

# Molecular phylogeny of Camphorosmeae (Camphorosmoideae, Chenopodiaceae): Implications for biogeography, evolution of C<sub>4</sub>-photosynthesis and taxonomy

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**Abstract** Camphorosmeae constitute a species-rich tribe of Chenopodiaceae-Camphorosmoideae that consists mostly of subshrubs and annuals, distributed in steppes and semi-deserts of Australia, Eurasia, North Africa, southern Africa and North America. We study (1) the relationships of Camphorosmeae to major lineages of the closely related Salsoloideae and (2) the diversification of the tribe with focus on the non-Australian members using sequence variation of five different markers (*rbcl* gene, *ndhF* gene, *atpB-rbcL* spacer, *psbB-psbH* spacer, ITS) and morphological characters. The cpDNA analyses revealed six early-branching lineages in Camphorosmoideae/Salsoloideae (Camphorosmeae, Salsoleae s.str., Caroxyloneae, *Salsola kali* clade, *Nanophyton* clade, *Salsola genistoides* clade) and supported partly (*ndhF* and *atpB-rbcL* spacer) the sister-group relationship of Camphorosmeae and all Salsolean clades. The distinctness of Camphorosmeae and Salsoleae s.l. is further supported by seed, stigma and pollen morphology. Molecular clock estimates point to an earlier radiation in Salsoleae s.l. (Early to Middle Oligocene) than in Camphorosmeae (Early Miocene). In Salsoleae s.l. early radiation might have been enhanced by multiple evolution of C<sub>4</sub>-photosynthesis which facilitated the spread into drier habitats of Eurasia. In Camphorosmeae, C<sub>4</sub>-photosynthesis likely evolved two times, probably in the Middle Miocene. During the Miocene Camphorosmeae spread from Eurasia to Australia, North America and at least two times to South Africa. Only the Australian lineage diversified, the others remained species-poor. The molecular trees congruently resolve three major clades of unclear relationship within Camphorosmeae, *Chenolea* clade (five widely disjunct and morphologically divergent C<sub>3</sub>-species, possibly remnants of old lineages), *Sclerolaena* clade (ca. 150 C<sub>3</sub>-species from Central Asia [3 spp.] and Australia [147 spp.], probably the results of a rapid radiation during the Pliocene) and *Bassia/Camphorosma* clade (ca. 23 C<sub>4</sub>-species and one C<sub>3</sub>/C<sub>4</sub>-intermediate which are widely distributed in Eurasia and southern Africa). The phylogenies show the artificial state of the current generic and subtribal classifications of Eurasian, North American and South African Camphorosmeae. All non-monotypic genera except *Camphorosma* and *Neokochia* were found to be polyphyletic. A revised classification of the tribe is proposed including reinstatement of the newly defined subfamily Camphorosmoideae, description of the new genera *Spirobassia* (1 sp.), *Eokochia* (1 sp.), *Grubovia* (3 spp.) and *Sedobassia* (1 sp.), and several new combinations and synonymizations.

**Keywords** BEAST analysis; *Eokochia*; *Grubovia*; molecular clock; Salsoloideae; *Sedobassia*; semi-deserts; *Spirobassia*; steppes

**Supplementary Material** Figures S1–S6 are available in the free Electronic Supplement to the online version of this article (<http://www.ingentaconnect.com/content/iapt/tax>).

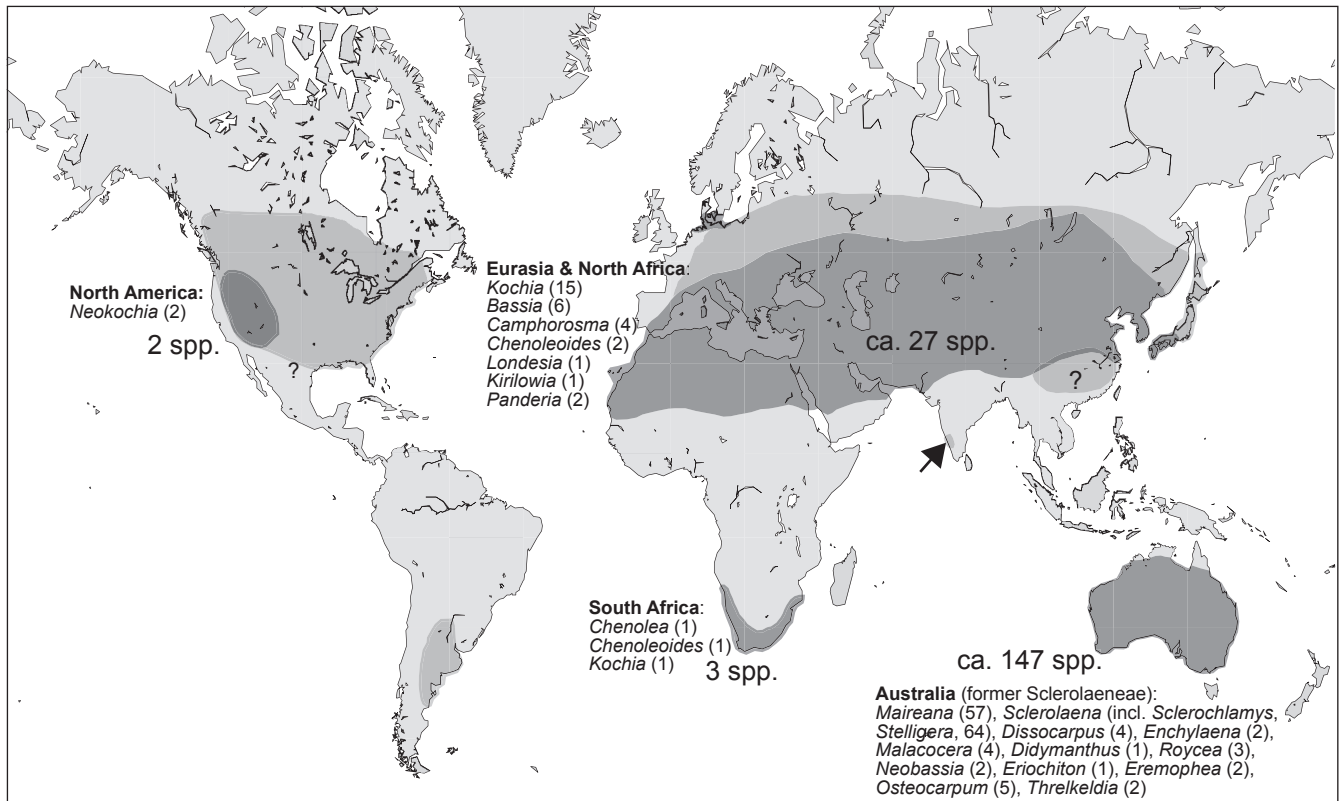
## ■ INTRODUCTION

Camphorosmeae (incl. Sclerolaeneae and Maireaneae) represent a species-rich tribe of Chenopodiaceae comprising ca. 19 genera and ca. 190 species (Scott, 1978; Kühn & al., 1993). Most species are dwarf shrubs or annuals, or more rarely perennial herbs. They have alternate leaves, inconspicuous, sessile flowers and variously appendaged nut-like fruits (Fig. 1). Camphorosmeae are confined to arid, saline or disturbed (ruderal) environments (Fig. 1). They are adapted to their habitats by a dense indumentum of dead hairs and leaves which are reduced in size and often succulent; some species are C<sub>4</sub>-plants. The distribution is centred in Australia, Eurasia and North Africa but also extends to other continents (Fig. 2). A few species are of limited economical interest: *Kochia scoparia* var. *trichophylla* is cultivated as an ornamental (summer-cypress); *Kochia*

*prostrata* (forage *Kochia*) is gaining increasing importance for improving rangelands in Central Asia (Gintzburger & al., 2003) and in the western U.S.A. (Utah State Univ., 2002), *Kochia indica* was introduced to North Africa (Quezel & Santa, 1962) as a high-yielding and salinity-tolerant forage plant and *K. scoparia* has given promising results on experimental farms in the Near East (Kafi & Jami-Al-Ahmadi, 2008); *Camphorosma monspeliaca* has been a traditional medicinal plant in East Mediterranean countries since medieval times due to its content of volatile oils which have antiasthmatic, expectorant, diaphoretic and other properties (Usher, 1974; Tajali & al., 2007).

**Position of Camphorosmeae within Chenopodiaceae.** — In traditional classifications Camphorosmeae were placed in subfam. Chenopodioideae because they share an annular embryo with the other tribes of this subfamily (e.g., Ulbrich, 1934; Kühn & al., 1993; for earlier systems see Kadereit & al., 2003: table 1).





**Fig. 2.** Distribution of Camphorosmeae (areas where Camphorosmeae have been introduced are shaded in light grey).

They were raised to a separate subfamily Camphorosmoideae by Scott (1978) with the argument that most of them differ from Chenopodioideae by having accrescent and appendaged fruiting perianths. Phylogenetic analyses of the Amaranthaceae/Chenopodiaceae alliance using different molecular markers (Kadereit & al., 2003, *rbcL*; Pratt, 2003, *ndhF*; Müller & Borsch, 2005, *matK-trnK* region) have revealed that Camphorosmeae are monophyletic and closely related to subfam. Salsoloideae, many species of which also have appendaged fruiting perianths. Therefore, Kadereit & al. (2003) included them in Salsoloideae. Molecular studies have also congruently shown that the enlarged Salsoloideae are sister to a clade comprising Suaedoideae and Salicornioideae. Initially, tribal relationships within Salsoloideae s.l. remained unclear. Insufficient sampling (Pratt, 2003, 6 spp.; Müller & Borsch, 2005, 3 spp., Kapralov & al., 2006, 9 spp.) or fragmentary representation of Camphorosmeae (P'yankov & al., 2001, 3 Camphorosmeae among 33 Salsoleae) did not allow reliable conclusions to be drawn. Based on the analysis of 10 Camphorosmeae and 12 Salsoleae, Kadereit & al. (2003) subdivided

the subfamily into three groups, namely Camphorosmeae and the provisional Salsoleae I and II. A detailed study (56 taxa) has recently been conducted by Akhani & al. (2007) for Salsoleae s.l. Based on ITS (internal transcribed spacer) and *psbB-psbH* spacer sequences it resolved Camphorosmeae (10 taxa) as sister to the traditional Salsoleae with high statistical support. Within Salsoleae, Akhani & al. (2007) substantiated two distinct clades, Salsoleae s.str. and Caroxyloneae, which had already been suggested in previous studies, albeit with low support and limited sampling (P'yankov & al., 2001; Kadereit & al., 2003).

**Relationships and classification within Camphorosmeae: morphological classifications.** — The more important classification systems of Camphorosmeae are compiled in Table 1. Endlicher (1837: 294) established Camphorosmeae with the genera *Camphorosma*, *Panderia*, *Sclerolaena*, *Anisacantha* and *Threlkeldia* as a subtribe of Chenopodieae, and defined it by ebracteolate flowers, vertical seeds and membranous testa. Moquin-Tandon (1840, 1849) raised it to tribal level and extended it by including genera with horizontal seeds: *Kochia*,

**Fig. 1.** Representative taxa of non-Australian Camphorosmeae, habit and environment. **A**, *Camphorosma lessingii* community, higher terrace of a sebkhah, E of Damascus, Syria, Oct. 2001; **B**, *Chenoleoides tomentosa* as a pioneer plant in higher coastal belt, northern Tenerife near Poris de Abona, Apr. 2003; **C**, *Chenolea diffusa* community, South Africa, Struisbaai, Heunignes River estuary, De Mond Nat., Sep. 2002; **D**, *Chenolea diffusa*, South Africa, Western Cape prov., lagoon near Uilenkraalsmond (note lack of inflorescences), Sep. 2006; **E**, *Bassia dasyphylla* (grey annual) in *Stipa krylovii* steppe (with *Panzeria lanata*, Lamiaceae), Russia, central Tuva, S of Kyzyl, Aug. 2003; **F**, *Bassia dasyphylla*, flowering, dito; **G**, *Kochia prostrata* in rocky steppe, southeastern Crimea near Opuk, Oct. 2003; **H**, *Bassia hyssopifolia*, fruiting, Uzbekistan, Aidar Kul', Oct. 2000; **I**, *Kochia villosissima* in Central Asian *Stipa orientalis* steppe, eastern Kazakhstan, near Zaysan lake, Sep. 2001; **J**, *Kochia angustifolia* in a dry saltmarsh, central Tuva, Chedar lake, Aug. 2003. Photographs by H. Freitag except C (L. Mucina) and I (M. Lomonosova).



inconsistent characters (presence or absence of perianth appendages, horseshoe-shaped versus annular embryos) and placed all Australian taxa in Kochiineae. Furthermore, he stressed the limited significance of the seed position character and showed that obviously closely related genera (e.g., *Kirilowia* and *Londesia*) were separated artificially in Moquin-Tandon's system, and that both character states are found in the same genus (e.g., in *Threlkeldia*). He accepted only some of the new Australian genera and merged others as sections of *Kochia* using the prefix "Austro-" (Table 1).

Scott (1978) raised Camphorosmeae to subfamily level and introduced the new tribes Sclerolaeneae and Maireaneae to include the Australian genera. These two subtribes were distinguished from each other by characters of the perianth appendages (wings, spines, lobes) and of the pericarp (membranous versus hardened), and from Camphorosmeae by "usually" having a shrubby habit, the absence of distinct inflorescences, and a modified fruiting perianth opposite the radicle. Scott maintained Camphorosminae and Kochiinae and provided a very detailed formal subdivision down to series. While stressing the importance of the structure of perianth appendages in the Australian genera, in Kochiinae he considered this character as less significant and included *Kochia* (with wings) as a section of *Bassia* (with spines) where *Londesia* and *Chenolea* (without appendages) were also included as sections. In floristic accounts, however, Scott's suprageneric classification was never used, and most authors also were reluctant to accept his broadened concept of *Bassia*. Finally, he transferred *Cycloloma* from Chenopodiaceae to Kochiinae on the basis of its accrescent, chartaceous and winged fruiting perianth.

Wilson (1984), in his account of Australian Chenopodiaceae, did not accept any further suprageneric subdivision of Camphorosmeae. He stated that "Australian genera are to some extent artificial" and that "the external characters of the fruiting perianth are extremely plastic ... [and] do not necessarily provide a basis for a natural description of genera." Finally, Kühn & al. (1993) recognized Camphorosmeae and Sclerolaeneae, the latter also containing Maireaneae. They maintained *Cycloloma* and a broadly circumscribed *Bassia*, excluding *Chenolea*. Recently, Chu & Sanderson (2008) raised the two native North American C<sub>3</sub>-species of *Kochia* from section level (Ulbrich, 1934) to the separate genus *Neokochia*.

A survey of the non-Australian taxa of Camphorosmeae recognized in this paper is given in Table 2. For an account of the historical classification of the Australian genera see also Cabrera & al. (2009: table 1). It appears that morphological approaches did not result in a satisfactory classification of Camphorosmeae due to the use of homoplasious and highly variable characters. The delimitation of most genera therefore remains unsettled.

**Relationships and classification within Camphorosmeae: molecular phylogenetic studies.** — In their *rbcL* study of the Amaranthaceae/Chenopodiaceae alliance that included ten species of Camphorosmeae, Kadereit & al. (2003) showed that the Australian genera (three genera represented) originated from a holarctic lineage. This result was substantiated by Kadereit & al. (2005) in an ITS analysis of 21 taxa including eight

samples of six Australian genera. They also showed that the Australian taxa are closely related to two annual species from Central Asia. The internal structure of the ITS tree remained unresolved due to limited sampling, except for the basal position of *Chenolea diffusa*.

A molecular study focussed on Australian Camphorosmeae using ITS (40 samples) and ETS (72 samples) was recently carried out by Cabrera & al. (2009). The resulting phylogenies did not support the current taxonomy of Australian taxa. They resolved several statistically supported clades but left other relationships unresolved. Many genera were shown to be polyphyletic. The authors suggested inclusion of *Stelligera*, *Babbagia*, *Sclerochlamys* and *Threlkeldia* into *Sclerolaena*, *Enchylaena* into *Maireana*, and *Neobassia* into *Eremophea* and *Sclerolaena*. However, generic delimitation remained problematic and of 15 morphological characters studied only the fruiting perianth proved to be in partial agreement with molecular relationships. The low resolution in the molecular trees was explained by the comparatively young age of the group, incomplete lineage sorting and the high degree of morphological homoplasy caused by strong selective pressures in the harsh environments.

**Morphology of Camphorosmeae.** — Camphorosmeae are either slightly to moderately lignified dwarf shrubs or annuals with ascending or spreading branches. The Australian, South African and American species are exclusively shrubby, whereas about 2/3 of the Eurasian taxa are annuals. Almost all annual organs including the tepals have a more or less dense indument of appressed or spreading hairs (see, e.g., Carolin, 1983). Indument characters such as density, shape and length of the trichomes are fixed in most species and determine the appearance of the respective plants (Fig. 1).

The alternate leaves (only a few Australian species have opposite leaves) rarely exceed 15 mm in length and 5 mm in width and are moderately to distinctly succulent. Thin and flat leaves without water-storing tissue occur in a few annual species only. For variation in leaf anatomy, see below.

The inflorescences are usually only moderately separated, the transition from leaves to bracts is gradual. The sessile, ebracteolate flowers are solitary or in axillary clusters of 2–3(5), sometimes above a dense ring of long spreading hairs produced from the axil of the subtending bract.

Flowers are mostly 1–2 mm in diameter and bisexual, but sometimes the lateral or the uppermost flowers are functionally female. In shape, they vary considerably among genera, from bowl-like to globular, ovoid, cylindrical and pocket-like. The perianth usually consists of five, more rarely four, membranous to scarious tepals which are fused for about 1/5 to 4/5 of their length and terminate in erect or incurved lobes. The four to five stamens are fused at the base into a delicate hypogynous disc, either have long and delicate or stout filaments, and unappendaged, mostly exerted anthers. The uni-ovulate ovary is either horizontally or, more rarely, vertically orientated and has a distinct style with two long, filiform stigmas covered by stigmatic papillae all around.

In the fruiting stage, the enlarged, persistent perianth surrounds the fruit and becomes an essential part of the diaspore

**Table 2.** Taxon names, distribution, life form, shape of perianth appendages, seed position, chromosome number and representation in the ...

Taxon name used in the sampling	Distribution	Life form
<b>Bassia</b> All.		
<i>aegyptiaca</i> Turki, El-Shayeb & Shehata, non All. 1770	N. Egypt (known from type locality only)	Subshrub
<i>dasyphylla</i> (Fisch. & C.A. Mey.) Kuntze	E. Kazakhstan–Mongolia	Annual
<i>eriophora</i> (Schrad.) Asch.	Egypt–S. Pakistan	Annual
<i>hirsuta</i> (L.) Asch.	Europe–S. Siberia	Annual
<i>hyssopifolia</i> (Pall.) Kuntze	Europe–W. China	Annual
<i>muricata</i> (L.) Asch.	Morocco–S. Iran	Annual
<i>sedoides</i> (Pall.) Asch.	Hungary–Siberia	Annual
<b>Camphorosma</b> L.		
<i>annua</i> Pall.	Hungary–E. Ukraine	Annual
<i>lessingii</i> Litv.	Transcaucasia–S. Siberia	Subshrub
<i>monspeliaca</i> L.	W. Europe–S. Siberia	Subshrub
<i>songorica</i> Bunge	Lower Volga–C. Asia	Annual
<b>Chenolea</b> Thunb.		
<i>diffusa</i> Thunb.	W. Namibia–S. Africa–Mozambique	Subshrub
<b>Chenoleoides</b> Botsch.		
<i>arabica</i> (Boiss.) Botsch.	Morocco–Iraq	Subshrub
<i>dinteri</i> (Botsch.) Botsch.	S. Africa	Subshrub
<i>tomentosa</i> (Lowe) Botsch.	Canary Islands–Morocco	Subshrub
<b>Kirilowia</b> Bunge		
<i>eriantha</i> Bunge	W. Kazakhstan–W. China	Annual
<b>Kochia</b> Roth		
<i>alata</i> Bates	N. America	Annual
<i>angustifolia</i> (Turcz.) Peschkova	S. Siberia–E. Mongolia	Annual
<i>densiflora</i> (Moq.) Aellen	S.E. Europe–C. Asia	Annual
<i>iranica</i> Bornm.	S. Iran–S. Pakistan	Annual
<i>indica</i> Wight	Libya–India	Annual
<i>krylowii</i> Litv.	Altai, Mongolia	Annual
<i>laniflora</i> (S.G. Gmel.) Borb.	C. Europe–E. Siberia	Annual
<i>littorea</i> (Makino) Makino	Korea, Japan	Annual
<i>melanoptera</i> Bunge	Tianshan–Mongolia	Annual
<i>odontoptera</i> Schrenk	W. Kazakhstan–W. China	Annual
<i>prostrata</i> (L.) Schrad.	S. Europa–China	Subshrub
<i>salsoloides</i> Fenzl	S. Africa	Subshrub
<i>saxicola</i> Guss.	S. Italy (Tyrrhenian Islands)	Subshrub
<i>scoparia</i> (L.) Schrad.	W. Europa–E. Asia	Annual
<i>stellaris</i> Moq.	C. Iran–W. China	Annual
<i>tianschanica</i> Pavl.	S.E. Kazakhstan–W. China	Subshrub
<i>villosissima</i> (Bong.) Serg.	S.E. Kazakhstan–W. China	Subshrub
<b>Londesia</b> Fisch. & C.A. Mey.		
<i>eriantha</i> Fisch. & C.A. Mey.	C. Iran–W. China	Annual
<b>Neokochia</b> (S. Watson) G.L. Chu & S.C. Sand.		
<i>americana</i> (S. Watson) G.L. Chu & S.C. Sand.	W. U.S.A.	Subshrub
<i>californica</i> (S. Watson) G.L. Chu & S.C. Sand.	California	Subshrub
<b>Panderia</b> Fisch. & C.A. Mey.		
<i>pilosa</i> Fisch. & C.A. Mey.	Turkey–W. China	Annual
<i>turkestanica</i> Iljin	Transcaucasia–W. China, Armenia	Annual

... molecular datasets of the Eurasian, African and North American Camphorosmeae.

Perianth appendages	Seed position	2n	Represented in the following datasets	Taxon name suggested here, for details see Conspectus
5 straight spines	Horizontal	?	Not represented	None – for the time being (see text)
5 straight spines	Horizontal	18	<i>rbcl</i> , <i>ndhF</i> , <i>atpB-rbcL</i> spacer, ITS	<i>Grubovia dasyphylla</i>
0 to 5 short spines	Horizontal	18	<i>atpB-rbcL</i> spacer,	<i>Bassia eriophora</i>
3 flat obtuse lobes	Horizontal	18	<i>rbcl</i> , <i>atpB-rbcL</i> spacer, ITS	<i>Spirobassia hirsuta</i>
5 uncinata spines	Horizontal	18	<i>atpB-rbcL</i> spacer, ITS	<i>Bassia hyssopifolia</i>
5 straight spines	Horizontal	?	<i>atpB-rbcL</i> spacer, ITS	<i>Bassia muricata</i>
5 flattened spines	Horizontal	18	<i>rbcl</i> , <i>ndhF</i> , <i>atpB-rbcL</i> spacer, ITS	<i>Sedobassia sedoides</i>
Absent	Vertical	12	<i>atpB-rbcL</i> spacer, ITS	<i>Camphorosma annua</i>
Absent	Vertical	12	ITS	? <i>Camphorosma lessingii</i>
Absent	Vertical	12, 60	<i>rbcl</i> , <i>ndhF</i> , <i>atpB-rbcL</i> spacer, ITS	<i>Camphorosma monspeliaca</i>
Absent	Vertical	12	<i>atpB-rbcL</i> spacer, ITS	<i>Camphorosma songorica</i>
5 short thick triangular wings	Horizontal	?	<i>atpB-rbcL</i> spacer, ITS	<i>Chenolea diffusa</i>
Absent	Horizontal	?	<i>atpB-rbcL</i> spacer, ITS	<i>Bassia arabica</i>
Absent	Horizontal	?	ITS	<i>Bassia dinteri</i>
Absent	Horizontal	?	<i>rbcl</i> , <i>ndhF</i> , <i>atpB-rbcL</i> spacer, ITS	<i>Bassia tomentosa</i>
Absent	Vertical	18	<i>atpB-rbcL</i> spacer, ITS	<i>Bassia lasiantha</i>
5 short wing-like tubercles	Horizontal	18	<i>atpB-rbcL</i> spacer, ITS	<i>Bassia scoparia</i>
5 small wings	Horizontal	18	<i>atpB-rbcL</i> spacer, ITS	<i>Bassia angustifolia</i>
5 tubercles or short wings	Horizontal	?	<i>rbcl</i> , <i>atpB-rbcL</i> spacer, ITS	<i>Bassia scoparia</i> s.l.
5 wings	Horizontal	?	<i>atpB-rbcL</i> spacer, ITS	<i>Bassia odontoptera</i>
5 short wings	Horizontal	?	<i>atpB-rbcL</i> spacer, ITS	<i>Bassia indica</i>
5 wings	Horizontal	18	<i>atpB-rbcL</i> spacer,	<i>Grubovia krylovii</i>
5 narrow wings	Horizontal	18	<i>atpB-rbcL</i> spacer, ITS	<i>Bassia laniflora</i>
5 short wings	Horizontal	?	Not represented	<i>Bassia littorea</i>
3(5) wings	Horizontal	18	<i>atpB-rbcL</i> spacer, ITS	<i>Grubovia melanoptera</i>
5 narrow wings	Horizontal	18	<i>atpB-rbcL</i> spacer, ITS	? <i>Bassia odontoptera</i>
5 wings	Horizontal	18, 36, 54	<i>rbcl</i> , <i>atpB-rbcL</i> spacer, ITS	<i>Bassia prostrata</i>
5 wings	Horizontal	?	ITS	<i>Bassia salsoloides</i>
5 wings	Horizontal	?	<i>rbcl</i> , <i>ndhF</i> , <i>atpB-rbcL</i> spacer, ITS	<i>Eobassia saxicola</i>
5 tubercles or short wings	Horizontal	18	<i>atpB-rbcL</i> spacer, ITS	<i>Bassia scoparia</i>
5 wings	Horizontal	18	<i>atpB-rbcL</i> spacer, ITS	<i>Bassia stellaris</i>
5 wings	Horizontal	?	<i>atpB-rbcL</i> spacer, ITS	<i>Bassia tianschanica</i>
5 wings	Horizontal	?	<i>atpB-rbcL</i> spacer, ITS	<i>Bassia villosissima</i>
Absent	Vert.–hor.	18	ITS	(?) <i>Bassia eriophora</i>
5 wings	Horizontal	18,36	<i>rbcl</i> , <i>ndhF</i> , ITS	<i>Neokochia americana</i>
5 wings	Horizontal	18	<i>atpB-rbcL</i> spacer, ITS	<i>Neokochia californica</i>
5 small wings	Vertical	18	<i>rbcl</i> , <i>ndhF</i> , <i>atpB-rbcL</i> spacer, ITS	<i>Bassia pilosa</i>
5 small wings	Vertical	18	Not represented	? <i>Bassia pilosa</i>

by formation of wings, spines or long hairs. Fleshy or woody fruiting perianths are known from Australian Camphorosmeae only. The flattened fruit itself has a horizontal, vertical or oblique position. The thin testa contains a large embryo which either is annular, horseshoe-shaped, hook-like or folded. In some species a rudimentary central perisperm is present.

**Distribution and ecology of Camphorosmeae.** — With ca. 14 genera and approximately 147 spp., Camphorosmeae are centered in Australia (Fig. 2) where they are an important element of the Eremaean floristic zone (Burbidge, 1960; Crisp & al., 1999; Kadereit & al., 2005; Cabrera, 2007). Molecular clock estimates in the latter two papers indicate that Camphorosmeae entered Australia during the Late Miocene or Early Pliocene, probably originating from Central Asian ancestors, and quickly expanded into arid and semi-arid regions of the continent. Outside Australia, Camphorosmeae are less species-rich with about 35–40 spp. (Scott, 1978; Kühn & al., 1993) distributed from southwestern Europe and northwestern Africa through the Mediterranean area and North Africa to East Asia (Table 2; Fig. 2) with extensions into adjoining areas along saline coastal habitats. Most species are xerophytes or halophytes in open plant communities of dry steppes, semi-deserts or in drier types of saltmarshes, preferably on soils with slightly or distinctly increased contents of soluble salts, in particular of sodium chloride, soda, or gypsum (Iljin, 1936; Grubov 2000; Zhu & al., 2003; pers. obs.). Only three species are found in South Africa, with two in semi-deserts and one in coastal habitats. Two species are native to southwestern North America, again on alkaline soils and in semi-deserts (Chu & Sanderson, 2008) (Fig. 2).

The Eurasian annuals *Kochia scoparia*, *Bassia hyssopifolia* and most likely also *B. hirsuta* were introduced to other continents. The first two species spread in ruderal sites, in particular in semi-arid regions of North America and Mexico (Mosyakin, 2003), South America (Soriano, 1948) and Australia (Wilson, 1984), and the last species invaded natural sea-shore ecosystems in the northeastern U.S.A. (Mosyakin, 2003). More recently, the subshrubby Australian *Maireana brevifolia* was collected in South Africa, Israel and the Canary Islands (H. Freitag, pers. obs.).

**C<sub>4</sub>-photosynthesis in Camphorosmeae.** — Since Volkens (1887), certain anatomical structures have been reported from several species of Camphorosmeae which much later, after the discovery of the C<sub>4</sub>-pathway (Hatch & Slack, 1966; Hatch, 1971), were understood as being associated with C<sub>4</sub>-photosynthesis and defined as the “kochioid” leaf type by Carolin & al. (1975) in contrast to the “austrobassoid” leaf type which is most common in Australian C<sub>3</sub>-taxa. In other Camphorosmeae the same authors also described the “atriplicoid” (in *Kirilowia*) and “salsoloid” (in *Camphorosma*) leaf type, and because of the deviating leaf anatomy they doubted the correct taxonomic placement of these taxa. In Kadereit & al. (2003) three C<sub>4</sub>-leaf types were accepted for Camphorosmeae, viz., the *Kochia prostrata*, the *Kochia laniflora*, and the *Kirilowia* type, but no further studies were carried out in the C<sub>3</sub>-species.

Kadereit & al. (2003) postulated that either two shifts from C<sub>3</sub>- to C<sub>4</sub>-photosynthesis or only one shift to C<sub>4</sub> and

one subsequent loss occurred in Camphorosmeae. They also found three different C<sub>4</sub>-leaf types within one C<sub>4</sub>-lineage and speculated that these might represent either different origins or different evolutionary stages of C<sub>4</sub>-anatomy within Camphorosmeae. The origin of C<sub>4</sub>-photosynthesis in Camphorosmeae was dated to the Early to Middle Miocene (21.6–14.5 Ma; Kadereit & al., 2003). This would mean that C<sub>4</sub>-Camphorosmeae represent a relatively old C<sub>4</sub>-lineage in Chenopodiaceae.

**Aims of this study.** — Molecular phylogenies using the chloroplast genes *ndhF* and *rbcL* with a broad outgroup sample, extended datasets for Salsoloideae and a detailed morphological survey are used to understand the phylogenetic relationships of Salsoleae s.str., Caroxyloneae and Camphorosmeae. We extend the ITS dataset of Kadereit & al. (2005) and generate an *atpB-rbcL* spacer dataset to investigate the phylogeny, biogeography and diversification of Camphorosmeae. The molecular phylogenies are used to estimate divergence times within Salsoloideae and Camphorosmeae to date the origin of major lineages, the age of the major biogeographical splits and the evolution of C<sub>4</sub>-photosynthesis. Based on the molecular phylogenies and a morphological survey of the Eurasian, North American and southern African genera of Camphorosmeae, a new classification of the non-Australian species is proposed.

## ■ MATERIALS AND METHODS

As the recent changes in the circumscription of genera were not or only partly adopted in the flora accounts of the regions where Camphorosmeae are important (e.g., the former U.S.S.R.: Czerepanov, 1995; China: Zhu & al., 2003; Middle East: Hedge & al., 1997) we use the traditional names *Kochia*, *Kirilowia*, *Londesia*, *Chenolea* and *Chenoleoides* in the main part of this paper, for convenience (see Table 2).

**Taxon sampling and outgroup choice.** — All recognized Old World species of Camphorosmeae (except *Bassia aegyptiaca*, *Kochia littorea* and *Pandertia turkestanica*) were sampled including several taxonomically critical taxa (see Table 2 and the Appendix with voucher and GenBank information for all five markers and their accessions).

- *rbcL* dataset: 129 sequences of the Amaranthaceae/Chenopodiaceae alliance, incl. 35 Salsoloideae representing 25 genera, 14 of which belong to Camphorosmeae (Table 2; Appendix). Sequences were mostly taken from Kadereit & al. (2003), 21 were newly generated for this study.

- *ndhF* dataset: 72 sequences of the Amaranthaceae/Chenopodiaceae alliance, incl. 42 Salsoloideae, representing 22 genera, 10 of which belong to Camphorosmeae. The sequences were partly taken from Hohmann & al. (2006), 45 were newly generated (see Appendix). For the *rbcL* and *ndhF* datasets two representatives of Achatocarpaceae were chosen as outgroup. The designation of outgroup followed the congruent results of family-wide phylogenetic studies on the Amaranthaceae/Chenopodiaceae alliance (Kadereit & al., 2003; Pratt, 2003; Müller & Borsch, 2005).

- The *atpB-rbcL* spacer dataset comprises thirty-five representatives of Camphorosmeae, eight of Salsoleae s.l., three of



Suaedoideae and six of Salicornioideae (a total of 52 sequences; Appendix). Seven outgroup sequences were taken from Kadereit & al. (2006) and Schütze & al. (2003), 45 were newly generated. Only four representatives of Australian Camphorosmeae were included to represent the Australian lineage of the tribe. The representatives of Salicornioideae (viz., *Kalidium foliatum*, *Allenrolfea occidentalis*, *Haloplepis perfoliata*, *Microcnemum coralloides*, *Tecticornia australasica*, and *Salicornia europaea*) and the representatives of Suaedoideae (viz., *Suaeda maritima*, *S. linifolia*, *Bienertia cycloptera*) were chosen as outgroups following the findings of previous molecular analyses (Kadereit & al., 2003; Schütze & al., 2003; Hohmann & al., 2006; Kapralov & al., 2006).

- *psbB-psbH* spacer: we generated 11 new *psbB-psbH* sequences and added 102 published by Akhiani & al. (2007). One representative each of Salicornioideae and Suaedoideae were chosen as outgroup.

- Combined cp data: we analysed 48 species representing 27 genera of Salsoloideae, incl. 18 samples of Camphorosmeae, and 4 representatives of Suaedoideae and Salicornioideae as outgroup. Only samples of which at least two of the four cp markers had been sequenced were included in this analysis.

- The ITS (internal transcribed spacer/5.8S region of nrDNA) dataset comprises 39 species of Camphorosmeae representing 12 currently recognized genera of Camphorosmeae. Sequences were partly taken from Kadereit & al. (2005); 17 were newly generated for this study. Due to the unclear sister-group relationship of Camphorosmeae (see individual results of the *rbcL*, *ndhF* and *atpB-rbcL* spacer analyses) an ingroup rooting approach with the *Chenolea* clade (*Bassia hirsuta*, *Neokochia californica*, *N. americana*, *K. saxicola*, *Chenolea diffusa*) as monophyletic outgroup was taken according to the combined cp analysis (Fig. 3) and an earlier ITS analysis in Kadereit & al. (2005).

**Plant material and DNA isolation.** — Total DNA was in most cases isolated from herbarium or silica gel-dried material using 20–50 mg leaf material. In a few cases DNA was extracted from fresh leaves or leaves preserved in saturated NaCl-CTAB solution supplemented with 200 mM sodium ascorbate (Thomson, 2002) using 50–100 mg. For DNA extraction the NucleoSpin plant DNA extraction kit (Macherey-Nagel) or DNeasy Plant Mini Kit (Qiagen) was used following the manufacturer's specifications.

**DNA amplification, sequencing and alignment.** — For amplification and sequencing protocols see Kadereit & al. (2003; *rbcL*), Hohmann & al. (2006; *ndhF*), Kadereit & al. (2005, 2006; ITS and *atpB-rbcL* spacer) and Schütze & al. (2003; *psbB-psbH* spacer). All obtained chromatograms were edited in Sequencher™ v.4.1.2 (GeneCodes Corp., Ann Arbor, Michigan, U.S.A.). Partial sequences of *ndhF* and *rbcL* were assembled to a consensus sequence for each taxon. The alignment for all markers was done in Sequencher. For *ndhF* and *rbcL* the alignment was straightforward and contained no ambiguous positions. The alignment of the *atpB-rbcL* spacer, ITS and *psbB-psbH* spacer needed manual correction due to a number of indels and relatively high variability in some parts. Ambiguously aligned nucleotide positions and mononucleotide

microsatellites in the *atpB-rbcL* and *psbB-psbH* spacers were excluded from the analyses.

**Phylogeny inference and divergence time estimation.**

— The aligned sequence data were analyzed for phylogenetic inference using the maximum likelihood (ML) algorithm implemented in PAUP\* v.4.10b (Swofford, 2002) for Apple computers. The appropriate nucleotide sequence evolution model was derived using the software program Modeltest (Posada & Crandall, 1998). The settings for the ML analyses are indicated in the legends of the respective trees.

Heuristic search settings were set to random addition of taxa and tree-bisection-reconnection (TBR) branch swapping for all datasets. To assess the reliability of clades of the ML trees, a ML bootstrap with random addition of taxa, TBR branch swapping and 100 replicates was conducted for the *atpB-rbcL* spacer, ITS and combined datasets. For the *rbcL*, *ndhF* and *psbB-psbH* spacer datasets a parsimony bootstrap with the following settings was performed: 100 replicates with heuristic search strategy, 10 random taxon-addition sequences each, maxtree option set to 10.000 (only *rbcL*), no maxtree limit for *ndhF* and *psbB-psbH* spacer.

The *rbcL*, *ndhF* and *atpB-rbcL* spacer datasets were used for divergence time estimation. Following the ML heuristic searches, a likelihood ratio test implemented in Modeltest (Posada & Crandall, 1998) was used to test for departure from clock-like evolution of the sequence data. In all cases, rate constancy among lineages was rejected. Therefore, a method that relaxes the null hypothesis of a uniform clock-like rate of molecular evolution, allowing different parts of a tree to have different rates, was implemented (see below).

For the calibration of the molecular clock the crown group age of the Amaranthaceae/Chenopodiaceae alliance was set to 65.0–56.5 Ma in the *rbcL* and *ndhF* analyses (Figs. S1, S3) based on pollen fossils (Srivastava, 1969; Nichols & Traverse, 1971; compare Kadereit & al., 2003: table 3). Furthermore, the fossil *Salicornites massalongoi* from Oligocene deposits (Principi, 1926) was used to fix the crown group age of Salicornioideae to 35.4–23.3 Ma. The *atpB-rbcL* spacer tree was calibrated using basal node estimates gained from the *rbcL* and *ndhF* analyses and the fossil *Salicornites massalongoi* to fix the crown group age of Salicornioideae (compare Fig. 5).

Two different approaches were used to determine divergence time estimations:

1. The program r8s (Sanderson, 2003) implements a semi-parametric smoothing method (penalized likelihood, PL; Sanderson, 2002). The optimal level of rate smoothing from the branch length data was estimated using the cross-validation procedure implemented in the software before estimating the ages. The smoothing factor was set to 1.0 for *rbcL*,  $3 \times 10^9$  for *ndhF* and 4.0 for the *atpB-rbcL* spacer. The calibrated nodes were fixed once with the minimum age of the fossils and once with the maximum age of the fossils. The single candidate tree with branch lengths in all analyses was the ML tree that resulted from the heuristic search described above.

2. The three datasets were additionally analysed using BEAST (Bayesian Evolutionary Analysis by Sampling Trees v.1.4.8; Drummond & 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 v.1.4.8 (BEAUti; implemented in BEAST, Drummond & Rambaut 2007). For the *ndhF* and *rbcL* analyses representatives of Amaranthaceae and Chenopodiaceae were defined as monophyletic in order to set the root at the split between Amaranthaceae/Chenopodiaceae and Achatocarpaceae. Furthermore, representatives of Salicornioideae were defined as monophyletic in order to be able to calibrate the crown group age of this subfamily. The substitution model parameters were set to GTR+G+I. The relaxed Bayesian clock was implemented with rates for each branch drawn independently from a lognormal distribution (Drummond & al., 2006). A birth and death prior was set for branch lengths. The root age was set to 65 Ma with a log normal prior distribution and the crown group age of Salicornioideae was fixed using the uniform prior distribution with the upper bound set to 35.4 and the lower bound set to 23.3 Ma. These calibrations were done according to the reliable fossils available (see above and Kadereit & al., 2003). Other priors were in default settings and the Monte Carlo Markov chain (MCMC; Drummond & 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 iterations, a burn-in of 10% and a sample frequency of 1000. After assessing convergence in Tracer v.1.4.1 (Rambaut & Drummond 2007) as described in the BEAST manual (Drummond & al., 2007), the maximum clade credibility tree was summarized in TreeAnnotator v.1.4.8 (Drummond & Rambaut, 2007) with a posterior probability (post. prob.) limit of 0.5 and summarizing mean node heights. The summary trees were edited in FigTree v.1.2.2 (Rambaut, 2006).

**Morphological studies.** — The morphological data found in the relevant taxonomic literature (Moquin-Tandon, 1840, 1849; Ulbrich, 1934; Iljin, 1936; Scott 1978; numerous extended flora accounts), were checked for all non-Australian species by standard methods in the laboratory and for most species complemented by own (HF) observations on habit and ecology in the field. In addition to the vouchers used in the molecular analyses, varying numbers of additional specimens have been studied depending on necessity or availability. However, the frame of the study did not allow the full study of critical groups, such as *Kochia scoparia* s.l. and *K. prostrata* s.l., in detail to solve their inherent taxonomic problems.

## ■ RESULTS

### Phylogeny inference and divergence time estimation. —

The *rbcL* matrix comprised 1343 characters and 131 taxa. The dataset contained 314 variable sites (23.4%) of which 133 (9.9%) occurred only in one sample. Within the 35 sampled Salsoloideae s.l., there were 204 (15.2%) variable sites, 120 (8.9%) of which occurred in one sample only. The trees resulting from the analysis with BEAST (Fig. S1) and the ML analysis (Fig. S2) are shown as online supplementary material. Both analyses

showed a nearly congruent topology. The main difference is that the *Salsola kali* clade, the *Salsola genistoides* clade, the *Nanophyton* clade and the Caroxyloneae form a basal grade in the ML analysis and a monophyletic group (with low support) in the BEAST analysis (Figs. S1, S2).

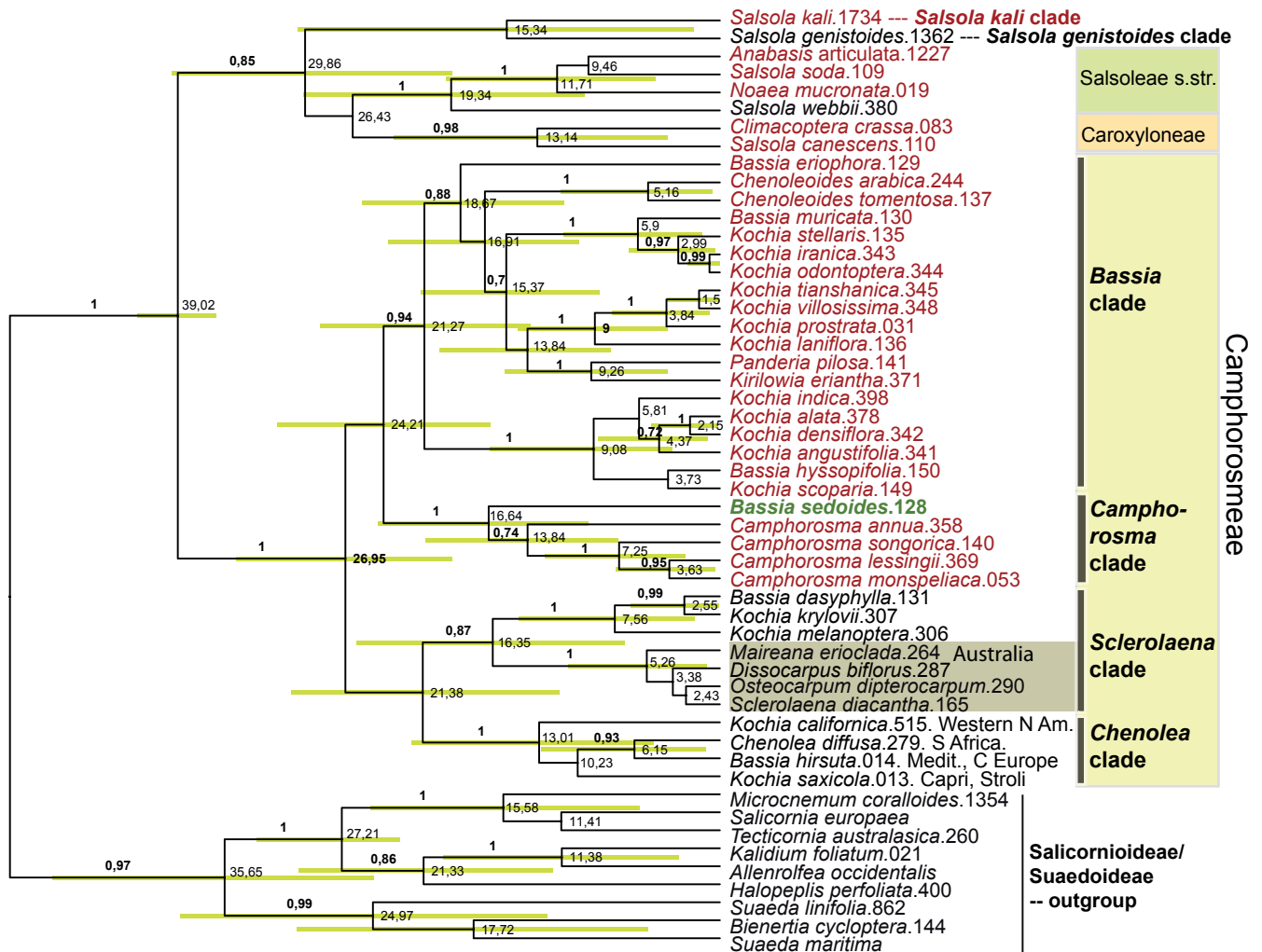
The *ndhF* matrix comprised 1899 characters and 74 taxa. The dataset contained 821 variable sites (43.2%) of which 294 (15.5%) occurred only in one sample. Within the 42 sampled Salsoloideae s.l., there were 510 (26.9%) variable sites, 225 (8.9%) of which occurred in one sample only. The complete trees resulting from the BEAST analysis (Fig. S3) and the ML analysis (Fig. S4) are presented as supplementary material. Both analyses showed a nearly congruent topology. The main difference is that in the BEAST analysis Caroxyloneae, the *Salsola kali* clade and *Nanophyton* form a monophyletic group while their relationship is not resolved in the ML tree (Figs. S3, S4).

The *atpB-rbcL* spacer matrix comprised 718 characters and 52 taxa. The dataset contained 251 variable sites (35%) of which 127 (17.7%) occurred only in one sample. Within the 43 sampled Salsoloideae s.l., there were 179 (24.9%) variable sites, 87 (12.2%) of which occurred in one sample only. Within the 35 sampled Camphorosmeae, there were 119 (16.6%) variable sites, 55 (7.7%) occurred only in one taxon. The ML tree and the tree resulting from the Bayesian analysis with BEAST showed identical topologies within Camphorosmeae. The poorly supported relationships of the major salsoloidean clades were slightly different. In the BEAST tree Salsoleae s.l. were monophyletic (with low support) while in the ML tree the monophyly of Salsoleae s.l. collapsed into a polytomy (Fig. 3, tree of the analysis with BEAST; Fig. S5, ML tree).

The aligned *psbB-psbH* spacer matrix included 98 Salsoleae s.l., 15 Camphorosmeae and one member each of Salicornioideae (*Microcnemum coralloides*) and Suaedoideae (*Suaeda maritima*) as outgroup. The 650 aligned base positions contained 127 parsimony-informative sites, 429 positions were constant and 94 positions showed character changes only in one sample. The resulting ML tree showed low overall resolution and contained only a few well-supported clades. The tree is shown in the online supplement (Fig. S6).

The aligned combined cp dataset comprised 48 taxa (26 Salsoleae s.l., 18 Camphorosmeae, 2 Suaedoideae [outgroup] and 2 Salicornioideae [outgroup]) and 4610 characters. The dataset contained 560 parsimony-informative sites, 3504 positions were constant and 546 positions showed character changes only in one sample. The resulting ML tree showed good overall resolution and high support in many parts of the tree (Fig. 4).

The ITS dataset includes sequences of 43 taxa of Camphorosmeae from 39 species, five of which are representative members of the large monophyletic Australian lineage (see under Plant material). The following two taxa had a number of missing sites at the 5' end due to sequencing problems: *Camphorosma monspeliaca* (Turkey accession, 235 bp) and *Kochia alata* (New Mexican accession, 84 bp). The following informative deletions and insertions were detected in the data matrix and additionally indicated on the ML tree (Fig. 5): *Chenolea* clade 3 bp insertion, *Sclerolaena* clade 2 bp deletion,



**Fig. 3.** Molecular phylogeny of Camphorosmeae derived from *atpB-rbcL* spacer sequences and a BEAST analysis. Posterior probabilities higher than 0.7 are indicated above branches (bold numbers), estimates of node ages are given behind the respective node. Red species represent C<sub>4</sub>-species, black C<sub>3</sub>-species and bold green C<sub>3</sub>/C<sub>4</sub> intermediate species. Corresponding bars represent 95% confidence intervals. The tree was calibrated using basal node estimates gained from the *rbcL* (Fig. S1) and *ndhF* (Fig. S3) analyses, and fossil *Salicornites massalongoi* to determine the crown group age of Salicornioideae.

*Sclerolaena* clade plus *Chenolea* clade 1 bp deletion (not shown in Fig. 5), *Neokochia californica* and *N. americana* 2 bp insertion, *Chenolea diffusa* and *Bassia hirsuta* 1 bp insertion, all *Camphorosma* species two 1 bp insertions, all *Camphorosma* species except *C. annua* 5 bp insertion, and *Kochia villosissima* and *K. tianshanica* 1 bp insertion. The aligned ITS matrix of 43 Camphorosmeae comprised 683 base positions. Of these 228 (33.4%) were polymorphic and 88 (12.9%) polymorphisms occurred only in one sample. The three rooting alternatives did not affect the topology within the ingroup.

The results of the molecular clock analyses of three different markers using two different dating approaches are shown in Table 3; Fig. 4; Figs. S1–S5. The two dating methods resulted in roughly similar age estimates. Among the three markers the estimates with the *rbcL* gene and the *atpB-rbcL* spacer showed mostly congruent results while the dating with the *ndhF* gene resulted in considerably older estimates.

**Morphological and taxonomical results.** — Morphological and taxonomical results are incorporated in the discussion. The new taxon names proposed in this study are shown in Fig. 5 and Table 2.

## DISCUSSION

**Major clades of Salsoloideae s.l. and the relationships of Camphorosmeae: molecular evidence.** — The individual and combined analyses of four cp markers (*rbcL*, *ndhF*, *atpB-rbcL* spacer, *psbB-psbH* spacer) revealed six major clades in Salsoloideae s.l.: Camphorosmeae, Salsoleae s.str., Caroxyloneae, *Salsola kali* clade, *Nanophyton* clade and *S. genistoides* clade (Figs. 3, 4; Figs. S1–S6). While Camphorosmeae, Salsoleae s.str., Caroxyloneae, the *Salsola kali* clade and the *Nanophyton* clade are recovered in all analyses, *Salsola genistoides* is

Camphorosmeae

Sclerolaena clade

Chenolea clade

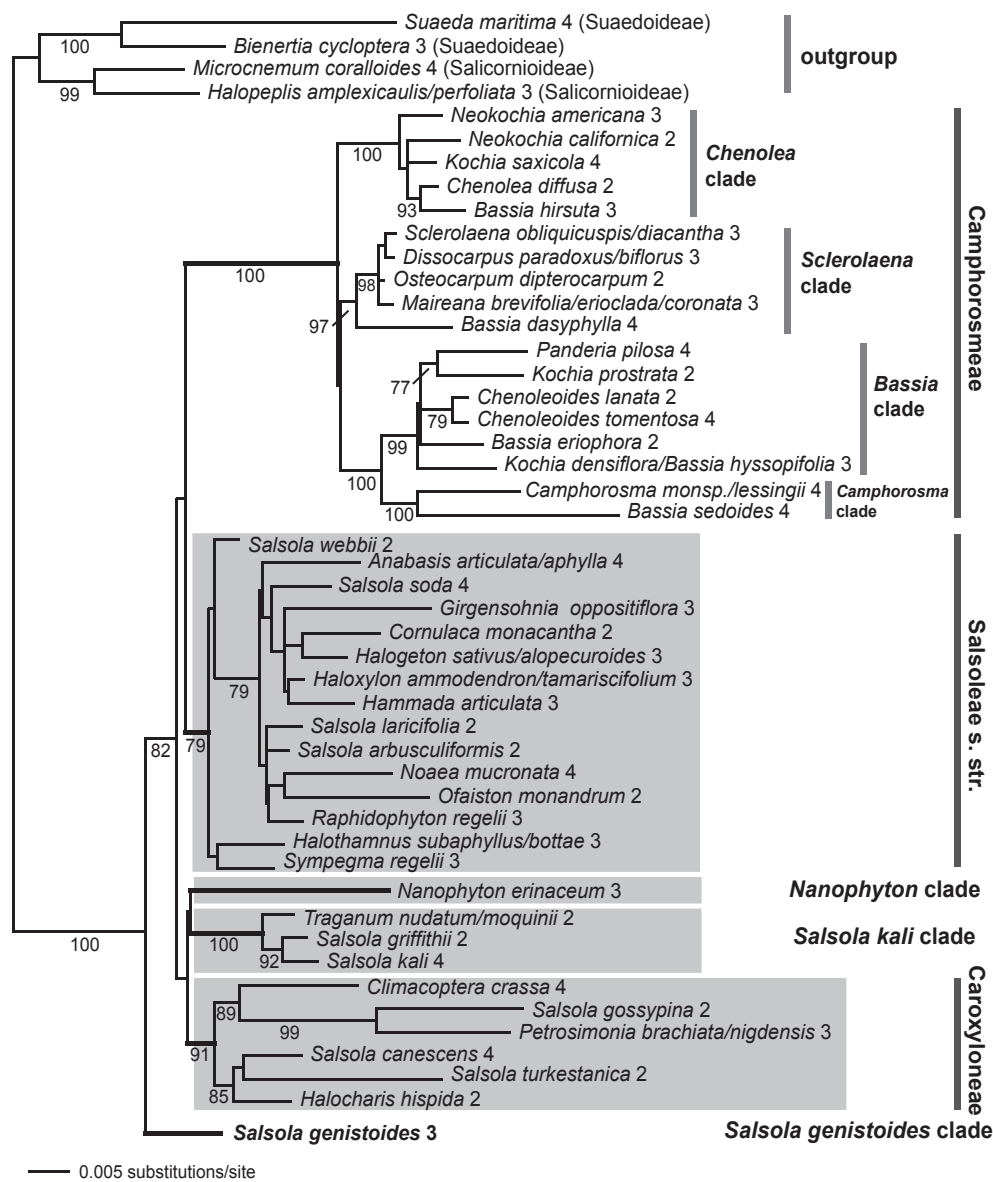
Salicornioideae/  
Suaedoideae  
-- outgroup

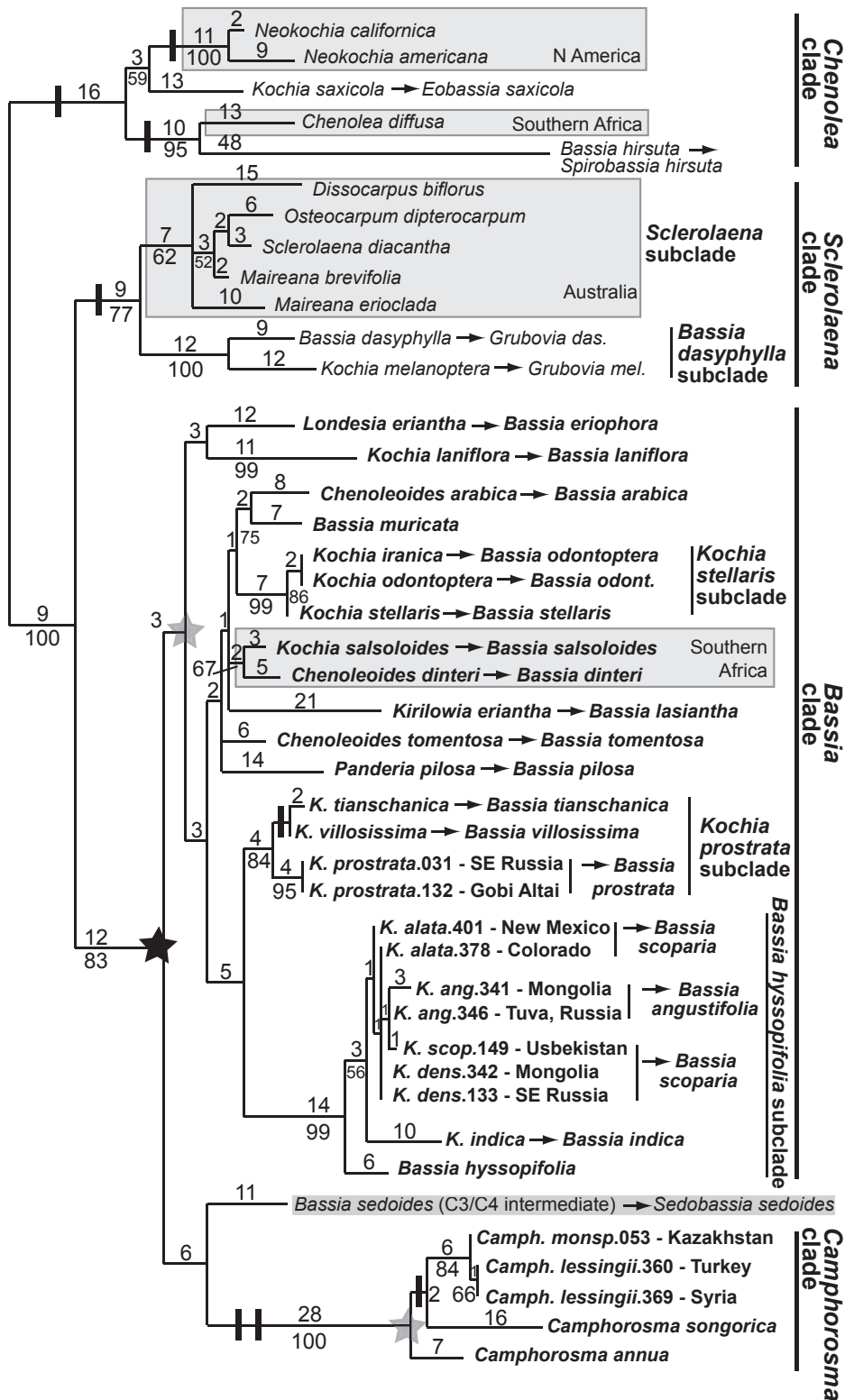
clearly nested in Salsoleae s.str. in the *ndhF* tree (Figs. S3, S4). Camphorosmeae are resolved in two different sister-group relationships: (1) sister to Salsoleae s.str. in the combined cpDNA analysis and *rbcL* tree (Fig. 4; Figs. S1, S2) and (2) sister to all other Salsoloideae in the *ndhF* and *atpB-rbcL* spacer datasets (Fig. 3; Figs. S3, S4). Bootstrap support for these basal relationships is weak or absent even in the combined analysis although most markers show sufficient overall variability. Therefore, our molecular results point to an early radiation in Salsoloideae s.l. giving rise to six major lineages (bold branches in Fig. 4).

There is some conflict between the six lineages found in our analyses based on cpDNA sequence data and the three tribes and their well-supported relationships found in a study by Akhani & al. (2007) which was based on a combined dataset of ITS and *psbB-psbH* spacer sequences. According to their combined tree, Camphorosmeae (represented by ten species from seven genera) are sister to a clade comprising

two well-supported lineages, which were named Salsoleae s.str. and Caroxyloneae. Furthermore, *Nanophyton* was nested within Caroxyloneae, being sister to *Halocharis*, the *Salsola kali* clade was nested within the Salsoleae s.str. and *Salsola genistoides* was not included. A sister-group relationship of Camphorosmeae and the rest of Salsoloideae (Salsoleae s.l.) was also found in our *ndhF* and *atpB-rbcL* spacer analyses, albeit with low or no support. However, in our cpDNA analyses the *Salsola kali* clade never groups with or within the Salsoleae s.str. as in the ITS analysis of Akhani & al. (2007). By comparing the individual trees (ITS tree and *psbB-psbH* tree) of Akhani & al. (2007) it became clear that their combined tree is almost identical with the ITS tree. Apparently, the latter suppresses the weak phylogenetic signal of the *psbB-psbH* spacer tree which deviates in a considerable number of clades and single accessions. The *Salsola kali* clade is, similarly to our findings, part of a basal polytomy including

**Fig. 4.** Maximum likelihood tree of Salsoloideae s.l. resulting from the combined analysis of four cp markers (*rbcL* and *ndhF* genes, *atpB-rbcL* spacer and *psbB-psbH* spacer sequences). ML analysis settings: GTR+G model; alpha shape parameter: 0.21; nucleotide frequencies: A = 0.3, C = 0.17, G = 0.18, T = 0.35; substitution rate matrix: AC = 1.17, AG = 1.89, AT = 0.21, CG = 0.87, CT = 2.33, GT = 1.0. ML bootstrap values >50 are shown below branches. Numbers after species (2, 3, 4) indicate how many of the four cp markers were sequenced. Thick branches indicate the six major clades of Salsoloideae s.l. Note that *Salsola genistoides* (bold) groups within Salsoleae s.str. in the *ndhF* tree (Figs. S3, S4).





**Fig. 5.** Maximum likelihood tree of Camphorosmeae derived from internal transcribed spacer (ITS) sequences. Settings: GTR+G+I model; alpha shape parameter: 0.742; nucleotide frequencies: A = 0.25, C = 0.25, G = 0.25, and T = 0.25; substitution rate matrix: AC = 1.05, AG = 2.94, AT = 2.01, CG = 0.49, CT = 5.5, GT = 1.0. ML bootstrap values >50 are shown below branches, number of character changes above branches. C<sub>4</sub>-species are in bold; black bars indicate indels that support this branch. Stars mark the two possible scenarios for the origin of C<sub>4</sub>-photosynthesis in Camphorosmeae; black star: one origin 24–14 Ma and one loss in *Bassia sedoides*; grey stars: two origins 21–8 Ma in the *Bassia* clade and 14–10 Ma in *Camphorosma*. Names following the arrows are new names proposed in this study. Thick branches indicate the six major clades of Salsoloideae s.l. Note that *Salsola genistoides* (bold) groups within Salsoleae s.str. in the *ndhF* tree (Figs. S3, S4).

**Table 3.** Results of the divergence time estimates in Ma (r8s-PL = semi-parametric rate smoothing method with penalized likelihood, BEAST = simultaneous estimation of tree topology and divergence times using Bayesian Evolutionary Analysis by Sampling Trees (BEAST v.1.4.8), description of the dating methods see chapter on divergence time estimation in Material and Methods; numbers given in brackets represent 95% confidence intervals; bold numbers indicate the minimum age of  $C_r$ -photosynthesis in Camphorosmeae)

Node	<i>rbcl</i> gene		<i>ndhF</i> gene		<i>atpB-rbcL</i> spacer		Geological epoch
	r8s-PL	BEAST	r8s-PL	BEAST	r8s-PL	BEAST	
Split between Suaedoideae/Salicornioideae and Salsoloideae	51.5–48.0	46.8 (55.1–38.8)	55.5–51.0	55.5 (64.1–46.1)	–	–	Middle Eocene
Crown group age Salsoloideae	40.5–37.2	36.1 (44.3–27.7)	43.6–39.4	41.6 (51.1–31.1)	–	–	Late Eocene
Stem age of Camphorosmeae	32.2–29.7	32.2 (40.4–23.5)	43.6–39.4	41.6 (51.1–31.1)	–	–	Late Eocene/Early Oligocene
Stem age of Salsoleae s.str.	32.2–29.7	32.2 (40.4–23.5)	37.5–30.4	36.8 (46.3–27.6)	–	–	Early Oligocene
Stem age of Caroxyloneae	40.5–37.2	30.7 (39.7–21.6)	33.1–30.4	31.5 (42.5–23.7)	–	–	Late Eocene/Early Oligocene
Stem age of <i>Salsola kali</i> clade	36.5–33.5	18.6 (32.1–5.3)	33.1–30.4	31.5 (42.5–23.7)	–	–	Oligocene–Middle Miocene
Stem age of <i>Nanophyton</i> clade	40.5–37.2	25.2 (32.6–21.6)	33.1–30.4	32.9 (42.5–23.7)	–	–	Late Eocene/Oligocene
Crown group age of Camphorosmeae	20.3–18.6	22.7 (30.2–16.2)	26.2–23.9	26.8 (35.8–18.0)	20.9–17.3	26.95 (34.8–19.3)	Early Miocene
Stem age of <i>Chenolea</i> clade	20.3–18.6	17.7 (25.1–10.7)	23.5–17.7	22.6 (32.2–13.6)	20.9–17.3	21.38 (30.8–11.5)	Early Miocene
Stem age of <i>Sclerolaena</i> clade	20.3–18.6	17.7 (25.1–10.7)	23.5–17.7	22.6 (32.2–13.6)	20.9–17.3	21.38 (30.8–11.5)	Early Miocene
Stem age of Australian Camphorosmeae	15.4–14.1	10.3 (17.3–4.5)	16.3–12.1	15.3 (24.0–6.5)	16.2–13.3	16.35 (28.2–8.9)	Middle Miocene
Crown group age of Australian Camphorosmeae	11.5–9.2	6.3 (11.0–2.1)	4.8–2.6	3.9 (8.1–0.8)	2.5–2.1	5.26 (10.9–0.9)	Late Miocene/Pliocene
Stem age of <i>Bassia</i> plus <i>Camphorosma</i> clade	20.3–18.6	22.7 (30.2–16.2)	26.2–23.9	26.8 (35.8–18.0)	20.9–17.3	26.95 (34.8–19.3)	Early Miocene
Stem age of <i>Camphorosma</i> clade and stem age of <i>Bassia</i> clade	15.4–14.2	19.2 (26.0–12.4)	23.2–17.1	20.1 (23.5–8.3)	20.2–16.8	24.21 (31.9–16.5)	Early–Middle Miocene
<b>Crown group age of the <i>Bassia</i> clade</b>	<b>9.0–8.3</b>	<b>12.7</b> (18.9–7.5)	<b>14.9–13.1</b>	<b>11.2</b> (19.0–4.2)	<b>19.0–15.8</b>	<b>21.27</b> (28.8–13.4)	<b>Miocene</b>
Split between <i>Bassia sedoides</i> and <i>Camphorosma</i> lineage	10.1–9.3	11.0 (18.3–4.4)	21.0–15.2	15.9 (23.5–8.3)	14.7–12.2	16.6 (24.8–9.7)	Middle Miocene
<b>Crown group age of <i>Camphorosma</i></b>	–	–	–	–	<b>11.8–9.8</b>	<b>13.8</b> (24.2–8.4)	<b>Middle Miocene</b>

Camphorosmeae and Salsoleae s.str./Caroxyloneae clade. *Nanophyton* also groups differently in the *psbB-psbH* tree where it is associated with *Salsola canescens*. Other species with distinctly different positions are, for example, *Rhaphidophyton regelii*, *Salsola soda*, *Seidlitzia florida*, *Anabasis setifera* (within the monophyletic *Anabasis* in the *psbB-psbH* tree), *Salsola vvedenskyi*, *S. chorassanica* and others. Bootstrap support especially of basal branches is mostly weak in the *psbB-psbH* spacer tree which certainly was the reason to combine this dataset with ITS.

To further investigate whether the *psbB-psbH* spacer shows results that are congruent with our markers, we generated eleven additional *psbB-psbH* sequences and re-aligned the alignment of Akhani & al. (2007) manually. Furthermore, we excluded a number of monosatellite regions and a few positions where an unambiguous alignment was not possible. The ML tree of this slightly enlarged *psbB-psbH* spacer dataset is included in the online supplementary material (Fig. S6). The major lineages found in this re-analysed dataset are a clade comprising Salsoleae s.str. and Caroxyloneae, the *Salsola kali* clade, the *Salsola genistoides* clade, and Camphorosmeae. The relationships among these clades are not resolved and bootstrap support is mostly very low, but these results do not conflict with our findings for cpDNA sequence data.

ITS is the only nuclear marker that has been applied to infer the phylogenetic relationships within Salsoloideae s.l. In their molecular study of 34 species of Salsoleae based on ITS sequences, P'yankov & al. (2001) found extremely high variation of the marker, especially in the ITS2 part. They excluded a fragment of ca. 80 base pairs from ITS2 because unambiguous alignment was not possible. The ITS alignment of Akhani & al. (2007, deposited at TreeBase), however, contained all nucleotide positions and comprised 141 sequences of Salsoloideae and 743 base pairs of which 68.8% were polymorphic. As the 232 constant characters almost exclusively belonged to the conserved 5.8S gene, this means that nearly 100% of the ITS1 and ITS2 positions were polymorphic. We suspect that ITS is too variable above tribal level in Salsoloideae to guarantee an unambiguous alignment. We calculated the number of changes and the homoplasy index of each variable character using the ITS-nexus-file of Akhani & al. (2007) deposited at TreeBase using PAUP\*. Of the variable positions, 60.5% underwent four or more character state changes, and the average number of character state changes was 6.8. This indicates that there is a high degree of base saturation in the data matrix. Accordingly, the consistency index and the retention index of the ITS dataset were extremely low, 0.303 and 0.224, respectively (Akhani & al., 2007).

In summary, the molecular analyses presented here are congruent with the analysis presented by Akhani & al. (2007) in resolving three major clades (Camphorosmeae, Caroxyloneae, Salsoleae s.str.) in Salsoloideae s.l. However, the cpDNA analysis presented here indicates that also the *Salsola kali* clade, the *Nanophyton* clade and the *Salsola genistoides* clade are early-branching major lineages. These conflicting clades probably need to be re-analysed because high variability of ITS might cause base saturation effects and ambiguous alignment.

We doubt that lack of informative characters in the cpDNA data causes this incongruence because the combined analysis confirmed the individual trees.

**Major clades of Salsoloideae s.l. and the relationships of Camphorosmeae: morphological evidence.** — Critical evaluation of morphological characters resulted in recognition of four diagnostic characters of seeds, stigmata, bracteoles and pollen that support a clear distinction between Camphorosmeae and the rest of Salsoloideae (here referred to as Salsoleae s.l.).

*Seeds.* — The seeds of Camphorosmeae contain an annular, horseshoe-shaped or folded embryo that surrounds a well to moderately developed perisperm. Salsoleae s.l. have a spirally coiled embryo and no perisperm or rudiments only. Spiral embryos associated with absence of perisperm are known from Salsoleae s.l. and Suaedoideae only.

*Stigmata.* — In Camphorosmeae the stigmata are usually filiform and always papillose on the entire surface whereas in Salsoleae s.l. they are mostly flattened and wider but bear papillae only on the inner surface. That group-specific distribution pattern of stigmatic papillae can be observed even in rare cases of flat stigmata in Camphorosmeae and of filiform stigmata in Salsoleae s.l. As in all other subfamilies of Chenopodiaceae the stigmata invariably are papillose over the entire surface, the peculiar stigma morphology of Salsoleae s.l. supports the monophyly of this lineage. The report of fully papillose stigmata in two species of *Salsola* sect. *Salsola* by Rilke (1999: 59) could not be confirmed.

*Bracteoles.* — Bracteoles are consistently lacking in Camphorosmeae but present in Salsoleae s.l. A similar distribution pattern of these character states is found in the sister subfamilies Suaedoideae (present) and Salicornioideae (absent).

*Pollen morphology.* — Although pollen morphology of Chenopodiaceae is known to be rather uniform, a comparative analysis of 81 Old World species by Dambach (1993) including 9 Camphorosmeae, 8 Caroxyloneae and 18 Salsoleae, indicated, that Camphorosmeae pollen differs significantly from Salsoleae s.l. Their pollen grains have larger diameter (>15 µm), a higher number of pores (usually >70), a smaller diameter of pores (usually <2000 nm), and a smaller number of spinulae per operculum (<15). Most of these differences were already found by Monoszon (1952).

Accordingly, there is strong morphological evidence for the separation of Salsoleae s.l. and Camphorosmeae. Therefore, we consider a sister-group relationship between Salsoleae and Camphorosmeae as found in three molecular datasets (ITS—see Akhani & al., 2007; *ndhF* and *atpB-rbcL* spacer) as most likely and suggest their re-classification into two subfamilies (see p. 71). However, previously identified synapomorphies of Camphorosmeae and Caroxyloneae, and of Camphorosmeae and Salsoleae s.str. (e.g., Kadereit & al., 2003) need to be considered. Camphorosmeae and Caroxyloneae have a similar indumentum and leaf morphology. At least in juvenile stages, leaves, stems and tepals of Camphorosmeae and Caroxyloneae are covered by an indumentum of long multicellular hairs which often are conspicuously articulate. In contrast, all other Salsoloideae are either glabrous or scabrous to hispidulous with short, thick-walled, unicellular trichomes, and they often have

tufts of curled multicellular hairs in their leaf axils. Leaves and cotyledons are more or less flattened in Camphorosmeae and Caroxyloneae but usually succulent and semiterete to terete in Salsoleae s.str. and in the *Salsola kali* clade. In *Nanophyton* leaves are needle-like and strongly sclerified. A sister-group relationship of Camphorosmeae and Caroxyloneae, however, is not supported in any of the molecular analyses.

A striking feature probably shared by Camphorosmeae, Salsoleae s.str. and the *Salsola kali* clade is the same C<sub>4</sub>-photosynthetic type, the NADP-ME subtype. Caroxyloneae have the NAD-ME subtype and *Nanophyton* is not known yet in that respect. To trace the evolution of the biochemical C<sub>4</sub>-photosynthetic type in Salsoloideae a more detailed analysis of this character is needed.

#### Origin and early diversification of Salsoloideae s.l. —

Each of the three subfamilies, Suaedoideae, Salicornioideae and Salsoloideae s.l., is distributed worldwide, predominantly in temperate and subtropical regions of the Northern Hemisphere. According to our estimates of divergence times, Salsoloideae s.l. split from Suaedoideae plus Salicornioideae already in the Early Tertiary, during the Middle Eocene (56–47 Ma; Table 3). In the predominantly warm and moist climate of the Eocene suitable habitats typical of modern Suaedoideae, Salicornioideae and Salsoloideae might have existed along the coasts and eventually also in the few and rather small semi-arid areas. Probably the common ancestors of Suaedoideae/Salicornioideae and Salsoloideae s.l. were distributed along the northern shores of the Tethys because early branching lineages of all three subfamilies still occur in this area (Schütze & al., 2003; Kadereit & al., 2006).

At the beginning of the Oligocene a global trend towards increasing aridity started. Three interacting processes were of major importance for the origin and spread of arid and intracontinental saline environments: (1) drop of temperature; (2) major tectonic events that altered the configuration of continents (e.g., retreat of the Tethys Sea) and led to greatly reduced precipitation in continental interiors; (3) increasing seasonality of climate caused by changes of oceanic currents and modifications of the atmospheric circulation (see, e.g., Frakes & al., 1992; Hallam, 1994; Mai, 1995; Willis & McElwain, 2002). Both Salsoloideae s.l. and Suaedoideae/Salicornioideae lineages were probably able to diversify in these newly forming and greatly expanding habitats. While modern Suaedoideae and Salicornioideae grow almost exclusively in saltmarshes, modern Salsoloideae s.l. are preferably adapted to steppes, semi-deserts and deserts, although some of them combine the properties of xerophytes and halophytes. We hypothesise that this strong ecological divergence of the two sister clades reflects an ancient ecological specialization which in both descendent lineages gave rise to evolutionarily successful sublineages.

The Salsoloideae s.l. started to diversify during the Late Eocene/Early Oligocene (Table 3) in semi-deserts, deserts and steppes. Most of them tolerate slightly to moderately saline conditions. It seems likely that this early radiation in Salsoleae s.l. was enhanced by the multiple evolution of C<sub>4</sub>-photosynthesis (Fig. 3; Figs. S1–S4) which might have facilitated the early spread into drier habitats. The diversification

of Camphorosmeae started during the Early Miocene which is considerably later than the diversification of the major Salsolean lineages (Table 3).

The oldest fossil evidences of Salsoloideae s.l. are *Salsola oeningensis*, *S. moquini* and *S. crenulata* (Heer, 1854: p. 75 & tab. 88, figs. 1, 1b, 2, 2b, 3, 3b). From the respective images we conclude that they probably represent slightly differing forms of the same taxon. They were found in coastal “upper molasse” sediments in the Bodensee area at the northwestern edge of the Alps which in that period started uplifting. These sediments were grouped into the Serravallian (Middle Miocene) and dated to 11.0–14.3 Ma (Montanari & al., 1997). The drawings of the well-preserved fruiting perianths with delicate overlapping wings do not allow us to assign them to Salsoleae or Camphorosmeae because the shape of the embryo in the fruit is not discernable. Accompanying fossils are, e.g., *Dodonea*, *Zizyphus*, *Ceratonia*, *Cercis* and *Ephedra* (“*Ephedrites*”). They indicate a semi-arid to semi-humid subtropical palaeoclimate similar to that of today’s southern Mediterranean area where today remnants of old lineages of Camphorosmeae (*Kochia saxicola*) and Salsoleae (*Salsola genistoides*, *S. webbii*) are found. In contrast to the fossils from the Bodensee area, we remain sceptical about the correct identification of *Salsola arctica* described by Heer (1870: 58, tab. 12, fig. 10) from Miocene sediments of Spitsbergen because the drawings are less convincing and the locality is situated in the Arctic (ca. 79° N).

**Phylogeny, biogeography and classification of Camphorosmeae: molecular evidence.** — The detailed molecular analyses of Camphorosmeae are based on two markers, the nrDNA marker ITS and the cpDNA marker *atpB-rbcL* spacer, on an almost complete sample of Eurasian, North American and southern African Camphorosmeae (Table 2), and on a small representative sample of the large group of Australian species (former *Sclerolaeneae*). The Australian representatives form a monophyletic group in all datasets (= *Sclerolaena* clade). A detailed molecular study of the Australian group using the external transcribed spacer (ETS; Cabrera, 2007; Cabrera & al., 2009) showed that all Australian Camphorosmeae form a monophyletic group that needs more variable markers to be fully resolved.

The combined cpDNA analysis (Fig. 4) and the ITS analysis (Fig. 5) congruently resolve three well to moderately supported major clades within Camphorosmeae:

1. *Chenolea* clade. The small *Chenolea* clade consists of the five widely disjunct C<sub>3</sub>-species *Bassia hirsuta*, *Kochia saxicola*, *Neokochia californica*, *N. americana* and *Chenolea diffusa*. The southern African *Chenolea diffusa* and the Eurasian *Bassia hirsuta* form a monophyletic group with high BS support of 95% only in the ITS tree (Fig. 5). The ITS tree additionally shows that the two North American species, *Neokochia americana* and *N. californica*, are sister species (BS 100%) and probably sister to the Central Mediterranean *K. saxicola*.

2. *Sclerolaena* clade. This large Australian lineage plus its small Central Asian sister clade consisting of *Kochia melanoptera*, *K. krylowii* and *Bassia dasyphylla*, contains exclusively C<sub>3</sub> species. The monophyly of the Australian clade is well supported in both datasets while the Central Asian clade



receives a much higher BS value in the *atpB-rbcL* spacer tree (Fig. 3). This result is additionally supported by the ETS tree of Cabrera & al. (2009).

3. *Bassia/Camphorosma* clade: This clade includes all Eurasian and southern African  $C_4$ -species plus the Eurasian  $C_3/C_4$ -intermediate *Bassia sedoides*. It receives moderate support in the ITS tree (Fig. 5), high support in the combined cpDNA tree (Fig. 4) but no statistical support in the *atpB-rbcL* spacer tree (Fig. 3). The *Bassia/Camphorosma* clade contains two distinct subclades, the *Camphorosma* subclade with *Camphorosma* and *Bassia sedoides*, and the *Bassia* subclade with the majority of the  $C_4$ -species (Figs. 3, 5). In the *Camphorosma* subclade, a sister-group relationship of *Camphorosma* and *Bassia sedoides* is highly supported in the *atpB-rbcL* spacer tree (Fig. 3) but receives no bootstrap support in the ITS analysis (Fig. 5). Under maximum parsimony the ITS topology changes (not shown): *Bassia sedoides* is resolved as sister to all  $C_4$ -species, and *Camphorosma* sister to the *Kochia scoparia* clade albeit without BS support. This contradicts all other topologies and might be due to a long-branch attraction artefact. However, in the strict consensus tree with 16 non-Australian taxa (Kadereit & al., 2005), *Bassia sedoides* also is sister to all other  $C_4$ -species. Within *Camphorosma*, the annuals *C. annua* and *C. songorica* form a basal grade, and the latter is sister to the perennial species.

The *Bassia* subclade contains only three statistically well-supported clades that are found in both datasets: (1) the *Kochia stellaris* subclade; (2) the *Kochia prostrata* subclade; and (3) the *Bassia hyssopifolia* subclade (Figs. 3, 5).

*Incongruencies* – The relationships of these three major clades (*Chenolea* clade, *Sclerolaena* clade and *Bassia/Camphorosma* clade) are somewhat conflicting in the different molecular analyses. In the *rbcL* analysis the *Chenolea* clade is sister to the *Bassia/Camphorosma* clade plus the *Sclerolaena* clade. ITS, *ndhF* and *atpB-rbcL* spacer data resolve the *Bassia/Camphorosma* clade as sister to the *Chenolea* clade plus *Sclerolaena* clade. Neither of these two groupings receives convincing statistical support. This lack of resolution in the backbone of Camphorosmeae, despite excellent taxon sampling and sufficient marker variability, is also evident in the combined cpDNA analysis (Fig. 4). This indicates the possibility of a “hard polytomy” at the base of the Camphorosmeae.

Other incongruencies between the *atpB-rbcL* spacer and ITS dataset are restricted to the *Bassia* subclade that shows relatively low resolution compared to the other clades (Figs. 3, 5). The *atpB-rbcL* spacer tree shows a close relationship of *Chenoleoides tomentosa* and *Ch. arabica* which is not supported by the ITS data but by morphology and anatomy (see below). Furthermore, the *atpB-rbcL* spacer tree shows a close relationship of *Pandertia pilosa* and *Kirilowia eriantha* which is neither supported by the ITS data nor by morphological or anatomical characters.

**Phylogeny, biogeography and classification of Camphorosmeae: conclusions and taxonomic consequences.** — The molecular results clearly uncover the artificial character of the current generic and subtribal classifications of Eurasian, North American and southern African Camphorosmeae. None of the

traditional camphorosmean genera, except for *Camphorosma* and, of course, the monotypic genera, are monophyletic. *Bassia* and *Kochia* are highly polyphyletic, with the former distributed among all clades, and the latter in most of them. *Chenoleoides* seems to be biphyletic but statistical support is lacking, and the monotypic genera *Londesia*, *Kirilowia* and *Pandertia* are nested within the *Bassia* subclade (Figs. 3, 5). In their recent study of the Australian genera, Cabrera & al. (2009) showed that this lineage is in need of a fundamental revision, too. However, they encountered similar problems in unraveling their phylogeny as Wilson (1975, 1984) did in classifying them by use of morphological characters. Wilson explained this phenomenon by invoking ongoing speciation in the comparatively young group associated with hybridization.

These results are not surprising because the delimitation of genera and subtribes in Camphorosmeae has long been disputed (see, Table 1, and the respective paragraph in the Introduction) caused by the growing awareness of the limited value of fruit and seed characters that traditionally were used to delimitate genera (Ulbrich, 1934; Wilson, 1975, 1984; Scott, 1978; Kühn & al., 1993). Scott (1978) already reduced the number of non-Australian genera of Camphorosmeae to five by including *Kochia*, *Londesia* and *Chenolea* into *Bassia*. Recently Chu & Sanderson (2008) raised the two North American species of *Kochia* sect. *Neokochia* to genus level which is supported by our data. However, further taxonomic changes are needed in order to keep the genera monophyletic.

We refrain from a new subtribal classification of Camphorosmeae and instead suggest three informal groups named after their main clades because morphological characters found in all representatives of a given group are poor, and species numbers are small to moderate. We decided to classify those *Kochia* and *Bassia* species that do not group in the *Bassia* subclade as new genera (*K. saxicola* → *Eokochia*; *Bassia hirsuta* → *Spirobassia*; *B. dasyphylla*, *K. krylovii* and *K. melanoptera* → *Grubovia*; *B. sedoides* → *Sedobassia*), and we included all traditional genera that group within the *Bassia* subclade into *Bassia*. This means that apart from *Kochia* p.p., *Londesia* and *Chenolea*, also *Pandertia* and *Kirilowia* are included in *Bassia*. In its new circumscription, *Bassia* is defined by the presence of three closely related  $C_4$ -leaf types, viz., the *Kochia* (*Bassia*) *prostrata*, the *K. (B.) laniflora* and the *Kirilowia* leaf types (Kadereit & al., 2003). Characters such as growth form, perianth appendages and seed position, however, can not be used to define the genus because they vary among species. The morphological details and formal taxonomic data will be given in the last chapter (revised classification).

**Biogeography and diversification of Camphorosmeae.** — Non-Australian Camphorosmeae are distributed mainly in the temperate and subtropical zones of the Northern Hemisphere where they grow in very diverse habitats ranging from coastal cliffs and saltmarshes to semi-deserts in Mediterranean-type climates and to various steppes and semi-deserts in climates with summer rain, from the fringe of the Sahara up to the alpine zone in Central Asia. Camphorosmeae probably evolved during the Late Eocene to Early Oligocene (Table 3). From the distribution of most early branching lineages in Eurasia (Fig. 5)

we conclude that the tribe originated in Eurasia and dispersed to southern Africa (2×), southwestern North America (1×) and Australia (1×). Evolutionary success of Camphorosmeae in the newly entered continents is extremely different. Although equally old or even older than the species-rich Australian lineage, the North American and southern African lineages remained (or became) species-poor (mono- or ditypic), while the Australian lineage diversified into 147 species. The phylogeny of the latter points to a rapid radiation of the Australian Camphorosmeae starting in the Late Miocene/Early Pliocene and a spread into the continent starting in the Southwest (Cabrera & al., 2010). Compared to the Australian lineage, the Eurasian C<sub>4</sub>-lineage with ca. 30 species also is relatively species-poor. This is all the more surprising as C<sub>4</sub>-photosynthesis and the annual life form only originated in this lineage which in other plant groups including the related Salsoleae s.l. apparently were key innovations to cope with unfavorable arid and semi-arid conditions.

• *Chenolea* clade: The *Chenolea* clade consists of species from western North America, southern Africa and Eurasia. In view of this geographical composition, one might suspect lab or analytical artefacts. The three genera and five species of this clade thus are strongly disjunct and several of them appear unrelated. Therefore, we repeated the sequencing and checked the sequences particularly carefully with the result that the clade was recovered in all analyses with moderate to good statistical support. These five species may be remnants of old lineages which suffered extensive extinction, possibly similar to what has been suggested for Betoideae (Kadereit & al., 2003; Hohmann & al., 2006) or the *Archiatriples* clade (Kadereit & al., 2010).

If we consider the *Chenolea* group as remnants of early lineages, their present-day ecology might represent the ancestral ecology of the whole tribe. Three out of the five species are halophytes (*Kochia saxicola*, *Chenolea diffusa*, *Bassia hirsuta*) and the two North American species are restricted to strongly alkaline habitats. Furthermore, *Kochia saxicola* and *Chenolea diffusa*, and probably also *Neokochia californica* are frost-sensitive species, and the two former are the only perennial Camphorosmeae known to grow exclusively in humid or semi-humid areas. We therefore assume that the earliest Camphorosmeae were coastal halophytes of a warm-temperate climate.

*Neokochia americana* and *N. californica*, with distinct wing-like appendages on the fruiting perianth, have long been considered as American representatives of *Kochia*. *Neokochia* differ from all perennial Eurasian species of the former *Kochia* in leaf anatomy which is characterized by a ring-like arrangement of secondary vascular bundles in combination with a typical C<sub>3</sub>-chlorenchyma (Chu & Sanderson, 2008). The closest relative of the two North American species remains unclear. It seems most likely, however, that *Neokochia* has its roots in the Mediterranean area where the other lineages except the southern African *Chenolea diffusa* are distributed. The origin of *Neokochia* (ca. 13 Ma; Fig. 3) is probably too recent for it to have reached North America via the North Atlantic land bridge (Tiffney & Manchester, 2001) as had been suggested

for the *Allenrolfea/Heterostachys* lineage within Salicornioideae (Kadereit & al., 2006). An eastern route as discussed by Hohmann & al. (2006) for *Aphanisma* (Betoideae) is unlikely because Asian relatives are lacking. We assume that this Mediterranean-western North American disjunction dates back to an early long-distance dispersal event. The two species of *Neokochia* are distinct in terms of morphology (Blackwell & al., 1978; Mosyakin, 2003; Chu & Sanderson, 2008), sequences (Figs. 3, 5) and leaf anatomy (Chu & Sanderson, 2008). Both species grow on alkaline soils in semi-deserts (Blackwell & al., 1978). A third taxon, raised by Rydberg (1906) from *K. americana* var. *vestita* S. Watson to species rank on the basis of a denser indumentum, was convincingly downgraded by Chu & Sanderson (2008) to a pubescent variant of *N. americana*.

*Kochia saxicola*, here defined as the new monotypic genus *Eokochia*, is endemic to three islands (Ischia, Capri and Stromboli) in the Tyrrhenian Sea (west coast of Italy), and is one of the rarest and most endangered plants in Italy (Pignatti, 1982). It grows on coastal rocks exposed to sea spray and strong winds. *Eokochia* has the habit of a weakly lignified subshrub with overhanging branches and has succulent leaves with C<sub>3</sub>-chlorenchyma and an unusual arrangement of vascular bundles: the two groups of compound lateral bundles are arranged in one plane with the central bundle (*Eokochia* type). The solitary flowers are born in the axil of regular leaves, and the fruiting perianth shows distinct wings.

*Chenolea diffusa* is a prominent species of intertidal estuaries, coastal rocks and foredunes around southern Africa from South Namibia to South Mozambique. The molecular data congruently show that it is most closely related to the Eurasian *Bassia hirsuta* and both split during the Middle Miocene. *Chenolea* grows as a prostrate, almost fully herbaceous perennial. The solitary flowers are located in the axils of regular leaves, and tepal appendages are absent. The flat leaves have a unique anatomy among Camphorosmeae, with numerous horizontally arranged vascular bundles located in a sharply separated aqueous tissue and a distinctly fenestrate C<sub>3</sub>-chlorenchyma (*Chenolea* type).

*Bassia hirsuta*, here classified in the new monotypic genus *Spirobassia*, is the most widespread species of the *Chenolea* clade. Its scattered distribution area ranges from the Roussillon in southern France along the northern Mediterranean coasts east to the shores of the Black Sea and the Caspian Sea, with an outlier along the southern coast of the North Sea and the western coasts of the Baltic Sea (Jalas & Suominen, 1980). From eastern Romania to South Siberia it extends into saline inland habitats in steppe environments. According to our own field experience in different parts of the area (HF) the species grows preferably in habitats enriched by decaying organic material, in particular in drift lines. *Bassia hirsuta* is the only annual species of the clade. It has leaves of the *Sclerolaena* type, three obtuse, thick, flattened outgrowths of the fruiting perianth, and unusually contorted infructescences. The name of the new genus refers to this last character. *Bassia hirsuta* exemplifies the adaptive potential of the annual life form: In the *Chenolea* clade it is the only species having invaded regions with harsh winters.

• *Sclerolaena* clade: The monophyletic, strictly perennial Australian group and three annual species from Central Asia constitute the *Sclerolaena* clade. They are possibly descendents of a formerly more diverse Eurasian lineage that was made up of perennials. As Kadereit & al. (2005) have pointed out, the ancestral lineage of Australian Camphorosmeae likely entered the continent from Central Asia. In a forthcoming biogeographical analysis, Cabrera & al. (2010) show that they started to diversify in the Southwest of the continent and spread northwards and eastwards with the onset of aridification. The estimates of divergence times congruently revealed that the onset of a rapid diversification of the Australian species during the Late Miocene/Pliocene (12–2 Ma; Table 3) started long after the split of the Australian and the Central Asian lineage during the Middle Miocene (16–10 Ma; Table 3).

*Bassia dasyphylla*, *Kochia melanoptera* and *K. krylowii* are combined into the new genus *Grubovia*. They show a limited distribution in Central Asia ranging from southwestern Siberia to northeastern China and south through eastern Kazakhstan, Kyrgistan and Mongolia to easternmost Tadjikistan, southeastern and central China. All species are annual xerophytes and grow in open steppe communities with summer rain, mainly on fine-textured or sandy soils containing usually small amounts of soluble salts only. They share the same  $C_3$ -*Sclerolaena* type leaf anatomy and superficially they look much alike. However, *Bassia dasyphylla* descends to lower altitudes with warm or even hot summers and produces horizontal spines on the fruiting perianth, whereas *Kochia melanoptera* and *K. krylowii* grow from the upper montane to the subalpine belts and can be distinguished by differing types of wing-like appendages on the fruiting perianth.

• *Bassia/Camphorosma* clade: The *Bassia/Camphorosma* clade consists of the small *Camphorosma* subclade and the much larger *Bassia* subclade that contains the majority of the Eurasian species. Whereas the former ranges from the western Mediterranean area to western Central Asia, the latter extends from the Canary Islands to Japan and contains two species from southern Africa. The *Camphorosma* subclade consists of two distinct lineages, *Bassia sedoides* and *Camphorosma*, while the *Bassia* subclade showed little resolution and only a few well-supported branches.

*Bassia sedoides* is here newly combined as the monotypic genus *Sedobassia*. Morphologically it is more similar to annual species of the *Bassia* subclade than to *Camphorosma*. It has five flattened spines on its fruiting perianth and occurs on slightly or moderately saline soils. Its isolated position in the molecular trees is corroborated by its peculiar  $C_3/C_4$ -intermediate leaf anatomy which is unique in Camphorosmeae (Carolin, 1983; H. Freitag, pers. obs.).

*Camphorosma* is the only traditional genus of Camphorosmeae that is monophyletic in the molecular tree. Its monophyly is further supported by a number of synapomorphies: a flattened and 4-lobed perianth, multicellular glandular hairs in the inflorescences (neither mentioned by Carolin, 1983 nor elsewhere),  $C_4$ -leaves of the *Camphorosma* type (H. Freitag, pers. obs.), and a diploid chromosome number of  $2n = 12$  which is unparalleled in the subfamily. *Camphorosma* is limited to

saline/alkaline soils. The perennial species are frost-resistant and penetrate deeply into continental steppes with moderate to severe winter frost. *Camphorosma annua* and *C. songorica* represent Southeast European/West Siberian vicariants in very open halophytic plant communities growing on soils which are wet in spring and dry out almost completely in summer. They differ only slightly, particularly in indumentum characters. Their distinction at specific rank was doubted but is supported by our molecular data. The two perennials *C. monspeliaca* and *C. lessingii* are prostrate shrubs growing in essentially the same habitat as the annual species. They also were considered geographical vicariants, with the first occurring from Northwest Africa and Spain to West Siberia, and the latter reported from more southern localities, from Anatolia to western Central Asia. Species rank of the latter was questioned by some authors (e.g., Hedge, 1997) because distinctive characters are somewhat weak. Our sample from the Syrian desert with several characters of *C. lessingii* (up to 1.5 m tall, branches not rooting) had the same sequences as a sample from Central Anatolia that fits morphologically into *C. monspeliaca*. Also, our specimen of *C. monspeliaca* from the northern edge of the Caspian Sea differs by one mutation only (Fig. 5). These facts highlight the need of further studies using a wider sampling. These should also include chromosome studies because decaploids as well as diploids have been reported from the Iberian Peninsula (Izuzquiza, 1990).

The *Kochia prostrata* subclade (here transferred to *Bassia* as suggested already by Scott, 1978) is distributed from the Iberian Peninsula up to central South Siberia, Central Asia and the northern parts of South Asia (Beguchev, 1971: map 1). The species grow in dry steppe and semi-desert communities, mainly on sandy and other coarsely textured non-saline soils from the lowlands up to subalpine altitudes. They often reach high coverage, and because of their palatability, high protein content and a remarkable resprouting ability from their shrubby base, they are most valuable components of the respective rangelands and are increasingly used for seeding on heavily overgrazed or otherwise depleted rangelands, e.g., in Uzbekistan (Gintzburger & al., 2003) and North America (e.g., Zobell & al., 2003). In different parts of the large distribution area many forms have evolved which differ in size, indumentum, shape and size of leaves, fruiting perianth wings, etc. They were treated by different authors in various ways as forms, varieties, subspecies (most concisely by Pratorov, 1971) or even species (Czerepanov, 1995). To understand the diversification of this lineage, a more detailed sampling and more variable molecular markers are necessary. The full geographical range should be sampled to include all other known morphological variants, as well as chromosome numbers because diploids, tetraploids and hexaploids have been recorded from the former U.S.S.R. (Takhtajan, 1990).

The *Bassia hyssopifolia* subclade contains *Bassia hyssopifolia* and the *Kochia scoparia* group, a clade consisting of four closely related and morphologically similar taxa; Fig. 5. We also treat the latter here under *Bassia*. The subclade consists of annual species and has a wide distribution area in Eurasia which ranges from the Iberian Peninsula to Japan. It is naturalized

on other continents with temperate semi-humid and semi-arid climates (see Fig. 2). *Kochia alata* was described from North America by Bates (1918), emended by Aellen (1943) and cited accordingly by Scott (1978). However, a detailed morphological analysis by Blackwell & al. (1978) as well as our molecular results (the sampling includes two accessions from North America) reveal that it is very similar to other species of the *Kochia scoparia* group (Fig. 5). *Kochia indica* was described by Wight (1852) from coastal South India, far outside the geographical range of the group. As the species' area extends from the East Mediterranean to northwestern India and no further records from the coast of tropical India were made, we assume that *K. indica* was introduced to the type area, probably by (sea)trade.

Most taxa of the *Bassia hyssopifolia* subclade occur in ruderal sites but their original habitats are open steppe communities, preferably around disturbed microsites such as rodent cavities. Only the Central Asian *K. angustifolia* and the East Asian *K. littorea* (the latter not included in our molecular analyses) are restricted to saltmarshes. *Bassia hyssopifolia* is the only species in the clade with uncinatate spines on the fruiting perianth. The *Kochia scoparia* group is well-known for its large variation in shape, size and indumentum of leaves, indumentum of leaf axils (very dense and long in *K. densiflora*), size and shape of wings on the fruiting perianth etc. which were treated in various ways by different authors. Our sampling included some conspicuous forms but was not large enough to resolve the taxonomy of the group. For morphological and ecological reasons, most likely only *K. scoparia*, *K. indica* and *K. littorea* deserve species rank.

The *Kochia stellaris* group with the three annuals *K. stellaris*, *K. iranica* and *K. odontoptera* (Fig. 5), inhabits chiefly sandy or loessic semi-deserts in middle and western Central Asia. The species differ mainly in shape of the wing-like tepal appendages and several authors (e.g., Hedge, 1997) include all of them into *K. stellaris*, or they recognize only *K. iranica* and *K. odontoptera* (Czerepanov, 1995). The ITS sequences of *K. iranica* and *K. odontoptera* (samples from the same locality in a temperate semi-desert of western Kazakhstan) are identical and the sequence of *K. stellaris* (sample from hot subtropical semi-deserts in Pakistani Baluchistan) differs in two base positions. The molecular data, therefore, support the close relationship of the taxa. Whether the three species are distinct requires further investigation.

*Kochia salsoloides* and *Chenoleoides dinteri* (both transferred to *Bassia*) are South African subshrubs which have been rarely collected. *Kochia salsoloides* is widely distributed in the Nama-Karoo where it grows along temporarily dry rivers. *Chenoleoides dinteri* is a rare plant in the fog desert of the Namib. In the ITS tree (Fig. 5) the two species form a monophyletic group, albeit without bootstrap support. Though they might have originated from one colonization event of a Mediterranean ancestor, they differ in morphology (e.g., presence of wings on the fruiting tepals in *Kochia salsoloides* and their absence in *Chenoleoides dinteri*), and in ecology.

*Chenoleoides tomentosa* and *Ch. arabica*, both included in *Bassia*, are rather similar in being prostrate subshrubs with

leaves which are densely covered by appressed silky hairs. They are distributed in semi-desert communities along the northern margin of the Saharo-Sindian floristic region on a wide variety of soils, the first in the Canary Islands including the Atlantic coast of Morocco, and the second further east from Libya to Iraq. Their close relationship is indicated in the *atpB-rbcL* spacer tree (Fig. 3) but not resolved in the ITS tree (Fig. 5). Most likely, the recently described *B. aegyptiaca* (Turki & al., 2006, name illegitimate) with short spines, which is known from the type locality only, also belongs here.

The remaining annual species are quite distinct from each other in morphology and ecology: *Bassia muricata* is an element of sand deserts in the Saharo-Sindian region. It germinates only after occasional winter rains and completes its life cycle in a few weeks. *Pandertia pilosa* and *Kirilowia eriantha*, here for the first time included in *Bassia*, represent a closely related pair of geographically vicariant annual species which is supported only in the *atpB-rbcL* spacer tree (BS 77%; Fig. 3). *Pandertia pilosa* is a typical Irano-Turanian floristic element from disturbed habitats. It has small and often wing-like tepal appendages. *Kirilowia eriantha* is an element of Central Asian steppes. It lacks tepal appendages and has long fasciculate hairs in the inflorescence. Both have vertical seeds, and their distribution ranges overlap slightly. *Pandertia turkestanica* (not included into the molecular analysis) differs from *P. pilosa* only in wing shape and indument (Iljin, 1936). Our morphological observations confirmed its questionable specific rank (e.g., Hedge, 1997) but further investigation is needed. The annual xerophytes *Bassia eriophora* and *Londesia eriantha*, the first not represented in the sampling, most likely are conspecific. They grow in extremely dry semi-deserts and differ only in the presence/absence of short tepaline spines which are hidden by long and dense hairs giving the fruits the aspect of small cotton balls. The first was described from cultivated plants grown from seeds most likely collected on Sinai and the latter from the eastern shore of the Caspian Sea suggesting vicariant Saharo-Sindian and Irano-Turanian species, respectively. Identity of the two species was first suspected by Boissier (1879: 927) who detected spiny and unarmed fruits in the same collection of *Bassia eriophora* from Sinai (*Schimper no. 133*), and later on accepted by Hedge (1997) and other authors. In our own collection of *Bassia eriophora* from a hot subtropical semi-desert in Pakistani Baluchistan we found both types of fruits even in the same individual, and in the molecular study of Akhani & al. (2007) both taxa have almost identical ITS sequences.

**Evolution of C<sub>4</sub>-photosynthesis.** — The identification of the photosynthetic syndrome in Camphorosmeae was based on the <sup>13</sup>C/<sup>12</sup>C carbon discrimination values taken from Akhani & al. (1997) and H. Freitag (unpub. data). The molecular data congruently show that all C<sub>4</sub>-species form a monophyletic group (*Bassia/Camphorosma* clade) including *Bassia sedoides*, the only C<sub>3</sub>/C<sub>4</sub>-intermediate of the tribe. The three traditional camphorosmean genera that included both C<sub>3</sub>- and C<sub>4</sub>-species, viz., *Bassia*, *Kochia* and *Chenolea*, are polyphyletic (Figs. 3, 5; see above). Obviously, the photosynthetic syndrome contains a strong phylogenetic signal in Camphorosmeae. It seems, however, not possible to decide which of the two C<sub>3</sub>-lineages

(*Sclerolaena* clade or *Chenolea* clade) are more closely related to the  $C_4$ -lineage (*Bassia/Camphorosma* clade) on the basis of molecular evidence (Figs. 3–5).

The  $C_3/C_4$ -intermediate *Bassia sedoides* is of major importance for the interpretation of the origin of  $C_4$ -photosynthesis in Camphorosmeae. Two possible interpretations are equally parsimonious in the topologies of the molecular trees, i.e., either two gains of  $C_4$ -photosynthesis (one along the branch leading to *Camphorosma* and one along the branch leading to all remaining  $C_4$ -species), or one gain at the stem of the *Bassia/Camphorosma* clade and one loss in *Bassia sedoides* (Fig. 5). Since *Camphorosma* has a distinct  $C_4$ -leaf type (H. Freitag, pers. obs.) we consider two separate origins more likely.

Kadereit & al. (2003) estimated that  $C_4$ -photosynthesis originated 21.6–14.5 Ma ago in Camphorosmeae. Their molecular clock approach was based on a clock-enforced ML tree that showed constant rates after pruning taxa with strongly deviating substitution rates. The present study with a much enlarged taxon sampling, different markers, different calibration points and two different molecular clock approaches gave similar results (Table 3). If we assume that  $C_4$ -photosynthesis arose twice in the Camphorosmeae, its origin is dated to at least 14–10 Ma in the ancestor of *Camphorosma* and to 21–8 Ma in the ancestor of the *Bassia* clade (Table 3). If  $C_4$ -photosynthesis arose only once in Camphorosmeae it must be postulated that this happened 24–14 Ma (Table 3; Fig. 5). In Salsoleae and Caroxyloneae the origin of  $C_4$ -photosynthesis is probably slightly older and dates back to the Oligocene/Miocene boundary (Table 3; Figs. S1–S4).

These estimates of the origin of  $C_4$ -photosynthesis in Camphorosmoideae during the Early to Middle Miocene correspond to estimates found for the early  $C_4$ -lineages in other  $C_4$ -plant groups (Sage, 2004; Christin & al., 2008). The emergence of  $C_4$ -lineages after the Oligocene/Miocene boundary corresponds to the finding that during this period the  $CO_2$  partial pressure dropped under the critical value of 500–600 ppm (Pagani & al., 2005; Tiplle & Pagani, 2007) at which the  $CO_2$  concentration in the atmosphere becomes problematic in hot and dry environments (Ehleringer & al., 1997; Sage, 2004; Osborne & Beerling, 2006). Probably more important, increased aridity and seasonality of the climate in Eurasia might have enhanced the multiple origin of  $C_4$ -lineages during the Miocene (Behrensmeier & al., 2007; Huang & al., 2007; Kürschner & al., 2008; Passet & al., 2009) not only in grasses but also in chenopods.

Within the *Bassia/Camphorosma* clade ca. 23  $C_4$ -species evolved. In comparison to other partly even younger but species-rich  $C_4$ -lineages in Chenopodiaceae, such as *Atriplex*, *Suaeda* and  $C_4$ -lineages of Salsoleae s.l. this represents a small number of species. The origin of  $C_4$ -photosynthesis in the *Bassia/Camphorosma* clade is associated with innovations regarding structure and shape of leaves. These offer an array of phylogenetically informative anatomical characters, with four different  $C_4$ -leaf types, one  $C_3/C_4$ -intermediate and five  $C_3$ -leaf types that are most valuable taxonomic characters at generic and species level in Camphorosmeae (H. Freitag & G. Kadereit, unpub. data). Variation in leaf anatomy will be treated in a separate paper.

## ■ TAXONOMIC CONCLUSIONS

The necessary new combinations and diagnoses of new genera in non-Australian Camphorosmeae, based on the present study, are listed below. Listing of full synonymy is not attempted.

**Subfam. Camphorosmoideae** Scott in Feddes Repert. 89: 102. 1978.

Emended description: Differing from the otherwise similar Salsoloideae by absence of bracteoles, filiform stigmata with stigmatic papillae on the entire surface, annular or folded embryo engirdling the perisperm and by pollen grains with larger diameter (>15  $\mu$ m), higher number of pores (usually >70), smaller diameter of pores (usually <2000 nm), and smaller number of spinulae per operculum (>15).

Circa 147 spp. in Australia, ca. 27 spp. in Eurasia including North Africa, 3 spp. in South Africa, 2 spp. in North America; a few naturalized species worldwide (Fig. 2).

### Species group 1 (*Chenolea* group)

*Chenolea* Thunb., Nov. Gen. Pl. 1: 10. 1781 – Type: *Chenolea diffusa*.

Perennial, mat-forming herb with rooting stems; without distinct inflorescences, leaves densely packed, flat, with one central and numerous lateral bundles embedded in aqueous tissue and surrounded by fenestrate chlorenchyma ( $C_3$  *Chenolea* type); flowers usually solitary, fruiting perianth star-shaped by 5 short, thick, wing-like appendages. One species.

*Chenolea diffusa* Thunb., Nov. Gen. Pl. 1: 10. 1781; southern Africa.

*Spirobassia* Freitag & G. Kadereit, **gen. nov.** – Type: *Spirobassia hirsuta*.

Genus novum a generibus affinis infructescentiis contortis, perianthii appendicibus tribus obtusis provis et substitutionibus in sequentia ITS perspicue diversa est.

Annual; leaves with one central and numerous peripheral bundles ( $C_3$  *Sclerolaena* type); fruiting perianth with 3 obtuse tepal appendages; infructescence contorted. One species, North Mediterranean to South Siberia. The genus name refers to the contorted fruiting inflorescences.

*Spirobassia hirsuta* (L.) Freitag & G. Kadereit, **comb. nov.**  $\equiv$  *Chenopodium hirsutum* L., Sp. Pl.: 221. 1753  $\equiv$  *Bassia hirsuta* (L.) Asch. in Schweinfurth, Beitr. Fl. Aethiop.: 187. 1867  $\equiv$  *Echinopsilon hirsutum* (L.) Moq. in Ann. Sci. Nat., Bot., ser. 2, 2: 127. 1834.

*Neokochia* (Ulbr.) G.L. Chu & S.C. Sand. in Madroño 55: 255. 2009 ('2008')  $\equiv$  *Kochia* sect. 3 *Neokochia* Ulbr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 16c: 535. 1934 – Type: *Neokochia americana*.

Dwarf shrubs; leaves with  $C_3$  *Sclerolaena* type or the related *Neokochia americana* type that differs by thick-walled

aqueous tissue; fruiting perianth 5-winged. Two species, south-western North America.

*Neokochia americana* (S. Watson) G.L. Chu & S.C. Sand. in Madroño 55: 255. 2009 ('2008') ≡ *Kochia americana* S. Watson in Proc. Amer. Acad. Arts 9: 93. 1874.

= *K. vestita* A. Nelson in J.M. Coulter & A. Nelson, New Man. Bot. Centr. Rocky Mt.: 165. 1909.

*Neokochia californica* (S. Watson) G.L. Chu & S.C. Sand. in Madroño 55: 255. 2009 ('2008').

*Eokochia* Freitag & G. Kadereit, **gen. nov.** – Type: *Eokochia saxicola*.

Genus novum inter genera affines foliorum nervis lateralibus duobus compositis singulariter est.

Weakly lignified dwarf shrub with overhanging branches; leaves highly succulent, almost terete, with one central and two complex lateral bundles (C<sub>3</sub> *Eokochia* type); perianth 5-winged. One species, Central Mediterranean. The genus name was chosen because this species evidently is a relict of a very old lineage.

*Eokochia saxicola* (Guss.) Freitag & G. Kadereit, **comb. nov.** ≡ *Kochia saxicola* Guss., Enum. Pl. Inarim.: 275, t. 13. 1855 ≡ *Bassia saxicola* (Guss.) A.J. Scott in Feddes Repert. 89: 108. 1978.

### Species group 2 (*Sclerolaena* group)

*Grubovia* Freitag & G. Kadereit, **gen. nov.** – Type: *Grubovia dasyphylla*.

Plantae *Spirobassia hirsuta* similes sed infructescentiis non contortis, appendicibus quinque aliformibus vel spiniformibus et substitutionibus in sequentiis ITS, *rbcL*, *atpB-rbcL* et *ndhF* bene differt.

Annuals; leaves with one central and numerous peripheral bundles (C<sub>3</sub> *Sclerolaena* type); infructescence not contorted; fruiting perianth with 5 wings or spines. Three species, Central Asia. The new genus is named in honour of the recently deceased outstanding Russian botanist Valeriy Ivanovich Grubov (1917–2009) who greatly contributed to the knowledge of the flora of Central Asia.

*Grubovia dasyphylla* (Fisch. & C.A. Mey.) Freitag & G. Kadereit, **comb. nov.** ≡ *Kochia dasyphylla* Fisch. & C.A. Mey. in Enum. Pl. Nov. 1: 12. 1841 ≡ *Bassia dasyphylla* (Fisch. & C.A. Mey.) Kuntze, Revis. Gen. Pl. 2: 546. 1891.

= *Echinopsilon divaricatum* Kar. & Kir. in Bull. Soc. Imp. Naturalistes Moscou 14: 760. 1841, nom. inval.

= *Bassia fiedleri* Aellen in Hegi, Ill. Fl. Mittl.-Eur., ed. 2, vol. 3(2): 713. 1968.

*Grubovia melanopectera* (Bunge) Freitag & G. Kadereit, **comb. nov.** ≡ *Kochia melanopectera* Bunge in Trudy Imp. S.-Peterburgsk. Bot. Sada 6(2): 417. 1880.

*Grubovia krylovii* (Litv.) Freitag & G. Kadereit, **comb. nov.** ≡ *Kochia krylovii* Litv. in Krylov, Fl. Altaya 5: 1121. 1909.

### Species group 3 (*Bassia/Camphorosma* group)

*Sedobassia* Freitag & G. Kadereit, **gen. nov.** – Type: *Sedobassia sedoides*.

A *Spirobassia* et *Grubovia* foliorum nervis lateralibus cellularis confinibus “Kranz”-formibus et substitutionibus in sequentiis ITS, *rbcL*, *atpB-rbcL* et *ndhF* diversa est.

Annual; leaves with Kranz-like innermost chlorenchyma layer bordering the vascular bundles (C<sub>3</sub>/C<sub>4</sub> intermediate *Sedobassia* type); fruiting perianth with 5 short spines. One species, Hungary to Siberia. The genus name emphasizes the similarity to genus *Bassia* where it was placed before and underlines its monotypic nature by incorporation of the species' epithet.

*Sedobassia sedoides* (Pall.) Freitag & G. Kadereit, **comb. nov.** ≡ *Salsola sedoides* Pall., Reise Russ. Reich 1: 492. 1771 ≡ *Bassia sedoides* (Pall.) Asch. in Schweinfurth, Beitr. Fl. Aethiop.: 187. 1867 ≡ *Echinopsilon sedoides* (Pall.) Moq. in Ann. Sci. Nat., Bot., ser. 2, 2: 127. 1834.

*Camphorosma* L., Sp. Pl.: 122. 1753 – Type: *Camphorosma monspeliaca*.

Annuals or perennials; leaves with peripheral bundles and almost closed Kranz layer (C<sub>4</sub> *Camphorosma* type); inflorescence with glandular hairs, fruiting perianth flattened, 4-lobed, unappendaged. Three (four) species, West Mediterranean to Central Asia.

*Camphorosma monspeliaca* L., Sp. Pl.: 112. 1753.

*Camphorosma lessingii* Litv. in Trudy Bot. Muz. Imp. Akad. Nauk 2: 96. 1905.

More work is needed to ascertain the separation of this species from *C. monspeliaca*.

*Camphorosma annua* Pall., Ill. Pl.: 67. 1803.

*Camphorosma songorica* Bunge in Trudy Imp. S.-Peterburgsk. Bot. Sada 6(2): 415. 1880.

*Bassia* All. in Mélanges Philos. Math. Soc. Roy. Turin 3: 177. 1766 – Type: *B. aegyptiaca* ≡ *B. muricata*.

= *Kochia* Roth in J. Bot. (Schrader) 3(2): 307. 1801 ('1800').

= *Willemetia* Maerkl. in J. Bot. (Schrader) 3(2): 329. 1801 ('1800'), nom. inval.

= *Echinopsilon* Moq. in Ann. Sci. Nat., Bot., ser. 2, 2: 127. 1834, nom. illeg.

= *Londesia* Fisch. & C.A. Mey., Index Sem. Hort. Petrop. 2: 40. 1835.

= *Pandertia* Fisch. & C.A. Mey., Index Sem. Hort. Petrop. 2: 46. 1835, **syn. nov.**

= *Kirilowia* Bunge in Del. Sem. Hort. Dorpat.: 7. 1843, **syn. nov.**

= *Chenoleoides* (Ulbr.) Botsch. in Bot. Zhurn. (Moscow & Leningrad) 61: 1408. 1976.

Annuals or perennials; leaves with different C<sub>4</sub> “kochioid” types; fruiting perianth unappendaged or with 5 wings or spines. Circa 20 species, West Mediterranean to East Asia.

***Bassia aegyptiaca*** Turki & al. in Fl. Medit. 16: 279. 2006, nom. illeg., non *B. aegyptiaca* All.

The identity of this species, reported from one locality only, is questionable.

***Bassia angustifolia*** (Turcz.) Freitag & G. Kadereit, **comb. nov.** ≡ *Kochia scoparia* (L.) Schrad. var. *angustifolia* Turcz., Fl. Baical.-Dahur. 2(2): 33. 1856 ≡ *Kochia angustifolia* (Turcz.) Peschkova, Stepnaya Fl. Baikal'skoi Sibiri: 53. 1972.

The taxon is well separated from *B. scoparia* by filiform leaves with 2-layered aqueous tissue, and by growing in Central Asian saltmarshes.

***Bassia arabica*** (Boiss.) Maire & Weiller in Maire (ed.), Fl. Afr. Nord 8: 54. 1962 ≡ *Chenolea arabica* Boiss., Diagn. Pl. Orient., sér. 1, 12: 97. 1853 ≡ *Chenoleoides arabica* (Boiss.) Botsch. in Bot. Zhurn. (Moscow & Leningrad) 61: 1409. 1976.

***Bassia dinteri*** (Botsch.) A.J. Scott in Feddes Repert. 89: 108. 1978 ≡ *Chenolea dinteri* Botsch. in Bot. Zhurn. (Moscow & Leningrad) 58: 1463. 1973 ≡ *Chenoleoides dinteri* (Botsch.) Botsch. in Bot. Zhurn. (Moscow & Leningrad) 61: 1409. 1976.

***Bassia eriophora*** (Schrad.) Asch. in Schweinfurth, Beitr. Fl. Aethiop.: 187. 1867 ≡ *Kochia eriophora* Schrad. in Neues J. Bot. 3(3–4): 86 & t. 3. 1809.

= *Londesia eriantha* Fisch. & C.A. Mey., Index Sem. Hort. Petrop. 2: 40. 1835.

= *Bassia eriantha* (Fisch. & C.A. Mey.) Kuntze, Rev. Gen. Pl. 2: 546. 1891.

***Bassia hyssopifolia*** (Pall.) Kuntze, Revis. Gen. Pl. 2: 547. 1891 ≡ *Salsola hyssopifolia* Pall., Reise Russ. Reich. 1: 491. 1771 ≡ *Echinopsilon reuterianum* Boiss. in Boissier & Reuter, Pugill. Pl. Afr. Bor., Hispan.: 105. 1852.

***Bassia indica*** (Wight) A.J. Scott in Feddes Repert. 89: 108. 1978 ≡ *Kochia indica* Wight, Icon. Pl. Ind. Orient. 5(2): 5, t. 1791. 1852.

= *Bassia joppensis* Bornm. & Dinsm. in Repert. Spec. Nov. Regni Veg. 17: 274. 1921.

***Bassia laniflora*** (S.G. Gmel.) A.J. Scott in Feddes Repert. 89: 108. 1978 ≡ *Salsola laniflora* S.G. Gmel., Reise Russland 1: 160. 1774 ≡ *Kochia laniflora* (S.G. Gmel.) Borbás, Balaton Fl.: 340. 1900.

= *Kochia arenaria* (Maerkl.) Roth in J. Bot. (Schrader) 3(2): 307. 1801 ('1800').

***Bassia lasiantha*** Freitag & G. Kadereit, **nom. nov.** ≡ *Kirilowia eriantha* Bunge in Del. Sem. Hort. Dorpat.: 8. 1843. A new

name is required because of *Bassia eriantha* (Fisch. & C.A. Mey.) Kuntze.

= *Londesia eriantha* Fisch. & C.A. Mey.

***Bassia littorea*** (Makino) Freitag & G. Kadereit, **comb. nov.** ≡ *Kochia scoparia* (L.) Schrad. var. *littorea* Makino in Bot. Mag. (Tokyo) 23: 12. 1909 ≡ *Kochia littorea* (Makino) Makino in Bot. Mag. (Tokyo) 27: 254. 1913.

The species differs from *Bassia scoparia* by distinctly succulent leaves with hypodermis and 2-layered aqueous tissue made up of elongated cells, furthermore by zig-zag shape of inflorescences and by growing in periodically flooded coastal saltmarshes.

***Bassia muricata*** (L.) Asch. in Schweinfurth, Beitr. Fl. Aethiop.: 187. 1867 ≡ *Salsola muricata* L., Mant. Pl.: 54. 1767 ≡ *Bassia aegyptiaca* All., Mélanges Philos. Math. Soc. Roy. Turin 3: 178. 1766 & 5: 93. 1770.

***Bassia odontoptera*** (Schrenk) Freitag & G. Kadereit, **comb. nov.** ≡ *Kochia odontoptera* Schrenk in Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint Pétersbourg 1: 361. 1843.

= *Bassia iranica* (Bornm.) Bornm. in Repert. Spec. Nov. Regni Veg. 17: 276. 1921.

= *Kochia iranica* Bornm. in Bull. Hérb. Boissier, sér. 2, 8: 546. 1908.

Further studies are required to check if the species is distinct from *B. stellaris*.

***Bassia pilosa*** (Fisch. & C.A. Mey.) Freitag & G. Kadereit, **comb. nov.** ≡ *Pandertia pilosa*, Index Sem. Hort. Petrop. 2: 46. 1835, **syn. nov.**

= *Kochia monticola* Boiss., Diagn. Pl. Orient. 1(7): 82. 1846.

Most likely the following taxon is conspecific: *Pandertia turkestanica* Iljin, Izv. Bot. Sada Akad. Nauk S.S.S.R. 30: 364. 1932.

***Bassia prostrata*** (L.) A.J. Scott in Feddes Repert. 89: 108. 1978 ≡ *Salsola prostrata* L., Sp. Pl.: 222. 1753 ≡ *Kochia prostrata* (L.) Schrad. in Neues J. Bot. 3(4): 85. 1809.

The widespread and polymorphic group requires a deeper study.

***Bassia salsoloides*** (Fenzl) A.J. Scott in Feddes Repert. 89: 108. 1978 ≡ *Kochia salsoloides* Fenzl, Nov. Stirp. Dec. Vind.: 74. 1839.

***Bassia scoparia*** (L.) A.J. Scott in Feddes Repert. 89: 108. 1978 ≡ *Chenopodium scoparium* L., Sp. Pl.: 221. 1753 ('*scoparia*') ≡ *Kochia scoparia* (L.) Schrad. in Neues J. Bot. 3(4): 85. 1809.

= *K. sieversiana* (Pall.) C.A. Mey. in Ledebour, Fl. Altaic. 1: 415. 1829.

= *K. scoparia* var. *densiflora* Moq. in Candolle, Prodr. 13(2): 131. 1849.

= *K. densiflora* auct.

= *K. alata* Bates in Amer. Bot. (Binghamton) 24: 52. 1918.

Further studies are required to elucidate the infraspecific grouping.

**Bassia stellaris** (Moq.) Bornm. in Repert. Spec. Nov. Regni Veg. 17: 276. 1921 ≡ *Kochia stellaris* Moq., Chenop. Monogr. Enum.: 93. 1840.

**Bassia tianschanica** (Pavlov) Freitag & G. Kadereit, **comb. nov.** ≡ *Kochia tianschanica* Pavlov, Vestn. Akad. Nauk Kazahsk. S.S.R. 8: 17. 1950.

**Bassia tomentosa** (Lowe) Maire & Weiller in Maire, Fl. Afr. Nord 8: 53. 1962 ≡ *Suaeda tomentosa* Lowe in Trans. Cambridge Philos. Soc. 6: 534. 1838 ≡ *Chenolea tormentosa* (Lowe) Maire in Emberger & Maire, Cat. Pl. Maroc: 973. 1941 ≡ *Chenoleoides tomentosa* (Lowe) Botsch. in Bot. Zhurn. (Moscow & Leningrad) 61: 1409. 1976.

= *Chenolea canariensis* Moq., Chenop. Monogr. Enum.: 96. 1840.

= *Chenolea lanata* (Masson) Moq. in Candolle, Prodr. 13(2): 129. 1849.

**Bassia villosissima** (Bong. & C.A. Mey.) Freitag & G. Kadereit, **comb. nov.** ≡ *K. prostrata* var. *villosissima* Bong. & C.A. Mey., Verz. Saisang-nor Pfl.: 67. 1841 ≡ *K. villosissima* (Bong. & C.A. Mey.) Serg., Fl. Zapadnoi Sibiri 12(2): 3260. 1964 ≡ *K. prostrata* subsp. *grisea* Prato var. *villosissima* Bong. & C.A. Mey. in Burygin, Izen' Kochia prostrata: 8–9. 1971.

### Excluded species

*Bassia pulverulenta* H. Lindb. in Acta Soc. Sci. Fenn., Ser. B, Opera Biol. 2(7): 12. 1946.

= *Salsola inermis* Forssk. in Meikle, Fl. Cyprus 2: 1392. 1985.

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**Appendix.** Taxa sampled for each marker in alphabetical order. Voucher details are given only for newly generated sequences. Lab numbers and GenBank accession numbers (in bold if sequence was newly generated) are given for all samples studied.

Taxon, Lab number, voucher, GenBank accession number.

**rbcL:** *Achatocarpus praecox* Griseb., AY270142; *Acroglochin chenopodioides* Schrad., chen 127, AY270049; *Aerva javanica* (Burm. f.) Schultes, AC 014, AY270050; *Agriophyllum squarrosum* (L.) Moq., chen 054, AY270051; *Allenrolfea occidentalis* Kuntze, chen 095, AY270052; *Alternanthera caracasana* Kunth, AC 058, AY270053; *Alternanthera pungens* Kunth, AC 061, AY27054; *Amaranthus greggii* S. Watson, AC 059, AY270055; *Amaranthus tricolor* L., X53980; *Anabasis articulata* (Forssk.) Moq., chen 1227, G. Kadereit & J.W. Kadereit 2006/5 (MJG), Spain, Almería prov., Cabo de Gata, **HM630092**; *Anthochlamys multinervis* Rech. f., chen 042, AY270056; *Aphanisma blitoides* Nutt. ex Moq., chen 310, AY270057; *Arthrocnemum macrostachyum* (Morice) K. Koch, chen 023, AY270058; *Atriplex coriacea* Forssk., chen 038, AY270045; *Atriplex halimus* L., chen 278, AY270059; *Atriplex patula* L., X15925; *Atriplex prostrata* L., X55831; *Atriplex spongiosa* F. Muell., chen 158, AY270060; *Atriplex undulata* (Moq.) D. Dietr., chen 167, AY270061; *Axyris prostrata* L., chen 118, AY270062; *Bassia dasyphylla* (Fisch. & C.A. Mey.) Kuntze, chen 131, AY270150; *Bassia hirsuta* (L.) Asch., chen 014, H. Freitag 28.077 (KAS), NW.Kazakhstan, Ural'sk prov., Shalkar lake, **HM630093**; *Bassia sedoides* (Pall.) Asch., chen 128, AY270063; *Beta nana* Boiss. & Heldr., chen 309, AY270065; *Beta vulgaris* L. subsp. *maritima* Thell., chen 049, AY270065; *Bienertia cycloptera* Forssk., chen 144, AY270066; *Blutaparon vermiculare* (L.) Mears, AC 053, AY270067; *Bosea yervamora* L., AC 072, AY270069; *Calicornema capitata* (Moq.) Hook. f., AC 055, AY270070; *Camphorosma monspeliaca* L., chen 053, AY270071; *Celosia argentea* L., AC 090, AY270072; *Ceratocarpus arenarius* L., chen 466, HM587594; *Chamissoa altissima* (Jacq.) Kunth var. *altissima*, AC 043, AY270073; *Charpentiera obovata* Gaudich., B.A. Prigge 15251, AY270074; *Charpentiera ovata* Gaudich., B.A. Prigge 15252, AY270075; *Chenoleoides tomentosa* (Lowe) Botsch., chen 137, AY270076; *Chenopodium acuminatum* Willd., chen 183, AY270077; *Chenopodium auricomum* Lindl., chen 258, AY270078; *Chenopodium bonus-henricus* L., chen 051, AY270079; *Chenopodium coronopus* Moq., chen 721, HM587595; *Chenopodium desertorum* (J. Black) J. Black ssp. *anidiophyllum* (Aellen) Paul. G. Wilson, chen 254, AY270042; *Chenopodium foliosum* Asch., chen 117, AY270081; *Chenopodium frutescens* C.A. Mey., chen 210, AY270082; *Chenopodium sanctaeflorae* Johow, chen 194, AY270043; *Chenopodium urbicum* L., chen 821, HM587596; *Climacoptera crassa* (M. Bieb.) Botsch., chen 083, AY270083; *Corispermum filifolium* C.A. Mey. ex A.K. Becker, chen 148, AY270084; *Deeringia amaranthoides* (Lam.) Merrill, AC 044, AY270085; *Dissocarpus paradoxus* (R. Br.) Ulbr., chen 163, AY270089; *Dysphania ambrosioides* (L.) Mosyakin & Clemants, chen 822, HM587599; *Dysphania botrys* (L.) Mosyakin & Clemants (= *Chenopodium botrys* L.), chen 116, AY270080; *Dysphania cristata* (F. Muell.) Mosyakin & Clemants (= *Chenopodium cristatum* (F. Muell.) F. Muell.), chen 256, AY270046; *Dysphania glomulifera* (Nees) Paul G. Wilson, chen 277, AY270086; *Froelichia floridana* (Nutt.) Moq., AC 016, AF132089; *Girgensohnia oppositiflora* (Pall.) Fenzl, chen 033, AY270087; *Gomphrena elegans* Mart., Th. Borsch 3545, AY270088; *Gomphrena haageana* Klotzsch, chen 068, AY270089; *Gomphrena serrata* L., AC 011, AY270090; *Guilleminia densa* (Willd.) Moq., AC 051, AY270091; *Hablitzia tamnoides* M. Bieb., AC 018, AY270092; *Halimione pedunculata* (L.) Aellen, chen 034, AY270093; *Halocharis hispida* Bunge, chen 085, H. Freitag 30.117 (KAS), Uzbekistan, ca. 85 km ssw of Tashkent, outskirts of Gulistan, **HM630094**; *Haloecnemum strobilaceum* (Pall.) M. Bieb., chen 444, AY270094; *Halogeton sativus* Moq., chen 1229, G. Kadereit & J.W. Kadereit 2006/13 (MJG), Spain, Granada prov., near Baza, Jabalcon, **HM630095**; *Haloplepis amplexicaulis* Ung.-Sternb. ex Ces., Passer. & Gibelli, G. Kadereit 2002/14, AY270095; *Halostachys belangeriana* (Moq.) Botsch., chen 864, W. Wucherer 2004 (KAS), Kazakhstan, Syrdarya valley near Aral Lake, 1 km W of Amanotkel', **HM630096**; *Halothamnus bottae* Jaub. & Spach, chen 351, N. Kilian 4499 (B), Yemen, Socotra, **HM630097**; *Haloxylon tamariscifolium* (L.) Pau, chen 196, H. Freitag 27.236 (KAS), Spain, Almería prov., Sierra de Alhama, **HM630098**; *Ibid.*, chen 1230, G. Kadereit & J.W. Kadereit 2006/18 (MJG), **HM630099**; *Hebanthe occidentalis* (R.E. Fr.) Borsch & Pedersen var. *occidentalis*, AC 008, AY270097; *Hemichroa diandra* R. Br., Blaylock 383, AY270098; *Hermibstaedia glauca* (Wendl.) Reichenb. ex Steudel, AC 041, AY270099; *Holmbergia tweedii* Speg., chen 193, AY270100; *Iresine palmeri* S. Watson, AC 054, AY270101; *Kalidium caspicum* (L.) Ung.-Sternb., chen 089, AY270102; *K. densiflora* (Moq.) Aellen, chen 133, H. Freitag 28.321 (KAS), Russia, Saratov prov., near Pugachev, AY489264; *Kochia prostrata* (L.) Schrad., chen 031, AY270104;

## Appendix. Continued.

- Kochia saxicola* Gruss., chen 013, cultivated at Bot. Garden Kassel (KAS), from Italy, Capri Is. **HM630100**; *Krascheninnikovia ceratoides* (L.) Gueldenst., chen 012, AY270105; *Maireana brevifolia* (R. Br.) Paul G. Wilson, chen 143, AY270106; *Microcnemum coralloides* (Loscoc & Pardo) Buen, chen 2002/15, *G. Kadereit & J.W. Kadereit 2002/15* (MJG), Spain, Aragón prov., Acaniz, Laguna de Guallar, **HM630101**; *Microgynoecium tibeticum* Hook. f., chen 119, AY270107; *Monolepis nuttalliana* Greene, chen 125, AY270108; *Nanophyton erinaceum* (Pall.) Bunge, chen 1346, *B. Neuffer & al. OSBU 18050* (OSBU), Russia, Tuva Rep., w of Kysyl at river Jenissej, **HM630102**; *Neokochia americana* (S. Watson) G.L. Chu & S.C. Sand., chen 076, AY270103 (as *Kochia americana* S. Watson); *Nitrophila occidentalis* S. Watson, *D. Pratt 204*, AY270109; *Noaea mucronata* (Forssk.) Asch. & Schweinf., chen 019, AY270110; *Nototrichum humile* Hillebr., *B.A. Prigge 15249*, AY270111; *Ojaiston monandrum* (Pall.) Moq., chen 020, AY270112; *Oreobliton thesioides* Durieu & Moq., chen 093, AY270113; *Pandera pilosa* Fisch. & C.A. Mey., chen 141, AY270114; *Patellifolia patellaris* (Moq.) A.J. Scott, Ford-Lloyd & J.T. Williams, chen 2023, *G. Kadereit & J.W. Kadereit (2006/6)*, Spain, Almería prov., Cabo de Gata, **HM630103**; *Petrosimonia nigdensis* Aellen, chen 025, AY270116; *Phaulothamnus spinescens* A. Gray, M97887; *Pleuropetalum sprucei* (Hook. f.) Standley, AC 020, AY270117; *Polycnemum majus* A. Braun ex Bogenh., AY270118; *Polycnemum perenne* Litv., chen 078, AY270119; *Pseudoplantago friesii* Suess., AC 040, AY270120; *Ptilotus manglesii* (Lindl.) F. Muell., AC 015, AY270121; *Pupalia lappacea* A. Juss., AC 036, AY270122; *Raphidophyton regelii* (Bunge) Iljin, chen 075, AY270123; *Rhagodia drummondii* Moq., chen 159, AY270124; *Roycea divaricata* Paul G. Wilson, chen 818, Herbarium NSW 594030, **HM630104**; *Salicornia dolichostachya* Moss, Spie 2, AY270125; *Salsola canescens* (Moq.) Spach, chen 110, AY270127; *Salsola genitoides* Juss. ex Poir., chen 281, AY270128; *Salsola kali* L., chen 059, AY270129; *Salsola laricifolia* Litv. ex Drobov, chen 249, AY270130; *Salsola soda* L., chen 109, *H. Freitag 27.205* (KAS), Spain, Sevilla prov., sw of Venta de la Cruz, **HM630105**; *Salsola vermiculata* L., chen 072, AY270131; *Sarcocornia blackiana* (Ulbr.) A.J. Scott, chen 292, AY270149; *Sarcocornia utahensis* (Tidestr.) A.J. Scott, *D. Pratt 196*, AY270126; *Scleroblitum atriplicinum* (F. Muell.) Ulbr., chen 274, AY270044; *Sclerolaena obliquispis* (R. Anders.) Ulbr., chen 027, AY270132; *Sericostachys scandens* Gilg & Lopr., AC 042, AY270134; *Spinacia oleracea* L., Zurawski et al. (1981); *Suaeda altissima* (L.) Pall., chen 121, AY270135; *Suaeda aralocaspica* (Bunge) Freitag & Schütze (= *Borszczowia aralocaspica* Bunge), chen 145, AY270066; *Suaeda crassifolia* (Pall.), chen 147, AY270136; *Suaeda linifolia* Pall., chen 862, *H. Freitag 28.092* (KAS), N.W. Kazakhstan, Ural'sk prov., Shalkar lake, **HM630106**; *Suaeda maritima* ("macrocarpa") (L.) Dumort., chen 146, AY270137; *Sympegma regelii* Bunge, chen 036, AY270138; *Tecticornia australasica* (Moq.) Paul G. Wilson, chen 260, AY270139; *Tecticornia disarticulata* (Paul G. Wilson) K.A. Sheph. & Paul G. Wilson, chen 289, *S. Jacobs 8729* (NSW), Australia, New South Wales, North Far Western Plains, near Tibooburra, **HM630107**; *Tecticornia indica* (Willd.) K.A. Sheph. & Paul G. Wilson (= *Halosarcia indica* (Willd.) Paul G. Wilson), chen 123, AY270096; *Tecticornia peltata* (Paul G. Wilson) K.A. Sheph. & Paul G. Wilson (formerly misidentified as *Halosarcia montiformis* Paul G. Wilson), chen 160, AY270133; *Tecticornia triandra* (F. Muell.) K.A. Sheph. & Paul G. Wilson (= *Pachycornia triandra* (F. Muell.) J. Black), chen 265, AY270047; *Teloxys aristata* (L.) Moq., chen 293, AY270140; *Tidestromia lagunosa* (Nutt.) Standl., AC 052, AY270141;
- ndhF**: *Agathophora alopecuroides* Bunge, chen 300, *H. Freitag 30.108* (KAS), N.Jordan, 140 km e of Irbid at road Irbid-Safawi, **HM630036**; *Agriophyllum squarrosum* (L.) Moq., chen 054, AY858623; *Amaranthus palmeri* S. Watson., AF194821; *Anabasis aphylla* L., chen 022, *H. Freitag 28.117* (KAS), Kazakhstan, Ural'sk prov., near Kalmykovo at Ural river, **HM630037**; *Anthochlamys multinervis* Rech. f., chen 042, *H. Freitag 13.979* (KAS), Iran, Kavir Nat. Park, near Mobarakiyeh, **HM630038**; *Aphanisma blitoides* Nutt. ex Moq., chen 310, AY858628; *Arthrocnemum macrostachyum* (Moric.) K. Koch, chen 2002/7, AY858619; *Atriplex spongiosa* F. Muell., chen 158, Hort. Bot. Berg. Stockholm 117; 0006303, **HM630039**; *Axyris prostrata* L., chen 118, AY858615; *Bassia dasyphylla* (Fisch. & C.A. Mey.) Kuntze, chen 131, G. & S. Miede 96-203-02 (Hb. Miede, KAS), Mongolia, Gobi Altai, **HM630040**; *Bassia sedoides* (Pall.) Asch., chen 128, *H. Freitag 28.035* (KAS), NW.Kazakhstan, Ural'sk, prov., Shalkar lake, **HM630041**; *Beta vulgaris* L., *G. Kadereit 99/255* (MJG), N-Germany, Baltic Sea, **HM630042**; *Bienertia cycloptera* Bunge, chen 144, DQ097399; *Bosea yervamora* L., AC 072, DQ097397; *Camphorosma lessingii* Litv., chen 369, DQ097398; *Charpentiera obovata* Gaudich., *B.A. Prigge 15251*, AY858621; *Chenoleoides tomentosa* (Lowe) Botsch., chen 137, *H. Freitag 27.256* (KAS), Spain, Canary Is., Lanzarote, **HM630043**; *Chenopodium acuminatum* Willd., chen 183, AY858614; *Climacoptera brassia* (M. Bieb.) Botsch., chen 083, DQ097403; *Corispermum filifolium* C.A. Mey. ex A.K. Becker, chen 148, *H. Freitag 28.702* (KAS), N.Turkey, Samsun prov., near Bafra, **HM630044**; *Cornulaca monacantha* Delile, chen 373, *Mathew 2946* (KTUH), Kuwait, 10 km from Al-Subiah-Kuwait city road, **HM630045**; *Cyathobasis fruticulosa* (Bunge) Aellen, chen 082, *H. Freitag 28.887* (KAS), C. Turkey, Kayseri prov., near Yeşilhisar, **HM630046**; *Cycloloma atriplicifolia* J.M. Coult. (GCI), chen 157, Bot. Garden Kassel, seeds from Hort. Bot. Berg. Stockholm 116; 0006302 (KAS), **HM630047**; *Dissocarpus paradoxus* (R. Br.) Ulbr., chen 163, DQ097404; *Dysphantia glomulifera* (Nees) Paul G. Wilson, chen 277, *S. Jacobs 8738* (NSW), Australia, New South Wales, North Western Plains, **HM630048**; *Enchylaena tomentosa* R. Br., chen 166, *N. Schmalz 214* (MJG), Australia., North. Territ., Uluru Nat. Park, **HM630049**; *Girgensohnia oppositiflora* Fenzl., chen 033, *H. Freitag 26.282* (KAS), Kazakhstan, 60 km w of Almaty, **HM630050**; *Hablitzia tamnoides* M. Bieb., chen 361, Bot. Garden Mainz (MJG), **HM630051**; *Halocnemum strobilaceum* (Pall.) M. Bieb., chen 324, AY858616; *Haloepelis perfoliata* Bunge ex Schweinf. & Asch., chen 400, AY858617; *Halothamnus bottae* Jaub. & Spach, chen 351, *N. Kilian 4499* (B), Yemen, Socotra, **HM630052**; *Kalidium caspicum* (L.) Ung.-Sternb., chen 089, AY858618; *Kochia americana* S. Watson, chen 076 + 370, DQ097402; *Kochia saxicola* Guss., chen 013, Bot. Garden Kassel (KAS), from Italy, Capri Is., **HM630053**; *Microgynoecium tibeticum* Hook. f., chen 874, G. & S. Miede 03-059-11 (Hb. Miede, KAS), China, Xizang (Tibet), Tso basin s of Raka Tsangpo Tsabasang, **HM630054**; *Monolepis nuttalliana* Greene, chen 125, Bot. Garden Kassel, seeds from Univ. Hohenheim (KAS), **HM630055**; *Nanophyton erinaceum* Bunge, chen 301, *Lomonosova 2001/16* (NS, KAS), E.Kazakhstan, Zaisan dist., Shilikta valley, **HM630056**; *Nitrophila occidentalis* S. Watson, chen 204, AY959893; *Noaea mucronata* (Forssk.) Asch. & Schweinf., chen 019, *H. Freitag 28.716* (KAS), N.Turkey, Çorum prov., near Sungurlu, **HM630057**; *Pandera pilosa* Fisch. & C.A. Mey., chen 141, *H. Freitag 18.894* (KAS), Pakistan, Baluchistan prov. near Kalat, **HM630058**; *Petrosimonia brachiata* Bunge, chen 084, *H. Freitag 28.621* (KAS), E.Turkey, Kars prov., Aras valley near Kağızman, **HM630059**; *Suaeda aralocaspica* (Bunge) Freitag & Schütze (= *Borszczowia aralocaspica* Bunge), chen 145, AY270066; *Pleuropetalum sprucei* Standl., chen AC 020, AY959891; *Polycnemum perenne* Litv., chen 078, AY858634; *Rhaphidophyton regelii* (Bunge) Iljin, chen 075, *Baranov 364* (TASM), Kazakhstan, Karatau Mts., **HM630060**; *Salicornia* sp., chen 357, AY858620; *Salsola arbuscula* Pall., chen 185, *Freitag 27.015* (KAS), N.Tadzhikistan, Fergana valley, 30–35 km ene of Khodzhtent, **HM630061**; *Salsola arbusculiformis* Drob., chen 176, *H. Freitag 26.210* (KAS), SE.Kazakhstan, Taldy-Kurgan dist., 60 km w Dzharkent (Panfilov) at road to Saryozek, **HM630062**; *Salsola canescens* (Moq.) Spach, chen 110, DQ097405; *Salsola cyrenaica* Maire & Weiller subsp. *antalyensis* Freitag & Duman, chen 354, *Duman 6838* (GAZI, KAS), S.Turkey, Antalya prov., betw. Finike and Kale, **HM630063**; *Salsola genitoides* Juss. ex Poir., chen 281, *J. Hensen s.n.* (KAS), Spain, Almería prov., Campo de Tabernas, **HM630064**; *Salsola gossypina* Bunge ex Boiss., chen 106, *Moussavi & Tehrani s.n.* (TARI, KAS), **HM630065**; *Salsola griffithii* (Bunge) Freitag & Khani, chen 206, *H. Freitag 18.595* (KAS) Pakistan, Baluchistan prov., Makran, 60 km ssw of Panjgur, **HM630066**; *Salsola gymnosachala* Maire ex Zolotar. & Murat, chen 355, *J. Escallier s.n.* (TFMC), SW.Morocco, Atlantic coast near Sidi Ifni, **HM630067**; *Salsola kali* L., chen 059, DQ097401; *Salsola laricifolia* Turcz. ex Litv. chen 249, *Helmecke s.n.* (HAL), Mongolia, Aimak Omnogobi, **HM630068**; *Salsola merxmulleri* Aellen, chen 221, *L. Mucina 6905/4* (KAS), S.Africa, Western Cape prov., Rocher Pan, **HM630069**; *Salsola monoptera* Bunge, chen 177, *B. Dickoré 4681* (M), China, Xizang (Tibet), **HM630070**; *Salsola oppositifolia* Desf., chen 495, *Z. Turki s.n.* (KAPIS), N.W.Egypt, coast near Sollum, **HM630071**; *Salsola papillosa* Willk., chen 098, *H. Freitag 27.231* (KAS), Spain, Almería prov., 20 km sw of Almería, **HM630072**; *Salsola soda* (L.) Pall., chen 109, *H. Freitag 27.205* (KAS), Spain, Sevilla prov., Guadaluquivir valley, Isla Mayor, **HM630073**; *Salsola spinescens* Moq., chen 349, *N. Kilian 3642* (B), Yemen, Socotra, **HM630074**; *Salsola turkestanica* Litv., chen 181, *H. Freitag 27.012* (KAS), NE.Tadzhikistan, Fergana valley 30–35 km ene of Khodzhtent, **HM630075**; *Salsola verrucosa* M. Bieb., chen 201, *H. Freitag 28.606* (KAS), E.Turkey, Kars prov., 6 km nw of Kağızman, **HM630076**; *Salsola webbia* Moq., chen 380 (no voucher), *L. Baena s.n.* 9.9.2003 (fresh leaf sample), Spain, Granada prov., Cabo Sacratif, **HM630077**; *Scleroblitum atriplicinum* (F. Muell.) Ulbr., chen 274, AY858611; *Sclerolaena diacantha* Benth., chen 165, *N. Schmalz 239* (MJG) Australia, North. Territ., Kulgera, **HM630078**; *Spinacia oleracea* L., AY090621; *Suaeda altissima* Pall., chen 121, *H. Freitag 28.601* (KAS), E.Turkey, Erzincan prov., 6 km ese of Erzincan, **HM630079**; *Suaeda maritima* (L.) Dumort., chen 146, DQ097400; *Sympegma regelii* Bunge, chen 036, DQ097406; *Teloxys aristata* (L.) Moq., chen 293, AY858612; *Traganum moquini* Webb. ex Moq., chen 026, *H. Freitag 27.274* (KAS), Spain, Canary Is., Lanzarote, **HM630080**;
- atpB-rbcL spacer**: *Allenrolfea occidentalis* (S. Watson) Kuntze, AY181810; *Anabasis articulata* (Forssk.) Moq., chen 1227, *G. Kadereit & J.W. Kadereit 2006/5* (MJG), Spain, Almería prov., Cabo de Gata, **HM629974**; *Bassia eriophora* (Schrud.) Asch., chen 129, *Mathew 2794* (KTUH, KAS), Kuwait, Sulaiqbikhat,

## Appendix. Continued.

**HM629975**; *Bassia dasphylla* (Fisch. & C.A. Mey.) Kuntze, chen 131, G. & S. Miede 96-203-02 (KAS, hb. Miede), Mongolia, Gobi Altai, **HM629976**; *Bassia hirsuta* (L.) Asch., chen 014, H. Freitag 28.077 (KAS), NW.Kazakhstan, Ural'sk prov., Shalkar lake, **HM629977**; *Bassia hyssopifolia* (Pall.) Volkens, chen 150, H. Freitag 30.046 (KAS), Uzbekistan, near Tashkent, **HM629978**; *Bassia muricata* (L.) Asch., chen 130, M. Al-Dosari 1664 (KTUH, KAS), Kuwait, **HM629979**; *Bassia sedoides* (Pall.) Asch., chen 128, H. Freitag 28.035 (KAS), NW. Kazakhstan, Ural'sk prov., Shalkar lake, **HM629980**; *Bienertia cycloptera* Bunge, chen 144, H. Akhani s.n. (Hb. Akhani, KAS), Iran, Kavir Nat.Park near Mobarakiyeh, **HM629981**; *Camphorosma annua* Pall., chen 358, G. Kadereit 2003/2 (MJG), Hortobágyi Nat. Park, Hungary, **HM629982**; *Camphorosma monspeliaca* L., chen 053, H. Freitag 31.152 (KAS), Syria, 60 km ne of Damascus, **HM629983**; *Camphorosma lessingii* Litv., chen 369, H. Freitag 28.799 (KAS), Turkey B4, Aksaray prov., southern edge of Tuz Gölü near Eskil, **HM629984**; *Camphorosma songorica* Pall., chen 140, H. Freitag 28.034 (KAS), NW.Kazakhstan, Ural'sk prov., beside Shalkar lake, **HM629985**; *Chenolea diffusa* Thunb., chen 279, L. Mucina 6914/1 (MJG; KAS), S. Africa, Western Cape prov., **HM629986**; *Chenoleoides arabica* (Boiss) Botsch., chen 244, A. Danin 12.2000, Israel, Sinai, Arod, **HM629987**; *Chenoleoides tomentosa* (Lowe) Botsch., chen 137, H. Freitag 27.256 (KAS), Spain, Canary Is., Lanzarote, **HM629988**; *Climacoptera crassa* (M. Bieb.) Botsch. s.l., chen 083, H. Freitag 30.115 (KAS), Uzbekistan, Gulistan ssw of Tashkent, **HM629989**; *Dissocarpus biflorus* F. Muell. var. *biflorus*, chen 287, S. Jacobs 8726 (NSW), Australia, New South Wales, North Far Western Plains, Sturt Nat. Park., **HM629990**; *Haloepelis perfoliata* (Forssk.) Bunge ex Schweinf. & Asch., chen 400, H. Freitag & G. Kothe 18.546 (KAS), Pakistan, Baluchistan prov., Makran Coastal Plain near Jivani, **HM629991**; *Kalidium foliatum* (Pall.) Moq., chen 021, AY181809; *Kirilowia eriantha* Bunge, chen 371, K.H. Rechinger 17.705 (W), Afghanistan, Ghazni prov., near Okak, **HM629992**; *Kochia scoparia* (L.) Schrad. (= *K. alata* J.M. Bates, chen 378, *Libing Zhang s.n.* (no voucher), U.S.A., Colorado, Fort Collins, foothill, **HM629993**; *Kochia angustifolia* (Turcz.) Peschkova, chen 341, W. Hilbig 9/02 (KAS, hb. Hilbig), E.Mongolia, Dornod dist., 50–60 km E Choybalsan, **HM629994**; *Kochia densiflora* (Moq.) Aellen, chen 342, W. Hilbig 75/02 (KAS, hb. Hilbig), Mongolia, E.Mongolia, Dornod dist., wnw of Sangjiu-dalai nuur, **HM629995**; *Kochia indica* Wight, chen 398, H. Freitag 7462 (KAS), E.Afghanistan, Jalalabad, **HM629996**; *Kochia iranica* Schrenk., chen 343, Freitag 26.472b (KAS), Kazakhstan, Kzyl-Orda dist., near Zhana Darya, **HM629997**; *Kochia krylovii* Litv., chen 307, A. Ebel s.n. (HAL, KAS), Mongolia, Kobdo dist., **HM629998**; *Kochia laniflora* (S.G. Gmel.) Borb., chen 136, H. Freitag 28.310 (KAS), Russia, Saratov prov., Krasnyi Kut, **HM629999**; *Kochia melanoptera* Bunge, chen 306, M. Lomonosova 175/2001 (NS, KAS), E.Kazakhstan, Zaisan dist., **HM630000**; *Kochia odontoptera* Schrenk., chen 344, H. Freitag 26.472a (KAS), Kazakhstan, Kzyl-Orda dist., near Zhana Darya, **HM630001**; *Kochia prostrata* (L.) Schrad., chen 031, H. Freitag 28.254 (KAS), Russia, Volgograd prov., El'ton lake, **HM630002**; *Kochia saxicola* Guss., chen 013, cult. in Kassel (KAS), from Italy, Capri Is., **HM630003**; *Kochia scoparia* (L.) Schrad., chen 149, H. Freitag 30.145 (KAS), Uzbekistan, near Tashkent, **HM630004**; *Kochia stellaris* Moq., chen 135, H. Freitag 18.911 (KAS), Pakistan, Baluchistan prov., Kalat dist., **HM630005**; *Kochia tianschanica* Pavl., chen 345, H. Freitag 26.419 (KAS), Kazakhstan, Chimkent dist., Karatau Mts. near Osyk, **HM630006**; *Kochia villosissima* (Bong. & C.A. Mey.) Serg. (= *K. prostrata* var. *villosissima* Bong. & C.A. Mey., chen 348, M. Lomonosova 130 (NS, KAS), E.Kazakhstan, Kurchum dist., Bukumbai Mts., **HM630007**; *Maireana erioclada* (Benth.) Paul G. Wilson, chen 264, S. Jacobs 8699 (NSW), Australia, New South Wales, South Far Western Plains, near Balranald, **HM630008**; *Microcnemum coralloides* (Loscovs & Pardo) Font Quer, chen 1354, AY181811; *Neokochia californica* (S. Watson) G.L. Chu & S.C. Sand., chen 515, E. Cypher s.n. 05.08.2004 (KAS), U.S.A., California, Fresno Co., **HM630009**; *Noaea mucronata* (Forssk.) Asch. & Schweinf., chen 019, H. Freitag & N. Adigüzel 28.716 (KAS), Turkey A5, Çorum prov., 16 km WSW Sungurlu, **HM630010**; *Osteocarpum dipterocarpum* (F. Muell.) Volkens, chen 290, S. Jacobs 8731 (NSW), Australia, New South Wales, North Far Western Plains, near Tibooburra, **HM630011**; *Pandertia pilosa* Fisch. & C.A. Mey., chen 141, H. Freitag & G. Kothe 18.894 (KAS), Pakistan, Baluchistan prov., Kalat, **HM630012**; *Salicornia europaea* L., AY181815; *Salsola canescens* (Moq.) Spach, chen 110, H. Freitag 28.800 (KAS, GAZI), C.Turkey, Aksaray prov., southern edge of Tuz Gölü, **HM630013**; *Salsola genistoides* Juss. ex Poir., chen 1362, G. Kadereit 2006/19 (MJG), Spain, Almería prov., Sierra de Alhamilla, **HM630014**; *Salsola kali* L., chen 1734, G. Kadereit 2000/103 (MJG), Denmark, Jütland prov., Fjerritslev, **HM630015**; *Salsola soda* L., chen 109, H. Freitag 27.205 (KAS) Spain, Sevilla prov., Guadalquivir valley, Isla Mayor, **HM630016**; *Salsola webbii* Moq., chen 380 (no voucher), L. Baena s.n. 9.9.2003 (fresh leaf sample), Spain, Granada prov., Cabo Sacratif, **HM630017**; *Sclerolaena diacantha* (Nees) Benth., chen 165, N. Schmalz 239 (MJG), Australia, North Territ., Kulgera, **HM630018**; *Suaeda linifolia* Pall., chen 862, AY181805; *Suaeda maritima* (L.) Dumort., AY181758; *Tecticornia australasica* (Moq.) Paul G. Wilson, chen 260, AY181812;

**ITS**: *Bassia dasphylla* (Fisch. & C.A. Mey.) Kuntze, chen 131, AY489195; *Bassia hirsuta* (L.) Asch., chen 014, AY489196; *Bassia hyssopifolia* (Pall.) Volkens, chen 150, AY489197; *Bassia muricata* (L.) Asch., chen 130, AY489198; *Bassia sedoides* Kuntze, chen 128, AY489199; *Camphorosma annua* Pall., chen 358, G. Kadereit 2003/2 (MJG), Hortobágyi National Parc, Hungary, **HM630019**; *Camphorosma lessingii* Litv., chen 369 (KAS), H. Freitag 31.152, 60 km ne of Damascus, Syria, **HM630020**; *Camphorosma lessingii* Litv., chen 360, H. Freitag 28.799 (KAS), Turkey B4, Aksaray prov., S edge of Tuz Gölü near Eskil, **HM630021**; *Camphorosma monspeliaca* L., chen 053, AY489200; *Camphorosma songorica* Pall., chen 140, AY489201; *Chenolea diffusa* Thunb., chen 139, AY489202; *Chenoleoides arabica* (Boiss) Botsch., chen 138, AY489203; *Chenoleoides dinteri* (Botsch.) Botsch., chen 514, N. Jürgens 22636 (PRE), Richtersveld, Boegoe Twin South, South Africa, **HM630022**; *Chenoleoides tomentosa* (Lowe) Botsch., chen 137, AY489204; *Dissocarpus biflorus* F. Muell., chen 287, AY489205; *Kirilowia eriantha* Bunge, chen 074, AY489209; *K. alata* Bates → see *Kochia scoparia* (L.) Schrad.; *Kochia americana* S. Watson, chen 076, AY489210; *Kochia angustifolia* (Turcz.) Peschkova, chen 346, Lomonosova s.n. 09/1989 (NS, KAS), Russia, Tuva Rep., Cheder lake, **HM630023**; *Kochia angustifolia* (Turcz.) Peschkova, chen 341, W. Hilbig 9/02 (KAS, hb. Hilbig), E.Mongolia, Dornod dist., 50–60 km e of Choybalsan, **HM630024**; *Kochia densiflora* → see *Kochia scoparia*; *Kochia indica* Wight, chen 512, H. Freitag 7462 (KAS), E.Afghanistan, near Jalalabad, **HM630026**; *Kochia iranica* Bornm., chen 343, H. Freitag 26.472b (KAS); Kazakhstan, Kzyl-Orda dist., near Zhana Darya, **HM630027**; *Kochia laniflora* Borbás, chen 136, AY489214; *Kochia melanoptera* Bunge, chen 306, AY489215; *Kochia odontoptera* Schrenk., chen 344, H. Freitag 26.472a (KAS), Kazakhstan, Kzyl-Orda dist., near Zhana Darya, **HM630028**; *Kochia prostrata* (L.) Schrad., chen 031, AY489216; *Kochia prostrata* (L.) Schrad., chen 132, Miede 96-038-05 (KAS, Hb. Miede), Mongolia, Gobi Altai, **HM630029**; *Kochia salsoloides* Fenzl, chen 584, DAMB Shearing 1356 (PRE), S. Africa, Cape Prov., Beaufort West dist., **HM630030**; *Kochia saxicola* Guss. chen 013, AY489217; *Kochia scoparia* (L.) Schrad. (= *K. densiflora* auct.), chen 133, AY489212; *Kochia scoparia* (L.) Schrad. (= *K. densiflora* auct.), chen 342, W. Hilbig 75/02 (HAL, KAS), E.Mongolia, Dornod dist., wnw of Sangjiu-dalai nuur, **HM630025**; *Kochia scoparia* (L.) Schrad., chen 149, AY489218; *Kochia scoparia* (L.) Schrad. (syn. *K. alata* Bates), chen 378, *Libing Zhang s.n.* (21. Aug. 2003; no voucher), U.S.A., Colorado, Fort Collins, foothill, **HM630031**; *Kochia scoparia* (L.) Schrad. (syn. *K. alata* Bates), chen 401, Th. Borsch & al. 3429 (BONN, KAS), U.S.A., New Mexico, Dona Ana, **HM630032**; *Kochia stellaris* Moq., chen 135, AY489219; *Kochia tianschanica* Pavlov ex Iljin, chen 345, H. Freitag 26.419 (KAS), Kazakhstan, Chimkent dist., Karatau Mts., foothills near Osyk, **HM630033**; *Kochia villosissima* (Bong & C.A. Mey.) Serg., chen 348, M. Lomonosova 130 (NS, KAS), E.Kazakhstan, Kurchum dist., Bukumbai Mts., **HM630034**; *Maireana brevifolia* (R. Br.) Paul G. Wilson, chen 430, EF613600; *Maireana erioclada* (Benth.) Paul G. Wilson, chen 264, AY489222; *Neokochia californica* (S. Watson) G.L. Chu & S.C. Sand., chen 515, E. Cypher s.n. 05.08.2004 (KAS), U.S.A., California, Fresno Co., **HM630035**; *Osteocarpum dipterocarpum* (F. Muell.) Volkens, chen 290, AY489226; *Pandertia pilosa* Fisch. & C.A. Mey., chen 141, AY489227; *Sclerolaena diacantha* (Nees) Benth., chen 165, AY489231;

**psbB-psbH spacer**: *Bassia dasphylla* Kuntze, chen 131, G. & S. Miede 96-203-02 (Hb. Miede, KAS), Mongolia, Gobi Altai, **HM630081**; *Bassia hirsuta* (L.) Asch., chen 014, H. Freitag 28.077 (KAS), NW.Kazakhstan, Ural'sk prov., Shalkar lake, **HM630082**; *Bassia sedoides* Schrad., chen 128, H. Freitag 28.035 (KAS), NW.Kazakhstan, Ural'sk prov., Shalkar lake, **HM630083**; *Chenolea diffusa* Thunb., chen 279, L. Mucina 6914/1 (MJG; KAS), S. Africa, Western Cape prov., **HM630084**; *Kochia saxicola* Gruss., chen 013, cultivated at Bot. Garden Kassel (KAS), from Italy, Capri Is., **HM630086**; *Nanophyton erinaceum* (Pall.) Bunge s.l., chen 1346, B. Neuffer & al. OSBU 18050 (OSBU), Russia, Tuva Rep., slopes w of Kysyl, **HM630088**; *Nanophyton grubovii* U. Prato, chen 347, M. Lomonosova s.n. Sept 1989 (NS, KAS), Russia, Tuva Rep., Ersin dist., Khol'vill., **HM630087**; *Neokochia americana* (S. Watson) G.L. Chu & S.C. Sand., chen 076 + 370, Breckle 2756 (KAS), U.S.A., Utah, Box Elder Co., Curlew Valley, **HM630091**; *Neokochia californica* (S. Watson) G.L. Chu & S.C. Sand., chen 515, E. Cypher s.n. 05.08.2004 (KAS), U.S.A., California, Fresno Co., **HM630085**; *Osteocarpum dipterocarpum* (F. Muell.) Volkens, chen 290, S. Jacobs 8731 (NSW), Australia, New South Wales, North Far Western Plains near Tibooburra, **HM630089**; *Salsola genistoides* Juss. ex Poir., chen 1362, G. Kadereit 2006/19 (MJG), Spain, Almería prov., Sierra de Alhamilla, **HM630090**; for all other accessions and of the *psbB-psbH* spacer tree we refer to Akhani & al. (2007).