SYSTEMATICS AND PHYLOGENY

Phylogeny, biogeography and systematics of Dysphanieae (Amaranthaceae)

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Abstract After a rather turbulent taxonomic history, Dysphanieae (Chenopodioideae, Amaranthaceae) were established to contain five genera, four of which are monospecific (*Cycloloma*, *Neomonolepis*, *Suckleya*, *Teloxys*) and geographically restricted, and the fifth genus, *Dysphania*, having a nearly worldwide distribution and comprising ca. 50 species. This study investigates the phylogeny, biogeography and taxonomy of Dysphanieae. We studied specimens from 32 herbaria to infer morphological differences and distribution areas of the species and sampled 121 accessions representing 39 accepted species of the tribe for molecular phylogenetic analyses. The molecular phylogeny tested generic relationships of the tribe and infrageneric relationships of *Dysphania* on the basis of two plastid DNA markers (*atpB-rbcL* spacer, *rpl16* intron) and two nuclear ribosomal markers (ETS, ITS) and was also used for an ancestral area reconstruction with BioGeoBEARS. Three of the monospecific genera (*Neomonolepis*, *Suckleya*, *Teloxys*) form a basal grade and appear to be relictual lineages of the tribe, while *Cycloloma* is nested within *Dysphania*. The ancestral area reconstruction favors a widespread ancestry for Dysphanieae, and the relictual lineages in Asia (*Teloxys*) and North America (*Neomonolepis*, *Suckleya*) might be explained by a wide distribution across Beringia during the Late Oligocene/Early Miocene. *Dysphania* likely originated in North America; however, the simultaneous diversification into three major clades, an Asian/African, an American and an Australian/African clade, indicates a widespread ancestor at the crown node of *Dysphania*. Our taxonomic revision results in four accepted genera in Dysphanieae, *Dysphania*, *Neomonolepis*, *Suckleya* and *Teloxys*. The sectional subdivision for *Dysphania* is revised. We subdivide the genus into five sections, *D.* sect. *Adenois* (13 spp.), *D.* sect. *Botryoides* (10 spp.), *D.* sect. *Dysphania* (17 spp.), *D.* sect. *Incisa* (2 spp.) and *D.* sect. *Margaritaria* (4 spp.); three strongly deviating species remain unplaced and need further attention.

Keywords *Cycloloma*; *Dysphania*; infrageneric classification; long-distance dispersal; molecular clock; molecular phylogeny; *Neomonolepis*; *Suckleya*; taxonomy; *Teloxys*

Supporting Information may be found online in the Supporting Information section at the end of the article.

INTRODUCTION

Dysphanieae is a tribe of subfam. Chenopodioideae belonging to the now widely circumscribed Amaranthaceae (incl. Chenopodiaceae: Morales-Briones & al., 2020). According to extensive molecular studies, it includes the genus *Dysphania* R.Br. and four monotypic genera: *Cycloloma* Moq., *Neomonolepis* Sukhor., *Suckleya* A.Gray and *Teloxys* Moq. (Kadereit & al., 2010; Fuentes-Bazan & al., 2012a,b; Sukhorukov & al., 2018a). The vast majority of the members of Dysphanieae were previously part of *Chenopodium* L. s.l., with many species transferred from *Chenopodium* to *Dysphania* by Mosyakin & Clemants (2002, 2008), Verloove & Lambinon (2006) and Uotila (2013). Further investigations based on morphological and carpological data allowed the description of new species of *Dysphania* from the Himalayas and Tibet (Sukhorukov, 2012b, 2014; Uotila, 2013; Sukhorukov & al., 2015), and Australia (Dillon & Markey, 2017), and to confirm or contradict

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the species status of some taxa (Sukhorukov & al., 2018b, 2019a,b). To date, *Dysphania* is one of the largest genera in Chenopodioideae, comprising ca. 50 species (Sukhorukov & al., 2018b).

Dysphanieae is geographically widespread on all continents excluding Antarctica, with predominant distribution in the subtropics and tropical mountainous deserts (Fig. 1). The greatest species diversity, all *Dysphania*, is in Australia and New Zealand with 17 native and three naturalized species (Wilson, 1984; Shepherd & Wilson, 2008). In North America, there are seven native species in four genera, including the monospecific *Cycloloma* (Mosyakin, 2003), *Neomonolepis* (Holmgren, 2003, as part of *Monolepis*) and *Suckleya* (Chu, 2003), and eight naturalized species in two genera, including *Teloxys* (Clemants & Mosyakin, 2003). In South America (plus Tristan da Cunha), there are at least 12 native species and three aliens (including *Cycloloma*) documented (Aellen, 1973; Simón, 1996; Múlgura & Marticorena, 2008). The centre of diversity of *Dysphania* in Asia has been recently revealed in the Himalayas and Tibet, where eight native and two alien species occur (Uotila, 2013; Sukhorukov, 2014; Sukhorukov & Kushunina, 2014; Sukhorukov & al., 2015); in addition, one native species is widespread in South-West Asia (Uotila, 2013), and two more aliens have been reported from Iran (Rahiminejad & al., 2004), Japan (Clemants, 2006) and India (Ramayya & Rajagopal, 1969; Ravi & Anilkumar, 1990). *Teloxys* is widespread in the deserts of Central Asia, with many records in temperate Eurasia (e.g., Iljin & Aellen, 1936; Grubov, 1966; Sukhorukov, 2014). From the Arabian Peninsula, only three native and two introduced species are mentioned by Boulos (1996). The number of species given for Africa is relatively low: five native and four introduced species (three native and three introduced species in tropical Africa: Brenan, 1954; Lebrun & Stork, 1991; Friis & Gilbert, 2000; Sukhorukov & al., 2018b; one native and two introduced species in North Africa: Dobignard & Chatelain, 2011). Europe is the region poorest in native species including only *Dysphania botrys* (L.) Mosyakin & Clemants, but with a number of other Dysphanieae (*Cycloloma*, *Dysphania*, *Teloxys*) naturalized to at least some degree (Aellen, 1960; Uotila, 2001, 2011; Sukhorukov, 2014).

Almost all morphological characters of Dysphanieae (Fig. 2) are similar to many other members of Chenopodioideae; e.g., flat leaves, thyrsoid inflorescences, mostly three to five free or more or less fused perianth segments, short (0.2–0.3 mm) anthers, thin parenchymatous pericarp, subglobose to lenticular seeds with copious perisperm and usually annular embryo. However, most Dysphanieae, i.e., the species of *Dysphania*, are known to produce glandular white hairs and/or yellow or orange subsessile glands; these glands contain essential oils that provide a characteristic aromatic odour, often persisting in herbarium specimens for years. Four other genera, *Cycloloma*, *Neomonolepis*, *Suckleya* and *Teloxys*, are reported to lack such glands or glandular hairs, but *Suckleya* and *Teloxys* bear papillae that are rare in almost all other Chenopodioideae (Reimann & Breckle, 1988; Simón, 1997; Sukhorukov, 2012a, 2014). Pollen morphology is relatively

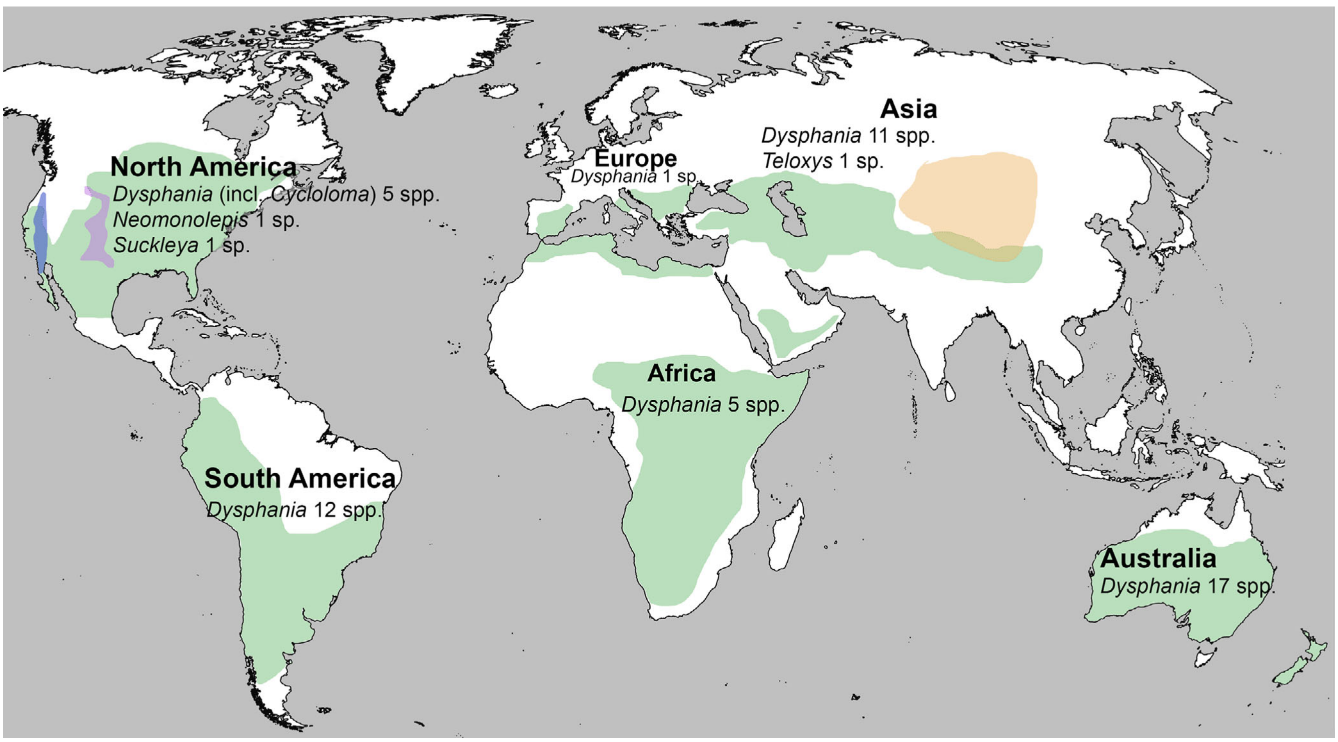

Fig. 1. Worldwide distribution and species diversity of Dysphanieae (green = *Dysphania* [incl. *Cycloloma*], blue = *Neomonolepis*, lilac = *Suckleya*, beige = *Teloxys*). Species numbers refer to species currently known. Only native species and native areas are included.

uniform in all Chenopodioideae, and species of Dysphanieae and Chenopodieae fall into the same group (e.g., Perveen & Qaiser, 2012). Mosyakin & Tsymbalyuk (2004) studied pollen of nine species of Dysphanieae and observed that pollen grains in *Dysphania* are morphologically rather uniform, but some species and groups of species can still be distinguished by their pollen morphology. Although *Dysphania* shares the same floral histogenesis with Chenopodieae (Mahabale & Solanky, 1954; Eckardt, 1967, 1968), a set of reproductive characters of Dysphanieae in its recent circumscription differentiates it from almost all other Chenopodioideae (Fuentes-Bazan & al., 2012b). Fruits and seeds of Dysphanieae are distinguished by different hairs and papillae (if present) on the pericarp surface and absence of cell wall stalactites in the exotestal layer of the seed coat (Sukhorukov & Zhang, 2013).

Two basic chromosome numbers have been reported for Dysphanieae, $x = 8$ and $x = 9$. Both *Suckleya suckleyana* (Torr.) Rydb. (Bassett & Crompton, 1970) and *Teloxys aristata* (L.) Moq. (e.g., Probatova & al., 2004; Ankova & Zykova, 2018) have $x = 9$ and are diploids with $2n = 18$. *Cycloloma atriplicifolium* (Spreng.) J.M.Coult. is reported to have a tetraploid number $2n = 36$ (Löve & Löve, 1982).

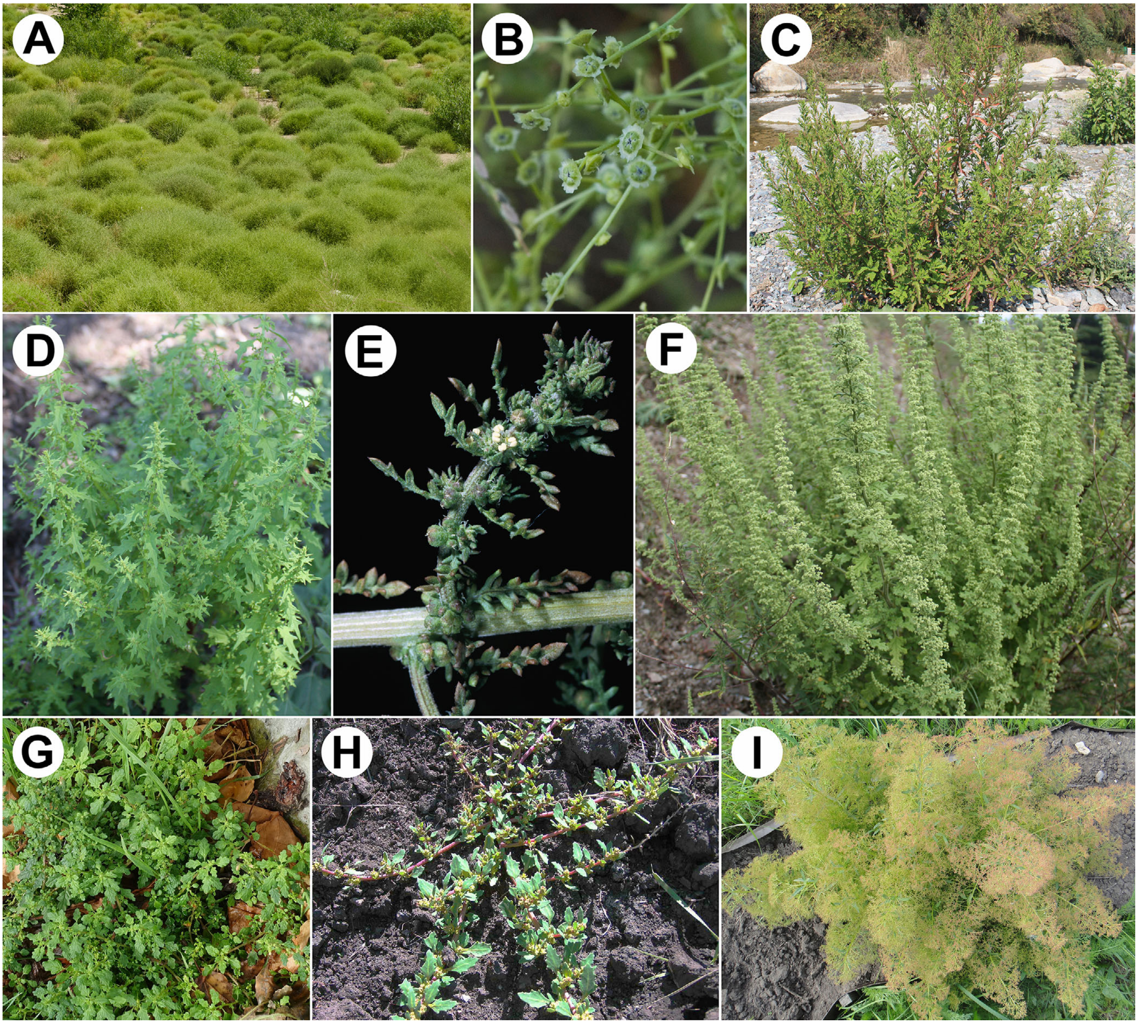

Fig. 2. Representative species of Dysphanieae. **A**, Population of *Cycloloma atriplicifolium*; **B**, Detail of the infructescence of *C. atriplicifolium*; U.S.A., Indiana Dunes State Park, 25 August 2012, M. Huft; **C**, *Dysphania ambrosioides*; India, Uttarakhand State, Dehradun, February 2017, A. Sukhorukov (reproduced by the written permission of PhytoKeys Editorial Office); **D**, *D. graveolens*; Mexico, Teotihuacan, September 2018, A. Sukhorukov; **E**, *D. multifida*; U.S.A., California, 2004, J. DiTomaso; **F**, *D. neglecta*; Nepal, Mid-West, Mugu Distr., September 2013, A. Sukhorukov; **G**, *D. pumilio*; Switzerland, Geneva, October 2019, P. Uotila; **H**, *Suckleya suckleyana*; Canada, Alberta Prov., Fort Macleod, 21 August 2005, R. Bielesch; **I**, *Teloxys aristata*; Russia, Irkutsk Prov., August 2017, E. Bayandina.

As to *Dysphania*, only small numbers of taxa have been studied, and, in addition, single counts only are available of several taxa. Further, misidentifications are common, and somatic polyploidy is possible (see Palomino & al., 1990), so the figures should be interpreted with caution, and not all reports have been accepted below. Most counts from American *Dysphania* species show the basic number $x = 8$. The tetraploid number $2n = 32$ has been reported for *D. multifida* (L.) Mosyakin & Clemants and *D. ambrosioides* (L.) Mosyakin & Clemants (Grozeva & Cvetanova, 2013 and references therein), *D. chilensis* (Schrad.) Mosyakin & Clemants (Voroshilov, 1942), *D. venturii* (Aellen) Mosyakin & Clemants (Giusti, 1988) and for *D. graveolens* (Willd.) Mosyakin & Clemants (e.g., Giusti, 1970; Keener, 1970). The octoploid number $2n = 64$ has been counted for *D. anthelmintica* (L.) Mosyakin & Clemants (Voroshilov, 1942; Kawatani & Ohno, 1950) and *D. retusa* (Juss. ex Moq.) Mosyakin & Clemants (Giusti, 1970). However, several counts indicate $x = 9$: the tetraploid number $2n = 36$ for *D. multifida* from Bulgaria (Grozeva & Cvetanova, 2013) and the hexaploid number $2n = 54$ for *D. mandonii* (S.Watson) Mosyakin & Clemants (Giusti, 1970). Reliable diploid counts do not seem to exist of American taxa.

Numerous counts of the Eurasiatic *D. botrys* and African/Arabian *D. schraderiana* (Schult.) Mosyakin & Clemants resulted in $x = 9$ and $2n = 18$ (e.g., Grozeva & Cvetanova, 2013 and references therein). A report of *D. procera* (Hochst. ex Moq.) Mosyakin & Clemants from Africa gives the tetraploid number $2n = 36$ (Auquier & Renard, 1975). The two studied Australian species are diploids, with both $x = 8$ and $x = 9$ reported: *D. pumilio* (R.Br.) Mosyakin & Clemants with $2n = 16$ (Giusti, 1970; Keener, 1974) and $2n = 18$ (many recent counts, e.g., Rahiminejad & al., 2004; Grozeva & Cvetanova, 2013), and *D. carinata* (R.Br.) Mosyakin & Clemants with $2n = 16$ (Kawatani & Ohno, 1962).

Some species of *Dysphania* produce secondary metabolites that play a role for human health, albeit in very different ways. *Dysphania ambrosioides* (Mexican tea), for example, contains essential oils used as tea, spice or in traditional medicine with numerous applications (e.g., Boutkhil & al., 2009 and references therein). Ascaridol is a major component of the essential oil and shows amoebicidal activity (Ávila-Blanco & al., 2014). *Dysphania botrys* is a traditional as well as a potentially new medicinal plant that might be explored for cancer treatment (Morteza-Semnani, 2015). Other species of *Dysphania*, *D. glomulifera* (Nees) Paul G.Wilson and *D. littoralis* R.Br., were shown to contain high concentrations of cyanid (McKenzie & al., 2007). The concentration in *Dysphania* plants, especially during dry seasons, is high enough to kill cattle and sheep after consuming less than 200 g of fresh plant (McKenzie & al., 2007).

Taxonomic history of *Dysphania* and related genera. — *Dysphania* was described by Robert Brown as a genus "related to chenopods" and consisted of one species, *D. littoralis* (Brown, 1810). Simultaneously with *Dysphania*, Brown (1810) described a new section *Orthosporum* R.Br. for Australian species of *Chenopodium* with a vertical seed embryo. Taxa of *Ch*. sect. *Orthosporum* were said to differ from *Dysphania* in the number of perianth lobes and stamens. Spach (1836) emphasised the aromatic odour of certain chenopods and placed them in two genera, *Ambrina* Spach and *Botrydium* Spach. In Moquin-Tandon (1840), the "hairy" taxa of the tribe Anserineae were recognized as several genera, such as *Ambrina*, *Cycloloma* and *Roubieva* Moq., but none of the "hairy" species was included in *Chenopodium*. However, Moquin-Tandon (1840) did not mention Australian taxa of *Chenopodium* sect. *Orthosporum*. Later, he regarded seed orientation position as a key character in the subtribal classification of tribus Chenopodieae (≡ Anserineae) (Moquin-Tandon, 1849). The genera with vertical seeds were included in subtribe 'Bliteae' and those with horizontal seeds in subtribe 'Beteae', independent of the type of indumentum (Table 1).

The placement of the genus *Dysphania* has been uncertain and far from constant (Table 1). Bentham & Hooker (1880) placed it in Illecebraceae (now a part of extended Caryophyllaceae: Greenberg & Donoghue, 2011). Pax (1889) described Dysphanieae as a tribe of Caryophyllaceae subfam. Alsinoideae and included only *Dysphania* with three species. Later, Pax (1927) claimed that *Dysphania* is intermediate between Chenopodiaceae and Caryophyllaceae, describing it as a family on its own, Dysphaniaceae. However, Aellen (1930a) pointed out that *Dysphania* has a close relationship to *Chenopodium*, and placed *Dysphania* as a section in *Chenopodium*, which already included *Ch*. sect. *Orthosporum* from Australia. He also divided *Dysphania* into two sections of *Chenopodium* by describing a new *Ch*. sect. *Tetrasepalae* Aellen for species with four sepals, i.e., *D. rhadinostachya* (F.Muell.) A.J.Scott and *D. inflata* (Aellen) A.J.Scott (= *D. rhadinostachya* subsp. *inflata* (Aellen) Paul G.Wilson), and reducing *Ch*. sect. *Dysphania* to include only the species with three sepals (Aellen, 1930b). He proposed that *Ch*. sect. *Tetrasepalae* is a link between *Ch*. sect. *Dysphania* and *Ch*. sect. *Orthosporum*. Black (1934) accepted Aellen's concept, but also raised the possibility of maintainig *Dysphania* as a genus that included the sections *Orthosporum* and *Tetrasepalae*. However, further taxonomic development led in an opposite direction: Pax & Hoffmann (1934) accepted the family Dysphaniaceae. Aellen (1961) subsequently changed his mind and treated his previous section at family level. Family status was later rendered superfluous by Eckardt (1967), who included *Dysphania* in Chenopodiaceae and regarded its generic status separate from *Chenopodium* as debatable. However, Scott (1978a) again recognized *Dysphania* as a separate genus and divided it into three sections (*D*. sect. *Dysphania*, sect. *Tetrasepalae* (Aellen) A.J. Scott, sect. *Caudatae* A.J.Scott) on the basis of the number of perianth segments and the orientation of the seed embryo. Even Kühn & al. (1993) accepted *Dysphania* as a genus in its traditional delimitation.

The four genera of the Anserineae (Moquin-Tandon, 1840) were added by Standley (1916), who described one more "glandular-pubescent" genus within Chenopodiaceae, *Meiomeria* Standl. Since then, the hairy species were treated in various ways as separate genera and sections or as a subgenus of

Chenopodium (Table 1). *Roubieva* and *Meiomeria* were later included in *Chenopodium* as sections. *Cycloloma* kept its generic rank, but was included in subfam. Camphorosmioideae by Scott (1978b), mainly because of the horizontal wing on the perianth segments, and was followed by Kühn & al. (1993). However, Mosyakin (2003) noted that the development of the wing in *Cycloloma* seems to be different from the mode of development of a similar wing (or other appendages) in taxa of Camphorosmioideae and expressed an opinion that *Cycloloma* is more closely related to *Chenopodium* in the broad sense. *Teloxys* was sometimes included in *Chenopodium* as a subsection or section (e.g., Iljin & Aellen, 1936; Aellen, 1960;

Table 1. Historical overview of classifications in the present Dysphanieae (Amaranthaceae). – Genera and sections belong to Chenopodiaceae tr. Chenopodieae if not otherwise stated (marked with bold). (Continued to the right on next page.)

Moquin-Tandon, 1840 (**Anserineae**)	Moquin-Tandon, 1849	Bentham & Hooker, 1880 (Euchenopodieae)	Pax, 1889 (**Caryophyllaceae**) Volkens, 1893 (Chenopodiaceae)	Standley, 1916	Pax & Hoffmann, 1934 (**Dysphaniaceae**) Ulbrich, 1934 (Chenopodioideae)
	Dysphania (Chenopodieae subtr. 'Bliteae')	*Dysphania* (**Illecebraceae tr. Pollichieae**)	*Dysphania* (**Caryophyllaceae subfam. Alsinoideae**)		*Dysphania* (**Dysphaniaceae**)
	Blitum sect. *Orthosporum* (Chenopodieae subtr. 'Bliteae')	*Chenopodium* sect. *Orthosporum*	*Chenopodium* sect. *Orthosporum*	*Chenopodium* [unranked] *Carinata*	*Chenopodium* sect. *Orthosporum*
					Chenopodium sect. *Tetrasepala*
Ambrina sect. *Adenoïs* (**Anserineae**)		*Chenopodium* sect. *Ambrina*	*Chenopodium* sect. *Ambrina*	*Chenopodium* [unranked] *Ambrosioidia*	*Chenopodium* sect. *Ambrina*
Roubieva (**Anserineae**)	*Roubieva* (Chenopodieae subtr. 'Bliteae')	*Roubieva*		*Roubieva*	*Chenopodium* sect. *Roubieva*
Cycloloma (**Anserineae**)	*Cycloloma* (Chenopodieae subtr. 'Beteae')	*Cycloloma*	*Cycloloma*	*Cycloloma*	*Cycloloma*
Ambrina sect. *Botryoïs* (**Anserineae**)	*Chenopodium* sect. *Botryoïs* (Chenopodieae subtr. 'Beteae')	*Chenopodium* sect. *Botrydium*	*Chenopodium* sect. *Botrydium*	*Chenopodium* [unranked] *Botryes*	*Chenopodium* sect. *Botryoides*
				Chenopodium [unranked] *Incisa*	
				Meiomeria	*Meiomeria*
			Monolepis p.p.	*Monolepis* p.p.	*Monolepis* p.p.
		Suckleya (**Atripliceae**)	*Suckleya* (**Atripliceae**)	*Suckleya* (**Atripliceae**)	*Suckleya* (**Atripliceae**)
Teloxys (**Anserineae**)	*Teloxys* (Chenopodieae subtr. 'Beteae')			*Chenopodium* [unranked] *Aristata*	*Teloxys*

Mosyakin, 1993). Furthermore, Moldenke (1946) described a new genus *Neobotrydium* Moldenke that was substituted for the illegitimate name *Botrydium*, with the single species *N. botrys* (L.) Moldenke (≡ *Dysphania botrys*).

Weber (1985) concluded that the glandular taxa of *Chenopodium* should be treated as a separate genus together with *Teloxys*, but did not consider *Dysphania* at all. Wilson (1983), after carefully studying the Australian species, discussed again the lack of clear differences between *Chenopodium* sect. *Orthosporum* and *Dysphania*, but he retained the generic division (Wilson, 1984). Later, disagreeing with Weber's suggestion that sect. *Orthosporum* should be placed in *Teloxys*, he wrote: "I consider the two groups to be generically distinct and that the American species should be placed in *Teloxys*

Table 1. Continued from the left from previous page.

Aellen, 1961 (**Dysphaniaceae**) Aellen, 1960 (Chenopodiaceae)	Scott, 1978a (Chenopodieae) Scott, 1978b (**Camphorosmeae**)	Simón, 1996 (*Chenopodium* subg. *Ambrosia*)	Mosyakin & Clemants, 2002 (Chenopodiaceae)	Zhu & Sanderson, 2017	This study (**Amaranthaceae tr. Dysphanieae**)
Dysphania (**Dysphaniaceae**)	*Dysphania* sect. *Dysphania* + sect. *Caudatae*		*Dysphania* sect. *Dysphania*	*Dysphania* (**Neobotrydieae**)	*Dysphania* sect. *Dysphania*
Chenopodium sect. *Orthosporum*	*Chenopodium* subg. *Ambrosia* sect. *Orthosporum*	*Chenopodium* subg. *Ambrosia* sect. *Orthosporum*	*Dysphania* sect. *Orthospora*		
Chenopodium sect. *Tetrasepala*	*Dysphania* sect. *Tetrasepala*				
Chenopodium sect. *Ambrina*	*Chenopodium* subg. *Ambrosia* sect. *Ambrina*	*Chenopodium* subg. *Ambrosia* sect. *Adenois* subsect. *Adenois*	*Dysphania* sect. *Adenois*	*Ambrina* (**Neobotrydieae**)	*Dysphania* sect. *Adenois*
Chenopodium sect. *Roubieva*	*Chenopodium* subg. *Ambrosia* sect. *Roubieva*	*Chenopodium* subg. *Ambrosia* sect. *Adenois* subsect. *Roubieva*	*Dysphania* sect. *Roubieva*	*Roubieva* (**Neobotrydieae**)	
Cycloloma	*Cycloloma* (**Camphorosmeae**)			*Cycloloma* (**Neobotrydieae**)	
Chenopodium sect. *Botryoides* subsect. *Botrys*	*Chenopodium* subg. *Ambrosia* sect. *Botryoides* subsect. *Botrys*	*Chenopodium* subg. *Ambrosia* sect. *Botryoides* subsect. *Botrys*	*Dysphania* sect. *Botryoides* subsect. *Botrys*	*Neobotrydium* (**Neobotrydieae**)	*Dysphania* sect. *Botryoides*
			Dysphania sect. *Botryoides* subsect. *Incisa*		*Dysphania* sect. *Incisa*
	Chenopodium subg. *Ambrosia* sect. *Margaritaria*	*Chenopodium* subg. *Ambrosia* sect. *Margaritaria*			*Dysphania* sect. *Margaritaria*
	Chenopodium subg. *Ambrosia* sect. *Meiomeria*	*Chenopodium* subg. *Ambrosia* sect. *Meiomeria*			unplaced
	Monolepis p.p.			*Monolepis* p.p. (Chenopodieae)	*Neomonolepis*
				Suckleya (Chenopodieae subtr. Suckleyinae)	*Suckleya*
Chenopodium sect. *Botryoides* subsect. *Teloxys*	*Chenopodium* subg. *Ambrosia* sect. *Botryoides* subsect. *Teloxys*	*Chenopodium* subg. *Ambrosia* sect. *Botryoides* subsect. *Teloxys*	*Dysphania* sect. *Botryoides* subsect. *Teloxys*	*Teloxys* (**Neobotrydieae**)	*Teloxys*

and the Australian in *Dysphania* (or *Dysphania* and *Orthosporum*)" (Wilson, 1987: 79).

Mosyakin & Clemants (2002, 2008) concluded that all species of *Chenopodium* with glandular hairs as well as *Teloxys* belong in *Dysphania*. Finally, based on morphological characters (indumentum, inflorescence details, seed embryo position), Zhang & Zhu (2016) and Zhu & Sanderson (2017) reinstated *Ambrina*, *Neobotrydium* and *Roubieva* at generic rank, and Zhu & Sanderson (2017) included them, with *Cycloloma* and *Dysphania*, in tribe Neobotrydieae G.L.Chu.

Kadereit & al. (2010) showed that the monotypic genus *Suckleya*, earlier generally included in Atripliceae, belongs to Dysphanieae, and Sukhorukov & al. (2018a) moved *Monolepis spathulata* A.Gray, a species of the small genus *Monolepis* Schrad. (at that time part of *Blitum* L.) to Dysphanieae as a monotypic genus *Neomonolepis*.

Objectives of this study. — The aims of this study are to (1) provide a robust phylogenetic tree of Dysphanieae based on two nuclear ribosomal and two plastid DNA markers including species representing all four genera of the tribe as well as a representative number of species from all sections of *Dysphania*, (2) conduct a biogeographical analysis of the tribe, (3) test the current generic classification of Dysphanieae, and (4) suggest a new infrageneric classification of *Dysphania*.

■ MATERIALS AND METHODS

Plant material, sampling and outgroups. — We used leaf fragments taken from herbarium specimens or from material collected during recent field trips and dried in silica gel. Altogether 121 accessions were included in the phylogenetic analyses representing all genera, sections and 39 accepted species of Dysphanieae. Voucher information for all accessions is given in Appendix 1. Our sampling covers ~80 % of the currently recognized species of Dysphanieae according to recent taxonomic treatments. We included multiple accessions for problematic or widespread species to test their monophyly. Representatives of all three genera of Axyrideae, *Axyris* (five accessions representing two species), *Ceratocarpus* (three accessions representing *C. arenarius*) and *Krascheninnikovia* (five accessions representing the two subspecies of *K. ceratoides*) were included as outgroups according to Kadereit & al. (2010) (Appendix 1). Appendix 1 also gives an overview of sequences newly generated for this study and sequences included from previous molecular studies with GenBank accession numbers.

Sequencing and phylogenetic inference. — Total DNA was extracted from 20 mg dried leaf-material using the DNeasy Plant Mini Kit (QIAGEN, Venlo, Netherlands) following the manufacturer's specifications. PCR was carried out in a T-Professional or T-Gradient Thermocycler (Biometra, Jena, Germany). Table 2 gives the details of primer sequences, PCR recipe and cycler programme for each marker. PCR products were checked on 1% agarose gels and purified subsequently using the NucleoSpin Gel and PCR clean-up-Kit (Macherey-Nagel, Düren, Germany) following the manufacturers manual. DNA sequences were obtained using the Big Dye Terminator v.3.1 Cycle Sequencing Kit (Applied Biosystems, Thermo Fisher Scientific, Schwerte, Germany) in combination with the primers detailed in Table 2 following a purification step using Illustra Sephadex G-50 Fine DNA Grade (Cytiva, Thermo Fisher Scientific, Schwerte, Germany). DNA fragments were sequenced using an automatic capillary sequencer GA3130XL (Applied Biosystems) following the Sanger method. Forward and reverse sequences were edited and merged to consensus sequences, then compiled in preliminary alignments using Sequencher v.4.1.4 (Gene Codes Corporation). All preliminary marker alignments were then subjected to automatic alignment using MAFFT (v.7.402) on CIPRES. The alignments were checked once more and corrected manually where needed. For the combined alignment, see supplementary Appendix S1.

The chloroplast dataset consisting of the *atpB*-*rbcL* spacer and *rpl16* intron sequences and the nuclear dataset consisting of ITS (internal transcribed spacer) and ETS (external transcribed spacer) were initially analysed separately. For all accessions that had been successfully sequenced for both partitions (plastid and nuclear), a combined analysis was conducted. For all three datasets (plastid, nuclear, combined), the best substitution model was inferred using jModeltest (v.2.1.6) on CIPRES Science Gateway v.3.3 (https://www.phylo.org, Miller & al., 2010). Maximum likelihood phylogenetic analyses were then performed using RAxML-HPC2 on XSEDE (v.8.2.12) including bootstrapping (Stamatakis, 2014) with GTR+Γ+I for the nuclear dataset, GTR+Γ for the plastid dataset and HKY+Γ+I for the combined dataset selected as the best substitution models under the Akaike information criterion.

Divergence times were estimated using a Bayesian uncorrelated lognormal relaxed clock under a birth–death speciation process (Nee & al., 1994; Gernhard, 2008). This tree is based on the combined data matrix with only one accession per species included. For each aligned locus, the best substitution model was determined using PartitionFinder v.2 (Lanfear & al., 2017). The GTR+Γ+I model was suggested as the most appropriate model for the ETS and *atpB*-*rbcL* datasets, while the GTR+Γ model was selected for the ITS and *rpl16* datasets. A secondary calibration was used as dating prior, being obtained from Kadereit & al. (2012), that constrains the age estimate for the most recent common ancestor (MRCA) of Dysphanieae at 34 Ma (95% highest posterior density [HPD]: 18.24–38.63 Ma). We selected a normal distribution prior for the secondary calibration with a standard deviation of 8, equivalent to the 95% HPD estimate of Kadereit & al. (2012). This calibration was chosen because it includes the early-branching lineages *Teloxys* and *Suckleya*, five representatives of *Dysphania* and a wide outgroup sampling of Amaranthaceae s.l. The age estimate found in this study covers mean node ages for the stem of Dysphanieae found in other studies (Morales-Briones & al., 2020: 33.9 myr; Kadereit & al., 2010: 37.1 myr [plastid data] and 25.1 myr [nuclear data]). Two independent MCMC analyses were run, each of 20 million generations, sampling every 20,000. Input files were generated with BEAUti v.2.4.5

(Bouckaert & al., 2014) and analyses ran using BEAST v.2.4.5 (Bayesian Evolutionary Analysis by Sampling Trees; Bouckaert & al., 2014) on the CIPRES Science Gateway v.3.3 (https://www.phylo.org, Miller & al., 2010). Output log files were analysed using Tracer v.1.6 (Rambaut & Drummond, 2013) to assess convergence and effective sample size of all parameters. As "burn-in", 25% of samples were removed prior to combining the independent runs using LogCombiner v.2.4.5 (Bouckaert & al., 2014). The MCC tree was generated using TreeAnnotator v.2.4.5 (Bouckaert & al., 2014).

Ancestral area analysis. — Species distribution was assessed from literature, the online database Australasian Virtual Herbarium (https://avh.chah.org.au/) and study of herbarium specimens housed in AD, AQ, B, BCN, BEI, BM, C, E, G, GLM, H, HAL, K, KAS, LE, M, MJG, MO, MPU, MSB, MW, NSW, P, PERTH, S, STU, TARI, TUH, UPS, W, WU and Z. Eight broad geographic regions reflecting the worldwide distribution of Dysphanieae were coded as follows: A = Asia: Siberia and Mongolia; B = Asia: Himalayas and Tibet; C = Asia: Irano-Turanian Region and Mediterranean;

Table 2. Primer sequences, PCR recipe and cycler program for each marker.

Marker	Primer	Primer sequence 5′–3′	Author	PCR recipe (all in µl)	Cycler program
ITS	F: ITS18S R: ITS28S	CCT TMT CAT YTA GAG GAA GGA G CCG CTT ATT CAT ATG CTT AAA	Blattner, 1999	ddH2O: 16.33 $MgCl_2$ [25 mM]: 2.5 σ-Buffer: 2.5 dNTPs (10 mM each): 0.5 σ-Taq Enzym DNA-Polymerase: 0.17 DNA: 1.0 Primer (F + R): 0.5 (20 µM) each DMSO: 1.0	94°C, 1 min 35 cycles 94°C, 30 s 52°C, 50 s 72°C, 1 min 94°C, 30 s 52°C, 72 s 72°C, 8 min 10°C, ∞
ITS1 ITS2	F: ITS A R: ITS C F: ITS B R: ITS D	GGA AGG AGA AGT CGT AAC AAG G GCA ATT CAC ACC AAG TAT CGC CTT TTC CTC CGC TTA TTG ATA TG CTC TCG GCA ACG GAT ATC TCG	Blattner, 1999	ddH2O: 16.58 $MgCl_2$ [25 mM]: 1.5 σ-Buffer: 2.5 dNTPs (10 mM each): 0.25 σ-Taq Enzym DNA-Polymerase: 0.17 DNA: 2.0 Primer (F + R): 0.5 (50 µM) each DMSO: 1.0	94°C, 1 min 35 cycles 94°C, 20 s 55°C, 30 s 72°C, 1 min 94°C, 20 s 55°C, 80 s 72°C, 8 min 10°C, ∞
ETS	F: ETS 18S II R: ETS Atriplex Int.	CTC TAA CTG ATT TAA TGA GCC ATT CGC A CGT GTG AGT GGT GAT TGG TT	Zacharias & Baldwin, 2010	ddH2O: 16.25 $MgCl_2$ [25 mM]: 2.5 σ-Buffer: 2.5 dNTPs (10 mM each): 0.25 σ-Taq Enzym DNA-Polymerase: 0.25 DNA: 2.0 Primer (F + R): 0.5 (50 µM) each DMSO: 0.25	94°C, 1 min 35 cycles 94°C, 30 s 52°C, 50 s 72°C, 1 min 94°C, 30 s 52°C, 72 s 72°C, 8 min 10°C, ∞
atpB-rbcL spacer	F: atpB-rbcL spacer F R: atpB.rbcL spacer R	GAA GTA GTA GGA TTG ATT CTC CAA CAC TTG CTT TAG TCT CTG	Xu & al., 2000	ddH2O: 18.6 $MgCl_2$ [25 mM]: 1.2 σ-Buffer: 2.5 dNTPs (10 mM each): 0.25 σ-Taq Enzym DNA-Polymerase: 0.2 DNA: 1.0 Primer (F + R): 0.5 (50 µM) each DMSO: 0.25	94°C, 1 min 35 cycles 94°C, 30 s 52°C, 50 s 72°C, 1 min 94°C, 30 s 52°C, 72 s 72°C, 8 min 10°C, ∞
rpl16 intron	F: rplF71 R: rplR1516	GCT ATG CTT AGT GTG TGA CTC GTT G CCC TTC ATT CTT CCT CTA TGT TG	Shaw & al., 2005	ddH2O: 17.8 $MgCl_2$ [25 mM]: 2 σ-Buffer: 2.5 dNTPs (10 mM each): 0.25 σ-Taq Enzym DNA-Polymerase: 0.2 DNA: 1.0 Primer (F + R): 0.5 (50 µM) each DMSO: 0.25	Temp., time, ramp [°C/s] 80°C, 5 min, 5.0 35 cycles 95°C, 1 min, 5.0 50°C, 1 min, 0.3 65°C, 4 min, 5.0 65°C, 5 min 8°C, ∞

Table 3. Distribution areas of species of Dysphanieae included in the molecular and biogeographical analyses and the coding used for the analysis with BioGeoBears.

Species	Sequence_ID	Distribution	Coding
Axyris amaranthoides L.	AxamarAC647_3015	Siberia and Mongolia	A
A. prostrata L.	Axpros0118	Himalayas and Tibet	B
Ceratocarpus arenarius L.	CearenAC649_3050	Irano-Turanian Region	C
Dysphania ambrosioides (L.) Mosyakin & Clemants	Dyambr2786	South America	F
D. anthelmintica (L.) Mosyakin & Clemants	Dyanth2795	Southern U.S.A., Mexico and West Indies	D
D. atriplicifolia (Spreng.) G.Kadereit, Sukhor. & Uotila	Cy2791	Mexico, U.S.A. and southern Canada	D
D. bhutanica Sukhor.	Dybhut2998	Himalayas and Tibet	B
D. botrys (L.) Mosyakin & Clemants	Dybotr2999	Irano-Turanian Region and Mediterranean	C
D. carinata (R.Br.) Mosyakin & Clemants	Dycari3425	Eastern Australia	E
D. chilensis (Schrad.) Mosyakin & Clemants	Dychil2796	South America	F
D. congestiflora S.J.Dillon & A.S.Markey	Dycofl3501	Western Australia	E
D. congolana (Hauman) Mosyakin & Clemants	Dycong3306	East and Central Africa	G
D. cristata (F.Muell.) Mosyakin & Clemants	Dycris3528	Australia	E
D. geoffreyi Sukhor.	Dygeof3309	Himalayas and Tibet	B
D. glandulosa Paul G.Wilson	Dyglan3537	Western Australia	E
D. glomulifera (Nees) Paul G.Wilson	Dyglom3523	Australia	E
D. graveolens (Willd.) Mosyakin & Clemants	Dygrav2073	Mexico and southern U.S.A.	D
D. himalaica Uotila	Dyhima2773	Himalayas and Tibet	B
D. kalpari Paul G.Wilson	Dykalp3508	Central Australia	E
D. littoralis R.Br.	Dylitt3432	Eastern Australia	E
D. mandonii (S.Watson) Mosyakin & Clemants	Dymand2781	Peru, Bolivia, northern Argentina and northern Chile	F
D. melanocarpa (J.M.Black) Mosyakin & Clemants	Dymela3409	Australia	E
D. multifida (L.) Mosyakin & Clemants	Dymult2789	South America	F
D. multiflora (Moq.) G.Kadereit, Sukhor. & Uotila	Dymufl3014	Himalayas	B
D. neglecta Sukhor.	Dynegl3010	Himalayas	B
D. nepalensis (Colla) Mosyakin & Clemants	Dynepa3011	Hindukush – Himalayas, and China	B
D. plantaginella F.Muell.	Dyplan3522	Australia	E
D. platycarpa Paul G.Wilson	Dyplat3411	Central Australia	E
D. procera (Hochst. ex Moq.) Mosyakin & Clemants	Dyproc2772	East and Central Africa, South Arabia	G
D. pseudomultiflora (Murr) Verloove & Lambinon	Dypseu2783	Southern Africa	H
D. pumilio (R.Br.) Mosyakin & Clemants	Dypumi3513	Australia	E
D. rhadinostachya (F.Muell.) A.J.Scott	Dyrhad3414	Australia	E
D. saxatilis (Paul G.Wilson) Mosyakin & Clemants	Dysaxa3517	Western Australia	E
D. schraderiana (Schult.) Mosyakin & Clemants	Dyschr3048	East and Central Africa, South Arabia	G
D. simulans F.Muell. & Tate	Dysimu3421	Central Australia	E
D. sphaerosperma Paul G.Wilson	Dyspha3530	Central and Western Australia	E
D. tibetica (A.J.Li) Uotila	Dytibe2769	Himalayas and Tibet	B
D. truncata (Paul G.Wilson) Mosyakin & Clemants	Dytrun3424	Central Australia	E

(Continues)

Table 3. Continued.

Species	Sequence_ID	Distribution	Coding
D. valida Paul G.Wilson	Dyvali3433	Eastern Australia	E
Krascheninnikovia ceratoides (L.) Gueldenst. subsp. *ceratoides*	KrceraAC608_0012	Siberia – Irano-Turanian Region	C
K. ceratoides subsp. *lanata* (Pursh) H.Heklau	KrcerassplanaAC628_1887	Western U.S.A. and Canada	D
Neomonolepis spathulata (A.Gray) Sukhor.	MoSPATH	Southwestern U.S.A. and northwestern Mexico	D
Suckleya suckleyana (Torr.) Rydb.	Susuck2000	Central U.S.A.	D
Teloxys aristata (L.) Moq.	Tearis0293	Siberia and Mongolia	A

A, Asia: Siberia and Mongolia; B, Asia: Himalayas and Tibet; C, Asia: Irano-Turanian Region and Mediterranean; D, North America incl. Mexico; E, Australia; F, South America; G, East and Central Africa, South Arabia; H, Southern Africa.

D = North America incl. Mexico; E = Australia; F = South America; G = East and Central Africa, South Arabia; H = Southern Africa (Table 3, Fig. 1). Ancestral range estimation (ARE) was conducted using the time-calibrated tree representing 39 species of Dysphanieae and 5 of Axyrideae included in this analysis with only one accession per species using BioGeoBEARS (Matzke, 2013, 2014) in R v.3.3.2 (R Core Team, 2016). We ran the analysis under a dispersal-extinction cladogenesis (DEC) model, dispersal-vicariance (DIVALIKE) model and BAYAREA (BAYAREALIKE) model. We did not consider a second run adding the parameter "j" (founder-event speciation) for each biogeographic model because of the conceptual and statistical problems of this parameter outlined by Ree & Sanmartín (2018). Out of the three models explored in this study, the DIVALIKE model was the best fit based on the Akaike information criterion and likelihood ratio test results. The analyses were unconstrained (without possible dispersal routes or ancestral areas assumed *a priori*). In three independent runs, we allowed the inferred ancestor to occupy a maximum of two, three and four areas, respectively, even though the maximum number of areas occupied by any extant species was one.

Morphological studies. — Our studies included macro-morphological characters from the herbaria listed above. Micromorphological and anatomical features studied included pericarp and perianth (for methods, see Sukhorukov, 2014) and trichomes. For the latter, we used SEM microscopy in the laboratory of Electron Microscopy at the Lomonosov Moscow State University.

■ RESULTS

Phylogenetic inference. — The plastid marker alignment consisted of 116 accessions and 1569 bp, the nuclear marker alignment had 120 accessions and 1262 bp and the combined alignment, which consisted only of those accessions represented in both separate datasets, had 107 accessions and 2831 bp (suppl. Appendix S1). The phylogenetic tree resulting from the combined dataset (Fig. 3) shows an overall better resolution than the trees resulting from the individual datasets (plastid tree, suppl. Fig. S1; nuclear tree, suppl. Fig. S2). There are only few instances of topological conflict between the plastid and nuclear trees that received considerable bootstrap support (BS > 75). However, these have implications for the backbone of the Dysphanieae tree and are therefore mentioned in detail below.

Dysphanieae, comprising *Dysphania* (incl. *Cycloloma*), *Neomonolepis*, *Suckleya* and *Teloxys*, is well supported (BS 100) in the ML trees of all three datasets (Fig. 3, suppl. Figs. S1, S2). *Teloxys* and *Neomonolepis* are successively sister to the remainder of Dysphanieae with *Teloxys* branching first in the plastid tree (suppl. Fig. S1) and second in the nuclear tree (suppl. Fig. S2). As a result of this topological conflict, the sister-group relationship of *Teloxys* to the remainder of Dysphanieae (incl. *Neomonolepis*) received low support in the combined analysis because the monophyly of the remainder of Dysphanieae (incl. *Neomonolepis*) was only weakly supported (BS 64; Fig. 3). Excluding these two conflicting monotypic genera from the analyses does not change the topology of the remaining clades. *Suckleya* and *Dysphania* are sister genera (BS 80; Fig. 3) in all analyses, and *Cycloloma* is always nested in *Dysphania* as sister to a clade comprising species from South and North America (Fig. 3, suppl. Figs. S1, S2). Within *Dysphania*, overall resolution and support of the tree resulting from the combined dataset is improved, in comparison to the tree topologies resulting from the separate datasets, indicating that they show a congruent phylogenetic signal. Conflict affecting the backbone of *Dysphania* is found in the position of a branch consisting of *D. graveolens* and *D. mandonii*. There are three major clades in *Dysphania*: An Asian/African clade consisting of nine species (clade 1 in Fig. 3), an American clade including seven species (clade 2 in Fig. 3) and an Australian/African clade with 20 species (clade 3 in Fig. 3). While clades 1 and 3 are well supported, clade 2 receives only low support due to the conflicting position of the *D. graveolens*/*D. mandonii* branch. This branch resolves as sister to clade 1 in the plastid tree (BS 72; suppl. Fig. S1) and as part of clade 2 in the nuclear tree (BS 59; suppl. Fig. S2). Although this conflicting topology received only low support, it likely prevents a resolved backbone within *Dysphania*, which means that the phylogenetic relationships of the three major clades remain unclear. Clade 2 consists of species from South and North America and also includes the North American *Cycloloma atriplicifolium*. Differentiation is poor between the morphologically similar *Dysphania ambrosioides* and *D. chilensis*. The Australian/African clade 3 consists of 17 Australian species with 3 African species (*D. congolana* (Hauman) Mosyakin & Clemants, *D. pseudomultiflora* (Murr) Verloove & Lambinon, *D. schraderiana*) nested among them. Apart from clade 1, which is unresolved at the backbone, the *Dysphania* clades show considerable internal resolution.

Ancestral area analysis. — In the biogeographical analysis, the reduced and dated tree showed the same topology as the combined ML tree (Figs. 3, 4). According to our dating, the Dysphanieae started to diversify ca. 18 million years ago

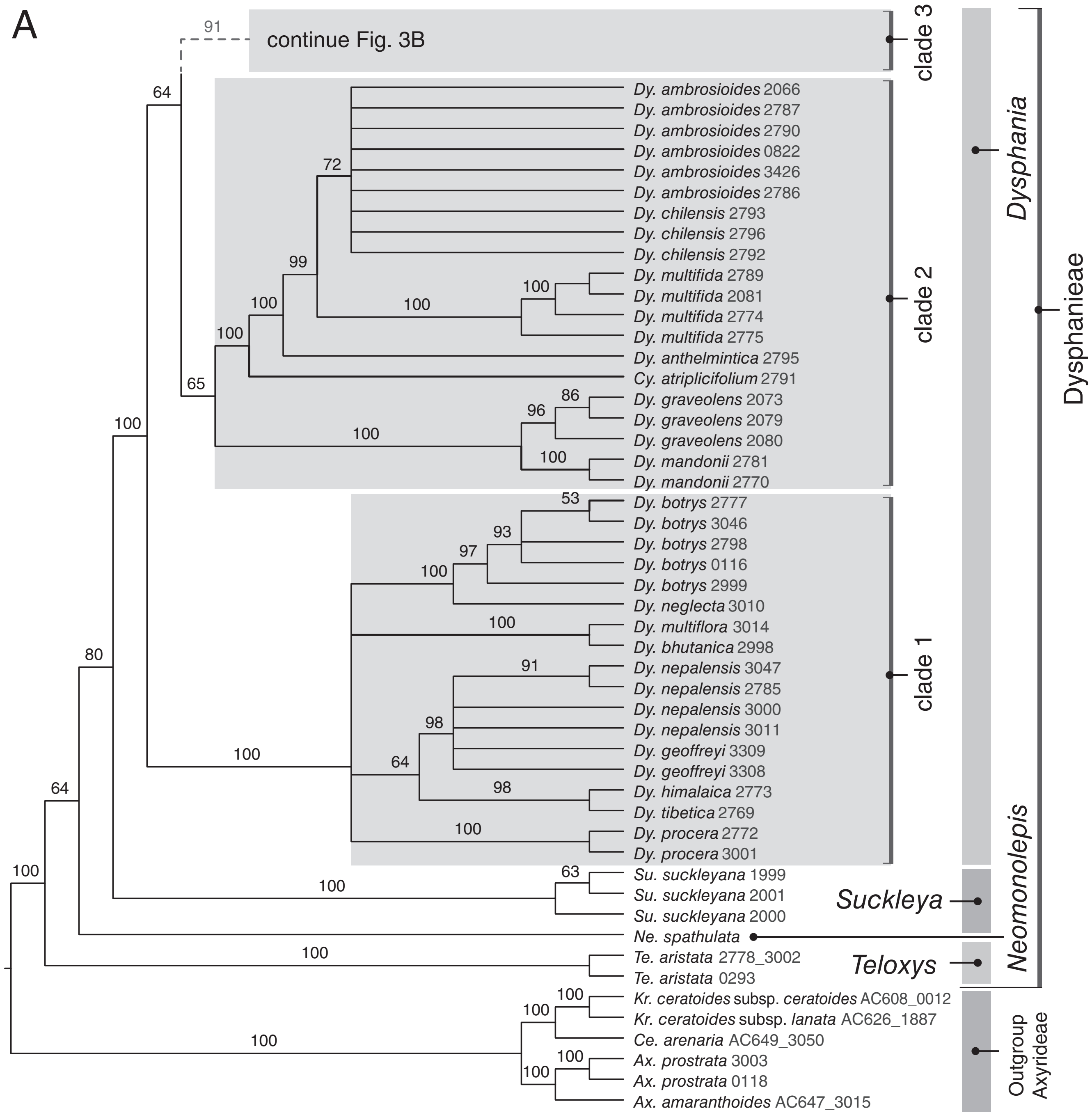

Fig. 3. Phylogenetic tree resulting from a maximum likelihood analysis of combined plastid and nuclear data of 101 Dysphanieae samples representing 39 species of the tribe. Representatives of Axyrideae serve as outgroup. Bootstrap support values >50 are given above branches.

and *Dysphania* 10 million years ago. The DIVALIKE model received the best likelihood scores compared to the other models in all three runs, and the lowest when four ancestral areas were allowed (−56.56; versus −66.37.12 for DEC and −116.88 for BAYAREALIKE). The reconstructed ancestral area for the stem node of Dysphanieae was Asia (areas A–C) and North America (D) with the ancestral areas ABCD receiving the highest score of 53.2 and ACD = 17.6; see Fig. 4); for the crown node, it was Siberia, Mongolia/North America (AD) with the highest score of 100. The ancestral area of the stem node of *Dysphania* showed the highest score for North America (D = 98.8), while the ancestral area of the crown node of *Dysphania* remains uncertain with BDEG receiving the highest score of 34.2. Within the American clade of *Dysphania* (clade 2), South America seems to have been colonized twice from North America, and within the

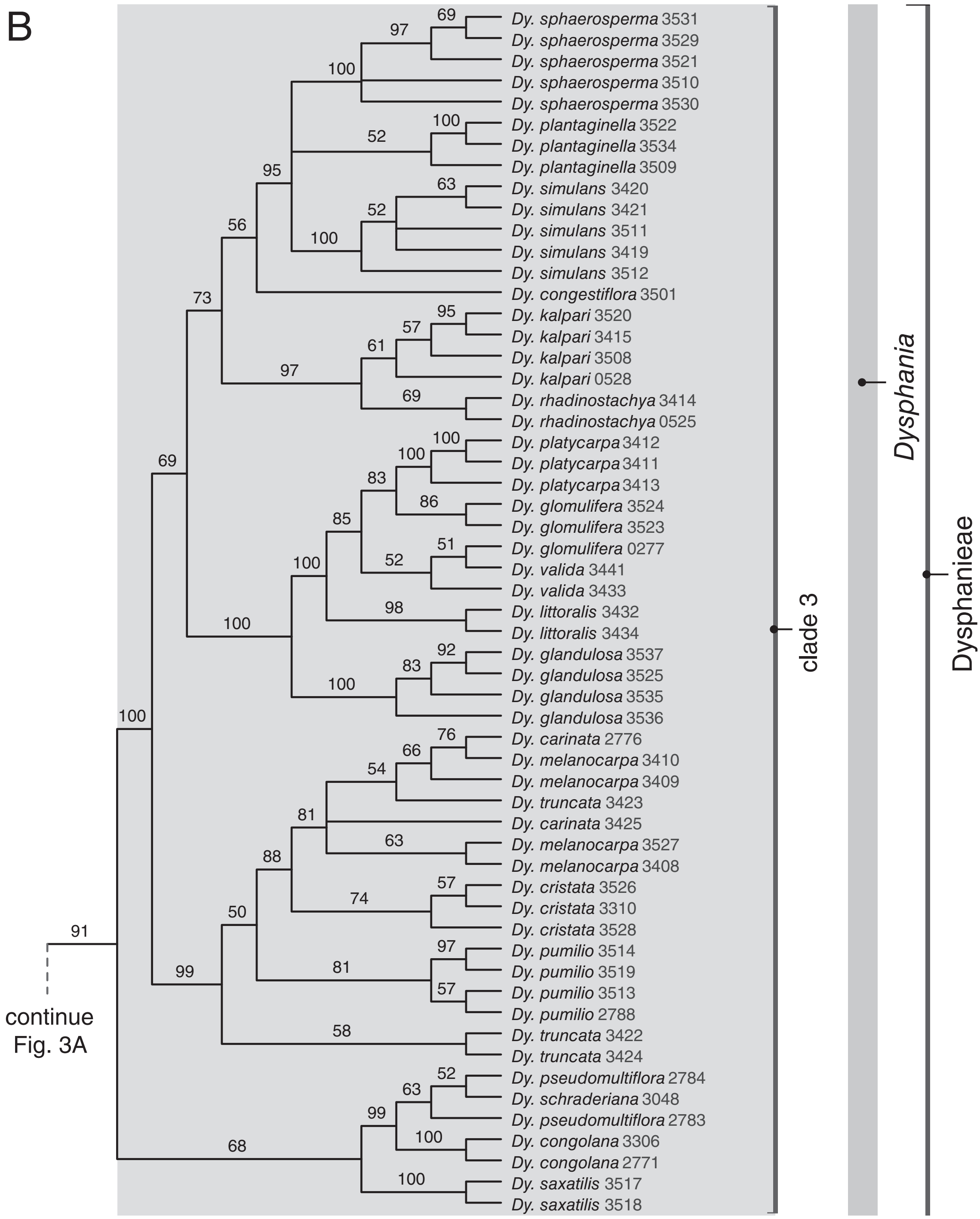

Fig. 3. Continued.

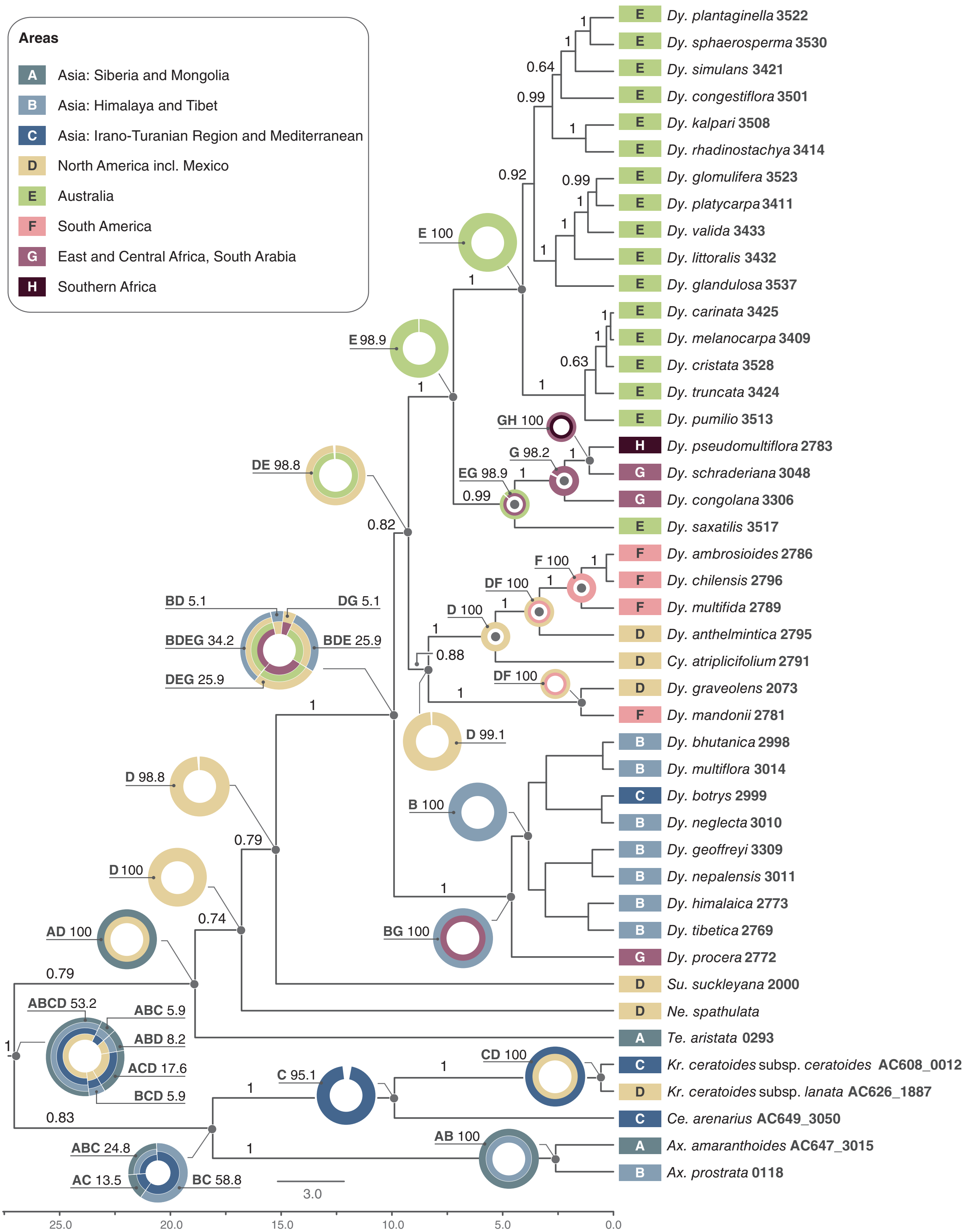

Fig. 4. Results of the ancestral range estimation (ARE) under the DIVALIKE model and with a maximum of four ancestral areas allowed, run with BioGeoBEARS based on a time-calibrated tree representing 44 species and subspecies of Dysphanieae with only one accession per species. Numbers above branches represent posterior probabilities.

Australian clade of *Dysphania* (clade 3), Africa has been colonized from Australia (Fig. 4). For the Asian clade (clade 1 in Fig. 3), the Himalayas/Tibet and East and Central Africa and South Arabia were inferred as ancestral; however, internal resolution of this clade is lower compared to the other two.

■ DISCUSSION

Phylogenetic history and diversification of Dysphanieae. — Molecular phylogenetic studies of Chenopodioideae consistently agreed that the tribe Dysphanieae included the genera *Cycloloma*, *Dysphania*, *Suckleya* and *Teloxys* (Kadereit & al., 2010, 2012; Fuentes-Bazan & al., 2012a; Morales-Briones & al., 2020). Only recently, it was discovered that one more genus, *Neomonolepis*, also belongs to Dysphanieae (Sukhorukov & al., 2018a). These previous results are supported here with a substantially broadened sampling of the large genus *Dysphania* (Fig. 3). While the monophyly of Dysphanieae is always well supported (including our study), there is either low support or conflict between nuclear and chloroplast data concerning the branching order of the first two lineages, *Teloxys* and *Neomonolepis*. Both are monospecific genera of small, annual, non-aromatic herbs. While the native distribution range of *Teloxys* is Central Asia, *Neomonolepis* is found in the southwestern United States and Mexico (Baja California; Fig. 1). The following, successively branching lineage is the monospecific annual genus *Suckleya*, which is distributed through the southern-central United States (Fig. 1). With a view to the ancestral area reconstruction, which favoured a North American/Asian stem and a North American/Siberian-Mongolian distribution for the crown node of Dysphanieae, we interpret these three old and species-poor lineages as relictual decendants of an ancestral lineage with a wider distribution across Beringia. The stem and crown of the Dysphanieae date back to the Late Oligocene and Early Miocene, respectively (Fig. 4), a period when warm-temperate groups migrated via the Beringia Land Bridge. The disjunct distribution of early-branching Dysphanieae (Fig. 4) is therefore consistent with the availability of the Bering Land Bridge (Wen, 1999; Sanmartín & al., 2001) and supported by other taxa with an Asian/North American disjunction of similar age (Wen & al., 2016 and references therein).

Although we allowed a maximum of four combined areas, the ancestral area analysis showed a high score for North America (D = 98.8) for the stem node of *Dysphania*. From its ancestral area in North America (Fig. 4), the genus spread worldwide. A broad ancestral range at the crown node of *Dysphania* would probably explain the simultaneous diversification on different continents (Fig. 3), viz. North Africa/Asia (clade 1), America (clade 2) and Australia (clade 3). The phylogeny reveals that the North American Dysphanieae as well as the African Dysphanieae are not monophyletic. Native to North America are the already mentioned relictual old Dysphanieae lineages *Neomonolepis* and *Suckleya* with closest relatives in Central Asia and also the much younger *Cycloloma atriplicifolium*, which seems to have originated during the Late Miocene from within a North American Dysphania clade and will hence be included in *Dysphania*. Native to Africa is a Late Miocene lineage consisting only of *Dysphania procera*, which is sister to the Asian *Dysphania* species, and a Pliocene lineage originating from Australia consisting of three species, one of which is distributed in South Africa. This younger African lineage is sister to the Australian species *D. saxatilis* (Paul G.Wilson) Mosyakin & Clemants. From a geographical point of view this might be surprising, but easy to accept on the basis of morphological characters. Already Wilson (1983) had difficulty placing his new species *Chenopodium saxatile* Paul G.Wilson in any of the existing Australian sections. He compared it also with the African *Chenopodium congolanum* (Hauman) Brenan, recognizing several common features. The biogeographical analysis allows two interpretations for this Australian/African clade. Either the ancestor of the three African species dispersed from Australia to Africa, in which case the typical morphology of this lineage evolved in Australia, or the ancestor of the lineage comprising *D. saxatile* and the three African species dispersed from Australia to Africa. In the latter case, morphological traits of this group could have evolved in Africa, and *D. saxatile* represents a dispersal event back to Australia.

The phylogenetic trees (Figs. 3, 4) resulting from the combined analysis of plastid and nuclear data resolves all American species of *Dysphania* in one clade depicting the phylogenetic signal of the nuclear data (suppl. Fig. S2). The ancestral area reconstruction suggests that within *Dysphania* South America was reached during the Pliocene/Quaternary two times independently within the two subclades: 1, *D. mandonii* and *D. graveolens*, and 2, *D. ambrosioides*, *D. chilensis*, *D. multifida*, *D. anthelmintica*, *Cycloloma atriplicifolium*. Morphological data support the distinction of the two subclades. Main differences between the species of these subclades exist in the type of inflorescence, perianth characters and pericarp surface. The species of subclade 1 have paniculate inflorescences, flowers in loose, compound dichasial cymes, abortive at the tip of ultimate branches, the perianth opened in fruiting stage, perianth lobes with prominent appendages on the back and the pericarp smooth and glabrous. By contrast, species in subclade 2 have spiciform inflorescences, all flowers developed, ± dense glomerules (flowers seldom single), the perianth closed in fruiting stage and the pericarp covered with yellow glandular hairs, sometimes together with simple hairs.

The morphological circumscription of Dysphanieae. — After a rather turbulent taxonomic history (see Introduction and Table 1), Mosyakin & Clemants (2002, 2008) suggested assembling all species of *Chenopodium* with glandular hairs as well as *Teloxys* in *Dysphania*. The molecular results clearly indicate that they were correct in recognizing *Dysphania* and *Teloxys* as a natural lineage, albeit not as congeneric since also *Suckleya* and *Neomonolepis* belong to this lineage. Together, these four genera make up the tribe Dysphanieae, which can be distinguished from other Chenopodioideae by a combination

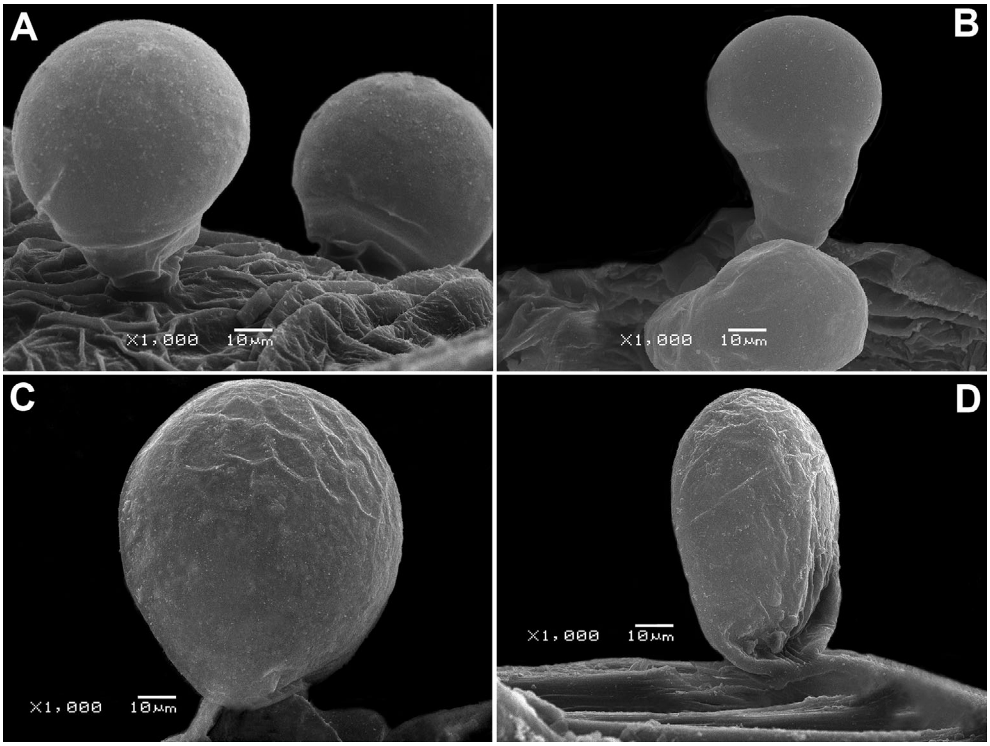

Fig. 5. SEM images of gland and hair types in Dysphanieae. **A**, Subsessile glands on the perianth of *Dysphania graveolens*; Mexico, September 2018, *A. Sukhorukov s.n.* (MW); **B**, Short, multicellular glandular hairs on the stem of *D. atriplicifolia*; Romania, Turda, *G. & J. Wolff 1018* (MW); **C**, A papilla on the stem of *Suckleya suckleyana*; U.S.A., New Mexico, July 1984, *Hill 14611* (GH); **D**, A papilla on the stem of *Teloxys aristata*; Russia, Tambov Prov., August 2001, *A. Sukhorukov s.n.* (MW).

of diverse trichomes (Fig. 5). It seems that only *Neomonolepis*, which is a glabrous herb, is a clear exception to this, and this monospecific genus is sister to all other Dysphanieae according to the nuclear sequence data (suppl. Fig. S2). Contrary to other Dysphanieae, flowers of *Neomonolepis* and *Suckleya* are unisexual, and the perianth of the female flowers of *Neomonolepis* abortive.

Subsessile, yellow- or orange-coloured glands containing essential oils are found in almost all species of *Dysphania* (Fig. 5A). As to *Cycloloma atriplicifolium* (combined into *Dysphania* below), we discovered in the course of this study that this species has short-stipitate, white glandular hairs (lacking essential oils) of the same shape as in *Dysphania* (Fig. 5B). They are easily overlooked, being scattered and mainly present on young parts of the stem, flower bases and perianths. Because *Cy. atriplicifolium* is nested among species with oil-containing glandular hairs, we assume that in *Cy. atriplicifolium* the oil secretion was lost. The inflated unicellular trichomes (Fig. 5C), mentioned by Chu & al. (1991) as a peculiar character of *Suckleya*, are in fact intermixed with multi-celled glandular hairs. *Teloxys aristata* is described as a glabrous herb (Iljin & Aellen, 1936; Grubov, 1966), but is hairy at the base of the stem, the number of cells varying from one (Fig. 5D) to several, and the apical cell is inflated. In *Dysphania*, many species have in addition to the glands often also other types of trichomes (multicellular glandular and simple hairs, and papillae) (Simón, 1997; Sukhorukov, 2012a,b, 2014; Sukhorukov & Zhang, 2013; Sukhorukov & al., 2015).

■ TAXONOMIC TREATMENT

Our molecular and morphological study is the first comprehensive attempt to disentangle phylogenetic relationships within Dysphanieae and to translate these findings into a modern taxonomic treatment. Our results strongly confirm the acceptance of only four genera within the tribe – *Dysphania*, *Neomonolepis*, *Suckleya* and *Teloxys*. The characters mentioned by Zhang & Zhu (2016) and Zhu & Sanderson (2017), e.g., the shape of the subsessile glands ("gland-grains"), or position of seed embryo (horizontal vs. vertical) in *Ambrina*, *Neobotrydium* and *Dysphania* are not genus-specific, and there are no distinct characters supporting the existence of *Ambrina*, *Roubieva* and *Neobotrydium* (Sukhorukov & al., 2018b). Below we provide an updated circumscription of Dysphanieae, with an improved generic key and nomenclatural synonymies. A new sectional subdivision of the largest genus *Dysphania* is also included.

Key to genera

1. Plants glabrous; flowers unisexual, female flowers with reduced perianth .... ***Neomonolepis***

1. Plants pubescent, at least in basal parts or in inflorescence; flowers bisexual, unisexual or polygamous, all flowers with properly developed perianth 2
2. Flowers strictly unisexual (plants monoecious); perianth of female flowers zygomorphic, enlarged, flattened and triangular in fruit stage; seeds ca. 3 mm ....***Suckleya***
2. Flowers bisexual or polygamous; perianth actinomorphic, not enlarged and flattened in fruit stage; seeds 0.3–1.6 mm.. 3
3. Plants not aromatic, with papillae and short multicellular white hairs mostly localized on lower parts of the stem; branches usually bifurcate, terminating with long arista; all flowers solitary .... ***Teloxys***
3. Plants mostly aromatic, with glandular hairs and usually yellow or orange subsessile glands, and multicellular simple hairs; branches mostly not bifurcate, if bifurcate, short and not terminating with long arista; flowers in simple or compound cymes or dense glomerules...........***Dysphania***

Dysphanieae Pax in Engler & Prantl, Nat. Pflanzenfam. 3(1b): 92. 1889 ≡ Dysphaniaceae Pax in Bot. Jahrb. Syst. 61: 230. 1927 – Type: *Dysphania* R.Br.

= Suckleyinae G.L.Chu & Stutz in Amer. J. Bot. 78(1): 65. 1991 – Type: *Suckleya* A.Gray.

= Neobotrydieae G.L.Chu in Chu & Sanderson, Gen. New Evol. System World Chenopod.: 72. 2017 – Type: *Neobotrydium* Moldenke.

Dysphania R.Br., Prodr.: 411. 1810 – Type: *Dysphania littoralis* R.Br.

= *Roubieva* Moq. in Ann. Sci. Nat., Bot., ser. 2, 1: 292. 1834 ≡ *Ambrina* Spach, Hist. Nat. Vég. 5: 295. 1836, nom. superfl. & illeg. – Type: *Roubieva multifida* (L.) Moq. (≡ *Dysphania multifida* (L.) Mosyakin & Clemants).

= *Cyclolepis* Moq. in Ann. Sci. Nat., Bot., sér. 2, 1: 203. 1834, nom. illeg., non Gillies ex D.Don 1832 ≡ *Cycloloma* Moq., Chenop. Monogr. Enum.: 17. 1840 – Type: *Cycloloma platyphyllum* (Michx.) Moq. (= *C. atriplicifolium* (Spreng.) J.M.Coult. ≡ *Dysphania atriplicifolia* comb. nov.).

= *Botrydium* Spach, Hist. Nat. Vég. 5: 298. 1836, nom. illeg., non Wallr. 1815 ≡ *Neobotrydium* Moldenke in Amer. Midl. Naturalist 35: 330. 1946 – Type: *Neobotrydium botrys* (L.) Moldenke (≡ *Dysphania botrys* (L.) Mosyakin & Clemants).

= *Meiomeria* Standl. in Britton & al., N. Amer. Fl. 21: 7. 1916 – Type: *Meiomeria stellata* Standl. (≡ *Dysphania stellata* (Standl.) Mosyakin & Clemants).

Description. – Annuals or short-lived perennial herbs, more or less covered with simple multicellular hairs and stalked glandular hairs/subsessile glands, sometimes glabrescent, usually aromatic. Stems rarely somewhat woody in lower part, erect, ascending, decumbent or prostrate, branched (rarely ± simple), not jointed, not spiny, not fleshy. Leaves alternate, usually petiolate; blade lanceolate, oblanceolate, ovate or elliptic, entire or lobed to pinnatisect, margins entire, sinuate, dentate or serrate, base cuneate to truncate, apex obtuse, acute or acuminate. Inflorescences terminal, loosely paniculate, of simple or compound dichasial cymes, or spiciform and of dense axillary glomerules; glomerules may be subtended by reduced leaves (sometimes referred to as "leaflike bracts"). Flowers bisexual or sometimes polygamous (at least functionally). Perianth segments 1–5, rarely 6–9 (*D. stellata*), free or variously connate from the base, flat to variously keeled with longitudinal or rarely (*D. atriplicifolia*) transverse outgrowths. Stamens 0–5. Ovary superior; style short or ± absent, stigmas 1–5, filiform. Fruits 1-seeded, often enclosed in perianth; pericarp adherent or non-adherent, membranous, smooth, papillate, with glands, glandular hairs or rarely with simple hairs (*D. atriplicifolia*). Seeds horizontal or vertical (rarely oblique), globose to lenticular or ellipsoidal; seed coat reddish brown or black, smooth to rugose, rarely reticulate with deep pits (*D. dissecta*); outer cell walls of the testal layer without stalactites; embryo annular or almost straight, with copious farinose perisperm.

Note. – The inclusion of *Cycloloma* within *Dysphania* is stated for the first time, and two peculiarities of *Cycloloma* – circular wing-like outgrowth on the perianth evidently enhancing anemochory, and presence of long simple hairs on the pericarp, missing in all Chenopodioideae – emend the description of *Dysphania*.

1. ***Dysphania*** sect. ***Adenois*** (Moq.) Mosyakin & Clemants in Ukrayins'k. Bot. Zhurn. 59(4): 382. 2002 ≡ *Ambrina* sect. *Adenois* Moq., Chenop. Monogr. Enum.: 39. 1840 ≡ *Chenopodium* [unranked] *Ambrosioidia* Standl. in Britton & al., N. Amer. Fl. 21: 26. 1916 ≡ *Chenopodium* [subg. *Ambrosia*] sect. *Adenois* (Moq.) L.E.Simón in Anales Jard. Bot. Madrid 54: 138. 1996 – Type (designated by Simón in Anales Jard. Bot. Madrid 54: 138. 1996): *Chenopodium ambrosioides* L. (≡ *Dysphania ambrosioides* (L.) Mosyakin & Clemants).

= *Roubieva* Moq. in Ann. Sci. Nat., Bot., sér. 2, 1: 292. 1834 ≡ *Ambrina* Spach, Hist. Nat. Vég. 5: 295. 1836, nom. superfl. & illeg. ≡ *Chenopodium* sect. *Ambrina* Benth. & Hook.f., Gen. Pl. 3(1): 51. 1880 ≡ *Chenopodium* sect. *Roubieva* (Moq.) Rouy in Rouy & Foucaud, Fl. France 12: 53. 1910 ≡ *Chenopodium* [subg. *Ambrosia* sect. *Adenois*] subsect. *Roubieva* (Moq.) L.E.Simón in Anales Jard. Bot. Madrid 54: 138. 1996 ≡ *Dysphania* sect. *Roubieva* (Moq.) Mosyakin & Clemants in Ukrayins'k. Bot. Zhurn. 59(4): 382. 2002 – Type: *Roubieva multifida* (L.) Moq. (≡ *Dysphania multifida* (L.) Mosyakin & Clemants).

= *Chenopodium* sect. *Nigrescentia* Aellen in Acta Bot. Acad. Sci. Hung. 19: 3. 1973 – Type: *Chenopodium burkartii* (Aellen) Worosch. (≡ *Dysphania burkartii* (Aellen) Mosyakin & Clemants).

Description. – Annuals or perennials, with subsessile glands and glandular and multicellular simple hairs. Stems sometimes woody in the lower part, erect to ascending or procumbent, variously branched. Leaves short-petiolate (in inflorescence sessile); blades entire, lobed or pinnatifid, oblong-ovate, oblong or lanceolate, margins almost entire to sinuate or dentate, base cuneate, apex acute or fairly obtuse. Inflorescences more or less spiciform, leafy, or branches leafless; flowers clustered in dense sessile glomerules, sometimes some flowers solitary. Perianth segments (3–)4–5, basally connate for 1/4–3/4 of their length, cucullate, or fused to form sac surrounding the fruit, abaxially rounded or keeled, rarely with transverse wing, glabrous or with glands or multicellular hairs. Stamens 4–5. Stigmas 2–5. Pericarp ± loose. Seeds mostly horizontal, sometimes vertical, up to 1.3 mm, subglobose to obovoid; seed coat black, smooth or indistinctly sculptured.

Included species. – 13 species: *Dysphania ambrosioides* (L.) Mosyakin & Clemants (2*n* = 32), *D. anthelmintica* (L.) Mosyakin & Clemants (2*n* = 64), ***D. atriplicifolia*** (Spreng.) G.Kadereit, Sukhor. & Uotila, **comb. nov.** (≡ *Salsola atriplicifolia* Spreng., Nachtr. Bot. Gart. Halle: 35. 1801 ≡ *Cycloloma atriplicifolium* (Spreng.) J.M.Coult. in Mem. Torrey Bot. Club 5: 143. 1894) (2*n* = 36), *D. bonariensis* (Hook.f.) Mosyakin & Clemants ex Sukhor. (not analysed), *D. burkartii* (Aellen) Mosyakin & Clemants (not analysed), *D. chilensis* (Schrad.) Mosyakin & Clemants (2*n* = 32), *D. microcarpa* (Phil.) Mosyakin & Clemants (not analysed), *D. multifida* (L.) Mosyakin & Clemants (2*n* = 32), *D. oblanceolata* (Speg.) Mosyakin & Clemants (not analysed), *D. retusa* (Juss. ex Moq.) Mosyakin & Clemants (2*n* = 64) (not analysed), *D. sooana* (Aellen) Mosyakin & Clemants (not analysed), *D. tomentosa* (Thouars) Mosyakin & Clemants (not analysed) and *D. venturii* (Aellen) Mosyakin & Clemants (2*n* = 32) (not analysed). – *Dysphania anthelmintica* and *D. atriplicifolia* are distributed in North America, *D. tomentosa* on Tristan da Cunha, the other species in South America. *Dysphania ambrosioides* is widespread as naturalized species in the tropics and subtropics including southern North America, and *D. multifida* in southern North America, the Mediterranean Europe, Australia, northern and southern Africa. *Dysphania chilensis* is reported as naturalized in coastal areas of the southwestern U.S.A. (e.g., Clemants & Mosyakin, 2003).

Notes. – In the molecular anlaysis, *Dysphania atripicifolia* was sister to the other species of *D.* sect. *Adenois*; in addition, it has unique morphological charaters within the genus, which might allow to recognize a subsection for it. However, there are several American species, three of them morphologically distinctive, that were not included in our analysis, and due to lack of this information, no further division of *D.* sect. *Adenois* was adopted. *Dysphania anthelmintica*, sometimes considered only a variety of the polymorphic species *D. ambrosioides*, proved to be sister to the remaining taxa of the group, i.e., *D. ambrosioides*, *D. chilensis* and *D. multifida*. *Dysphania anthelmintica* is morphologically much closer to the two first species than to *D. multifida*. However, *D. anthelmintica* is quite well distinguished from *D. ambrosioides* and *D. chilensis* by regularly lobed leaves and leafless branches of the inflorescence. Furthermore, according to the few chromosome counts available, it might be octoploid, whereas the others are tetraploids. Even their native areas appear different: *D. anthelmintica* grows in North America round the Gulf of Mexico, *D. chilensis* originates from the southern part of South America, while the indigenous area of *D. ambrosioides* is probably in South America. *Dysphania ambrosioides* and *D. anthelmintica* have been cultivated as medicinal plants, but many of the plants cultivated under the name *Chenopodium anthelminticum* L. or *Dysphania anthelmintica* seem to be misidentified and belong to *D. ambrosioides*.

The molecular difference between *Dysphania multifida* and *D. ambrosioides* + *D. chilensis* agrees with their considerable morphological differences in leaf shape and perianth characters, which in earlier treatments led to their placements in different sections or even in different genera. *Dysphania bonariensis* and *D. microcarpa* share a flattened, elongated and hardened, always closed perianth with *D. multifida*.

Dysphania ambrosioides and *D. chilensis* are morphologically close to each other. *Dysphania ambrosioides* is polymorphic and obviously taxonomically heterogeneous, while *D. chilensis* has been sometimes misunderstood. Further, there are several species, not included in our analysis, that are morphologically fairly similar to *D. ambrosioides*, as *D. oblanceolata* and *D. tomentosa*. *Dysphania burkartii*, *D. retusa*, *D. sooana* and *D. venturii* are morphologically well-separate from *D. ambrosioides* even though usually placed near it, for instance, Aellen (1973) included them into *D.* sect. *Ambrina*, except for *D. burkartii* (as *Chenopodium burkartii*), which was placed in a monotypic *D.* sect. *Nigrescentia* mainly because it turns blackish when pressed. Additional morphological and molecular studies are needed for proper understanding of the variation and taxonomy of this section.

2. ***Dysphania*** sect. ***Botryoides*** (C.A.Mey.) Mosyakin & Clemants in Ukrayins'k. Bot. Zhurn. 59(4): 383. 2002 ≡ *Chenopodium* sect. *Botryoides* C.A.Mey. in Ledebour, Fl. Altaic. 1: 410. 1829 ≡ *Chenopodium* sect. *Botrys* W.D.J.Koch, Syn. Fl. Germ. Helv.: 607. 1837 ≡ *Ambrina* sect. *Botryois* Moq., Chenop. Monogr. Enum.: 36. 1840 ≡ *Chenopodium* sect. *Botryois* Moq. in Candolle, Prodr. 13(2): 72. 1849 ≡ *Chenopodium* [unranked] *Botryes* Standl. in Britton & al., N. Amer. Fl. 21: 25. 1916 ≡ *Chenopodium* [sect. *Botryoides*] subsect. *Botrys* (W.D.J.Koch) Aellen & Iljin in Komarov, Fl. URSS 6: 46. 1936 ≡ *Dysphania* subsect. *Botrys* (W.D.J.Koch) Mosyakin & Clemants in Ukrayins'k. Bot. Zhurn. 59(4): 383. 2002 – Type: *Chenopodium botrys* L. (≡ *Dysphania botrys* (L.) Mosyakin & Clemants).

= *Botrydium* Spach, Hist. Nat. Vég. 5: 298. 1836, nom. illeg., non Wallr. 1815 ≡ *Chenopodium* sect. *Botrydium* Benth. & Hook.f., Gen. Pl. 3(1): 51. 1880 ≡ *Neobotrydium* Moldenke in Amer. Midl. Naturalist 35: 330. 1946 – Type: *Neobotrydium botrys* (L.) Moldenke (≡ *Dysphania botrys* (L.) Mosyakin & Clemants).

Description. – Annuals, with multicellular simple and glandular hairs and subsessile glands. Stems mostly erect, branched. Leaves with fairly short petiole; blades ovate to elliptic, shallowly to deeply lobate, lyrate-sinuate, sinuate-dentate, erose-dentate, or pinnatifid, occasionally entire, base cuneate to truncate, apex ± obtuse. Inflorescence mainly terminal, mostly leafless, loosely paniculate, composed of compound small dichasial cymes and solitary flowers; rarely ultimate branches bifurcate, sterile (*D. tibetica*). Perianth segments free to variously connate, more or less navicular, flat to swollen abaxially, with glandular hairs/subsessile glands and often multicellular hairs, sometimes narrow lobes. Stamens (1–)5. Stigmas 2. Pericarp ± adherent. Seeds mostly horizontal, sometimes vertical, rarely oblique, 0.5–1.1 mm, orbicular or slightly ovate in outline, lenticular, margin obtuse to truncate; seed coat brown, red or black, smooth or faintly reticulate.

Included species. – 10 species: *Dysphania bhutanica* Sukhor., *D. botrys* (L.) Mosyakin & Clemants ($2n = 18$), *D. geoffreyi* Sukhor., *D. himalaica* Uotila, *D. kitiae* Uotila (not analysed), ***D. multiflora*** (Moq.) G.Kadereit, Sukhor. & Uotila, **comb. nov.** (≡ *Chenopodium multiflorum* Moq. in Candolle, Prodr. 13(2): 75. 1849), *D. neglecta* Sukhor., *D. nepalensis* (Colla) Mosyakin & Clemants, *D. procera* (Hochst. ex Moq.) Mosyakin & Clemants ($2n = 36$), *D. tibetica* (A.J.Li) Uotila. – Most species are distributed mainly in the Himalayas and adjacent China; *C. botrys* occurs in Central Asia to the Arabian Peninsula and Mediterranean Europe and Africa, and *D. procera* in eastern Africa and the adjacent Arabian Peninsula.

Notes. – Up to now *Dysphania* sect. *Botryoides* included also a few American taxa, usually as *D.* subsect. *Incisa*. Removing this group does not cause marked changes in the morphological description of *D.* sect. *Botryoides*, the most important change being the absence of sterile inflorescence branches ending with a knot of an abortive flower. Furthermore, the area of *D.* sect. *Botryoides* is now limited to Asia (including the Arabian Peninsula), East Africa (*D. procera*) and North Africa and southern Europe (*D. botrys*). The latter species occurs as introduced in North America. Even though *D. kitiae* has several special features, as deeply divided leaves and a strong keel in the apical part of the perianth, it seems to belong to *D.* sect. *Botryoides*. Recognizing *D. multiflora* at species rank was confirmed by molecular characters but supposed on the basis of leafy inflorescences; it was earlier included in the polymorphic *D. nepalensis* (e.g., Uotila, 2013; Sukhorukov & Kushunina, 2014; Sukhorukov & al., 2019a).

3. ***Dysphania*** sect. ***Dysphania*** ≡ *Chenopodium* sect. *Dysphania* (R.Br.) Aellen in Bot. Jahrb. Syst. 63: 486. 1930 – Type: *Dysphania littoralis* R.Br.

= *Chenopodium* sect. *Orthosporum* R.Br., Prodr.: 407. 1810 ≡ *Dysphania* sect. *Orthospora* (R.Br.) Mosyakin & Clemants in Ukrayins'k. Bot. Zhurn. 59(4): 382. 2002 – Type (designated by Ulbrich in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 16c: 494. 1934): *Chenopodium carinatum* R.Br. (≡ *Dysphania carinata* (R.Br.) Mosyakin & Clemants).

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

= *Chenopodium* sect. *Tetrasepalae* Aellen in Bot. Jahrb. Syst. 63: 490. 1930 ≡ *Dysphania* sect. *Tetrasepalae* (Aellen) A.J.Scott in Bot. Jahrb. Syst. 100: 218. 1978 – Type (designated by Scott in Bot. Jahrb. Syst. 100: 218. 1978): *Dysphania inflata* (Aellen) A.J.Scott (= *D. rhadinostachya* subsp. *inflata* (Aellen) Paul G.Wilson).

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

Description. – Annual or short-lived perennials, with multicellular simple and glandular hairs and glands. Stems prostrate, procumbent or erect. Leaves almost sessile to fairly short petiolate; blade elliptic to ovate, entire or variously lobed, margin entire to sinuous, base cuneate or truncate, apex obtuse. Inflorescence spiciform, axillary and terminal, of compact, ± sessile glomerules. Flowers bisexual or functionally female. Perianth segments 1–5, free to variously connate, cucullate to navicular, in fruit stage swollen or enlarged and hardened, sometimes prominently keeled or winged, glabrous, variously glandular or with multicellular hairs. Stamens 0–2. Stigmas 1–2, short. Pericarp mostly ± adherent. Seeds vertical, oblique or horizontal, globular, ellipsoidal or lenticular, 0.3–0.6 mm; seed coat smooth.

Included species. – 17 species: *Dysphania carinata* (R.Br.) Mosyakin & Clemants, *D. congestiflora* S.J.Dillon & A.S.Markey, *D. cristata* (F.Muell.) Mosyakin & Clemants, *D. glandulosa* Paul G.Wilson, *D. glomulifera* (Nees) Paul G.Wilson, *D. kalpari* Paul G.Wilson, *D. littoralis* R.Br., *D. melanocarpa* (J.M.Black) Mosyakin & Clemants, *D. plantaginella* F.Muell., *D. platycarpa* Paul G.Wilson, *D. pumilio* (R.Br.) Mosyakin & Clemants ($2n = 16, 18$), *D. pusilla* (Hook.f.) Mosyakin & Clemants (not analysed), *D. rhadinostachya* (F.Muell.) A.J.Scott, *D. simulans* F.Muell. & Tate, *D. sphaerosperma* Paul G.Wilson, *D. truncata* (Paul G.Wilson) Mosyakin & Clemants, *D. valida* Paul G.Wilson. – All species are endemic to Australia, excluding *D. pusilla*, which is probably endemic to New Zealand; *D. pumilio* and *D. carinata* are frequently naturalized in other continents, *D. pumilio* also in New Zealand.

Notes. – The exclusion of *Dysphania saxatile* from the other Australian taxa makes *D.* sect. *Dysphania* morphologically more homogeneous, e.g., in inflorescence morphology. *Dysphania pusilla* is the only species of the section not analysed by us. It is regarded as morphologically related to *D. pumilio* (Wilson, 1983; Webb & al., 1988; De Lange, 2020), even though rather different in habit, leaf form, seeds size and number of perianth segments (usually only 4 segments instead of usually 5 in *D. pumilio*). Also, preliminary DNA data based on one marker (nrDNA ITS) places it with *D. pumilio* (De Lange, 2020).

4. ***Dysphania*** sect. ***Incisa*** (Standl.) G.Kadereit, Sukhor. & Uotila, **comb. & stat. nov.** ≡ *Chenopodium* [unranked] *Incisa* Standl. in Britton & al., N. Amer. Fl. 21: 25. 1916 ≡ *Dysphania* [sect. *Botryoides*] subsect. *Incisa* (Standl.) Mosyakin & Clemants in Ukrayins'k. Bot. Zhurn. 59(4): 383. 2002 – Type: *Chenopodium incisum* Poir. (= *Dysphania graveolens* (Willd.) Mosyakin & Clemants).

Description. – Annuals, with subsessile glands and thin multicellular simple hairs. Stems erect, branched. Leaves with rather short petiole; blade lanceolate to ovate or elliptic, sinuate-pinnatifid or laciniate-pinnatifid to deeply dentate, sinuate or entire, base truncate or cuneate, apex obtuse to acuminate. Inflorescence paniculate, axillary and terminal, loose, of dichasial few-flowered cymes and single flowers, often with ultimate branches ending with a small knot (abortive flower). Perianth segments 5, basally shortly connate, abaxially fairly flat but often with prominent appendage(s) in the apical part, with subsessile glands. Stamens 0–5. Stigmas 2. Pericarp rugose, adherent. Seeds horizontal, 0.5–0.8 mm, depressed-globose; seed coat dark brown.

Included species. – 2 species: *Dysphania graveolens* (Willd.) Mosyakin & Clemants (2*n* = 32) in southern North America and *D. mandonii* (S.Watson) Mosyakin & Clemants (2*n* = 54) in South America (Argentina, Bolivia, Chile, Peru).

Notes. – *Dysphania graveolens* and *Teloxys aristata* resemble each other in having long sterile ultimate branches of the inflorescence. This similarity led Aellen (1960) to include *D. graveolens* (as *Chenopodium graveolens* Willd.) in *Chenopodium* sect. *Botryoides* subsect. *Teloxys* (Moq.) Aellen & Iljin (now genus *Teloxys*). Also *Dysphania tibetica* from *D.* sect. *Botryoides* has sterile ultimate inflorescence branches (Uotila, 2013). This character seems to have developed convergently in different lineages of the tribe and led to a somewhat different result: In *D.* sect. *Incisa*, the ultimate branches are terminated by an abortive flower visible as a knot; in *D. tibetica*, the sterile branches are short, somewhat hooked; and in *Teloxys*, they are long, needle-like aristae. Morphologically, the species of *D.* sect. *Incisa* are relatively similar to those of *D.* sect. *Botryoides* and more dissimilar with the other American section *D.* sect. *Adenois*. Scott (1978a) merged *D.* sect. *Incisa* under *D.* subsect. *Botrys*, and Mosyakin & Clemants (2008) regarded it as a subsection in *D.* sect. *Botryoides*.

5. ***Dysphania*** sect. ***Margaritaria*** (Brenan) G.Kadereit, Sukhor. & Uotila, **comb. nov.** ≡ *Chenopodium* sect. *Margaritaria* Brenan in Kew. Bull. 11: 166. 1956 – Type: *Chenopodium congolanum* (Hauman) Brenan (≡ *Dysphania congolana* (Hauman) Mosyakin & Clemants).

Description. – Annuals, with multicellular simple hairs and subsessile glands. Stems mostly erect, sometimes prostrate, branched mostly in lower part, branches often long, spreading. Leaves short-petiolate; blade lanceolate to ovate or elliptic, deeply pinnatifid to entire with sinuate to lobed margins, base cuneate, apex obtuse to subacute. Inflorescence axillary and terminal, narrowly paniculate, composed of compound dichasial cymes and solitary flowers. Perianth segments 4 or 5, free near to the base, navicular, abaxially somewhat swollen to cristately keeled, with subsessile glands or multicellular hairs. Stamens 0–5. Stigmas 2. Pericarp thin, adherent to the seed, sometimes glandular. Seeds vertical or horizontal, 0.6–1.0 mm, lenticular to semiglobose; seed coat black or brown, finely and reticulately rugulose or smooth.

Included species. – 4 species: *Dysphania congolana* (Hauman) Mosyakin & Clemants, *D. pseudomultiflora* (Murr) Verloove & Lambinon, *D. saxatilis* (Paul G.Wilson) Mosyakin & Clemants, *D. schraderiana* (Schult.) Mosyakin & Clemants (2*n* = 18). – *Dysphania saxatilis* is a West-Australian species largely inhabiting rocky places like hillslopes, hill tops and escarpments of tablelands; the three others are in Africa, with differing distribution patterns: foothills and mountains of tropical Africa (*D. congolana*; Sukhorukov & al., 2016), southern Africa (*D. pseudomultiflora*; Sukhorukov & al., 2019b), and foothills and mountains of eastern Africa and southwestern mountains of the Arabian Peninsula, with secondary distribution in Europe and West Asia (*D. schraderiana*).

Notes. – Brenan (1956) considered that the tropical African *Chenopodium congolanum* is in some respects a morphological link between *C.* sect. *Botryoides* and *C.* sect. *Orthosporum* and proposed a new section *C.* sect. *Margaritaria* for it. Wilson (1983) was uncertain of the placement of *Chenopodium saxatile* and considered options between *Dysphania* s.str. and *Chenopodium* sect. *Orthosporum*, sect. *Botryoides* and sect. *Margaritaria*. He solved the difficulty by emending *C.* sect. *Orthosporum* to cover also *C. saxatile*, e.g., by accepting also 4 perianth segments and 2 stamens, and allowing more open lateral branches of the inflorescence. Zhang & Zhu (2016) moved *Dysphania saxatile* to *Neobotrydium*.

Dysphania sect. *Margaritaria* is small but morphologically heterogeneous. *Dysphania pseudomultiflora* and *D. schraderiana* are fairly similar with usually pinnatifid leaves, mostly leafless inflorescence, 5 carinate to cristate perianth segments and horizontal seeds. By contrast, *D. congolana* and *D. saxatile* have less-lobed leaves, leafy inflorescences, four somewhat swollen perianth segments, and vertical seeds. Some other characters break this grouping. The perianth segments of *D. saxatile* have multicellular simple hairs but no glands, while in the other species simple hairs are missing but glands are present. *Dysphania congolana* has a smooth pericarp, while the other species have papillate pericarp.

Neomonolepis Sukhor. in PhytoKeys 109: 121. 2018 – Type: *Neomonolepis spathulata* (A.Gray) Sukhor. (≡ *Monolepis spathulata* A.Gray ≡ *Blitum spathulatum* (A.Gray) S.Fuentes, Uotila & Borsch).

Description. – Non-aromatic, small, glabrous, annuals. Stem branched or not, lateral branches (if present) ascending. Leaves short-petiolate to sessile; blade spathulate-oblong, margin entire. Inflorescence leafy (bracts similar to stem leaves) composed of axillary, small glomerules; flowers sessile or shortly pedicellate, with unisexual, pistillate and staminate flowers mixed in small glomerules. Male flowers with 2-lobed hyaline perianth, stamens 1–2, anthers 0.10–0.15 mm long. Female flowers with reduced perianth, stigmas 2(–3). Fruits ca. 0.5 mm, almost globose; pericarp blackish, papillate, easily ruptured. Seeds vertical, 0.4 × 0.3 mm; seed coat reddish, smooth, with tiny irregular pits, outer cell walls of the testal layer with stalactites. Embryo vertical.

One species, *Neomonolepis spathulata* (A.Gray) Sukhor.; western North America (Holmgren, 2003).

Suckleya A.Gray in Proc. Amer. Acad. Arts 11: 103. 1876 – Type: *Suckleya suckleyana* (Torr.) Rydb. (≡ *Obione suckleyana* Torr.).

Description. – Annuals, with inflated papillate cells and multicellular glandular hairs, lacking essential oils (Fig. 5C). Stems prostrate or ascending, diffusely branched. Leaves usually fairly long-petiolate; blade rhombic-ovate to suborbicular, repand-dentate. Inflorescence of axillary glomerules; flowers unisexual, monoecious, with pistillate and staminate flowers mixed in glomerules. Staminate flowers usually with 4 free perianth segments, 4 stamens and sometimes rudimentary ovary. Pistillate flowers zygomorphic, with 4 somewhat fleshy perianth segments, which become fused, enlarged and compressed in fruit; ovary ovoid, stigmas 2. Fruit enclosed by the enlarged perianth, ovate to triangular-ovate, compressed; pericarp thin, adnate to the seed. Seeds vertical, to 3 mm; seed coat brown, smooth; outer cell walls of the testal layer without stalactites. Embryo subannular, surrounding the copious perisperm, radicle superior.

Suckleya has a zygomorphic female perianth and flattened fruits that differentiate it from other Dysphanieae.

One species, *Suckleya suckleyana* (Torr.) Rydb. ($2n = 18$); midwestern U.S.A. and southern Alberta, Canada (Chu & al., 1991; Chu, 2003).

Teloxys Moq. in Ann. Sci. Nat., Bot., ser. 2, 1: 289. 1834 ≡ *Chenopodium* sect. *Teloxys* (Moq.) Beck in Reichenbach, Icon. Fl. Germ. Helv. 24: 116. 1908 ≡ *Chenopodium* [unranked] *Aristata* Standl. in Britton & al., N. Amer. Fl. 21: 25. 1916 ≡ *Chenopodium* [sect. *Botryoides*] subsect. *Teloxys* (Moq.) Aellen & Iljin in Komarov, Fl. URSS 6: 47. 1936 ≡ *Dysphania* [sect. *Botryoides*] subsect. *Teloxys* (Moq.) Mosyakin & Clemants in Ukrayins'k. Bot. Zhurn. 59(4): 383. 2002 – Type: *Teloxys aristata* (L.) Moq. (≡ *Chenopodium aristatum* L.).

Description. – Non-aromatic, small annuals, richly branched and tumble-weed in habit, the stem base covered with papillae and multicellular simple hairs (Fig. 5D), other parts ± glabrous. Leaves subsessile; blade up to 6 cm, linear, narrowly oblong or spathulate, often folded on the ventral side, margin entire. Inflorescence terminal, paniculate; flowers sessile or short-pedicellate in loose dichotomous cymes, ultimate branches usually sterile, terminating with acicular apices, sometimes (in wet habitats) without acicular apices. Perianth segments 5, free to base, hyaline, sometimes pinkish, glabrous, abaxially subcarinate. Styles 2(3). Fruit compressed-spherical; pericarp tightly adjoining the seed and separating from it when rubbed, smooth. Seeds horizontal, 0.7–0.8 mm, margin keeled, seed coat reddish-black, smooth; outer cell walls of the testal layer without stalactites. Embryo horizontal, rarely obliquely or vertically orientated.

One species, *Teloxys aristata* (L.) Moq. ($2n = 18$); distributed in Central Asia and more or less established as an alien in many parts of temperate Eurasia and North America.

Uncertain placements. — Most of the Dysphanieae species that were not included in our analysis are morphologically so closely related to the studied species of *Dysphania* that it is possible to list them in the present sectional division of *Dysphania*. However, three American species of Dysphanieae have specialized morphological features that indicate that they obviously belong to *Dysphania*, but their placements in the present sectional grouping remain uncertain. They are briefly discussed here.

Dysphania minuata (Aellen) Mosyakin & Clemants (≡ *Chenopodium minuatum* Aellen).

Aellen (1973) described *Chenopodium minuatum* as a member of *C.* sect. *Ambrina*, but later Simón (1996) proposed to transfer the species to the African *C.* sect. *Margaritaria*. In addition to some morphological features similar to *C. congolanum*, she pointed out possible phytogeographic relationships across the Atlantic Ocean: *Chenopodium minuatum* was described and known only from the Atlantic coastal regions of eastern Brazil (Simón, 1995); however, it is probably more widespread in tropical South America. A fairly robust specimen from northern Peru (Prov. Piura, Piura, 1865, *R. Spruce*, BM!, G!), seems to belong to *D. minuata*. Sukhorukov & al. (2016) did not consider *D. minuata* closely related to the African *D. congolana* despite the morphological similarity in leaf shape and vertical seed embryo position. However, *D. minuata* deviates from the South American *D.* sect. *Adenois* in leaf characters, branching of the inflorescence and hairy perianth, and its placement pends molecular confirmation.

Dysphania dissecta (Moq.) Mosyakin & Clemants (≡ *Ambrina dissecta* Moq. ≡ *Chenopodium dissectum* (Moq.) Standl. = *Chenopodium bipinnatifidum* Moric. ex Moq.).

Small, branched annual with glandular and multicellular hairs. Leaves sparsely pinnatisect, lobes linear, as wide as the rachis, with few very short secondary lobes, apex and lobes obtuse. Flowers dense on short paniculate branches in leaf axils, subsessile. Perianth segments 5, deeply split, not contiguous, abaxially swollen in fruit stage. Seeds ca. 1 mm, globose, with prominently reticulate surface, pits deep. Similar seeds are not known in other Dysphanieae. *Dysphania dissecta* is known from Mexico, in mountainous areas from the State of Puebla to the State of Coahuila. Standley (1916) placed *Chenopodium dissectum*, together with *C. botrys*, in his *C.* [unranked] *Botryes*; instead, Mosyakin & Clemants (2008) included *D. dissecta* in *Dysphania* subsect. *Incisa*, together with *D. graveolens* and *D. mandonii*.

Dysphania stellata (S.Watson) Mosyakin & Clemants (≡ *Chenopodium stellatum* S.Watson ≡ *Meiomeria stellata* (S.Watson) Standl.).

Small, branched annual with glandular and multicellular hairs. Leaves subsessile, linear, entire, obtuse. Flowers densely

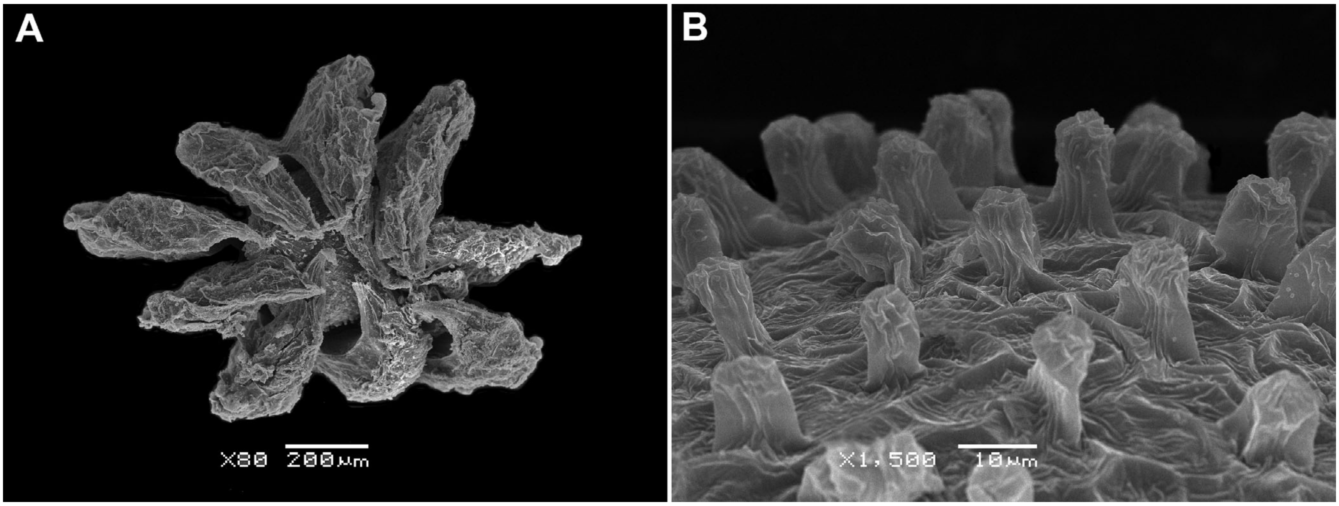

Fig. 6. SEM images of the perianth and pericarp ultrasculpture of *Dysphania stellata*. **A**, Perianth in fruit stage with 9 winged segments; **B**, Papillae on the pericarp; Mexico, Coahuila, 1800, *E. Palmer 1155* (LE).

on spiciform branches in leaf axils, subsessile; perianth segments 6–9 (Fig. 6A), almost free, concave, linear, not contiguous, strongly swollen abaxially and becoming winged and dentate in fruit. Pericarp with tubular papillae. Seeds vertical, 0.3–0.4 mm. Flowers deviate from other Dysphanieae in particular as to the high number of perianth segments. Additionally, this species drastically differs in having tubular pericarp papillae (Fig. 6B) that are not mentioned in any American *Dysphania* (only *D. dissecta* was not studied). Such papillae are very similar to those of *D. schraderiana* (Sukhorukov, 2014: plate 8, fig. 6). Watson (1883) stated that the species is allied to *Chenopodium carinatum* (≡ *Dysphania carinata*). Standley (1916) described a new genus *Meiomeria* for it, which was generally accepted since Scott (1978a) transferred it back to *Chenopodium* as the monotypic *C.* sect. *Meiomeria*. When transferred to *Dysphania* Mosyakin & Clemants (2008) did not place it in any section.

■ AUTHOR CONTRIBUTIONS

PU, APS and GK designed the project. JMD, PU, APS and GK contributed samples. NB, AAK and GK conducted lab work and molecular data analyses. PU and APS conducted morphological analyses. PU, APS and GK contributed to the biogeographical and taxonomic part. PU, APS and GK wrote the draft; all authors approved and contributed to the final version of the paper. — PU, https://orcid.org/0000-0002-3707-0454; APS, https://orcid.org/0000-0003-2220-826X; AAK, https://orcid.org/0000-0002-0653-3655; GK, https://orcid.org/0000-0003-0094-8769

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Appendix 1. Sequence identification numbers and isolate numbers, voucher details and GenBank accession numbers of taxa sampled. Names follow new taxonomy.

Taxon name with taxonomic authority, Seq_ID, Isolate number, ITS, ETS, *atpB-rbcL* spacer, *rpl16* intron GenBank accession numbers for samples for which sequences have been taken from GenBank only. An asterisk (*) indicates a sample included in biogeography analysis. A dash (–) indicates missing data.

Axyris amaranthoides L., AxamarAC647, AC647, HE577370, –, –, –; ***Axyris prostrata*** L., AxprosAC529, AC529, HE577369, –, –, –; ***Ceratocarpus arenarius*** L., CearenAC649, AC649, HE577365, –, –, –; ***Ceratocarpus arenarius***, CearenAC531, AC531, HE577364, –, –, –; ***Krascheninnikovia ceratoides*** (L.) Gueldenst., KrceraAC608, AC608, HE577366, –, –, –, * (combined with Chen0012); ***Krascheninnikovia ceratoides***, Krcera0012, Chen0012, –, –, MK635457, –, * (combined with CearenAC531); ***Krascheninnikovia ceratoides*** subsp. ***lanata*** (Pursh) H.Heklau, KrcerassplanaAC626, AC626, HE577368, –, –, –.

Appendix 1. Continued.

Taxon name with taxonomic authority, Seq_ID, Isolate number, country: largest political subdivision/locality, *collector(s)* + *number* (Herbarium and voucher sheet number), ITS, ETS, *atpB-rbcL* spacer, *rpl16* intron GenBank accession numbers for newly sequenced specimens. An asterisk (*) indicates a sample included in biogeography analysis. A dash (–) indicates missing data. States of Australia and U.S.A. given with official abbreviations. BG = Botanical Garden.

Axyris amaranthoides L., Axamar3015, Chen3015, Mongolia: North Mongolia, *W. Hilbig 246/83* (HAL 56454), –, MK692777, MK635354, –, *; ***Axyris prostrata*** L., Axpros0118, Chen0118, Mongolia: Gobi Altai, *G. & S. Miehe 96-140-04* (KAS), MK802948, –, MK635355, MK784573, *; ***Axyris prostrata***, Axpros3003, Chen3003, Mongolia: Central Mongolia, *W. Hilbig & Z. Schamsran s.n.* (HAL 48537), –, MK692778, MK635356, MK784574; ***Ceratocarpus arenarius*** L., Cearen3050, Chen3050, Mongolia: Khovd Prov., *W. Hilbig & Z. Schamsran s.n.* (HAL 101082), –, MK692779, MK635357, –, *; ***Dysphania ambrosioides*** (L.) Mosyakin & Clemants, Dyambr0822, Chen0822, Portugal: Azores/Sao Miguel (seed sample from Berlin-Dahlem BG leg. *Royl 6394*, cult. in BG Mainz), –, (MJG), MK802950, –, MK635361, MK784576; ***Dysphania ambrosioides***, Dyambr2786, Chen2786, Tanzania: Tanga Prov./West Usambara, *K. Vainio-Mattila, K. Lahti & O. Vainio 96-151* (H 1692978), MK802952, MK692781, MK635363, MK784578, *; ***Dysphania ambrosioides***, Dyambr2790, Chen2790, Japan: Tokyo (seed sample from Tokyo BG, cult. in Helsinki BG), *P. Uotila 29969* (H 1393031), MK802954, MK692783, MK635365, MK784580; ***Dysphania ambrosioides***, Dyambr2066, Chen2066, U.S.A.: CA/Butte County, *Lowell Ahart 9413* (JEPS), MK802951, –, MK635362, MK784577; ***Dysphania ambrosioides***, Dyambr3426, Chen3426, India: Himachal Pradesh/20 km SW of Dehra Dun, *P. Uotila 17666* (H 1101255), MK802955, MK692784, MK635366, MK784581; ***Dysphania ambrosioides***, Dyambr3504, Chen3504, Argentine: Mendoza/Malargüe, *C.B. Passera s.n.* (MERL 37468), MK802956, MK692785, –, –; ***Dysphania ambrosioides***, Dyambr2787, Chen2787, England: Surrey/Kew (seed sample from Royal BG Kew, cult. in Helsinki BG), *P. Uotila 28757* (H 1260955), MK802953, MK692782, MK635364, MK784579; ***Dysphania anthelmintica*** (L.) Mosyakin & Clemants, Dyanth2795, Chen2795, U.S.A.: NC/Conine Creek, *H.E. Ahlee 52014 & J.G. Haesloop* (H 1036364), MK802957, –, MK635367, MK784582, *; ***Dysphania atriplicifolia*** (Spreng.) G.Kadereit, Uotila & Sukhor., Cyatri2791, Chen2791, U.S.A.: MN/Houston Co., *S.R. Ziegler & M.F. Leykom 1838* (H 1206836), MK802949, MK692780, MK635358, MK784575, *; ***Dysphania atriplicifolia***, Cyatri2892, Chen2892, U.S.A.: IL/Henderson Co., *T.G. Lammers 7464* (F), –, –, MK635359, –; ***Dysphania atriplicifolia***, Cyatri2893, Chen2893, U.S.A.: WI/Vernon Co., *S.R. Ziegler & M.F. Leykom 1616* (H 1206837), –, –, MK635360, –; ***Dysphania bhutanica*** Sukhor., Dybhut2998, Chen2998, Bhutan: Thimphu, *A.J.C. Grierson & D.G. Long 2828* (K), MK802958, MK692786, MK635368, MK784583, *; ***Dysphania botrys*** (L.) Mosyakin & Clemants, Dybotr0116, Chen0116, Turkey: Konya/road to Karapinar, *H. Freitag & Adigüzel 28769* (KAS), MK802959, –, MK635369, MK784584; ***Dysphania botrys***, Dybotr2798, Chen2798, Kyrgyzstan: Jalal-Abad region/Kyzyl-Jar, *P. Uotila 47905* (H 1747524), MK802961, –, MK635370, –; ***Dysphania botrys***, Dybotr2777, Chen2777, Austria: Niederösterreich/Vöslau, *W. Till 90228* (WU), MK802960, –, –, MK784585; ***Dysphania botrys***, Dybotr2999, Chen2999, Kyrgyzstan: Jalal-Abad Region, *P. Uotila 47502* (MW), MK802962, MK692787, MK635371, MK784586, *; ***Dysphania botrys***, Dybotr3046, Chen3046, Russia: Kursk prov./Zheleznogorsk, *N.I. Degtyarev s.n.* (MW), MK802964, MK692789, MK635373, MK784588; ***Dysphania carinata*** (R.Br.) Mosyakin & Clemants, Dycari3425, Chen3425, South Africa: Johannesburg/Soweto, *I. Sahi s.n.* (H 1763504), MK802966, MK692790, MK635375, MK784590, *; ***Dysphania carinata***, Dycari2776, Chen2776, Yemen: Lahij/55 km from Habilayn towards Labus, *M. Thulin, M. Ghebrehiwet & A.N. Gifri 9264* (UPS 125313), MK802965, –, MK635374, MK784589; ***Dysphania chilensis*** (Schrad.) Mosyakin & Clemants, Dychil2796, Chen2796, Chile: Región de Maule/Tricao, *M. Valdes (Hernández 204)* (H 1690741), MK802967, MK692793, MK635378, MK784591, *; ***Dysphania chilensis***, Dychil2792, Chen2792, Chile: Región de Maule/Cordillera de los Andes, *C. Hernández 203* (H 1690734), –, MK692791, MK635376, –; ***Dysphania chilensis***, Dychil2793, Chen2793, Chile: Santiago/Laguna de Aculéo, *C. Hernández 210* (H 1690732), –, MK692792, MK635377, –; ***Dysphania congestiflora*** S.J.Dillon & A.S.Markey, Dycofl3501, Chen3501, Australia: WA, *A. Markey & S. Dillon FM 9709* (PERTH 08730105), MK802968, MK692794, MK635379, –, *; ***Dysphania congolana*** (Hauman) Mosyakin & Clemants, Dycong2771, Chen2771, Ethiopia: Gojjam Region/near Sekela, *M. Thulin & A. Hunde 3970* (H 1377076 & UPS), MK802969, –, MK635380, MK784592; ***Dysphania congolana***, Dycong3306, Chen3306, Burundi: Prov. Muramwya/Bugarama, *M. Reekmans 11051* (BR), MK802970, MK692795, MK635381, MK784593, *; ***Dysphania congolana***, Dycong3307, Chen3307, Burundi, *M. Reekmans 11227* (BR), –, MK692796, –, –; ***Dysphania cristata*** (F.Muell.) Mosyakin & Clemants, Dycris0256, Chen0256, Australia: NSW/Coonamble, *S. Jacobs 8653* (NSW 491980), –, –, MK635382, MK784594; ***Dysphania cristata***, Dycris3310, Chen3310, Australia: SA/32.05090°S 140.15977°E, *J. McDonald 1409/26B* (MJG 020875), –, MK692797, MK635383, MK784595; ***Dysphania cristata***, Dycris3526, Chen3526, Australia: WA/Giralia Station at S end of Exmouth Gulf, *M. Maier GIR 107-X* (PERTH 07451172), MK802972, MK692798, MK635384, MK784596; ***Dysphania cristata***, Dycris3528, Chen3528, Australia: WA/Lake Mason Station 56 km NNE of Sandstone, *D.J. Edinger & G. Marsh, DJE 4638A* (PERTH 06872980), MK802973, MK692799, MK635385, MK784597, *; ***Dysphania geoffreyi*** Sukhor., Dygeof3308, Chen3308, Bhutan: Upper Mo Chu distr., *Sinclair & Long s.n.* (E 00151629), MK802974, MK692800, MK635386, –; ***Dysphania geoffreyi***, Dygeof3309, Chen3309, China: Yunnan/Nada, *Chungtien-Lijiang-Dali- Expedition 324* (K), MK802975, MK692801, MK635387, MK784598, *; ***Dysphania glandulosa*** Paul G.Wilson, Dyglan3535, Chen3535, Australia, WA/13.2 km from Yalgoo, *G. Byrne 3563* (PERTH 08387729), MK802977, MK692803, MK635389, MK784600; ***Dysphania glandulosa***, Dyglan3536, Chen3536, Australia: WA/12.7 km E of Mt. Narryer Station Homestead, *A.S. George 17439* (PERTH 05981301), MK802978, MK692804, MK635390, –; ***Dysphania glandulosa***, Dyglan3537, Chen3537, Australia: WA/Meekatharra, *G. Byrne 308* (PERTH 07153201), MK802979, MK692805, MK635391, MK784601, *; ***Dysphania glandulosa***, Dyglan3525, Chen3525, Australia: WA/Gidgee Road, *D.J. Edinger & G. Marsh DJE 4862* (PERTH 06930026), MK802976, MK692802, MK635388, MK784599; ***Dysphania glomulifera*** (Nees) Paul G.Wilson, Dyglom0277, Chen0277, Australia: NSW/Hermidale, *S. Jacobs 8738* (NSW 490542), MK802980, –, MK635392, MK784602; ***Dysphania glomulifera***, Dyglom3523, Chen3523, Australia: WA/Gibson Desert, *C.P. Campbell* 2429 (PERTH 06288871), MK802981, MK692806, MK635393, MK784603, *; ***Dysphania glomulifera***, Dyglom3524, Chen3524, Australia: WA/Doolgunna Station Gascoyne, *D.J. Edinger 4337* (PERTH 07112580), MK802982, MK692807, MK635394, MK784604; ***Dysphania graveolens*** (Willd.) Mosyakin & Clemants, Dygrav2073, Chen2073, Mexico: Veracruz/Perote, *M. Nee 32944* (JEPS & UC), MK802983, –, MK635395, MK784605, *; ***Dysphania graveolens***, Dygrav2079, Chen2079, U.S.A.: NM/Luna Co., *J. Travis Columbus 525* (JEPS & UC), MK802984, –, MK635396, –; ***Dysphania graveolens***, Dygrav2080, Chen2080, U.S.A.: AZ/Mohave Co., *L.C. Higgins 24017* (JEPS & UC), MK802985, –, MK635397, MK784606; ***Dysphania himalaica*** Uotila, Dyhima2773, Chen2773, India: Ladakh/Rupshu, *L.Klimeš 99-27-9a* (H 1757588), MK802986, –, MK635398, –, *; ***Dysphania kalpari*** Paul G. Wilson, Dykalp0276, Chen0276, Australia: NSW/ca. 75 km N of Bourke, S.*W.L. Jacobs 8734* (NSW 490547), –, –, –, MK784607; ***Dysphania kalpari***, Dykalp0528, Chen0528, Australia: WA/Austin, *S.W.L. Jacobs 9185* (MJG 018697 & NSW 594047), MK802987, –, MK635399, MK784608; ***Dysphania kalpari***, Dykalp3508, Chen3508, Australia: WA/Mt. Methwin, *N. Gibson 6872 & al.* (PERTH 08795010), MK802989, MK692809, MK635401, MK784610, *; ***Dysphania kalpari***, Dykalp3520, Chen3520, Australia: WA/27°24′S 120°38′E, *G. Byrne 2232* (PERTH 07809360), MK802990, MK692810, MK635402, MK784611; ***Dysphania kalpari***, Dykalp3415, Chen3415, Australia: WA/Austin, *A.A. Mitchell 1518* (AD 234148), MK802988, MK692808, MK635400, MK784609; ***Dysphania littoralis*** R.Br., Dylitt3432, Chen3432, Australia: Qld./ Idalia National Park, *R.J. Fensham 6182* (AQ 876272), MK802991, MK692811, MK635403, MK784612, *; ***Dysphania littoralis***, Dylitt3434, Chen3434, Australia: Qld/N of Yeppoon, *A.R. Bean 31614* (AQ 823544), MK802992, MK692812, MK635404, MK784613; ***Dysphania mandonii*** (S.Watson) Mosyakin & Clemants, Dymand2770, Chen2770, Bolivia: La Paz/Bautista Saavedra Prov. *J. Krach 8378* (H 1661944), MK802993, –, MK635405, MK784614; ***Dysphania mandonii***, Dymand2781, Chen2781, Bolivia: La Paz/José Ramón Loayza Prov., *St. G. Beck 22974* (H 1704706), MK802994, MK692813, MK635406, MK784615, *; ***Dysphania melanocarpa*** (J.M.Black) Mosyakin & Clemants, Dymela3408, Chen3408, Australia: SA/Gairdner-Torrens, *H.P. Vonow & N.R. Neagle BS721-452* (AD 241113), MK802995, MK692814, MK635407, MK784616; ***Dysphania melanocarpa***, Dymela3409, Chen3409, Australia: SA/E of main Serpentine Lakes, *D.E. Murfet 7693* (AD 267507), MK802996, MK692815, MK635408, MK784617, *; ***Dysphania melanocarpa***, Dymela3410, Chen3410, Australia: SA/W from Mt Hoare, *P.D. Canty BS23-39262* (AD 120888), MK802997, MK692816, MK635409, MK784618; ***Dysphania melanocarpa***, Dymela3527, Chen3527, Australia: WA/E of Mt. Royal, *W.A. Thompson & N.N. Sheehy 629* (PERTH 08571945), MK802999, MK692818, MK635410, MK784619; ***Dysphania melanocarpa***, Dymela3429, Chen3429, Australia: WA/W of Yeo Camp, *H.R. Tölken 6046*

Appendix 1. Continued.

(H 1559880), MK802998, MK692817, –, –; ***Dysphania multifida*** (L.) Mosyakin & Clemants, Dymult2774, Chen2774, Greece: Makedonia/Halkidiki, *M. Koistinen 1997/285* (H 1720089), MK803001, –, MK635413, –; ***Dysphania multifida***, Dymult2789, Chen2789, Chile: Región de Maule/San Miguel de Colín, *C. Hernández 208* (H 1690726), MK803003, MK692820, MK635415, –, *; ***Dysphania multifida***, Dymult2775, Chen2775, Spain: Malaga/Fuengirola, *P. Uotila 42552* (H 1695061), MK803002, –, MK635414, MK784621; ***Dysphania multifida***, Dymult2081, Chen2081, U.S.A.: CA/Butte County, *V.H. Oswald 9981* (JEPS), MK803000, –, MK635412, –; ***Dysphania multiflora*** (Moq.) G.Kadereit, Sukhor. & Uotila, Dymufl3014, Chen3014, Nepal: Jumla/Jumla village, *A. Sukhorukov s.n.* (MW), –, MK692819, MK635411, MK784620, *; ***Dysphania neglecta*** Sukhor., Dynegl3010, Chen3010, Nepal: Jumla/Nigregar, *A. Sukhorukov s.n.* (MW), MK802963, MK692788, MK635372, MK784587, *; ***Dysphania nepalensis*** (Colla) Mosyakin & Clemants, Dynepa2785, Chen2785, Nepal: Mustang/Mukhtinath village, *A. Sukhorukov s.n.* (H 1750722), MK803004, –, MK635416, MK784622; ***Dysphania nepalensis***, Dynepa3000, Chen3000, India: Kashmir/Leh, *H. Hartmann 4015* (G), MK803005, –, MK635417, –; ***Dysphania nepalensis***, Dynepa3047, Chen3047, China: Qinghai/Gonghe, *T.N. Ho & al.* (E 00067214), MK803007, –, MK635419, MK784623; ***Dysphania nepalensis***, Dynepa3011, Chen3011, Bhutan: Bumthang, *Ch. Parker 7118* (E), MK803006, MK692821, MK635418, –, *; ***Dysphania plantaginella*** F.Muell., Dyplan3509, Chen3509, Australia: WA/Yamada rockhole, *N. Gibson 6871 & al.* (PERTH 08794855), MK803008, MK692822, MK635420, MK784624; ***Dysphania plantaginella***, Dyplan3522, Chen3522, Australia: WA/Tent Island Nature Reserve, *N. Godfrey NG 57/15* (PERTH 08752850), MK803009, MK692823, MK635421, MK784625, *; ***Dysphania plantaginella***, Dyplan3532, Chen3532, Australia: WA/Giralia Station, *M. Maier, K. McCreery & B. Muir GIRB-08* (PERTH 07515758), –, –, MK635422, –; ***Dysphania plantaginella***, Dyplan3533, Chen3533, Australia: WA/Ord River, *T. Handasyde & A.N. Start, TH 00 227* (PERTH 06193331), –, MK692824, –, –; ***Dysphania plantaginella***, Dyplan3534, Chen3534, Australia: WA/Oyster stacks car park, *J. English 157* (PERTH 07694474), –, MK692825, MK635423, MK784626; ***Dysphania platycarpa*** Paul G.Wilson, Dyplat3411, Chen3411, Australia: SA/29 km S of Innamincka, *D.J. Duval, D. Murfet, T. Croft, P. Winter & M. Thorpe 864* (AD 214659), MK803010, MK692826, MK635424, MK784627, *; ***Dysphania platycarpa***, Dyplat3412, Chen3412, Australia: SA/Mt. Sarah Station, *R. Bates 46907* (AD 99815056), MK803011, MK692827, MK635425, MK784628; ***Dysphania platycarpa***, Dyplat3413, Chen3413, Australia: SA/Goyder Lagoon, *R. Bates 71698* (AD 206499), MK803012, MK692828, –, MK784629; ***Dysphania procera*** (Hochst. ex Moq.) Mosyakin & Clemants, Dyproc2772, Chen2772, Burundi: Gankuzo/Gitwenge (seed sample from Liege BG, cult. in Helsinki BG), *P. Uotila 33696* (H 1590138), MK803013, MK692829, MK635426, MK784630; ***Dysphania procera***, Dyproc3001, Chen3001 (=chen3012, 3013), Yemen: Shahará, *J.R. Wood 2502* (BM & E), MK803014, –, MK635427, MK784631, *; ***Dysphania pseudomultiflora*** (Murr) Verloove & Lambinon, Dypseu2783, Chen2783, South Africa: Transvaal/Pretoria, *K.A. Dahlstrand 1288* (H 1039200), –, MK692830, MK635428, MK784632, *; ***Dysphania pseudomultiflora***, Dypseu2784, chen2784, Namibia: Windhoek, *M. Juva s.n.* (H 1731422), –, –, –, MK784633; ***Dysphania pseudomultiflora***, Dypseu3305, Chen3305, South Africa: Eastern Cape/Albany, *R.D.A. Bayliss 8675* (BR-16053632), –, MK692831, –, –; ***Dysphania pumilio*** (R.Br.) Mosyakin & Clemants, Dypumi2788, Chen2788, Australia: Tas/East Coast, *W.M. Curtis* (H 1669458), MK803015, –, MK635430, –; ***Dysphania pumilio***, Dypumi0255, Chen0255, Australia: NSW/Coonamble, *S. Jacobs 8651* (NSW 491981), –, –, MK635429, MK784634; ***Dysphania pumilio***, Dypumi3049, Chen3049, Czech Republic: Moravia, *F. Dvořák s.n.* (MW), MK803016, MK692832, –, –; ***Dysphania pumilio***, Dypumi3513, Chen3513, Australia: WA/Manjimup, *R.J. Cranfield 14546* (PERTH 05600154), MK803017, MK692833, MK635431, MK784635, *; ***Dysphania pumilio***, Dypumi3514, Chen3514, Australia: WA/Watheroo National Park, *G.J. Keighery* (PERTH 05703662), MK803018, MK692834, MK635432, MK784636; ***Dysphania pumilio***, Dypumi3519, Chen3519, Australia: WA/Manjimup town centre, *R.J. Cranfield 26678* (PERTH 08461422), MK803019, MK692835, MK635433, MK784637; ***Dysphania rhadinostachya*** (F.Muell.) A.J.Scott, Dyrhad0525, Chen0525, Australia: WA/118 km NNE of Carnarvon, *S. Jacobs 9167* (MJG 018698 & NSW 594049), MK803020, –, MK635434, MK784638; ***Dysphania rhadinostachya***, Dyrhad3414, Chen3414, Australia: SA/Lake Eyre, *D.J. Duval, D. Murfet, T. Croft, P. Winter, M. Thorpe 891* (AD 214625), MK803021, MK692836, MK635435, MK784639, *; ***Dysphania rhadinostachya***, Dyrhad3416, Chen3416, Australia: WA/Carnarvon, *R. & K. Chinnock 16* (AD 98701214), MK803022, MK692837, –, –; ***Dysphania saxatilis*** (Paul G.Wilson) Mosyakin & Clemants, Dysaxa3418, Chen3418, Australia: WA/ Von Treuer Tableland, *H.R. Tolken 6152* (AD 98006341), MK803023, MK692838, –, –; ***Dysphania saxatilis***, Dysaxa3430u3417, Chen3430 (H) & Chen3417 (AD), Australia: WA/124.6 km W of Neale Junction, *H.R. Tolken 6042* (H 1559839 & AD 98004534), MK803024, MK692839, –, –; ***Dysphania saxatilis***, Dysaxa3517, Chen3517, Australia: WA/SE of Yalgoo, *A. Markey & S. Dillon 5469* (PERTH 08488738), MK803025, MK692840, MK635436, MK784640, *; ***Dysphania saxatilis***, Dysaxa3518, Chen3518, Australia: WA/SW of Tom Price, *J. Fairhead & P. Anderson BES 00424* (PERTH 08431000), MK803026, MK692841, MK635437, MK784641; ***Dysphania schraderiana*** (Schult.) Mosyakin & Clemants, DyschrAC387, AC387, Ethiopia: –, *M. Wondafrash 2255* (B), HE577349, –, –, –; ***Dysphania schraderiana***, Dyschr2794, Chen2794, Russia: Moscow distr. (seed sample from BG of Inst. Pl. Med., Vilar, cult. in Helsinki BG), *P. Uotila 28695* (H 1259578), –, –, MK635438, –; ***Dysphania schraderiana***, Dyschr3048, Chen3048, Russia: Moscow/Botanical Garden, *Yu. Alexeev s.n.* (MW), MK803027, MK692842, MK635439, MK784642, *; ***Dysphania simulans*** F.Muell. & Tate, Dysimu3419, Chen3419, Australia: SA/Clayton station, H.P. Vonow 2353 & al. (AD 99736045), MK803028, MK692843, MK635440, MK784643; ***Dysphania simulans***, Dysimu3420, Chen3420, Australia: SA/Lake Eyre, *F.J. Badman 5158* (AD 99235095), –, MK692844, MK635441, MK784644; ***Dysphania simulans***, Dysimu3421, Chen3421, Australia: SA/Salt-gypsum lake off the Oodnadatta Track, *R. Bates RB46908* (AD 99815057), MK803029, MK692845, MK635442, MK784645, *; ***Dysphania simulans***, Dysimu3511, Chen3511, Australia: WA/S side of Lake Kerrylyn Tate, *N. Gibson 6869 & al.* (PERTH 08794839), MK803030, MK692846, MK635443, MK784646; ***Dysphania simulans***, Dysimu3512, Chen3512, Australia: WA/Samphire Tate, *R.J. Cranfield 5980* (PERTH 02586347), –, MK692847, MK635444, –; ***Dysphania simulans***, Dysimu3515, Chen3515, Australia: WA/Lorna Glen Station Tate, *D.J. Edinger & G. Marsh DJE 3321* (PERTH 06464858), –, –, MK635445, –; ***Dysphania spec.***, Dyspec3503, Chen3503, Argentina: Mendoza/Uspallata, *F.A. Raig 11429* (MERL 42014), –, MK692848, –, –; ***Dysphania sphaerosperma*** Paul G.Wilson, Dyspha3510, Chen3510, Australia: WA/Lake Kerrylyn, *N. Gibson 6870 & al.* (PERTH 08794847), MK803031, MK692849, MK635446, MK784647; ***Dysphania sphaerosperma***, Dyspha3521, Chen3521, Australia: WA/SE of Cane River Homestead, *D.J. Edinger 1607* (PERTH 05435870), MK803032, MK692850, MK635447, MK784648; ***Dysphania sphaerosperma***, Dyspha3529, Chen3529, Australia: WA/NW of Mt. Amy, *S. Dillon, A. Markey CR 9199* (PERTH 08432473), MK803033, MK692851, MK635448, MK784649; ***Dysphania sphaerosperma***, Dyspha3530, Chen3530, Australia: WA/Pilbara, *N.G. Walsh 6573 & al.* (PERTH 08085706), MK803034, MK692852, MK635449, MK784650, *; ***Dysphania sphaerosperma***, Dyspha3531, Chen3531, Australia: WA/6.5 km NE of Mt. Turner, *M. Maier BES 00001* (PERTH 08437173), MK803035, MK692853, MK635450, MK784651; ***Dysphania tibetica*** (A.J.Li) Uotila, Dytibe2769, Chen2769, India: Ladakh/Rupshu, *L. Klimeš s.n.* (H 1757589), MK803036, –, MK635451, –, *; ***Dysphania truncata*** (Paul G.Wilson) Mosyakin & Clemants, Dytrun3422, Chen3422, Australia: SA/Innamincka Regional Reserve, *M. Barnett BS612-319* (AD 224049), MK803037, MK692854, MK635452, MK784652; ***Dysphania truncata***, Dytrun3423, Chen3423, Australia: SA/Cordillo Downs, *D.J. Duval, M.J. Thorpe & T.S. Te 1217* (AD 224912), MK803038, MK692855, MK635453, MK784653; ***Dysphania truncata***, Dytrun3424, Chen3424, Australia: SA/off Borefield Road, *R. Bates 46881* (AD 99909269), MK803039, MK692856, MK635454, MK784654, *; ***Dysphania valida*** Paul G.Wilson, Dyvali3433, Chen3433, Australia: Qld/30 km S of Morven on Boatman road, *J.L. Silcock JLS 1107* (AQ 825529), MK803040, MK692857, MK635455, MK784655, *; ***Dysphania valida***, Dyvali3441, Chen3441, Australia: Qld/E of Windorah, *A.R. Bean 30223* (AQ 822308), MK803041, MK692858, MK635456, MK784656; ***Krascheninnikovia ceratoides***, Krcera3051, Chen3051, Mongolia: Govi-Altai Prov., *E. Jäger* (HAL 57753), –, –, MK635458, –; ***Krascheninnikovia ceratoides subsp. lanata*** (Pursh) H.Heklau, Krcerassplana1887, Chen1887, U.S.A.:NM/San Miguel, *J.B. Nelson 23554 & al.* (HAL 100339), –, MK692859, MK635459, –, *; ***Neomonolepis spathulata*** (A.Gray) Sukhor., MoSPATH, MoSPATH, U.S.A.: CA/Susanville, *I.Yu. Koropachinsky & al. 404* (MHA), MH675518, –, MH152575, *; ***Suckleya suckleyana*** (Torr.) Rydb., Susuck2000, Chen2000, U.S.A.: NM/Tres Piedras, *J.E. Larson 6492* (RM), MK803042, MK692861, –, MK784658, *; ***Suckleya suckleyana***, Susuck2001, Chen2001, U.S.A.: NM, *B.E. Nelson 66396* (RM), –, MK692862, –, MK784659; ***Suckleya suckleyana***, Susuck1999, Chen1999, U.S.A.: WY, *B.E.Nelson 56487* (F), –, MK692860, –, MK784657; ***Teloxys aristata*** (L.) Moq., Tearis0293, Chen0293, Mongolia: Ulaanbaatar, *B.B. Neuffer & H. Hurka 11.727* (KAS), MK803043, –, MK635460, MK784660, *; ***Teloxys aristata***, Tearis2778, Chen2778, Russia: Altai Republic/Altai near river Chuya (Cuja), *A. Tribsch & F. Essl 9924* (WU), MK803044, –, –, MK784661; ***Teloxys aristata***, Tearis3002, Chen3002, Mongolia: Zentralaimak, W. Hilbig, *Z. Schamsran* (HAL 45266), –, –, MK635461, –.