.e., genus, subgenus, or section). Sukhorukov (2006) found that the position of the radicle is strongly correlated with the degree of concrescence of the two bracts. The radicle is always orientated toward the point where the concrescent part passes into the free part. Furthermore, Sukhorukov (2006) found that the degree of concrescence of the two bracts can vary considerably within species.

In contrast to the cosmopolitan *Atriplex* the smaller genera have rather limited distribution areas (Table 1). *Atriplex* has greatest taxonomic diversity in Australia, North America, South America, and Eurasia. In South Africa, the genus seems to be less diverse, but in this region and also in South America, a region of high diversity, the genus has not been extensively

studied so far. The evolution of C₄ photosynthesis might have played a major role in the evolutionary success of the genus because the majority of *Atriplex* species perform C₄ photosynthesis and C₄ *Atriplex* are distributed worldwide. Unlike most other groups of C₄ Chenopodiaceae, *Atriplex* has typical Kranz anatomy with a layer of bundle sheath cells surrounding each vascular bundle and radially arranged palisade cells and relatively little variation in C₄ leaf types. This atriplicoid leaf type (Carolin et al., 1975) occurs in two variants, viz. the *Atriplex halimus* and the *A. dimorphostegia* types, respectively (Kadereit et al., 2003, compare with Khatib, 1959). The latter differs in the absence of a hypodermis. With limited sampling of the genus, Kadereit et al. (2003) estimated the origin of C₄ *Atriplex* to have occurred 11.5–7.9 Ma and Zacharias (2007) estimated it to have occurred 8.4–5.7 Ma.

Molecular analyses (Kadereit et al., 2003; Müller and Borsch, 2005) show that Chenopodioideae consist of only two tribes, Chenopodieae and Atripliceae. Other tribes that were previously assigned to this subfamily by Kühn et al. (1993), viz. Beteae and Camphorosmeae, clearly do not belong to Chenopodioideae. Beteae are now recognized at subfamilial rank (Kadereit et al., 2006), and Camphorosmeae either belong to subfam. Salsoloideae (Kadereit et al., 2003; Müller and Borsch, 2005; Kapralov et al., 2006; Akhiani et al., 2007) or should be recognized as a

subfamily of its own (Kadereit and Freitag, 2010). Representatives of Chenopodieae and Atripliceae are somewhat intermingled in the *rbcL* phylogeny by Kadereit et al. (2003), and neither Atripliceae nor Chenopodieae in their present circumscription after Kühn et al. (1993) seem to represent natural lineages. The sampling and resolution in Kadereit et al. (2003), however, was only sufficient to uncover the possible polyphyly of Atripliceae and *Chenopodium* and the presence of a basal grade mainly of members of the Chenopodieae but insufficient to come up with a new classification of the subfamily. A detailed cladistic analysis based on 78 morphological characters (Flores Olvera and Davis, 2001) suggested that Atripliceae and also *Atriplex* are paraphyletic and that both subtribes of Atripliceae, Atriplicinae, and Eurotiinae, are polyphyletic. A limited sampling within Chenopodieae and lack of additional evidence from other data sources restrained Flores Olvera and Davis (2001) from translating their results into a new classification of the tribe. Zacharias' (2007) and Zacharias and Baldwin's (in press) molecular analyses of Atripliceae showed that neither *Atriplex*, as traditionally recognized, nor the North American members of *Atriplex* constitute a monophyletic group.

This study aims to clarify the systematics and phylogeny of Atripliceae using a complete sampling of genera traditionally assigned to Atripliceae, extensive sampling of the large genus *Atriplex* and a broad sampling of other genera of Chenopodioideae. Three molecular markers (*rbcL* gene, *atpB-rbcL* spacer, and ITS) were sequenced and analyzed with the program BEAST v1.4.8 (Drummond and Rambaut, 2007), which estimates topology and branch lengths simultaneously from the data using a Bayesian Markov chain Monte Carlo (MCMC) analysis. The resulting topologies and dated major splits allowed us to obtain the first general idea of the historical biogeography and diversification of the cosmopolitan Atripliceae based on molecular evidence. With the aid of the molecular trees, we aim to understand the evolution of flower and fruit morphology, especially the evolution of persistent and strongly modified fruiting bracts and the evolution of separation of sexes within the tribe. Furthermore, we will investigate the origin and age of C_4 photosynthesis in *Atriplex*.

MATERIALS AND METHODS

Taxon sampling—We included all genera currently recognized and traditionally assigned to Atripliceae. We used multiple samples of *Atriplex* to represent the biogeographical and morphological diversity of this large and widespread genus. Furthermore, we included most genera currently assigned to Chenopodioideae with several samples of the large, polyphyletic genus *Chenopodium*.

We are in the fortunate situation that up to 50-yr-old herbarium material can be used for sequencing in Chenopodiaceae if the material was nicely dried and kept dry. Therefore, in this study, we mostly extracted DNA from herbarium material. In some cases, we used samples that were dried in silica gel, and for the Australian species of *Atriplex*, we used leaves preserved in saturated NaCl-CTAB solution supplemented with 200 mM sodium ascorbate (Thomson, 2002). Voucher information for all samples is listed in Appendix 1.

DNA extraction—For DNA extraction, the NucleoSpin plant DNA extraction kit (Macherey & Nagel, Düren, Germany) or the DNeasy Plant Mini Kit (Qiagen, Valencia, California, USA) was used following the manufacturer's specifications, or samples were extracted using the CTAB extraction protocol of Doyle and Doyle (1987).

Amplification and sequencing—For amplification and sequencing protocols of the *rbcL* gene, we refer to Kadereit et al. (2003) and for the *atpB-rbcL* spacer and ITS to Kadereit et al. (2005, 2006), Mavrodiev et al. (2005), and Zacharias and Baldwin (in press).

Alignment—All obtained chromatograms were edited in the program Sequencer version 4.8 (GeneCodes Corp., Ann Arbor, Michigan, USA) or ABI Prism Sequence Navigator software (Applied Biosystems, Foster City, California, USA), and partial sequences of the *rbcL* gene were assembled to a consensus sequence for each taxon. The alignment for all three markers was done manually in Sequencer 4.8 and was straightforward due to moderate sequence variation (even in the mutational hotspots of the *atpB-rbcL* spacer). Indels were not coded in the ITS data set but treated as missing data. In the *atpB-rbcL* spacer data set, only six informative indels (outside the mutational hotspots of the spacer) were coded as transversions.

Phylogeny inference and divergence time estimation—The three data sets were analyzed separately using BEAST (Bayesian Evolutionary Analysis by Sampling Trees v1.4.8; Drummond and Rambaut, 2007), which simultaneously estimates tree topology and divergence times. The BEAST.xml input files (available from the corresponding author upon request) were created with the Bayesian Evolutionary Analysis Utility v1.4.8 (BEAUti; implemented in BEAST; Drummond and Rambaut, 2007). For the *rbcL* and *atpB-rbcL* spacer analyses representatives of Corispermoidae were chosen as outgroup according to the results of Müller and Borsch (2005) and Kadereit and Freitag (2010). The ingroup was defined as monophyletic to set the root at the split between Chenopodioideae and Corispermoidae. The substitution model parameters were set to those of GTR+G+I based on the program MODELTEST 3.7 (Posada and Crandall, 1998). The relaxed Bayesian clock was implemented with rates for each branch drawn independently from a lognormal distribution (Drummond et al., 2006). A birth and death prior was set for branch lengths. In the *rbcL* and *atpB-rbcL* spacer analyses the root age was set to 57–55 Ma with the uniform prior. This calibration was done according to earlier branch dating of the Amaranthaceae/Chenopodiaceae alliance that included the reliable fossils available (Kadereit et al., 2003; Kadereit and Freitag, 2010). In the ITS analysis, the root age was set to 30–29 Ma with the uniform prior according to the results of the *rbcL* and *atpB-rbcL* spacer analyses. Other priors were in default settings and the Markov chain Monte Carlo (MCMC; Drummond et al., 2002) was initiated on a random starting tree. The first runs were used to examine MCMC performance, and operators were adjusted as suggested by the output analysis. The final run was performed with 10 000 000 (*rbcL*) or 20 000 000 (*atpB-rbcL* spacer and ITS) iterations, a burn-in of 10% and a sample frequency of 1000. After assessing convergence in the program Tracer v1.4.1 (Rambaut and Drummond, 2007) as described in the BEAST manual (Drummond et al., 2007), the maximum clade credibility tree was summarized in the program TreeAnnotator v1.4.8 (Drummond and Rambaut, 2007) with a posterior probability (post. prob.) limit of 0.7 and summarizing mean node heights. The summary trees were edited in the program FigTree v1.2.2 (Rambaut, 2006).

Morphological and anatomical studies—Samples for morphological and anatomical studies were taken (with curatorial permission) from specimens of E, GH, K, LE, MHA, and MW or from collections made by the authors. Samples preserved in 70% ethanol from European Russia, the Mediterranean area, and Central Asia were included in the study. The fruit anatomy of numerous representatives of the tribe was studied comparatively. Anatomical sections were made by hand. Dry samples were soaked in an ethanol:glycerol:water (1:1:1) solution for several days prior to sectioning.

RESULTS

rbcL—The matrix comprised 1343 characters and 60 taxa. The three representatives of Corispermoidae were chosen as outgroup. The data set contained 229 variable sites (17.1%) of which 104 (7.7%) occurred in only one sample. The tree resulting from the analysis with BEAST is shown in Fig. 1. The *rbcL* analysis revealed a number of well-supported major clades within Chenopodioideae: Atripliceae, Axyrideae (trib. nov.), Chenopodieae I, Chenopodieae II, and Dysphanieae. Three species form clades on their own that cannot be assigned to any of these major clades. These are *Microgynoecium tibeticum*, *Chenopodium urbicum*, and *C. coronopus*. The placement of the latter two within Chenopodioideae requires further sampling because they do not group within the Chenopodieae clades. *Microgynoecium tibeticum* forms a well-supported clade with

Atripliceae and Chenopodieae I. A sister group relationship of *M. tibeticum* and Chenopodieae I is resolved in the *rbcL* tree, but this receives only weak support (post. prob. 0.76). Within Atripliceae a well-supported, basal split into two clades (the *Atriplex* clade and the *Archiatripliceae* clade) was found. The *Atriplex* clade contains the representatives of *Halimione* and *Atriplex* (including *Cremonophyton*) as well-supported sister lineages. The *Archiatripliceae* clade comprises *Archiatripliceae*, *Exomis*, *Manochlamys*, *Extriplex* (gen. nov. ined.), *Grayia*, and *Stutzia* (gen. nov. ined.).

***atpB-rbcL* spacer**—The matrix comprised 829 characters and 100 taxa. The three representatives of Corispermoidae were chosen as outgroups. The data set contained 291 variable sites (35.1%), of which 101 (12.2%) occurred in only one sample. The tree resulting from the Bayesian analysis with BEAST (Fig. 2) is largely congruent with the *rbcL* tree (Fig. 1). Like the *rbcL* analysis, the *atpB-rbcL* spacer analysis revealed the same major clades (Atripliceae, Axyrideae, Chenopodieae I, Chenopodieae II, and Dysphanieae) with high statistical support. The main difference between the *rbcL* analysis and the *atpB-rbcL* spacer analysis is the position of the Dysphanieae. They are resolved as sister to Axyrideae plus *Chenopodium urbicum* in the *atpB-rbcL* spacer analysis (with moderate support) and as sister to a clade comprising Chenopodieae I and II, Atripliceae, *Microgynoecium* and *Chenopodium coronopus* in the *rbcL* analysis. Again Atripliceae are most closely related to *Microgynoecium* and Chenopodieae I. The three clades form a polytomy. Atripliceae are subdivided into *Atriplex* clade and *Archiatripliceae* clade as in the *rbcL* analysis. Similar to the *rbcL* tree, the *Atriplex* clade shows a sister group relationship of *Halimione* and *Atriplex* (including *Cremonophyton*), and the *Archiatripliceae* clade comprises the same genera, as well as *Holmbergia*, which was not sampled for the *rbcL* analysis. The *Archiatripliceae* clade has lower support in the *atpB-rbcL* spacer tree than in the *rbcL* gene tree but has better resolution. *Archiatripliceae* is sister to the remaining genera. *Exomis*, *Manochlamys*, and *Holmbergia* form a well-supported monophyletic lineage and *Extriplex*, *Stutzia covillei* (comb. nov. ined.), and *Grayia* form a well-supported monophyletic lineage, but *Stutzia* is not supported. The position of *S. dioica* (comb. nov. ined.) remains unresolved.

ITS—The aligned ITS matrix of 122 Atripliceae and *Chenopodium frutescens* (a representative of Chenopodieae I) as outgroup, comprised 613 base positions. Of these, 234 (38.2%) were polymorphic, and 70 (11.4%) polymorphisms occurred in only one sample. The tree resulting from the Bayesian analysis with BEAST is shown in Fig. 3. As in the cp data analyses, the same two major clades of Atripliceae are resolved, the *Archiatripliceae* clade and the *Atriplex* clade. Within the *Archiatripliceae* clade, *Microgynoecium* is sister to *Archiatripliceae* plus the remaining genera. This sister group relationship receives only low statistical support (post. prob. 0.82). *Archiatripliceae* is sister to the remaining genera. Within the latter clade, only the North American C₃ Atripliceae (*Proatriplex*, *Grayia* [including *Zuckia*], *Extriplex*, and *Stutzia*) receive moderate statistical support. The relationships of *Exomis*, *Manochlamys*, *Holmber-*

gia, and the North American C₃ Atripliceae remain unclear (Fig. 3). Within the *Atriplex* clade, *Halimione* is sister to *Atriplex* (including *Cremonophyton*). Within *Halimione*, the annual *H. pedunculata* is sister to the perennial *H. portulacoides* and *H. verrucifera*. *Atriplex cana* and *Cremonophyton* seem to form a basal grade within *Atriplex*. There are a number of well-supported lineages within *Atriplex* that will be described in detail in the discussion. Among these are the C₄ species of the genus that form a well-supported monophyletic lineage (post. prob. 0.99; Fig. 3).

The molecular clock estimates for the major splits in Atripliceae gained from the three data sets are summarized in Table 3.

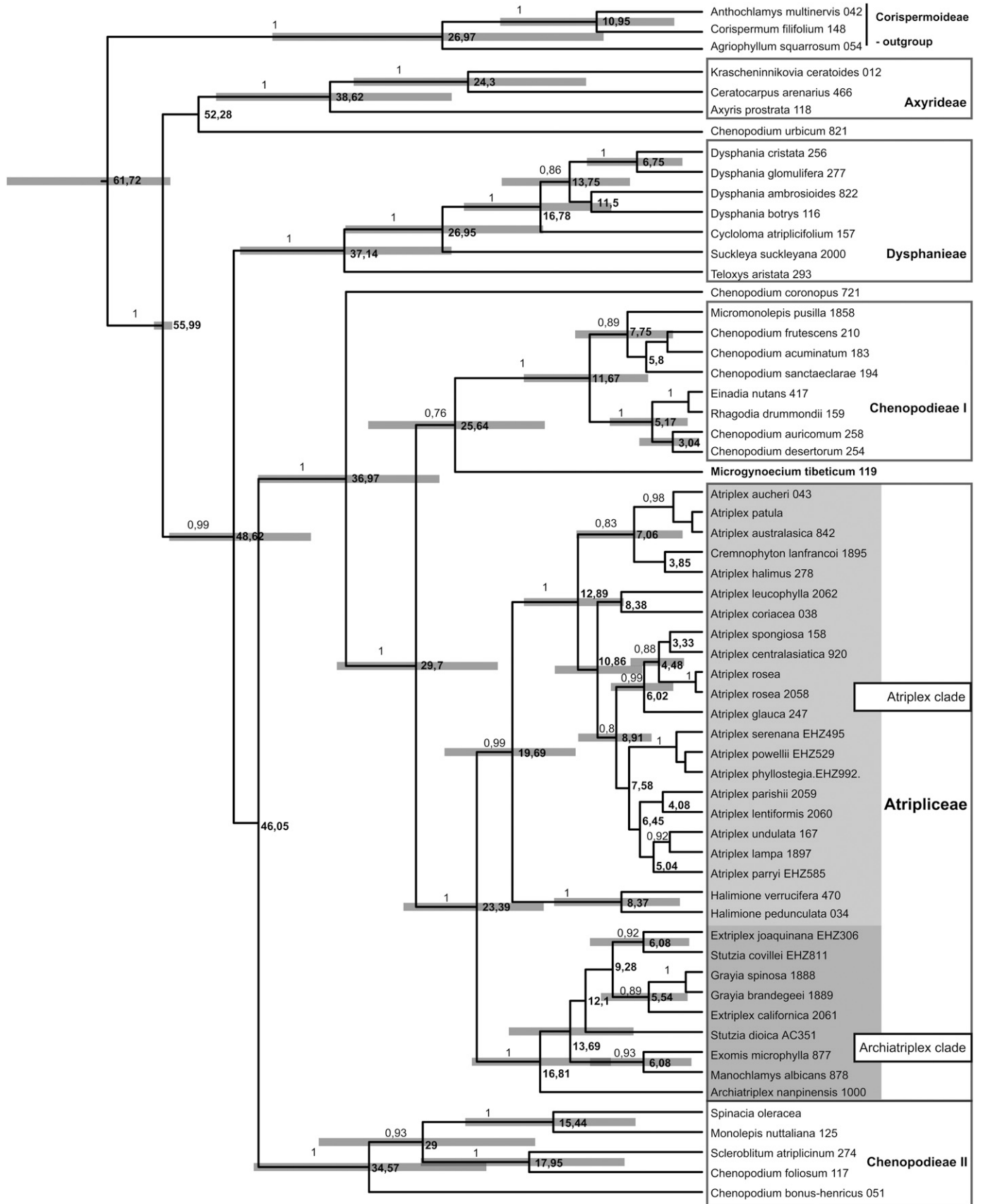
Morphological and anatomical studies of flowers and fruits—The results of our survey of flower morphology and fruit anatomy are presented in Table 4. They are mostly based on our own observations, but we also considered the relevant literature as indicated in Table 4.

DISCUSSION

A new circumscription of Atripliceae—The molecular data presented here show congruent results concerning the phylogenetic relationships of genera traditionally assigned to Atripliceae (Figs. 1–3). The following 10 genera are part of a well-supported Atripliceae clade: *Archiatripliceae*, *Atriplex* (including *Blackiella*, *Cremonophyton*, *Haloxanthium*, *Neopreissia*, *Obione*, *Pachypharynx*, *Senniella*, *Theleophyton*), *Exomis*, *Extriplex*, *Grayia* (including *Zuckia*), *Halimione*, *Holmbergia*, *Manochlamys*, *Proatriplex*, and *Stutzia*. The assignment of the Himalayan genus *Microgynoecium* to Atripliceae is not unambiguously supported by molecular data. Later, we make a case for the inclusion of *Microgynoecium* in Atripliceae on the basis of morphological data and weak support from the *atpB-rbcL* spacer and ITS (Figs. 2, 3). Three of the four genera traditionally classified as subtribe Eurotiinae, viz. *Axyris*, *Ceratocarpus*, and *Krascheninnikovia* (Table 2), and also *Spinacia* and *Suckleya* clearly do not belong to Atripliceae as circumscribed here. *Spinacia* seems to be closely related to the American and Siberian genus *Monolepis*, the Australian genus *Scleroblitum* and to representatives of *Chenopodium* subgenus *Blitum*. *Suckleya* is closely related to *Dysphania*, *Teloxys*, and *Cycloloma*. The three genera of subtribe Axyridinae (former Eurotiinae nom. illeg.) form a well-supported clade that is not closely related to any other clade of the Chenopodioideae but is part of a basal grade. Finally, *Holmbergia* is the only genus that was previously classified in Chenopodioideae but that clearly belongs to Atripliceae.

Within Atripliceae, the molecular analyses revealed that the 10 genera listed above fall into two clades, here named the *Archiatripliceae* clade and the *Atriplex* clade. These results corroborate the findings of Zacharias (2007) and Zacharias and Baldwin (in press), who showed this basal split in the tribe (with sampling focused on the American genera). The *Archiatripliceae* clade consists of a large number of small genera that show great morphological diversity and a widely disjunct distribution. These are *Archiatripliceae*, *Exomis*, *Extriplex*, *Grayia* (including *Zuckia*),

Fig. 1. Phylogeny of Chenopodioideae based on *rbcL* sequence data and a BEAST analysis. Posterior probabilities higher than 0.7 are indicated above branches, estimates of node ages are given behind the respective node, and the corresponding bars represent 95% confidence intervals. For the position of fossils used for calibration, see text.



Holmbergia, *Manochlamys*, *Proatriplex*, and *Stutzia* (Figs. 1–3; Tables 1, 2). The *Atriplex* clade contains the majority of species but only two genera, *Atriplex* and *Halimione*.

Excluded genera and their position within Chenopodioideae—*Spinacia*—*Spinacia* is a small genus of annual or biennial herbs distributed in the Irano-Turanian floristic region. *Spinacia oleracea* is widely known as an important vegetable cultivated nearly worldwide. The placement of the genus within Atripliceae has never been doubted because it has unisexual flowers and perianth-less female flowers with two rounded, connate bracts. These bracts are stout in *Spinacia*, often have 2–6 teeth along their margin and have been interpreted as sepals by some authors (Eichler, 1878; Cohn, 1914; Sherry et al., 1993; Sather et al., 2005). A closer look at the anatomy of this bract or perianth cover revealed five zones (Fig. 4A): an outer epidermis, a chlorenchyma, a sclerenchymatic parenchyma orientated perpendicular to its long axis, 1–2 crystalliferous layer(s) with 1–3 rhombic monocrystals and an inner epidermis. This bract anatomy of *Spinacia* is more complex than the bract anatomy found in species of *Atriplex* so far. The bracts of *Atriplex* do not possess crystalliferous layer(s), the crystals are dispersed in the parenchyma and occur only as druses. Also, there is no continuous sclerenchymatic parenchyma in the bracts of *Atriplex* species studied so far, except for *A. fera*. However, in *A. fera* the mechanical tissue consisting of many-layered true sclereids is orientated differently indicating the parallel evolution of this feature (Fig. 4B). Interestingly, *A. fera* had been included in *Spinacia* as *S. fera* L. (Linné, 1764) or *S. divaricata* Turcz. ex Moq. [nomen] (Moquin-Tandon, 1849).

A complex bract anatomy may be one character that separates *Spinacia* from Atripliceae, but the bract anatomy of some Atripliceae groups is not known yet. Further morphological characters that support the exclusion of *Spinacia* from Atripliceae are (1) absence of bladder hairs, (2) 4–5 styles vs. 2 (or more rarely 3) as in other Atripliceae, (3) a deviating chromosome number of $x = 6$ instead of $x = 9$ (Ellis and Janick, 1960; Fedorov, 1969; Turner, 1994), (4) a different branching pattern in the reproductive part (Urmi-König, 1981), and (5) a distinct pollen morphology (Flores Olvera et al., 2006).

In the molecular trees (Figs. 1, 2), *Spinacia* is nested among representatives of *Monolepis*, *Scleroblitum*, and *Chenopodium* subgenus *Blitum*. This is a rather heterogeneous clade within Chenopodioideae with a number of intercontinental disjuncts. Neither *Chenopodium* subgenus *Blitum* nor *Monolepis* have been sufficiently sampled in this study. Therefore, the resolution of the detailed phylogenetic relationships of *Spinacia* has to await further studies.

Suckleya—*Suckleya* is a monotypic genus with one succulent annual species that is distributed in western North America from southern Alberta to northwestern Texas. Chu et al. (1991) classified the genus within the monogeneric subtribe Suckleyinae of Chenopodieae based on its character combination of unisexual flowers, female flowers with four tepals, and superior radicles. This new subtribe of Chenopodieae was not accepted in subsequent treatments (e.g., Kühn et al., 1993). The place-

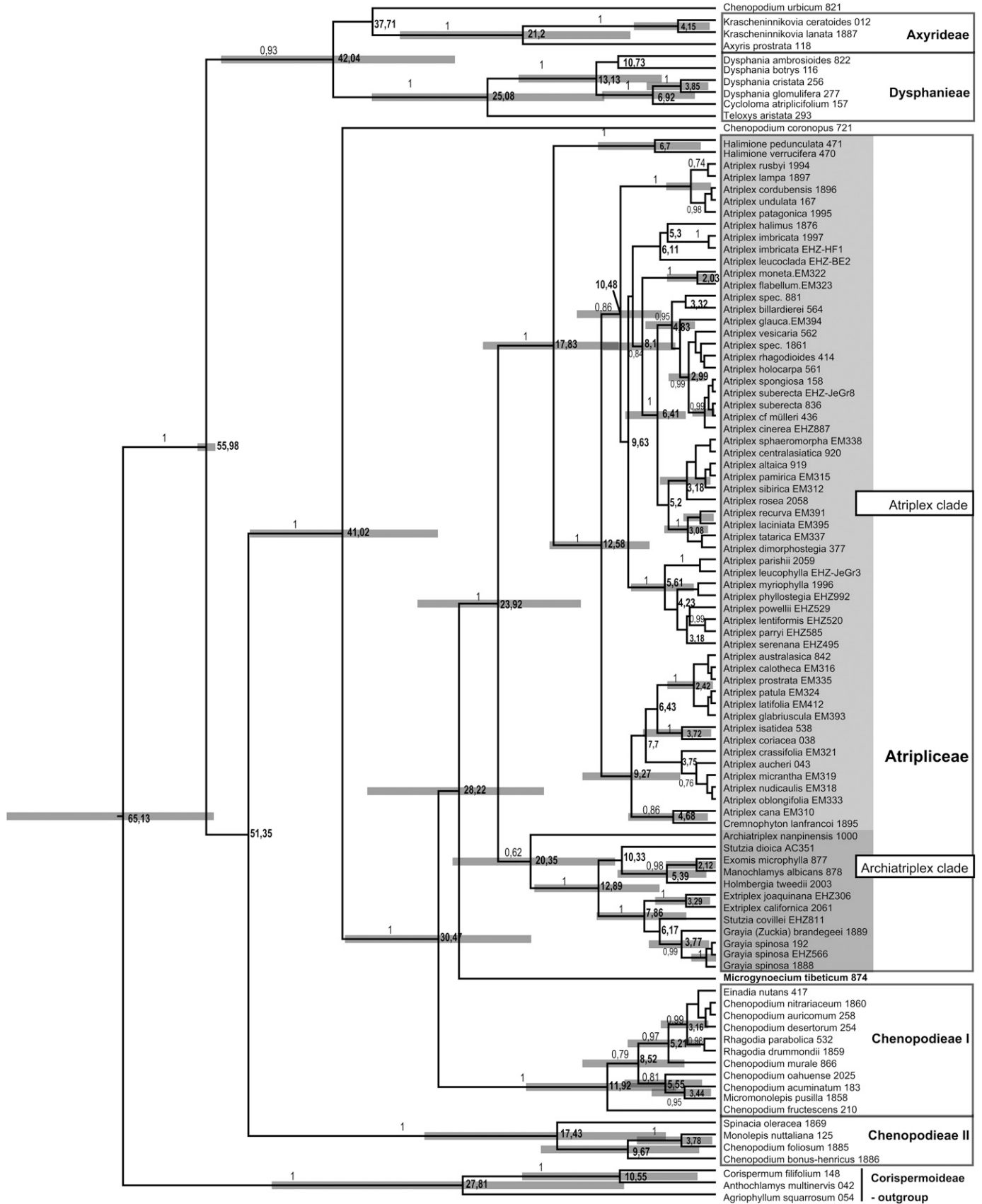
ment of the genus in Atripliceae, however, has also been questioned in a recent palynological analysis in which this genus differed from all other genera of Atripliceae in a remarkably small pollen diameter of 13–18 μm and a comparatively small number of pores of 28–36 (Flores Olvera et al., 2006). In their molecular study of North American Atripliceae Zacharias and Baldwin (in press) initially included a sample of *Suckleya suckleyana* but excluded it from the data set because of extensive sequence divergence. They suspected that the genus is more closely related to *Chenopodium*.

In our molecular analysis, *Suckleya* is closely related to *Dysphania*, *Cycloloma*, and *Teloxys* and therefore the exclusion from Atripliceae is clearly confirmed (Fig. 1). *Dysphania* and *Teloxys* (which is sometimes included in *Dysphania*) are characterized by the presence of typical glandular trichomes (Mosyakin and Clemants, 2002). *Suckleya*, however, has inflated unicellular trichomes (Chu et al., 1991), and *Cycloloma* has uniseriate trichomes (E. Zacharias and A. Sukhorukov, personal observation).

Axyridinae (*Axyris*, *Ceratocarpus*, and *Krascheninnikovia*)—Heklau and Röser (2008) conducted a morphological, morphometric, and molecular analysis of subtribe Axyridinae and found in a tree based on ITS sequence data that *Axyris*, *Ceratocarpus* and *Krascheninnikovia* form a well-supported clade in which *Krascheninnikovia* is sister to *Axyris* plus *Ceratocarpus*. This finding is only partly supported by our *rbcL* and *atpB-rbcL* data. Our molecular data support the monophyly of *Axyris*, *Ceratocarpus* and *Krascheninnikovia*, albeit *Axyris* is sister to *Ceratocarpus* plus *Krascheninnikovia* (Fig. 1). The Axyridinae are characterized by stellate hairs, which are missing in *Grayia*, a genus traditionally also classified in Eurotiinae (= Axyridinae; compare Table 1). Due to a limited outgroup sampling the position of *Grayia* remained unsettled in Heklau and Röser (2008). This study shows that *Grayia* is part of the *Archiatripliceae* clade and therefore remains within Atripliceae and that the Axyridinae are part of the basal grade of Chenopodioideae and not of Atripliceae. The exact placement of Axyridinae within Chenopodioideae has to be clarified in further molecular studies with an improved sampling of the large and obviously polyphyletic genus *Chenopodium*. Because of its isolated position within Chenopodioideae and because of its unique characters (stellate indumentum, absence of the “stalactites” in the outer cell walls of the testa in contrast to Chenopodieae and Atripliceae), this group is raised to tribal level, Axyrideae tribus nov. (see taxonomic section).

The split between *Axyris* and *Ceratocarpus* plus *Krascheninnikovia* is supported by flower and fruit morphology. The female flowers of *Ceratocarpus* and *Krascheninnikovia* lack a perianth, while in *Axyris* female flowers have a perianth that consists of three tepals. These tepals remain unchanged in the fruiting stage and do not develop into dispersal-enhancing structures. In *Axyris*, the pericarp adheres to the seed coat, and heterocarpy and heterospermy has been observed (Sukhorukov, 2005). Fruits on the same individual differ in the number of pericarp layers and the presence of sclereids, and the seeds differ

Fig. 2. Phylogeny of Chenopodioideae based on *atpB-rbcL* spacer sequence data and a BEAST analysis. Posterior probabilities higher than 0.7 are indicated above branches, estimates of node ages are given behind the respective node, and the corresponding bars represent 95% confidence intervals. For the position of fossils used for calibration, see text.



in thickness of the testa. In *Ceratocarpus* and *Krascheninnikovia* the female flowers are enclosed by two bracts that persist in the fruiting stage and fall off together with the fruit. Both genera have only one fruit/seed type, the pericarp is not adherent, and the testa is always thin and consists of two simple layers (Takhtajan, 1934; Butnik, 1981, 1991; A. Sukhorukov, unpublished results).

Our study clearly indicates that the typical female flower of Atripliceae with two persistent bracts arose two times independently in Chenopodioideae: (1) in the ancestor of Atripliceae (as defined here) and (2) in the common ancestor of *Ceratocarpus* and *Krascheninnikovia* (Fig. 1).

Relationships within Atripliceae—*Microgynoecium*—The relationships of *Microgynoecium* remained unclear in our molecular analyses. The monotypic genus is either resolved as sister to Chenopodieae I (with low support; Fig. 1), as sister to Atripliceae (without support; Fig. 2), or within Atripliceae, as sister to the *Archiatrilex* clade (with low support; Fig. 3). The morphological data, however, point to a closer affinity to Atripliceae than to Chenopodieae I and therefore support the topology found with the *atpB-rbcL* spacer and with ITS. Like the majority of Atripliceae, *Microgynoecium* has unisexual flowers with female flowers having two bracts and no perianth (Table 4). The bracts of the female flowers enclose the ovary in the fruiting stage and are slightly enlarged (A. Sukhorukov, personal observation). The female flowers are clustered in the axil of a subtending bract. This latter character is probably a plesiomorphic character state in the *Archiatrilex* clade (see below) and further supports the affinity of *Microgynoecium* to Atripliceae.

Microgynoecium grows in alpine meadows and disturbed sites in the Himalayan and Pamir mountains (Pratov, 1972; Zhu et al., 2003). Its unique fruit morphology with an irregular detachment of the pericarp from the seed coat is also known from some species of subf. Corispermioideae (Sukhorukov, 2007b). In Chenopodioideae, such detachment is found in *Axyris* and some species of *Chenopodium*; however, it is restricted to the upper part of the fruit (Sukhorukov, 2005; A. Sukhorukov, unpublished results).

***Archiatrilex* clade**—The *Archiatrilex* clade consists of *Archiatrilex*, *Exomis*, *Extriplex*, *Grayia* (including *Zuckia*), *Holmbergia*, *Manochlamys*, *Proatriplex*, and *Stutzia* (Figs. 1–3; compare also the findings in Zacharias and Baldwin, in press). All these genera are either monotypic (*Archiatrilex*, *Exomis*, *Holmbergia*, *Manochlamys*, *Proatriplex*) or consist of a few species only (Table 1). The *Archiatrilex* clade shows a disjunct distribution in Central China, North and South America, and South Africa. Most genera have relatively long branches, but their relationship remains partly unsettled due to short basal branches. This disjunctly distributed, species-poor clade, that consists of relatively old and morphologically heterogeneous lineages, probably represents the remnants of a formerly widely distributed and species-rich lineage (see below). Recovering the true phylogenetic relationships within the *Archiatrilex* clade is most likely hampered by rampant extinction in this lineage.

Archiatrilex—Chu (1987) discovered *Archiatrilex*, which is only known from a small area in northern Sichuan province of China, near Nanping. Its only species (*A. nanpinensis*) grows at an altitude of around 2100 m a.s.l. and was collected on the edges of bushy vegetation and on the banks of terraced farms. Chu (1987) recognized that this new genus represents a rather primitive member of the Atripliceae and pointed out that it has affinities to *Microgynoecium*. Both genera are small herbs and have foliaceous bracts that subtend several carpellate flowers. *Archiatrilex* is monoecious with the male flowers having five tepals and the female flowers having 3–4 tepals.

All the molecular trees presented here resolve *Archiatrilex* as sister to the other genera of the *Archiatrilex* clade, albeit with high statistical support only in the ITS data set (Fig. 3).

Holmbergia—Our molecular analyses showed that *Holmbergia* traditionally assigned to Chenopodieae (Table 2) belongs to Atripliceae. This placement supports previous molecular findings that were based on a smaller sample (Kadereit et al., 2003; Zacharias and Baldwin, in press). The assignment to Chenopodieae was based on the morphology of the female flowers in *Holmbergia*. These are ebracteate and have a perianth that consists of five tepals, which do not take part in fruit development. Ulbrich (1934) suspected *Holmbergia* to be a species of *Rhagodia* introduced to South America from Australia, and Scott (1978) placed *Holmbergia* in Rhagodiinae A. J. Scott, together with *Rhagodia* and *Einadia* from Australia and New Zealand. This new subtribe of Chenopodieae was based on the succulent pericarp and predominantly unisexual flowers. The anatomy of the pericarp is, however, different in *Rhagodia* and *Holmbergia*. While in *Rhagodia*, the pericarp has approximately three layers and is truly fleshy and spongy, the 3–5(6)-layered, undifferentiated pericarp of *Holmbergia* is dry, and the reddish appearance of the fruit is caused by the hard, dark red-brown testa (Fig. 4C). Berry-like fruits evolved several times in Chenopodiaceae in rather isolated positions. This character state does not seem to be phylogenetically informative in the family. The few berry-fruited taxa of Camphorosmeae, for example, represent three independent lineages (Cabrera et al., 2009). The monophyly of *Rhagodia* and/or *Einadia* and the relationships of these genera to Australian *Chenopodium* have not been resolved with molecular data yet. Our analyses, which included only a limited sample of these groups, indicate that *Rhagodia* and *Einadia* might be nested among Australian species of *Chenopodium* (Figs. 1, 2).

The closest relative of *Holmbergia* within the *Archiatrilex* clade remains unresolved. The genus is part of a polytomy consisting of *Exomis*, *Manochlamys*, and the North American representatives of this clade in the ITS analysis (Fig. 3) and sister to *Exomis* and *Manochlamys* in the *atpB-rbcL* analysis (Fig. 2). Morphologically, *Holmbergia* does not show particular similarities to any of the other genera of the *Archiatrilex* clade.

Exomis* and *Manochlamys—The two monotypic South African genera *Exomis* and *Manochlamys* have been treated under *Exomis* by Kühn et al. (1993). While *Exomis microphylla* is

Fig. 3. Phylogeny of Atripliceae based on ITS sequence data and a BEAST analysis. Posterior probabilities higher than 0.7 are indicated above branches, estimates of node ages are given behind the respective node, and the corresponding bars represent 95% confidence intervals. For the position of fossils used for calibration see text. Subgenus and section abbreviations: A = sect. *Atriplex*, At = sect. *Atriplicina*, Di = sect. *Dialyx*, O = sect. *Obione*, P = sect. *Pterochiton*, Ps = sect. *Psammophila*, Pt = subgen. *Pterotheca*, Sc = sect. *Sclerocalymna*, Se = sect. *Semibaccatae*, Sp = sect. *Spongiocarpus*, St = sect. *Stylosa*, Su = sect. *Suffruticosae*, T = sect. *Teutiopsis*, Te = sect. *Teutioides*, Th = sect. *Theleophyton*, nc = not classified.

found as a weed in gardens and hedges, *Manochlamys* grows on rocky or sandy hillsides, sand dunes, and along roads. The sister group relationship of the two subshrubby genera is supported by the *rbcL* data (Fig. 1) with moderate statistical support. *Manochlamys* and *Exomis* differ morphologically in the following three main characters (compare Aellen, 1939b; Aellen, 1967): (1) The female flowers of *Manochlamys* consist of two unequal fleshy bracts that later cover the fruit and a 2–4-lobed, membranous, small perianth, while the female flowers of *Exomis* are aggregated (1 to several) in the axils of two narrow-lanceolate bracts. The female flowers of *Exomis* either lack a perianth or have a strongly reduced, thin, translucent ring around the ovary or two small, thin, and translucent lobes opposite the bracts. (2) The inflorescence of *Manochlamys* is not leafy, while that of *Exomis* is leafy throughout. (3) The tepals of the male and bisexual flowers are connate in *Manochlamys*, while they are only basally united in *Exomis*. The two genera also differ in fruit anatomy. *Manochlamys* has a thick pericarp consisting of several layers of inflated, isodiametrical cells (Fig. 4D), while *Exomis* has a thin pericarp (also consisting of isodiametrical cells) with papillae-shaped bladder hairs. In both genera, the cells of the exotesta have numerous drops containing tannins (Fig. 4D). We consider *Manochlamys* and *Exomis* as morphologically and molecularly distinct and prefer—as had been suggested by Aellen (1939b)—to recognize both genera.

Proatriplex—*Proatriplex* is a western North American annual with clusters of female flowers enclosed by a pair of subtending bracts, female flowers with a perianth, and radicles pointing downward. Weber (1950) initially included *P. pleiantha* within *Atriplex* and hypothesized that it was a primitive member of the genus, but Stutz and Chu (in Stutz et al., 1990) emphasized its distinctness when they treated Weber's subgenus, *Proatriplex*, at genus rank. This view was also supported by Judd and Ferguson (1999). Zacharias and Baldwin (in press) showed it to be more closely related to the other North American genera of Atripliceae and *Holmbergia* than to *Atriplex*. In our study, the ITS data resolved *Proatriplex* as sister to the other North American members of the *Archiatripliceae* clade with moderate support.

Proatriplex has a distinct fruit anatomy (Fig. 4E). The pericarp is single-layered, compressed, and adheres tightly to the testa. The outer cell walls of the pericarp are thick. In cross section, the outline of the testa appears wavy, and its thickness varies between 20 and 35 μm . Such a wavy outline of the testa is uncommon in Chenopodioideae. It has been observed in *Chenopodium hybridum* and *C. simplex* in section *Grossefoveata* (A. Sukhorukov, unpublished data) but not in other members of Atripliceae. The cells of the exotesta have characteristic oblique cell wall fortifications (Fig. 4E).

Stutzia—Zacharias and Baldwin (in press) plan to replace the name *Endolepis* Torr. (1860), which is a later homonym of *Endolepis* Schleid. (1846), with *Stutzia* ined. These two species of *Stutzia* are western North American annuals with perianths in the female flowers, radicles pointing upward, and fused bracts; no other species in the *Archiatripliceae* clade shares this combination of characters. However, the relationships of *S. covillei* and *S. dioica* to each other and to other members of the *Archiatripliceae* clade are not well supported by the molecular data. In most analyses, they are part of the North American lineage within the *Archiatripliceae* clade (with the exception of *S. dioica* in the *atpB-rbcL* analysis, which shows it as sister to the *Holmbergia*, *Exomis*, and *Manochlamys* clade but with no statistical support).

Zacharias and Baldwin (in press) showed both species to be part of a grade with other sampled members having female flowers with perianths (*Holmbergia* and *Proatriplex*), although their relationships to each other were not clear. See Zacharias and Baldwin (in press) for further discussion of the systematics of this genus.

Morphologically, *Stutzia* is very similar to *Atriplex*. One difference is the presence of a small perianth in the female flowers, which is rare in *Atriplex*. The fruit anatomy is simple (as in most species of *Atriplex*) with a thin, one-layered pericarp and a thin testa (3–5 μm).

Extriplex—The two species of *Extriplex* have radicles that point laterally, 4-lobed perianths in the male flowers, perianthless female flowers, and are endemic to the California Floristic Province. The relationships of *E. joaquinana* (comb. nov. ined.) and *E. californica* (comb. nov. ined.) to each other and to other members of the *Archiatripliceae* clade are not consistent across the molecular data. The genus has high support in the *atpB-rbcL* spacer tree (Fig. 2) but no support in the ITS tree (Fig. 3). The *rbcL* analysis places *E. joaquinana* as sister to *Stutzia covillei* with moderate support and *E. californica* sister to *Grayia* with low support (Fig. 1). The combined nrDNA and cpDNA analysis of Zacharias and Baldwin (in press) showed that *Extriplex* is a well-supported clade. See Zacharias and Baldwin (in press) for discussion.

Grayia (including *Zuckia*)—The two sampled species of *Grayia* are shrubs from western North America with female flowers without perianth and radicles that point downward. As shown in Zacharias and Baldwin (in press), the molecular data resolve *Grayia* (including *Zuckia*) with high support. The sister relationship of *Grayia* is not clear. *Grayia* is sister to *Extriplex californica* with moderate support in the *rbcL* tree (Fig. 1). The *atpB-rbcL* spacer tree does not show the sister group relationships of *Grayia* with support (Fig. 2). The ITS tree shows *Grayia* as sister to *Extriplex* plus *S. dioica* with no support (Fig. 3). Zacharias and Baldwin (in press) showed *Grayia* as sister to *Extriplex* with low support. See Zacharias and Baldwin (in press) for further discussion.

Atriplex clade—*Halimione*—The distinctness of the three species today either classified as *Halimione* (Aellen, 1938a) or as *Atriplex* sect. *Halimus* and *Pedicellatae*, which is here supported by molecular evidence, had already been recognized 190 years ago. At that time, the oblong, entire, and greyish-coated leaves and the totally concrescent bracts were regarded as diagnostic characters separating *A. portulacoides* [= *Halimus portulacoides* (L.) Dumort.], *A. pedunculata* [= *H. pedunculatus* (L.) Wallr.], and *A. verrucifera* M. Bieb. [= *Halimus verruciferus* (M. Bieb.) Claus] from other species of *Atriplex* (Gray, 1821; Wallroth, 1822; Meyer, 1833; Claus, 1851). Since then, a large number of *Atriplex* species have been described, and some of these show these same character states. Therefore, these characters cannot be regarded as unique in *Halimione* any longer (Sukhorukov, 2006). However, Aellen (1938a), who combined the three species under the name *Halimione*, found an excellent additional feature that separates *Halimione* from all other species of *Atriplex*. He discovered that the pericarp is tightly adherent to the adaxial side of the bracts. This diagnostic character for *Halimione* was validated by later studies, but—maybe for reasons of difficult assessment in the field—rarely used in floristic treatments (e.g., Grossheim, 1949; Skripnik, 1987; Nikitin and Geldikhanov, 1988; Romo, 2002).

TABLE 3. Results of the divergence time estimates (in Ma) calculated with program BEAST v1.4.8 (numbers given in brackets represent 95% confidence intervals)

Node	<i>rbcL</i> gene	<i>atpB-rbcL</i> spacer	ITS	Geological epoch
Stem age of Atripliceae excl. <i>Microgynoecium</i>	29.7 (37.9–21.2)	28.22 (38.3–18.9)	Crown age of Atripliceae	Late Oligocene
Crown group age of Atripliceae excl. <i>Microgynoecium</i> (= stem age of <i>Archiatripliceae</i> clade and <i>Atriplex</i> clade)	23.4 (31.0–16.4)	23.9 (32.7–14.9)	incl. <i>Microgynoecium</i> set to 29 Ma	Early Miocene
Crown group age of the <i>Atriplex</i> clade (= stem age of <i>Atriplex</i> and <i>Halimione</i>)	19.7 (26.7–13.1)	17.8 (25.5–10.7)	24.8 (29.4–19.2)	Early to Middle Miocene
Crown group age of the <i>Archiatripliceae</i> clade	16.8 (23.9–9.5)	20.4 (28.9–11.1)	24.9 (29.0–19.6)	Early to Middle Miocene
Crown group age of <i>Atriplex</i>	12.9 (18.5–8.1)	12.6 (18.2–7.3)	19.3 (24.6–14.0)	Middle Miocene
Minimum age of C ₄ photosynthesis in <i>Atriplex</i>	10.9 (15.3–6.2)	10.5 (15.2–6.0)	14.1 (18.3–9.4)	Middle to Late Miocene

In our own anatomical studies, we discovered a second synapomorphic character for *Halimione*. The seed coat of *Halimione* is thin and membranous and consists of two layers of simple, isodiametrical, translucent cells. In contrast, the seed coat of *Atriplex* consists of a hard, conspicuous testa that contains tannin and is therefore brownish and a 2–3-layered endotegmen (Fig. 4 F, G). The simple seedcoat anatomy of *Halimione* is very unusual among Chenopodioideae (compare Netolitzky, 1926; Butnik, 1981) and certainly supports its separated position within the *Atriplex* clade.

The molecular data congruently resolve *Halimione* as sister to *Atriplex* with high statistical support (Figs. 1–3). Because *Halimione* is also morphologically well defined, we recognize *Halimione* as a genus separate from *Atriplex*. The subdivision of *Halimione* into two sections as has been proposed by Sukhorukov (2006), albeit within *Atriplex*, i.e., *Atriplex* sect. *Halimus* (S. F. Gray) Sukhor. (*A. portulacoides* L., *A. verrucifera* M. Bieb.) and *Atriplex* sect. *Pedicellatae* Sukhor. (*A. pedunculata* L.), is supported by the ITS tree (Fig. 3).

Former “satellite genera” of Atriplex—The molecular analyses presented here revealed that *Obione*, *Blackiella*, *Haloxanthium*, *Neopreissia*, *Senniella*, and *Theleophyton* are best considered as congeneric with *Atriplex*. Figure 3 shows the position of these genera within *Atriplex*. For all these genera, a placement within *Atriplex* has been suggested before (Kühn et al., 1993; Table 2). *Morrisiella* (Aellen, 1937/1938; = *Atriplex morrisii* R. Anderson) was not available for this study, and *Pachypharynx* Aellen was described on the basis of gall-infected specimens (Wilson, 1984).

Obione is the largest genus segregated from *Atriplex* with c. 100 species worldwide. Its separation from *Atriplex* has been controversial (for a summary, see Flores Olvera, 2003) and is handled differently in flora treatments. However, mostly it had been recognized as a taxon either at subgenus or section level, and only few authors have accepted genus rank (e.g., Moquin-Tandon, 1840, 1849; Ulbrich, 1934; Aellen, 1938b). *Obione* was described by Gaertner (1791) and comprised those species that show an inverted position of the radicle of the embryo (pointing upward), whereas in *Atriplex* the radicle points downward or laterally. Species classified within *Obione* (or *Atriplex* sect. *Obione*) do not form a monophyletic group in the ITS tree (Fig. 3), which clearly documents that *Obione* or sect. *Obione* does not represent a natural group and that the position of the radicle is highly variable within *Atriplex*, just like the connation of the bracts. As pointed out already, these two characters seem to be functionally connected (compare Sukhorukov, 2006).

The monotypic genus *Theleophyton* was described by Moquin-Tandon (1849) on the basis of *Atriplex* sect. *Theleophyton*

Hook. f. The generic status was not accepted in recent treatments (e.g., Kühn et al., 1993; Wilson, 1984), but the separation on section level was accepted (Wilson, 1984). *Atriplex (Theleophyton) billardierei* shows the following combination of unique morphological characters that distinguishes it from all other species within the genus: (1) young leaves with watery bladder hairs, (2) male flowers with five tepals that are connate for at least half of their length, (3) connate bracts of female flowers forming an urceolate structure in fruit, and (4) a seed that is initially orientated parallel to the bracts but which twists during ripening so that it is at right angles to the bracts at maturity. The molecular data (Fig. 3) reveal that *A. (Theleophyton) billardierei* is nested among Australian *Atriplex* species of sect. *Semibaccatae*. Its sister group was not resolved because of low resolution in terminal branches of the Australian clade. *Atriplex billardierei* is a prostrate herb that grows on sandy beaches just above high tide level on the coasts of Victoria, Tasmania, and New Zealand.

The three Australian genera *Senniella*, *Blackiella*, and *Morrisiella* were all described and classified within a new subtribe Spongiocarpinae by Aellen (1937/1938). The diagnostic character of the subtribe is the connate, spongy bracts of the female flowers. All three genera were not accepted in subsequent treatments of the group (e.g., Wilson, 1984; Kühn et al., 1993). Here we sampled two representatives of *Senniella* (*S. spongiosa* var. *spongiosa* and *S. spongiosa* var. *holocarpa*) and one of *Blackiella* (*B. conduplicata*), which all resolve in different positions nested within the C₄ clade of *Atriplex* (Fig. 3), indicating that spongy fruiting bracts evolved several times independently within the C₄ clade of *Atriplex*.

The Australian genera *Haloxanthium* and *Neopreissia* were described by Ulbrich (1934). In *Haloxanthium*, Ulbrich included two species, *H. quadrivalvatum* (Diels) Ulbrich and *H. fissivalve* (F. Muell.) Ulbrich, that both differ from *Atriplex* in having deeply divided and elaborately lobed bracts with basal teeth that become hard during ripening (Ulbrich, 1934: fig. 195 U–W). According to Ulbrich (1934), the entire glomerulate female inflorescence is dispersed like a burweed. Our molecular results show *H. fissivalve* (= *Atriplex fissivalvis*) clearly nested within the large clade of Australian *Atriplex* species (Fig. 3). Closely related species cannot be inferred because of the low resolution in this part of the tree. In *Neopreissia*, Ulbrich included two species, *N. isatidea* (Moq.) Ulbrich and *N. cinerea* (Poir.) Ulbrich, that both have sessile bracts with a thick turbinate stipe. Both species were included in our ITS analysis. They are nested within *Atriplex* and appear closely related to each other. Together with *A. nummularia* and *A. rhagodioides* they form a second Australian lineage within *Atriplex*. Neither *Haloxanthium* nor *Neopreissia* were accepted by Wilson (1984) and Kühn et al. (1993).

TABLE 4. Survey of flower and fruit characters in genera of Chenopodioideae; data are mostly based on our own observations and those of Kühn et al. (1993), Ulbrich, (1934), Welsh (2003), and Wilson (1984).

Taxon	Flowers						Fruit				Miscellaneous notes	
	Plant sex	Sex	Bisexual	Staminate	Pistillate: no. flws/bract or bract pair; no. tepals; no. stigmas	Perianth in fruit	Bract accrescence	Bract connation	Pericarp adherence	Seed position		Fruit inverted (radicle orientation)
<i>Atriplicaceae</i>												
<i>Archiatriplox</i> G.L. Chu	monoecious	unisexual	n/a	ebracteate; 5 tepals; 5 stamens	several/1 bract; 3-4 tepals; 2 stigmas	unchanged in fruit	n/a	n/a	pericarp adnate to seed	vertical	inferior radicle	
<i>Atriplex</i> L. a)	monoecious or dioecious	unisexual (seldomly with bisexual flws)	n/a	ebracteate; 3-5 tepals; 3-5 stamens	1/bract pair b); —; 3-5 tepals (if present)	unchanged in fruit	accrescent	free or fused	free	vertical (bibracteate) or rarely horizontal (ebracteate)	diverse positions (pointing upward, laterally, downward)	very distinct in bract's form, its hardness or conescent stage
<i>Cremnophyton</i> Brullo & Pavone	monoecious	unisexual	n/a	small bracts; 3-5 tepals; 4 stamens	1/bract pair; tepals absent; 2 stigmas	n/a	accrescent	free	bract surface adherent to the pericarp in lower fruit part	vertical	pointing upward	no dependence between bract connation and position of seed radicula
<i>Exomis</i> Fenzl ex Moq.	monoecious or dioecious (few bisexual flws)	unisexual	n/a	ebracteate; 5 tepals; 5 stamens	1/bract pair; 3-5 tepals or reduced to ring or lobes thin, translucent opposite the bracts	unchanged in fruit	accrescent	free	not adherent	vertical	pointing downward	2-4-layered undifferentiated pericarp; outer layer with papillae-shaped bladder hairs
<i>Extriplex</i> E.H. Zacharias	monoecious	unisexual	n/a	ebracteate; 4 tepals; 4 stamens	1/bract pair; tepals absent; 2 stigmas	n/a	accrescent	distinct to slightly connate	not adherent	vertical	pointing laterally	
<i>Grayia</i> Hook. and Arn. (incl. <i>Zuckia</i> Standl.)	dioecious or monoecious	unisexual	n/a	ebracteate; 4-5 tepals; 4-5 stamens	1/bract pair; tepals absent; 2 stigmas	n/a	accrescent	facial- mediane bract connation	free	vertical or horizontal	pointing downward	
<i>Halimione</i> Aellen	monoecious	unisexual	n/a	ebracteate; 4-5 tepals; 4-5 stamens	1/bract pair; tepals absent	n/a	accrescent	connate to the top	pericarp adherent to the bract	vertical	pointing upwards	seed coat thin, 2-layered, homogenous 3-5(6) layered, undifferentiated pericarp; cells flattened
<i>Holmbergia</i> Hicken	monoecious	unisexual	n/a	ebracteate; 5 tepals; 5 stamens	ebracteate; 5 tepals; 2 stigmas	unchanged in fruit	n/a	n/a	free	vertical	pointing downward	3-5(6) layered, undifferentiated pericarp; cells flattened
<i>Manochlamys</i> Aellen	polygamo- monoecious	unisexual	n/a	ebracteate; 4-5 tepals; stamens 5	1/bract pair; 2-4 tepals	n/a	accrescent	n/a	not adherent	vertical	pointing downward	3-5(6) layered, undifferentiated pericarp; cells spongy
<i>Microgynoeicum</i> Hook. f.	monoecious	unisexual	n/a	ebracteate; 5 tepals; 1-4 stamens	several flws/bract; 1 tepal; 2 stigmas	unchanged in fruit	slightly accrescent	n/a	not adherent	vertical	pointing laterally or upward	pericarp partly detached from seed coat

TABLE 4. Continued.

Taxon	Plant sex	Sex	Bisexual	Staminate	Pistillate: no. flws/bract or bract pair; no. tepals; no. stigmas	Flowers				Fruit				Miscellaneous notes
						Perianth in fruit	Bract accrescence	Bract connation	Pericarp adherence	Seed position	Fruit (radicle orientation)			
<i>Proatriplex</i> (W.A. Weber) Stutz & G. L. Chu	monoecious	unisexual	n/a	ebracteate; 5 tepals; 5 stamens	2-6/bract pair; 5 (or 4) hyaline tepals	unchanged in fruit	accrescent	united only at base	adherent to the seed coat	vertical	pointing downward	pericarp outgrowth in basal fruit part; stalactites of outer pericarpinal wall of testa oblique; big air cavities in seed		
<i>Stutzia</i> E.H. Zacharias	monoecious	unisexual	n/a	ebracteate; 5 tepals; 5 stamens	1/bract pair; (1-3(-5) hyaline tepals; 3-4 lobed	unchanged in fruit	accrescent	to middle or to top	not adherent	vertical	pointing upward			
Axyrideae <i>Axyris</i> L.	monoecious	unisexual	n/a	ebracteate; 3-5 tepals; 2-5 stamens	1/bract pair; 3 tepals	unchanged in fruit	not persistent, not accrescent	free	adherent to the seed coat	vertical	inferior	heterocarp and heterospermy; testa thick, without stalactites		
<i>Ceratocarpus</i> L.	monoecious	unisexual	n/a	ebracteate; 2 tepals; 1 stamen	1/bract pair; tepals absent	n/a	not accrescent	connate to top	not adherent	vertical	inferior	testa always thin, with 2 simple layers		
<i>Krascheninnikovia</i> Gueldenst.	monoecious	unisexual	n/a	ebracteate; 4 tepals	1/bract pair; tepals absent	n/a	slightly accrescent	connate 1/2 or more (almost to the top)	not adherent	vertical	inferior	testa always thin, with 2 simple layers		
Chenopodiaceae s.l. <i>Chenopodium</i> L.	polygamo-monoecious	bisexual or pistillate; bisexual (rarely unisexual, then terminal flower male or bisexual and lateral flws female)	ebracteate; perianth segments 3-5; stamens 5-3(-0); perianth green or hyaline, globose;	3-5 tepals; ≤5 stamens	ebracteate; (2-3-5 tepals	unchanged in fruit, or sometimes fleshy	n/a	n/a	not adherent, rarely tightly adherent	horizontal or vertical	inferior	pericarp membranous, mostly 1-2-layered		

TABLE 4. Continued.

Taxon	Plant sex	Flowers					Fruit					Miscellaneous notes
		Sex	Bisexual	Staminate	Pistillate: no. flws/bract or bract pair; no. tepals; no. stigmas	Perianth in fruit	Bract accrescence	Bract connation	Pericarp adherence	Seed position	Fruit inverted (radicle orientation)	
<i>Einaadia</i> Raf.	polygamo-monoecious	terminal flws of cluster	ebracteate; 4-5 tepals;	n/a	ebracteate; 4-5 tepals, no staminodes	fruit not enveloped by perianth	n/a	n/a	pericarp membranous or succulent; adherence not known	horizontal	embryo annular	
<i>Micromonolepis</i> Ulbr.	monoecious	bisexual, lateral ones pistillate	unisex	unisex	unisex	unchanged in fruit	n/a	n/a	adherent to the seed coat	vertical	embryo annular, radicle lateral	seed coat with hair-like outgrowth
<i>Monolepis</i> Schrad.	polygamo-monoecious	bisexual, some pistillate	1-3-lobed, or absent; 0-2 stamens; c)	n/a	n/a	unchanged in fruit	n/a	n/a	not adherent; loose when dry	vertical	embryo annular, radicle lateral	
<i>Rhagodia</i> R.Br.	dioecious	unisex	n/a	bracts small or absent; 5 tepals; 5 stamens	bracts small or absent; tepals 5; staminodes; 2 stigmas	perianth lobes expanded in fruit	n/a	n/a	not adherent	horizontal	embryo annular	pericarp succulent with spongy cells (fruits berry-like)
<i>Scleroblitum</i> Ulbr.	polygamo-monoecious	terminal bisexual, others female	unisex	unisex	n/a	perianth cartilaginous	n/a	n/a	?	vertical	inverted	pericarp thick and hard, testa membranous
<i>Spinacia</i> L.	dioecious or monoecious	unisex	n/a	ebracteate; 4-5 tepals; 4-5 stamens	bract-like perianth cover; 4-5 stigmas	hardened	cover accrescent	connate to the top	not adherent	vertical	superior	
<i>Dysphanieae</i>												
<i>Cycloloma</i> Moq.	polygamo-monoecious	bisexual, sometimes pistillate	unisex	unisex	unisex	perianth present in fruit, chartaceous with a broad horizontal annual ring	n/a	n/a	not adherent	horizontal	embryo annular	perianth segments form horizontally wings
<i>Dysphania</i> R.Br.	polygamo-monoecious	bisexual or pistillate	unisex	unisex	unisex	fruit enclosed by perianth	n/a	n/a	not adherent	vertical or horizontal	embryo annular, radicle lateral	

TABLE 4. Continued.

Taxon	Plant sex	Sex	Flowers				Fruit				Miscellaneous notes	
			Bisexual	Staminate	Pistillate: no. flws/bract or bract pair; no. tepals; no. stigmas	Perianth in fruit	Bract accrescence	Bract connation	Pericarp adherence	Seed position		Fruit inverted (radicle orientation)
<i>Teloxys</i> Moq.	monoecious	bisexual or pistillate	ebracteate; 3–5 perianth lobes; stamens 3–5; stigmas 2	n/a	ebracteate; 3–5 tepals; 2 stigmas	unchanged in fruit	n/a	n/a	not adherent	horizontal	embryo annular, radicle lateral	
<i>Suckleya</i> A. Gray	monoecious	unisexual	n/a	ebracteate; 3–4 tepals; 3–4 stamens	ebracteate; 4 tepals	tepals enlarged in fruit	n/a	n/a	not adherent	vertical	embryo horse-shoe shaped, radicle points upward	short and wide

^a Including: *Blackiella* Aellen, *Haloxanthium* Ulbr., *Morriella* Aellen, *Obione* Gaertner, *Pachypharynx* Aellen, *Semiella* Aellen, *Theleophyton* (Hook. f.) Moq.)
^b *Atriplex hortensis*, *A. sagittata*, *A. aucheri*—Dimorphic: pistillate flowers with perianth are ebracteate, pistillate flowers without perianth are between two bracts
^c Terminal flowers of cluster with 3 tepals and 2 stamens; lateral flowers of cluster with 1 tepal and 1 stamen; sometimes perianth lacking and/or stamens lacking

Major lineages within Atriplex and comments on the traditional sectional division—While the resolution within *Atriplex* is low in the *rbcL* and the *atpB-rbcL* spacer tree (Figs. 1, 2), there are a number of well-supported clades in the ITS tree (Fig. 3). However, low statistical support of basal branches within the ITS tree makes it impossible to draw any definite conclusion of the relationships of these well-supported lineages. There is a basal polytomy consisting of the following clades: (1) *Atriplex* (*Cremnophyton*) *lanfranconi* and *Atriplex cana* (two accessions; these two are resolved as a monophyletic group, albeit with very low support, Fig. 2), (2) *Atriplex* sect. *Atriplex* clade (4 spp.), (3) sect. *Teutliopsis* clade (17 species [18 accessions]), (4) C₄ clade (72 species [74 accessions]), (5) *Atriplex crassifolia* (Fig. 3). Although we included 100 accessions of *Atriplex* in the ITS data set, the genus is still not sufficiently sampled to infer an updated classification. Especially sections containing C₄ species are mostly polyphyletic and need further sampling (see below).

(1) *Cremnophyton* and *Atriplex cana*. The molecular data sets resolve the monotypic, Malta and Gozo endemic genus *Cremnophyton* as nested among C₃ species of *Atriplex*. The species probably is most closely related to *A. cana*, a species widely distributed in semideserts from western China to the eastern part of European Russia (Figs. 2, 3). Morphologically *Cremnophyton* and *A. cana* are not obviously similar to any other Eurasian *Atriplex*. Sukhorukov (2006) assumed that *A. cana* represents an old lineage of *Atriplex*, likewise Brullo and Pavone (1987) proposed that *Cremnophyton* represents a Tertiary (Oligocene/Miocene) relict. Although clearly resolved within *Atriplex*, both species branch off early within the genus (Figs. 2, 3).

Cremnophyton is a shrub and grows on limestone cliffs of Malta and Gozo (Brullo and Pavone, 1987), while *A. cana* is a dominant subshrub of certain plant formations in clayey, saline soils of Kazakhstani semideserts. Leaves of *Cremnophyton* are spatulate and entire as in *A. cana* but also as in *Halimione*. *Cremnophyton* differs from all other species of *Atriplex* (including *A. cana*) by the basic chromosome number of $x = 10$ (basic number in *Atriplex* is $x = 9$: Sukhorukov, 2006 and ref. therein) and by the presence of small bracts (only 1/4–1/5 the length of the petals) in male flowers (Brullo and Pavone, 1987). We found additional morphological characteristics of *Cremnophyton*. The bracts of the female flowers are sometimes unequal, the bracts adhere to the lower part of the fruit, and the radicle always points upward although the bracts are not connate along the margin. These two characters, direction of the radicle and degree of bract concrescence, have been found to be correlated in most *Atriplex* species with the result that the radicle points to the end of the concrescent part between the bracts (Sukhorukov, 2006). Because of its morphological and ecological distinctness, we consider *Cremnophyton lanfranconi* an unmistakable species within *Atriplex* (see taxonomic part).

Morphologically, cytologically, and anatomically *A. cana* is not very different from other Eurasian species of *Atriplex*. It should, however, be noted that *A. cana* shows—in contrast to other shrubby *Atriplex* species in Eurasia—light-brown seeds with a thin (5–10 μm) outer seed coat layer.

(2) *Atriplex* sect. *Atriplex* (formerly sect. *Dichospermum* (Ulbrich, 1934)) seems to represent a natural group of annual C₃ species (Fig. 3). According to Sukhorukov (2006), it contains three species, *A. hortensis* (type species of the section), *A. sagittata*, and *A. aucheri*. *Atriplex* sect. *Atriplex* is supported here. *Atriplex oblongifolia* is classified in *Atriplex* sect. *Teutliopsis*

(Sukhorukov, 2006). Here we find that this species is closely related to species of *Atriplex* sect. *Atriplex*. Traditionally, *Atriplex* sect. *Atriplex* is characterized by containing annual species with large hastate leaves and two types of female flowers. One type has two bracts and vertically orientated seeds and the other has 3–5 tepals and horizontally orientated seeds. In *A. oblongifolia*, only the first type of female flowers occurs. The placement of this species in the type section was already proposed by Schwarz (2003) based on molecular data. This tree topology implies that the second female flower type was probably lost in *A. oblongifolia*. Also in *A. sagittata*, the reduction of the second type of female flowers sometimes occurs (Sukhorukov, 1999).

(3) *Atriplex* sect. *Teutliopsis* also contains annual C_3 species. The inflorescences consist of mixed female and male flowers without a spatial separation of the sexes. There is only the perianthless type of female flowers; female flowers with a perianth occur very rarely in this group (Gustafsson, 1986; Medvedeva, 1996). The two bracts are only connate up to half of their length in fruit and remain herbaceous (Aellen, 1939a; Sukhorukov, 2006). *Atriplex* sect. *Teutliopsis* represents a well-supported, natural group. The inclusion of *A. davisii*, a formerly poorly known species, in this group is supported by morphological data (Sukhorukov, 2007a; Sukhorukov and Danin, 2009).

(4) The C_4 clade is well supported and contains the majority of *Atriplex* species (Fig. 3). The Eurasian species of this clade belong to several different sections (namely sect. *Sclerocaryma*, sect. *Psammophila*, sect. *Stylosa*, sect. *Pterochiton* and sect. *Obione*). These sections were separated, for example, by growth form, the degree of connation of the two bracts, and seed morphology and color. None of these sections seems to represent a natural group.

There are two distinct Australian lineages within the C_4 clade; these are named Australian *Atriplex* clade 1 and clade 2 (Fig. 3). Australian *Atriplex* clade 1 contains four species, *A. cinerea*, *A. isatidea*, *A. nummularia*, and *A. rhagodioides*. These are all large and widespread shrubs that belong to *Atriplex* sect. *Dialysex* and have been considered closely related by previous authors (Wilson, 1984; Aellen 1937/1938). Other morphologically similar species that have not been sampled here such as *Atriplex incrassata* F. Muell. or *A. amnicola* Paul G. Wilson, might belong to this clade, too. The Australian *Atriplex* clade 2 consists of 27 species classified in four different sections, viz. sect. *Spongiocarpus*, sect. *Semibaccatae*, sect. *Dialysex*, and the monotypic sect. *Theleophyton*. Section *Spongiocarpus*, sect. *Semibaccatae*, and sect. *Dialysex* are clearly polyphyletic. Thirty-one of 57 endemic species of Australian *Atriplex* were sampled for this study. Although this already represents a broad sampling, more variable markers and an increased sampling are needed to understand the phylogeny of *Atriplex* in Australia.

The American species and the Australian *Atriplex* clade 1 are sister to each other in a well-supported clade within the C_4 clade (Fig. 3). The American species belong to sect. *Obione* and sect. *Pterochiton*. Section *Pterochiton* is polyphyletic. Within the American clade, there are two North American lineages (one is well supported) and one well-supported South American lineage. The ITS and chloroplast results are not congruent; increased taxonomic sampling is necessary to understand the relationships among the American *Atriplex* lineages.

The molecular data suggests that the traditional sections of the C_4 species are largely polyphyletic and that a revised classification of the C_4 species of *Atriplex* is needed. Such a revision, however, needs a better resolved and sampled molecular tree.

(5) *Atriplex crassifolia*. Aellen (1939a) classified *A. crassifolia* with *A. patula* in sect. *Crassifolia*. Later the species was included in sect. *Teutliopsis* (Sukhorukov, 2006). We are unaware of distinct morphological characters that would justify a separation from sect. *Teutliopsis*.

Biogeography of Atripliceae and the evolution of C_4 -photosynthesis—Like other subfamilies of Chenopodiaceae studied with molecular data (Suaedoideae: Schütze et al. [2003]; Betoideae: Hohmann et al. [2006]; Salicornioideae: Kadereit et al., [2006]; Camphorosmoideae: Kadereit and Freitag, 2010). Atripliceae seem to have their roots in Eurasia. *Microgynoecium* is distributed in Tibet, Himalaya, and Pamir, and the early branching clades of both major lineages of Atripliceae, the *Atriplex* clade and *Archiatriples* clade, are also distributed in Eurasia (Fig. 3). In the *Archiatriples* clade, this is *Archiatriples*, which occurs in China, and in the *Atriplex* clade, these are *Halimione*, *Atriplex cana*, and *Cremnophyton*, and the *Atriplex* C_3 clades, which are (mostly) distributed in Eurasia. The Atripliceae started to diversify during the Early Miocene (Table 3). The *Atriplex* clade and the *Archiatriples* clade both are distributed worldwide—in Eurasia, North and South America, South Africa, and Australia (the latter only in the *Atriplex* clade). However, although of the same age, the two clades differ fundamentally in terms of internal divergence times and species diversification.

The *Archiatriples* clade comprises only 12 spp., eight of them found in North America. The North American species seem to form a monophyletic clade (North American C_3 clade). *Archiatriples* split from the rest of the clade c. 20.4–16.8 Ma. The relationships of *Exomis*, *Manochlamys*, *Holmbergia*, and the North American C_3 clade remain unresolved (see above). North America was either reached from South America or from South Africa, or its closest relative in Eurasia went extinct. North America was probably reached by the North American C_3 clade c. 12–10 Ma (Figs. 1–3). It likely slightly predates the arrival of the North American *Atriplex* C_4 lineage, which arrived c. 9 Ma (Fig. 3).

The *Atriplex* clade comprises c. 300 spp., the majority of them belonging to the C_4 lineage of *Atriplex*. The C_4 pathway likely arose only once in *Atriplex* (Fig. 3), and this C_4 lineage diversified, spread, and radiated on different continents. Branch dating of the molecular trees presented here shows that C_4 photosynthesis arose in *Atriplex* at least 14.1–10.9 Ma (Table 3). This dating of the C_4 origin in *Atriplex* supports the current view that the increased aridity and seasonality of the Miocene climate enhanced the origin of C_4 lineages (Osborne and Beerling, 2006; Behrensmeyer et al., 2007; Huang et al., 2007; Kürschner et al., 2008).

Australia was reached by C_4 *Atriplex* two times independently, once from Central Asia between 6.3 and 4.8 Ma, and once from Eurasia or America between 9.8 and 7.8 Ma (Fig. 3). The younger Australian *Atriplex* lineage (clade 2 in Fig. 3) radiated after its arrival on the continent and comprises most of the Australian species (G. Kadereit, unpublished results). The older Australian *Atriplex* lineage seems to comprise only a few species (clade 1 in Fig. 3). The arrival of *Atriplex* in Australia during the late Miocene agrees with the recent finding that the largest sthenurines kangaroo (*Procoptodon goliath*) was a browse specialist for *Atriplex* (Prideaux et al., 2009). The sthenurines kangaroos originated during the late Miocene and reached their highest diversity during the Pliocene spreading into the newly developing arid landscapes (Prideaux, 2004). The ITS tree presented here indicates that also the species-rich Australian *Atriplex* lineage radiated during the Pliocene (Fig. 3).

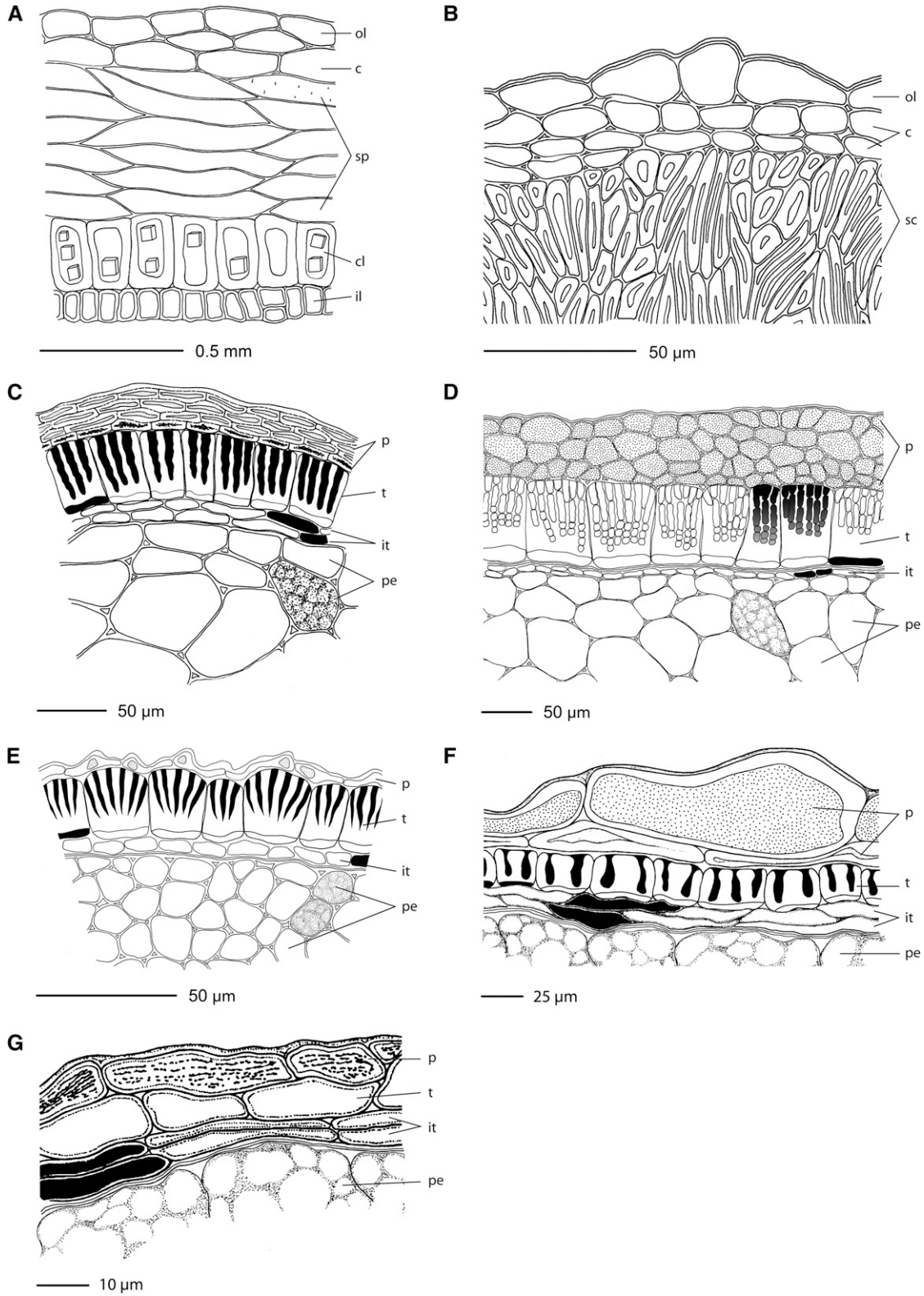


Fig. 4. Bract cover of (A) *Spinacia oleracea* and (B) *Atriplex fera*. Fruit/seed anatomy of (C) *Holmbergia tweedii*, (D) *Manochlamys albicans*, (E) *Proatriplex pleiantha*, and (F, G) *Atriplex centralasiatica* with evident heterospermy ([F] red seed, [G] yellow seed, pericarp deleted). Abbreviations: c, chlorenchyma; cl, crystalliferous layer; il, inner layer; it, integumental tepatum; ol, outer layer; p, pericarp; pe, perisperm; sc, sclerenchyma; sp, sclerenchymatic parenchyma; t, testa.

According to the ITS tree (Fig. 3), the Americas were reached by the *C₄ Atriplex* only once, either from Eurasia or Australia between 9.8 and 8.8 Ma. The tree topology does not allow us to specify the area of origin; however, we consider a northern hemispherical origin as more likely. South America may have been reached several times independently from North America (between 7.7–4.4 Ma and 6.0–5.2 Ma; Fig. 3). The American lineages radiated after their arrival on the continents.

Evolution of flower and fruit morphology in Chenopodioideae—Dioecy occurs in *Spinacia*, *Rhagodia*, *Grayia*, *Exomis*, and *Atriplex* (Table 4). From the scattered position of dioecious taxa in Chenopodioideae, mostly within clades that are predominantly monoecious or polygamo-monoecious, it seems obvious that dioecy evolved multiple times in the subfamily. The separation of sexes within the inflorescence is a common condition in Chenopodioideae, and it seems likely that the spatial differentiation of male and female inflorescence parts in monoecious taxa also evolved multiple times (cf. Kondorskaya, 1984). Many genera are either strictly monoecious or have mixed inflorescences with bisexual and unisexual flowers (Table 4). In contrast to this, species with exclusively bisexual flowers are relatively uncommon in Chenopodioideae and occur mainly in *Chenopodium* and *Dysphania*. Traditionally, Atripliceae were defined by unisexual flowers. Because this condition evolved several times in Chenopodioideae, viz. in Atripliceae, Axyrideae, *Suckleya*, *Spinacia*, and *Rhagodia* (compare Table 4), further characters are required to morphologically define the tribe. The second traditional character used to define Atripliceae is perianthless female flowers with a foliar cover of two bracts that persist and are modified during fruit ripening and become a constitutive part of the diaspores. There are a few species that have female flowers with a perianth (Table 4), but in Atripliceae as circumscribed here the perianthless female flowers with a foliar cover of two bracts are certainly the most common character state. However, in a few lineages, viz. *Microgynoecium*, *Archiatripliceae*, and *Proatriplex*, one bract or a pair of bracts subtend a cluster of female flowers. Because these genera probably represent old, relictual groups, it is tempting to speculate that a cluster of female flowers per bract could be the plesiomorphic condition of flower morphology in Atripliceae. However, this will be difficult to prove because of the unstable position of *Microgynoecium* in the trees and the rare occurrence of this character state in Chenopodioideae. Alternatively, it might represent an apomorphic condition that evolved independently in these lineages. The molecular analysis presented here revealed that female flowers with a persistent foliar cover evolved not only in Atripliceae, but also in the ancestor of *Ceratocarpus* and *Krascheninnikovia* and in *Spinacia*. These three lineages show distant positions from each other in the molecular trees, indicating that female flowers with a persistent foliar cover evolved three times independently in Chenopodioideae. Axyrideae (as defined here) are readily distinguished from Atripliceae by their characteristic indumentum of stellate hairs and by the absence of “stalactites” in the outer periclinal cell walls of the testa. A closer look at *Spinacia* revealed that it differs from Atripliceae in a set of prominent morphological and anatomical characters (see above) that further support its position outside the tribe.

Most representatives of Atripliceae have a 1- or few-layered and undifferentiated pericarp in the ripe fruits. However, members of the *Archiatripliceae* clade seem to be comparatively diverse in fruit anatomy. They differ in the adherence of the pericarp to

the seed coat and in the number of cell layers in the mature pericarp (Table 4). In contrast, the pericarp of the *Atriplex* clade is invariably simple (Fig. 4F). Within the *Atriplex* clade, *Halimione* evolved a pericarp that is tightly adherent to a thin, membranous testa (cf. Wunderlich, 1967; see above). In perennial *Atriplex*, the testa is normally thick and hard. In some annual species of *Atriplex*, heterospermy evolved. This character is found in several groups of Chenopodioideae (evident heterospermy in *Axyris*: Sukhorukov, 2005; latent heterospermy in Eurasian *Chenopodium*: A. Sukhorukov, pers. observation). In Atripliceae, a vertical orientation of the embryo is the predominant character state. A horizontal position has evolved in *Atriplex* (within sect. *Atriplex*) and in *Grayia* independently (Table 4). The rotation of the embryo orientation (radicle pointing upward, laterally or downward) likely arose in connection with a highly variable degree of bract connation multiple times in Atripliceae.

TAXONOMIC CONCLUSIONS

The results of this study made the following three taxonomic conclusions necessary:

(1) Atripliceae C. A. Mey.

The tribe Atripliceae is accepted here, albeit with a modified generic compilation. The following genera are included: *Archiatripliceae*, *Atriplex*, *Exomis*, *Extriplex*, *Grayia*, *Halimione*, *Holmbergia*, *Manochlamys*, *Microgynoecium*, *Proatriplex*, *Stutzia*. The subfamily status Atripliceae Falkovich and Kovalev (Falkovich and Kovalev, 2007) is not accepted here. The inclusion of *Blackiella*, *Haloxanthium*, *Neopreissia*, *Obione*, *Pachypharynx*, *Senniella*, and *Theleophyton* in *Atriplex* is supported by our results, while the inclusion of *Halimione* is rejected. The inclusion of *Cremnophyton* in *Atriplex* is proposed.

(2) *Atriplex lanfrancoi* (Brullo & Pavone) G. Kadereit et Sukhor., comb. nov.

Basionym: *Cremnophyton lanfrancoi* Brullo et Pavone, *Candollea* 42(2): 622 (1987).

(3) Tribe Axyrideae (Heklau) G. Kadereit & A. Sukhor., comb. & stat. nov.

Basionym: tribe Atripliceae, subtribe Axyridinae Heklau, *Taxon* 57(2): 572 (2008).

Typus: genus *Axyris* L., Sp. Pl. 979 (1753).

Included genera: *Axyris* L., *Ceratocarpus* L., *Krascheninnikovia* Gueldenst.

= subtribe Eurotiinae Moq. (sub Eurotieae) in DC., *Prodr.* 13(2): 119 (1849), nom. illeg.

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APPENDIX 1. Species sampled, voucher information, laboratory numbers and GenBank accessions. Sequences generated for this study are written in boldface. Herbarium abbreviations follow those of the Index Herbariorum. Abbreviations: Co., County; cult., cultivated; Nat., National; Prov., Province; SE, southeast.

- Taxon*, laboratory number, voucher (Herbarium), GenBank accession for (1) *rbcl* gene (2) *atpB-rbcL* spacer and (3) ITS; if more than one sample was used for a species then this is indicated by sample 1 and sample 2.
- Agriophyllum squarrosum* (L.) Moq., chen 054, *H. Freitag* 28.196a (KAS), SE Russia, Prov. Astrakhan, (1) AY270051, (2) **HM587612**; *Anthochlamys multinervis* Rech.f., chen 042, *H. Freitag* 13.979 (KAS), Iran, Kavir Nat. Park near Mobarakiyeh, (1) AY270056, (2) **HM587613**; *Archiatrilex nanpinensis* G.L. Chu, chen 1000, *Downie* 759 (ILL), China, Langkang, Nanping, Sichuan, (1) **HM587580**, (2) **HM587614**, (3) **HM587476**; *Atriplex acanthocarpa* (Torr.) S. Watson, EHZ-783, *E. Zacharias* 783 (UC), USA, New Mexico, Hidalgo Co., (3) **HM587477**; *Atriplex acutibractea* Anderson, chen 903, *S. Jacobs* 9340 (NSW), Australia, (3) **HM587478**; *Atriplex altaica* Sukhor., EM320/chen 919, *B. Shishkin & al.*, 08.1931 (MW), Russia, Altai, Kosch-Agach, (2) **HM587615**, (3) **HM587479**; *Atriplex angulata* Benth., chen 443, *S. Jacobs* 9113 (NSW), Australia, N. Far W. Plains, Stephens Creek, (3) **HM587480**; *Atriplex aucheri* Moq., sample 1: chen 043, *H. Freitag* 30.101 (KAS), Uzbekistan, c. 60 km SW Tashkent at road to Gulistan, (1) **HM587581**, (2) **HM587616**, sample 2: EM332, *A. Sukhorukov & al. s.n.*, 04.2000 (MW), Russia, prov. Astrakhan, Kharabali, (3) **HM587481**; *Atriplex australasica* Moq., sample 1: chen 842, *S. Jacobs* 9268 (NSW), Australia, NSW Central Coast, Broken River, Gerroa, (1) **HM587582**, (2) **HM587617**, (3) **HM587482**, sample 2: chen 672, *S. Jacobs* 9233, (NSW), Australia, NSW North Coast, North Creek Rd., (3) **HM587483**; *Atriplex belangeri* (Moq.) Boiss., EM 399, *M. Nazarov* 13457, 08.1930 (MW), Kazakhstan, Ber-Kazan, (3) **HM587484**; *Atriplex billardierei* Hook. f., chen 564, *A. M. Buchanan* 13863 (NSW), Australia, Planter Beach, Cockle Creek, (2) **HM587618**, (3) **HM587485**; *Atriplex calotheca* (Rafn) Fries, EM316, *N. Shvedchikova* 08.1988 (MW), Latvia, Mersrags, (2) **HM587619**, (3) **HM587486**; *Atriplex cana* C.A. Mey., sample 1: chen 1874, *B. Neuffer* 8890 (OSBU), Russia, Bazkumtschak, (3) **HM587487**, sample 2: EM310, *A. Sukhorukov & A. Seregin* R-64, 09.2002 (MW), Russia, prov. Volgograd, Elton (2) **HM587620**, (3) **HM587488**; *Atriplex canescens* (Pursh) Nutt., *Borsch, Müller & Pratt* 3431 (B. ISC), USA, Texas, Hwy 180 close to junction Hwy 375, (3) **HM587489**; *Atriplex centralasiatica* Iljin, chen 920, *M. Lomonosova* 190 (MW), IX.2001, Kazakhstan, distr. Tarbagatay, (1) **HM587583**, (2) **HM587621**, (3) **HM587490**; *Atriplex cinerea* Poir., sample 1: chen 435, *S. Jacobs* 9071 (NSW), Australia (3) **HM587491**, sample 2: EHZ-887, *Kuschel* 325 (UC), Australia, Victoria (cult. at UCBG), (2) **HM587622**, (3) HM005864; *Atriplex codonocarpa* Paul G. Wilson, chen 539, *S. Jacobs* 9166 (NSW), Australia, WA Carnarvon, Babbage Is., (3) **HM587492**; *Atriplex conduplicata* F. Muell., chen 442, *S. Jacobs* 9112 (NSW), Australia, N. Far W. Plains, Stephens Creek, (3) **HM587493**; *Atriplex confertifolia* (Torr. & Frém.) S. Watson, EHZ-522, *E. Zacharias* 522 (UC), USA, Utah, Garfield Co., (3) **HM587494**; *Atriplex cordubensis* Gand. & Stuck, chen 1896, *K. Kubitzki* 08-16 (HBG), Argentina, prov. Salta, San Carlos, (2) **HM587623**, (3) **HM587495**; *Atriplex coriacea* Forssk., chen 038, *H. Freitag* 19.596 (KAS); Egypt, Eastern desert, Wadi Hof (1) AY270045, (2) **HM587624**; *Atriplex crassifolia* Ledeb., EM321, *M. Lomonosova & A. Sukhorukov* 09.2000 (MW), Rusia, Novosibirsk prov., Karasuk, (2) **HM587625**, (3) **HM587496**; *Atriplex davisii* Aellen, EM472, *H. Freitag & Adiguel* 09.1997 (MW), Turkey, Amasya, (3) **HM587497**; *Atriplex deserticola* Phil, chen 1882, *R. Greissl* 701-04, (MJG), Chile, Toconao, (3) **HM587498**; *Atriplex dimorphostegia* Kar. & Kir., chen 377, *M. Al-Dosari* 1839 (KTUH), Kuwait, Al-Subiyah, (2) **HM587626**, (3) **HM587499**; *Atriplex eardleyae* Aellen, chen 440, *S. Jacobs* 9101 (NSW), Australia, N. Far W. Plains, Umberumberka Reservoir, (3) **HM587500**; *Atriplex elachophylla* F. Muell., chen 912, *S. Jacobs* 9353 (NSW), Australia, (3) **HM587501**; *Atriplex flabellum* Bunge ex Boiss., EM 323, *N.N. Kaden et al.* 69500, 08.1969 (MW), Kirghizia, Osh, (2) **HM587627**, (3) **HM587502**; *Atriplex fissivalvis* F. Muell., chen 905, *S. Jacobs* 9343 (NSW), Australia, N. Far W. Plains, Fowlers Gap, (3) **HM587503**; *Atriplex gardneri* (Moq.) D. Dietr., EHZ-660, *E. Zacharias* 660 (UC), USA, Utah, Salt Lake Co., (3) **HM587504**; *Atriplex glabriuscula* Edmondston, EM 393, *A. Schulz s.n.* (LE), Latvia (2) **HM587628**, (3) **HM587505**; *Atriplex glauca* L., sample 1: chen 247, *H. Freitag* 31.3.2001 (KAS), Spain (1) **HM587584**, (3) **HM587506**, sample 2: EM394, *V. Botschantzev* 09.1964 (LE), Egypt, Cairo (2) **HM587629**; *Atriplex gmelinii* C.A. Mey, chen 1878, *H. Freitag* 35.134 (KAS), S Korea, Jeollanam prov., Muan, (3) **HM587507**; *Atriplex halimus* L., sample 1: chen 278, *J. Hensen s.n.*, 31.03.01 (KAS), Salinas Santa Palo, SE Spain, (1) AY270059, (3) **HM587508**, sample 2: chen 1876, *G. Kadereit & J.W. Kadereit* 2006/23 (MJG), Spain, Almeria, Sierra de Alhamilla, (2) **HM587630**, (3) **HM587509**; *Atriplex herzogii* Standl., EHZ-HF7, *S. Beck* 22678 (KAS, LPB), Bolivia, Oruro Dept., Cercado Prov., (3) **HM587510**; *Atriplex holocarpa* F. Muell., chen 561, *S. Jacobs* 9189 (NSW), Australia, WA Austin, near Wiluna, (2) **HM587631**, (3) **HM587511**; *Atriplex hortensis* L., EM334, *A. Sukhorukov* 09.1998 (MW), Russia, Moscow, Pechatniki, (3) **HM587512**; *Atriplex hymenelytra* (Torr.) S. Watson, EHZ-606, *E. Zacharias* 606 (JEPS), USA, California, Inyo Co., (3) **HM587513**; *Atriplex hymenotheca* Moq., chen 536, *S. Jacobs* 9145 (NSW), Australia, WA Avon, Koorda, (3) **HM587514**; *Atriplex imbricata* D. Dietr., chen 1997/EHZ-HF1, *S. Beck* 21609 (KAS, LPB), Bolivia, Potosí Dept., Daniel Campos prov., salar de Myuni, (2) **HM587632**, (3) **HM587515**; *Atriplex inamoena* Aellen, chen 1875, *B. Neuffer* 3565 (OSBU), Egypt, Wadi 1b, (3) **HM587516**; *Atriplex intermedia* Anderson, chen 904, *S. Jacobs* 9342 (NSW), Australia, N. Far W. Plains, Stephens Creek, (3) **HM587517**; *Atriplex intracontinentalis* Sukhor., EM325, *M. Lomonosova & A. Sukhorukov* 09.2000 (MW), Kazakhstan, Ayaguz, (3) **HM587518**; *Atriplex isatidea* Moq., chen 538, *S. Jacobs* 9164 (NSW), Australia, (2) **HM587633**, (3) **HM587519**; *Atriplex laciniata* L., EM395, *Oellgaard* 07.1966 (MW), Dania, Laeso, (2) **HM587635**, (3) **HM587520**; *Atriplex laevis* C.A. Mey., EM326, *A. Sukhorukov* 09.1997 (MW), Russia, Moscow, Pechatniki, (3) **HM587521**; *Atriplex lampa* (Gilles ex Moq.) D. Dietr., chen 1897, *K. Kubitzki* 08-23, Argentina, San Juan prov., Las Flores, (1) **HM587585**, (2) **HM587634**, sample 2: chen 1898, *K. Kubitzki* 08-18, Argentina, Catamarca prov., Hualfin, (3) **HM587522**; *Atriplex latifolia* Wahlenb., EM412, V.V. Timofeeva 1673, 09.2002 (MW), Russia, Karelia, Kop, (2) **HM587636**, (3) **HM587523**; *Atriplex lehmanniana* Bunge, EM327, *K. Shatov & T. Efimova* 07.1969 (MW), Turkmenistam, Baba-Durmez, (3) **HM587524**; *Atriplex lentiformis* (Torr.) S. Watson, sample 1: chen 2060, *G. Kadereit* 2009/26, USA, California, South San Francisco Bay, Newark, (1) **HM587586**, sample 2: EHZ-520, *E. Zacharias* 520 (UC), USA, Utah, Washington Co., (2) **HM587637**, (3) HM005872; *Atriplex leptocarpa* F. Muell., chen 439, *S. Jacobs* 9100 (NSW), Australia, N. Far W. Plains, Umberumberka Reservoir, (3) **HM587525**; *Atriplex leucoclada* Boiss.,

- EHZ-BE2, *B. Ertter* 18793 (UC), Iran, Hamadan, (2) **HM587638**, (3) HM005860; *Atriplex leucophylla* D. Dietr., [sample 1](#): chen 2062, *G. Kadereit* 2009/38 (MJG), USA, California, Point Reyes, Limantour Beach (1) **HM587587**, [sample 2](#): EHZ-JeGr3, *J. Greenhouse s.n.* (JEPS), USA, California, Santa Barbara Co., (2) **HM587639**, (3) **HM587526**; *Atriplex lindleyi* Moq., chen 438, *S. Jacobs* 9099 (NSW), Australia, N. Far W. Plains, Broken Hill, (3) **HM587527**; *Atriplex littoralis* L., EM314, *N. Shvedchikova* 08.1988 (MW), Latvia, Tuya, (3) **HM587528**; *Atriplex micrantha* C.A. Mey., EM319, *A. Sukhorukov s.n.*, 10.1997 (MW), Russia, prov. Volgograd, Pallasovka, (2) **HM587640**, (3) **HM587529**; *Atriplex moneta* Bunge ex Boiss., EM322, *T. Efimova & K. Shatov* 08.1969 (MW), Turkmenistan, Baba-Durmaz, (2) **HM587641**, (3) **HM587530**; *Atriplex muelleri* Benth., [sample 1](#): chen 436, *S. Jacobs* 9083 (NSW), Australia, (2) **HM587642**, [sample 2](#): chen 670, *S. Jacobs* 9227 (NSW), Australia, QLD, Maranoa, Roma, (3) **HM587531**; *Atriplex myriophylla* Phil., chen 1996, *S. Beck* 11128 (KAS, LPB), Bolivia, prov. Murillo, La Paz Cota Cota, (2) **HM587643**; *Atriplex nessorhina* S.W.L. Jacobs, chen 913, *S. Jacobs* 9354 (NSW), Australia, N. Far W. Plains, Peery Lake, (3) **HM587532**; *Atriplex nudicaulis* Bogusl., EM318, *V. Vekhov* 09.1972 (MW), Russia, Karelia, Poyakonda, (2) **HM587644**, (3) **HM587533**; *Atriplex nummularia* Lindl., chen 415, *G. M. Towler* 323 (NSW), Australia, (3) **HM587534**; *Atriplex oblongifolia* Waldst. & Kit., EM333, *A. Sukhorukov* 09.1997 (MW), Russia, Volgograd, (2) **HM587645**, (3) **HM587535**; *Atriplex obovata* Moq., EHZ-743, *E. Zacharias* 743 (UC), USA, Utah, San Juan Co., (3) **HM587536**; *Atriplex pamirica* Iljin, EM315, *I.A. Raikova* 08.1953 (LE), Tajikistan, Chechekty (2) **HM587646**, (3) **HM587537**; *Atriplex parishii* S. Watson, [sample 1](#): chen 2059, *G. Kadereit* 2009/13 (MJG), USA, California, Alameda, Livermore, (1) **HM587588**, (2) **HM587647**, [sample 2](#): EHZ-FS2, *F. Sproul s.n.* (JEPS), USA, California, Riverside Co., (3) **HM587538**; *Atriplex parryi* S. Watson, EHZ-585, *E. Zacharias* 585 (JEPS), USA, California, San Bernardino Co., (1) **HM587589**, (2) **HM587648**, (3) **HM587539**; *Atriplex parvifolia* Kunth, EHZ-HF3, *S. Beck* 14369 (KAS, LPB), Bolivia, Oruro Dept., Cercado Prov., (3) **HM587540**; *Atriplex patagonica* D. Dietr., chen 1995, *F.-G. Schröder s.n.*, Argentina, Patagonia, Chubut, Salina Chica, (2) **HM587649**, (3) **HM587541**; *Atriplex patula* L., [sample 1](#): (1) X15925, [sample 2](#): EM324, *A. Sukhorukov* 10.2005 (MW), Russia, prov. Tambov, Michurinsk, (2) **HM587650**, (3) **HM587542**; *Atriplex phyllostegia* (Torr. ex S. Watson) S. Watson, EHZ-992, *E. Zacharias* 992 (UC), USA, Nevada, Churchill Co., (1) **HM587590**, (2) **HM587651**, (3) HM005870; *Atriplex polycarpa* S. Watson, E468, *J. Webber* (H), USA, California, (3) **HM587543**; *Atriplex powellii* S. Watson, EHZ-529, *E. Zacharias* 529 (UC), USA, Utah, Wayne Co., (1) **HM587591**, (2) **HM587652**, (3) **HM587544**; *Atriplex prostrata* Boucher ex DC., EM335, *A. Sukhorukov* 09.2002 (MW), Russia, Moscow, (2) **HM587653**, (3) **HM587545**; *Atriplex pseudocampanulata* Aellen, chen 838, *S. Jacobs* 9243 (NSW), Australia, S. Far W. Plains, Balranald, (3) **HM587546**; *Atriplex quinii* F. Muell., chen 908, *S. Jacobs* 9349 (NSW), Australia, N. Far W. Plains, Tibooburra, (3) **HM587547**; *Atriplex recurva* d'Urv., EM391 anonym (LE), Greece, Euboaea, (2) **HM587654**, (3) **HM587548**; *Atriplex rhagodioides* F. Muell., chen 414, *G. M. Towler & S. Jacobs* 322 (NSW), Australia, NSW Central Coast, cultivated: Mount Annan Bot. Garden, (2) **HM587655**, (3) **HM587549**; *Atriplex rosea* L., (1) X55831, chen 2058, *G. Kadereit* 2009/11, USA, California, Alameda, Livermore, (1) **HM587592**, (2) **HM587656**; *Atriplex rusbyi* Britton, chen 1994, EHZ-HF5, *S. Beck* 11335 (KAS), Bolivia, La Paz Dept., Murillo Prov., (2) **HM587657**, (3) HM005865; *Atriplex sagittata* Borkh., EM339, *A. Sukhorukov* 05.2000, (MW), Russia, Moscow, Pechatnik, (3) **HM587550**; *Atriplex schugnanica* Iljin, EM313, *S.S. Ikonnikov* 24, 09.1954 (MW), Tadjikistan, Sumyo, (3) **HM587551**; *Atriplex semibaccata* Moq., chen 535, *S. Jacobs* 9130 (NSW), Australia, NSW, Southern Tablelands, Willis, (3) **HM587552**; *Atriplex semilunaris* Aellen, chen 537, *S. Jacobs* 9151 (NSW), Australia, WA, Coolgardie, Moores Lake, (3) **HM587553**; *Atriplex serenana* A. Nelson ex Abrams, EHZ-495, *E. Zacharias* 495 (UC), USA, California, Tulare Co., (1) **HM587593**, (2) **HM587658**, (3) HM005868; *Atriplex sibirica* L., EM312, *L. Volosnova* 08.1982 (MW), Russia, Kaluga prov., (2) **HM587659**, (3) **HM587554**; *Atriplex sphaeromorpha* Iljin, EM338, 338A, *A. Sukhorukov* 09.2001 (MW), Kazakhstan, Dshanybek, (2) **HM587660**, (3) **HM587555**; *Atriplex spinibractea* Anderson, chen 915, *S. Jacobs* 9362 (NSW), Australia, North Western Plains, Nevertire, (3) **HM587556**; *Atriplex spec.*, chen 884, *L. Mucina* 6929/1 (MJG) South Africa, Eastern Cape, Gamtoos River, (3) **HM587557**; *Atriplex spongiosa* F. Muell., chen 158, *Hort.Bot. Berg. Stockholm* 117; 0006303, (1) AY270060, (2) **HM587661**, (3) **HM587558**; *Atriplex stipitata* Benth., chen 437, *S. Jacobs* 9095 (NSW), Australia, N. Far W. Plains, W of Cobar, (3) **HM587559**; *Atriplex sturtii* S.W.L. Jacobs, chen 910, *S. Jacobs* 9351 (NSW), Australia, N. Far W. Plains, Tibooburra, (3) **HM587560**; *Atriplex suberecta* I. Verd., [sample 1](#): EHZ-JeGr8, *J. Greenhouse s.n.* (JEPS), USA, California, Los Angeles Co., (2) **HM587662**, [sample 2](#): chen 836, *S. Jacobs* 9240 (NSW), Australia, South Western Plains, Lake Cargellico, (2) **HM587663**, (3) **HM587561**; *Atriplex tatarica* L., EM337, *A. Sukhorukov s.n.*, 09.2002, (MW), Russia, Moscow, (2) **HM587664**, (3) **HM587562**; *Atriplex turbinata* (R. Anderson) Aellen, chen 909, *S. Jacobs* 9350 (NSW), Australia, N. Far W. Plains, Tibooburra, (3) **HM587563**; *Atriplex undulata* (Moq.) D. Dietr., chen 167, *M. E. Múlgura* 2005 (SI, KAS); Argentina, La Pampa, (1) AY270061, (2) **HM587665**, (3) **HM587564**; *Atriplex velutinella* F. Muell., chen 906, *S. Jacobs* 9345 (NSW), Australia, N. Far W. Plains, Cobham Lake, (3) **HM587565**; *Atriplex vesicaria* Heward ex Benth., chen 562, *S. Jacobs* 9202 (NSW), Australia, Western Australia, Eucla, (2) **HM587666**; *Atriplex vesicaria* Heward ex Benth. subsp. *macrocytidia* Parr-Sm., chen 441, *S. Jacobs* 9103 (NSW), Australia, S. Far W. Plains, Broken Hill, (3) **HM587566**; *Axyris prostrata* L., chen 118, *G. & S. Miede* 96-140-04; Gobi Altai, Mongolei (Hb. Miede, KAS), (1) AY270062, (2) **HM587667**; *Ceratocarpus arenarius* L., chen 466, *H. Freitag* 33.017 (KAS), Russia, Tuva Rep., 15 km SSE Kyzyl (1) **HM587594**; *Chenopodium acuminatum* Willd., chen 183, *G. & S. Miede* 96-060-5 (Hb. Miede, KAS), Mongolia, Gobi Altai, (1) AY270077, (2) **HM587668**; *Chenopodium auricomum* Lindley, chen 258, *S. Jacobs* 8655 (NSW); Australia, New South Wales, North Western Plains (1) AY270078, (2) **HM587669**; *Chenopodium bonus-henricus* L., chen 051 and 1886, grown at Bot. Gard. Mainz, Germany (MJG), (1) AY270079, (2) **HM587670**; *Chenopodium coronopus* Moq., chen 721, Bot. Garden Berlin-Dahlem seed sample 687 (MJG), *leg. Royl* 6823, Spain, Canary Is., La Palma, Puerto Naos/El Remo, (1) **HM587595**, (2) **HM587671**; *Chenopodium desertorum* (J. Black) J. Black subsp. *anidiophyllum* (Aellen) Paul G. Wilson, chen 254, *S. Jacobs* 8650 (NSW); Australia, New South Wales, North Western Plains, (1) AY270042, (2) **HM587672**; *Chenopodium foliosum* Asch., [sample 1](#): chen 117, (1) AY270081, [sample 2](#): chen 1885, *W. Hilbig s.n.* (HAL), W Mongolia, Aimak, Charchiraa, w. of Ulaangom, (2) **HM587673**; *Chenopodium frutescens* C.A. Mey., chen 210, *A. Korolyuk s.n.* (NS), 23.6.2000; Tuva, Russia, (1) AY270082, (2) **HM587674**, (3) **HM587567**; *Chenopodium murale* L., chen 866, *W. Licht* 5801 (MJG), Italy, Gargano, (2) **HM587675**; *Chenopodium nitriaceum* (F. Muell.) Benth., chen 1860, *S. Jacobs* 9212 (NSW, MJG), Australia, NSW, near Balranald, (2) **HM587676**; *Chenopodium oahuense* (Meyren) Aellen, chen 2025, *S. Carlquist* 2085 (UC), USA, Hawaii, Kamehala, (2) **HM587677**; *Chenopodium sanctae-clarae* Johow, chen 194, (1) AY270043; *Chenopodium urbicum* L., chen 821, Bot. Garden Berlin-Dahlem seed sample 694 leg. *Raus* 242 (MJG), Greece, Aegean Sea, Nomos Evviva, (1) **HM587596**, (2) **HM587678**; *Corispermum filifolium* C.A. Mey. ex A.K. Becker, chen 148, *H. Freitag* 28.702 (KAS), Turkey A6 Samsun prov., near Bafra, (1) AY270084, (2) **HM587679**; *Cremonophyton lanfrancoi* Brullo & Pavone, chen 1895, *H. C. Weber s.n.*, Malta, Sliema, (1) **HM587597**, (2) **HM587680**, (3) **HM587568**; *Cycloloma atriplicifolium* J.M. Coult., chen 157, Bot. Garden Kassel, seeds from Hort. Bot. Berg. Stockholm 116; 0006302 (KAS), (1) **HM587598**, (2) **HM587681**; *Dysphania ambrosioides* (L.) Mosyakin & Clemants, chen 822, Bot. Garden Berlin-Dahlem seed sample 683 leg. *Royle* 6394 (MJG), Portugal, Azores, Sao Miguel, Ribeira Grande Lagoa das Fogo, (1) **HM587599**, (2) **HM587682**; *Dysphania botrys* (L.) Mosyakin & Clemants, chen 116, *Freitag & Adigüzel* 28.769 (KAS), Turkey, C4 Konya, road to Karapinar, AY270080, (2) **HM587683**; *Dysphania cristata* (F. Muell.) Mosyakin & Clemants, chen 256, *S. Jacobs* 8653 (NSW), Australia, North Western Plains, New South Wales, (1) AY270046, (2) **HM587684**; *Dysphania glomulifera* (Nees) Paul G. Wilson, chen 277, *S. Jacobs* 8738 (NSW) Australia, New South Wales, North Western Plains, (1) AY270086, (2) **HM587685**; *Einadia nutans* (R. Br.) A.J. Scott, chen 417, *G.M. Towler* 325 (NSW), Australia, central coast, cultivated Mt. Annan Botanical Garden (1) **HM587600**, (2) **HM587686**; *Exomis microphylla* (Thunb.) Aellen, chen 877, *L. Mucina* 081200/3 (MJG), South Africa, Western Cape prov., Darling, (1) **HM587601**, (2) **HM587687**, (3) **HM587569**; *Extriplex californica* (Moq.) E.H. Zacharias, [sample 1](#): chen 2061, *G. Kadereit* 2009/37 (MJG), USA, California, Point Reyes, (1) **HM587602**, (2) **HM587688**, [sample 2](#): EHZ-1025, *E. Zacharias* 1025 (JEPS), USA, California, San Mateo Co. (3) HM005850; *Extriplex joaquinana* (A. Nelson) E.H. Zacharias, EHZ-306, *E. Zacharias* 306, USA, California,

- Contra Costa Co., (1) **HM587603**, (2) **HM587689**, (3) HM005852; *Grayia brandegeei* A. Gray, [sample 1](#): chen 1889, *J. Coles s. n.* (COLO), USA, Colorado, Mesa, (1) **HM587604**, (2) **HM587690**, (3) **HM587570**, [sample 2](#): EHZ-H38, *N. Holmgren, J. Reveal & C. LaFrance* 2133 (UC), USA, Utah, Garfield Co., (3) HM005845; *Grayia spinosa* (Hook.) Moq., [sample 1](#): chen 192, *Larkesto s. n.* (BM), USA, California, Nevada, (2) **HM587691**, (3) **HM587571**, [sample 2](#): EHZ-566, *E. Zacharias 566* (UC), USA, Utah, Tooele Co., (2) **HM587692**, (3) HM005843, [sample 3](#): chen 1888; *B. Neely 4244* (COLO), USA, Colorado, Mouth of Gates of Lodore, (1) **HM587605**, (2) **HM587693**, (3) **HM587572**; *Halimione pedunculata* (L.) Aellen, [sample 1](#): chen 034, *G. Kadereit 2000/202* (MJG); Denmark, Kattegat, (1) AY270093, [sample 2](#): chen 471, *H. Freitag 33094* (KAS), Russia, Novosibirsk, 20 km north of Karasuk, (2) **HM587694**, (3) **HM587573**, [sample 3](#): EM336, *A. Sukhorukov 09.2002* (MW), Russia, prov. Volgograd, Elton, (3) **HQ008274**; *Halimione portulacoides* (L.) Aellen, EM385, *A. Sukhorukov s.n.*, 11.2006 (MW), Cyprus, Larnaca, (3) **HM587574**; *Halimione verrucifera* (M. Bieb.) Aellen, chen 470, *H. Freitag 33.092* (KAS), Russia, Novosibirsk, Karasuk, (1) **HM587606**, (2) **HM587695**, (3) **HM587575**; *Holmbergia tweedii* Spag., [sample 1](#): chen 2003, *A. Krapovickas & C.L. Cristobal 24545* (P), Argentina, Corrientes prov., Saladas rio Santa Lucia, (2) **HM587696**, [sample 2](#): EHZ-H17, *A. Krapovickas & A. Schinini 39143* (UC), Bolivia, (3) HM005842; *Krascheninnikovia ceratoides* (L.) Gueldenst., *B. Dickoré 12752*; Nanga Parbat area, Pakistan (Hb. Dickoré, KAS), chen 012, (1) AY270105, (2) **HM587697**; *Krascheninnikovia lanata* (Pursh) A. Meeuse & A. Smit, chen 1887, *B. Nelson 23554* (USCH, HAL 100339), USA, New Mexico, San Miguel County, Santa Fe Nat. Forest, (2) **HM587698**; *Manochlamys albicans* (Soland. in Ait.) Aellen, chen 878, *L. Mucina 200900/4* (MJG), South Africa, RSA, Northern Cape prov., Namaqua N, P., Kamieskroon, (1) **HM587607**, (2) **HM587699**, (3) **HM587576**; *Microgynoecium tibeticum* Hook.f., [sample 1](#): chen 119, *B. Dickoré 4284* (Hb. Dickoré, KAS), China, Tibet, Quinghai, (1) AY270107, [sample 2](#): chen 874, *G. & S. Miehe 03-059-11* (hb. Miehe, KAS), China, Xizang (Tibet), Tso basin s of Raka Tsangpo Tsabasang, (2) **HM587700**, (3) **HM587577**; *Micromonolepis pusilla* (Torr. ex S. Watson) Ulbr., chen 1858, *A. Tiehm 11763* (NSW), USA, Nevada, Humboldt River, (1) **HM587608**, (2) **HM587701**; *Monolepis nuttalliana* Greene, chen 125, Bot. Garden Kassel, seeds from Univ. Hohenheim (KAS), (1) AY27010, (2) **HM587702**; *Proatriplex pleiantha* (W.A. Weber) Stutz & G.L. Chu, [sample 1](#): chen 1857, *W. A. Weber 7651* (NSW), USA, Colorado, SW Towaoc, (3) **HM587578**, [sample 2](#): EHZ-H32, *R. Spellenberg & R. Corral 8185* (UC), USA, New Mexico, San Juan Co., (3) HM005836; *Rhagodia drummondii* Moq., [sample 1](#): chen 159, *N. Schmalz 194* (52) (MJG); Western Australia, Hayden, (1) AY270124, [sample 2](#): chen 1859, *S. Jacobs 9131* (NSW), Australia, Western Australia, near Meckering, (2) **HM587703**; *Rhagodia parabolica* R. Br., chen 532, *S. Jacobs 9208* (NSW), (2) **HM587704**; *Scleroblitum atriplicinum* (F. Muell.) Ulbr., chen 274, (1) AY858611; *Spinacia oleracea* L., (1) Zurawski et al. (1981), chen 1869, *G. Kadereit s.n.* (MJG), cult. at Botanical Garden University Mainz, (2) **HM587705**; *Stutzia covillei* (Standl.) E.H. Zacharias, EHZ-811, *E. Zacharias 811* (UC), USA, Nevada, Nye Co., (1) **HM587609**, (2) **HM587706**, (3) HM005839; *Stutzia dioica* (Nutt.) E.H. Zacharias, [sample 1](#): AC351, *L. Welp 6269* (NY), (1) **HM587610**, (2) **HM587707**, (3) **HM587579**, [sample 2](#): EHZ-H95, *C. Porter 9071* (UC), USA, Wyoming, Weston Co., (3) HM005838; *Suckleya suckleyana* Rydb., chen 2000; *J. E. Larson 6492*, USA, New Mexico, Tres Piedras, (1) **HM587611**; *Teloxys aristata* (L.) Moq., chen 293, *B. B. Neuffer & H. Hurka 11.727* (Hb. Hurka, KAS), Mongolia, Ulaanbaatar, (1) AY270140, (2) **HM587708**;