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Phylogenetic relationships and taxonomy of subfamily Zygophylloideae (Zygophyllaceae) based on molecular and morphological data

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Abstract. Phylogenetic analysis of noncoding *trn*L plastid DNA sequences and morphological data for 43 species of Zygophylloideae, representing most of the morphological and geographical variation in the subfamily, indicates that the currently recognised genera *Augea* (monotypic, southern Africa), *Tetraena* (monotypic, China), and *Fagonia* (c. 30 species, widespread), are embedded in *Zygophyllum* (c. 150 species, widespread). A generic classification based on six monophyletic and morphologically distinctive entities is proposed: *Roepera* with c. 60 species in Australia and southern Africa, *Zygophyllum* with c. 50 species in Asia, *Tetraena* with c. 40 species in Africa and Asia, *Augea* with a single species in southern Africa, *Melocarpum* with two species in the Horn of Africa region, and *Fagonia* with c. 30 species in both the Old and the New World. Scanning electron microscopy studies of testa structure provided important characters for the delimitation of some genera. New combinations (61) are made in *Roepera*, a resurrected genus originally described from Australia, one new name is proposed in *Zygophyllum*, 35 new combinations are made in *Tetraena*, and two new combinations are made in *Melocarpum* (previously *Zygophyllum* sect. *Melocarpum*).

Key words: Zygophyllaceae, Zygophylloideae, *Augea*, *Fagonia*, *Melocarpum*, *Roepera*, *Tetraena*, *Zygophyllum*, plastid DNA, *trn*L, morphology, phylogeny, taxonomy.

Zygophyllaceae, in the classification by Sheahan and Chase (1996, 2000), are a family of approximately 285 species subdivided into five subfamilies and about 27 genera. They consist of trees, shrubs and herbs mostly restricted to arid and semi-arid areas in the tropics and subtropics. According to recent molecular analyses, the family occupies an isolated position within the eurosid I clade, in which it is sister to *Krameria* (Soltis et al. 2000, Savolainen et al. 2000a, Savolainen et al. 2000b, APG 1998).

Zygophylloideae, as proposed by Sheahan and Chase (1996, 2000), are the largest subfamily in Zygophyllaceae and consist of about 180 species of shrubs, subshrubs and herbs currently grouped in four genera, monotypic *Augea* (South Africa), monotypic *Tetraena* (China), widespread *Fagonia* (c. 30 species), and likewise widespread *Zygophyllum* (c. 150

species). In previous classifications of Zygophyllaceae, such as those by Engler (1931) and Takhtajan (1996), a much wider circumscription of Zygophylloideae was used, including elements now placed in four other subfamilies, Larreoideae, Morkillioideae, Seetzenioideae and Tribuloideae. The circumscription of Zygophylloideae as proposed by Sheahan and Chase (1996, 2000) is used in this study, if not otherwise stated.

A strongly deviating view on the classification of Zygophyllaceae sensu lato was proposed by Khalkuziev (1990) on the basis of morphological data. Of the four genera mentioned above only *Fagonia* and *Zygophyllum* were placed in Zygophyllaceae, whereas *Augea* was placed in Tribulaceae and *Tetraena* in Tetradiclidaceae. This classification has no support in the molecular analyses and is not further considered here. Other alternative classifications involving *Augea* and *Tetraena* are the recognition of the monotypic subfamilies Augeoideae (Engler 1896, Schönland 1914, Engler 1931, Takhtajan 1996) and Tetraenoideae (Ma and Zhang 1990, Takhtajan 1996).

Some authors have questioned the monophyly of the large and morphologically diverse *Zygophyllum* (El Hadidi 1978; Thulin 1993; Sheahan and Chase 1996, 2000), but the genus, as understood and circumscribed by Engler (1931), has also been accepted by several authors who worked extensively on it (Zumbruch 1931, Van Huyssteen 1937, Oltman 1971, Van Zyl 2000). To accomodate the large range of variation, Engler (1931) subdivided *Zygophyllum* into 17 sections, whereas Van Huyssteen (1937) proposed a classification in two subgenera and 13 sections, mainly on the basis of fruit and filament characters.

In 1996 Sheahan and Chase published a study based on the analyses of morphological and *rbc*L DNA sequence data including *Augea*, one species of *Fagonia*, *Tetraena*, and two species of *Zygophyllum*. In their combined analysis *Fagonia* is sister to the rest of the subfamily, whereas *Z. fabago* (the type species of *Zygophyllum*) is sister to *Augea* and *Z. simplex* is sister to *Tetraena*. One of the conclusions drawn in this study is that *Z. simplex* may not in fact belong in *Zygophyllum*.

Sheahan and Chase (2000), in an expanded study, analysed both *rbc*L and *trn*L-F sequences from 36 members of Zygophyllaceae. From Zygophylloideae they included *Augea*, three species of *Fagonia*, *Tetraena*, and 15 species of *Zygophyllum*. In that study, Zygophylloideae were strongly supported as monophyletic, whereas *Zygophyllum* was polyphyletic with *Augea*, *Fagonia* and *Tetraena* embedded within it. The main groupings are the same in the different analyses, but the branching order within Zygophylloideae differed considerably between the *rbc*L and the *trn*L-F analyses. However, in the combined analysis the clade with all species of *Fagonia* is sister to a clade with *Z. robecchii* and *Z. hildebrandtii*, two species from the Horn of Africa region. *Augea* is there weekly supported as sister to the clade with *Fagonia* and the two species of *Zygophyllum* mentioned above. Three species of *Zygophyllum* from South Africa (*Z. leptopetalum*, *Z. hirticaule* and *Z. spinosum*) come out in a strongly supported clade as sister to three Australian species (*Z. fruticulosum*, *Z. billardieri* and *Z. glaucum*). The type of *Zygophyllum*, *Z. fabago*, forms a strongly supported clade with another Asian species, *Z. xanthoxylum*. Finally, *Tetraena* and *Z. simplex* appear in a strongly supported clade along with *Z. cylindrifolium*, *Z. decumbens*, *Z. album* and *Z. coccineum*. The last four species are distributed in Africa and southwestern Asia.

The results obtained by Sheahan and Chase (2000) clearly indicated that the generic classification within Zygophylloideae needed reconsideration. The aims of this study are to (1) clarify further phylogenetic relationships within Zygophylloideae by analysing both molecular and morphological data from an expanded sample of species, and (2) propose a new formal taxonomy at generic level for the subfamily based on monophyletic entities.

Materials and methods

Sampling of taxa. All species of Zygophylloideae analysed in the study by Sheahan and Chase (2000) are included in this study (Table 1). Our expanded sample of species comprises 19 additional species of *Zygophyllum* sensu lato and four additional species of *Fagonia*, i.e. a total of 43 species excluding the outgroups (Table 1). The additional species were selected to cover morphological and geographical variation within the subfamily. The 34 species of *Zygophyllum* sensu lato included represent 12 of the 17 sections recognised by Engler (1931) and 10 of the 13 sections recognised by Van Huyssteen (1937).

Choice of outgroup. The choice of outgroup is based on Sheahan and Chase (1996, 2000), who found the members of New World subfamily Larreoideae, *Bulnesia*, *Guaiacum*, *Larrea*, *Pintoa* and *Porlieria*, to be sister to Zygophylloideae, whereas the Old World subfamily Seetzeniodeae with the single genus *Seetzenia* was sister to both Larreoideae and Zygophylloideae. Members of these genera, with the exception of *Pintoa* (sister of *Larrea*) and *Porlieria* (sister of both *Bulnesia* and *Guaiacum*), are used as an outgroup in this study.

Morphological data. The morphological part of this study is mainly based on herbarium material from B, BM, E, K, P, S, UPS, W, and WU. A list of the specimens examined for morphological characters can be obtained from the corresponding author on request. *Augea* and various species of *Fagonia* and *Zygophyllum* have also been studied in the field.

A systematic search was made to find a total of 34 morphological characters (Table 2) that were putatively independent and discrete (e.g. Chapill 1989, Stevens 1991). The character coding is shown in Table 2. The distribution of the character states in these species is shown in Table 3. Several of the morphological characters are commented on below.

Stipules and leaves: Stipules (character 2) are found in all examined taxa, including *Augea*, which has been reported to lack stipules (Schönland 1914, Engler 1931, Schreiber 1966, Ronse Decraene et al. 1996). However, the stipules of *Augea* seem to be present only in young leaves; they soon dry out and disappear. Most taxa in this study have fused, opposite, herbaceous stipules that are more or less triangular. Young stipules are sometimes not completely fused and can therefore appear to vary within species and even individuals. Entirely free stipules are found only in the members of the outgroup and all members of *Fagonia*. Spinescent or pointed stipules (character 3) are characteristic of *Fagonia* and not found in any species of *Zygophyllum* sensu lato. The South African *Z. spinosum* has stiff stipules here coded as herbaceous or almost so. The stipules in *F. scoparia* are reduced but have nevertheless been coded like other species of *Fagonia*.

The leaf-blades/leaflets (character 4) of the studied species all exhibit a degree of xeromorphy and are either flat and leathery or terete and fleshy. Terete leaf-blades/leaflets may sometimes be grooved above. The number of leaflets (character 5) is usually constant within species, but particularly in some species of *Fagonia* it can vary. For example in *F. bruguieri*, 1, 2, and 3-foliolate leaves are found in most individuals. This is coded as polymorphic.

The petiole (character 6) of most species of *Zygophyllum* has a similar architecture as the leaflets. The somewhat terete and winged petiole (character 7), for example of *Z. fabago*, is coded as flat. In some species of *Zygophyllum* the base of the markedly attenuate leaflets can be petiolule-like (character 9). However, no species of *Zygophyllum* sensu lato except *Z. hildebrandtii* and *Z. robecchii* have been interpreted as having a petiolule. The shape of the leaflets did not provide any discrete characters, except for the acute versus obtuse apex (character 10) that seems to be a stable character in all species studied.

Sepals and petals: Persistent sepals (character 13) are found in *Augea*, the Australian species of *Zygophyllum*, and in South African species of *Z.* subgen. *Zygophyllum* sensu Van Zyl (2000). A few species of *Fagonia* are also characterised by persistent sepals.

The colour of petals (character 15) has usually faded on the herbarium specimens, and the coding is therefore in most cases based on field observations, label information, photographs and literature data. Petals with a red blotch are coded as being red and white or red and yellow.

Androecium and gynoecium: The shape of the apex of the basal appendages (character 21) of the filament is a character that is difficult to code when the appendages are split and lacerate. If the apex is lacerate the shape of the apex has been

Table 1. Zygophyllaceae species used in this analysis, together with information on voucher, geographical origin of plant material, and database accession numbers. Species for which sequences published by Sheahan and Chase (1996, 2000) were used are marked with an asterisk

Species	Voucher information	Database accession No.
*Augea capensis** Thunb.	Chase 718 (K) South Africa	AJ387945
*Bulnesia arborea** Engl.	Chase 641 (K)	AJ387947
Fagonia chilensis Hook. & Arn.	Penailillo s.n. (UTALCA) Chile	
Fagonia cretica L.	Davis 49662 (E) Libya	AY300767
Fagonia indica Burm.f.	Thulin et al. 9835 (UPS) Yemen	AY300768
Fagonia luntii Baker	Thulin et al. 9881 (UPS) Yemen	AY300769
Fagonia minutistipula Engl.	Giess & Müller 13952 (K) South Africa	AY300770
Fagonia pachyacantha Rydb.	Beier 103 (UPS) Mexico	AY300771
Fagonia scoparia Brandegee	Johnston 9461 (SD) Mexico	AY300772
*Guaiacum guatemalense** L.Planch., Rydb. & Vail	Chase 640 (K) USA	AJ387948
*Larrea tridentata** Coville	Thulin et al. 9012 (UPS) Yemen	AJ387971
*Melocarpum hildebrandtii** (Engl.) Beier & Thulin	Thulin et al. 9537 (UPS) Yemen	AY300773
Melocarpum robecchii (Engl.) Beier & Thulin	Chase 636 (K) USA	AJ387951
Roepera apiculata (F.Muell.) Beier & Thulin	Greder 18664 (K) Australia	AY233384
Roepera aurantiaca Lindl.	Greder 20900 (K) Australia	AY300774
*Roepera billardieri** (DC.) G.Don	R. 417 (Adelaide B.G.) Australia	AJ387964
Roepera compressa (J.M.Black) Beier & Thulin	Nicholls 809 (K) Australia	AY300775
Roepera eremaea (Diels) Beier & Thulin	Beier s.n. (UPS) Australia	AY300776
Roepera foetida (Schrad. & J.C.Wendl.) Beier & Thulin	Roux s.n. (K) South Africa	AY300777
*Roepera fruticulosa** (DC.) G.Don	Chase 2203 (K) Australia	AJ387969
*Roepera glauca** (F.Muell.) Beier & Thulin	Chase 2204(K) Australia	AJ387970
*Roepera hirticaulis** (Van Zyl) Beier & Thulin	Van Zyl 3894 (NBG) South Africa	AJ387972
Roepera iodocarpa (F.Muell.) Beier & Thulin	Symon 4607 (K) Australia	AY300778

Table 1 (continued)

Species	Voucher information	Database accession No.
Roepera leptopetala (Sond.) Beier & Thulin	Örtendahl 484 (K) South Africa	AY300779
Roepera morgsana (L.) Beier & Thulin	March 1450 (K) South Africa	AY300780
Roepera ovata (Ewart & J. White) Beier & Thulin	Melville 451 (K) Australia	AY300781
Roepera spinosa (L.) Beier & Thulin	Viviers 426 (K) South Africa	AY300782
*Seetzenia lanata** (Willd.) Bullock	Herman 3964 (K)	AJ387956
*Tetraena alba** (L.f.) Beier & Thulin	Thulin et al. 7977 (UPS) Yemen	AJ387963
*Tetraena coccinea** (L.) Beier & Thulin	Ryding 1347 (K) Eritrea	AJ387965
*Tetraena cylindrifolia** (Schinz) Beier & Thulin	Craven 3800 (WIND) South Africa	AJ387966
*Tetraena decumbens** (Delile) Beier & Thulin	Thulin et.al. 7981 (UPS) Yemen	AJ387967
Tetraena hamiensis (Schweinf.) Beier & Thulin	Thulin et al. 9840 (UPS) Yemen	AY300783
Tetraena madagascariensis (Baill.) Beier & Thulin	Keating Miller 2236 (K) Madagascar	AY300784
Tetraena madecassa (H.Perrier) Beier & Thulin	Lorence s.n. (K) Madagascar	AY300785
Tetraena migiurtinorum (Chiov.) Beier & Thulin	Thulin et al. 9553 (UPS) Yemen	AY300786
*Tetraena mongolica** Maxim.	Sheahan 1994 (K) China	AJ387959
*Tetraena simplex** (L.) Beier & Thulin	Chase 806 (K) Egypt	AJ387974
Zygophyllum atriplicoides Fisch. & C.A. Mey L.	Astanova s.n. (K) Tadzikistan	AY233385
*Zygophyllum fabago** L.	Chase 516 (K)	AJ387968
Zygophyllum gontscharovii Boriss.	Astanova s.n. (K) Tadzikistan	AY300787
Zygophyllum lehmannianum Bunge	June s.n. 1972 (K) Turkmenistan	AY300788
Zygophyllum miniatum Cham. & Schlecht.	June s.n. 1965 (K) Uzbekistan	AY300789
Zygophyllum ramosissimum Popov	Granitov s.n. (K) Turkmenistan	AY300790
Zygophyllum rosowii Bunge	Chaney 57 (K) Mongolia	AY300791
Zygophyllum subtrijugum (C.A.Mey.) Beier & Thulin	1955.07.30 s. leg. s.n. (K) Kazachstan	AY300792
*Zygophyllum xanthoxylum** (Bunge) Engl.	Chase 1700 (K) China	AJ387975

Table 2. Characters and character states used in the morphological analysis of Zygophylloideae

1.	Leaves on short shoots 0, not on short shoots 1
2.	Stipules entirely free 0, partly to entirely fused 1
3.	Stipules spinescent or pointed 0, herbaceous or almost so 1
4.	Leaf-blade/leaflets flattened 0, terete 1
5.	Leaves simple or 1-foliolate 0, 2-foliolate 1, 3-foliolate 2, 4- or more-foliolate 3
6.	Petiole present 0, absent 1
7.	Petiole flattened 0, terete and sometimes with a groove 1
8.	Joint between leaflet(s) and petiole distinct 0, not recognisable 1
9.	Petiolule present 0, absent 1
10.	Leaflet apex acute or pointed 0, obtuse to rounded or retuse 1
11.	Hairs of leaflet simple and eglandular 0, stellate 1, glandular 2, absent 3
12.	Sepal apex acute-attenuate 0, rounded-obtuse 1
13.	Sepals not persistent in fruit 0, persistent in fruit 1
14.	Sepals hairy and/or glandular 0, glabrous 1
15.	Petal colour violet 0, yellow 1, white 2, red 3, orange 4
16.	Number of petals five 0, four 1
17.	Petal ± apiculate or cuspidate 0, obtuse or rounded 1, deeply 3-lobed 2
18.	Number of stamens ten 0, eight 1, five 2
19.	Filament appendage absent 0, present 1
20.	Filament appendage split 0, undivided 1
21.	Apex of filament appendage truncate 0, acute or obtuse 1
22.	Margin of filament appendage entire 0, lacerate 1
23.	Filament appendage smooth 0, hairy 1, papillate-warty 2
24.	Ovary tomentose with eglandular hairs less than 1 mm long 0, glabrous 1, glandular 2, with eglandular hairs more than 2 mm long 3
25.	Disc papillate 0, without papillae 1
26.	Number of loculi of ovary three 0, four 1, five 2, ten 3
27.	Fruit a loculicidal capsule 0, a schizocarp 1
28.	Fruit shape obovoid 0, obconical 1, oblong-ellipsoid 2, globose 3, ovoid 4
29.	Fruit with exocarp extending as wings 0, exo- and endocarp extending as wings 1, not winged 2
30.	Testa with mucilage in the outermost cell layer 0, with mucilage beneath the outermost cell layer 1, without mucilage 2
31.	Outer testa with helical threads 0, without helical threads 1
32.	Outer testa with funnel- or rod-like structures 0, without funnel- or rod-like structures 1
33.	Aril present 0, aril absent 1
34.	Aril formed from a long narrow funicle 0, from a short and conspicuously widened funicle 1

determined by tracing a line along the tips of the fringes.

The pistils of the studied taxa often differ in size, shape and length of the style. However, these characters are often variable even within species and depend also on the degree of maturity of the pistil and are probably also not independent from character 28 and 29. They were therefore considered not possible to use in the analysis, as opposed to the study by Ronse Decraene et al. (1996).

Fruits: Fruit dehiscence in members of Zygophylloideae has previously been considered to be of a great taxonomic importance, but information found in the literature is sometimes conflicting. We have chosen to divide the fruits into two broad categories (character 27):

(1) Loculicidal capsule. Dehiscence takes place when the fruit is still attached to the plant and can develop in a more or less complete manner. In *Z. morgsana*, for example, the exocarp remains intact, and dehiscence of the fruit is therefore incomplete. In this case, dehiscence has been classified as septifragal by

Table 3. Data matrix for the terminal taxa with the characters numbered as in Table 2. Polymorphic states are represented by the letters as follows: a = 0/1, b = 0/2, c = 0/1/2, d = 1/2, e = 1/3, f = 1/2/3, g = 2/3, h = 1/2/4, i = 3/4, j = 0/2/3 and k = 0/3. Unknown states are coded "?" and inapplicable states are coded as "-"

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Bulnesia	1	0	1	0	e	0	1	0	0	0	0	0	0	0	1	0	1	0	1	1	a	1	1	a	1	2	1	g	1	?	1	1	1	-
Guaiacum	1	0	1	0	f	0	1	0	0	1	0	0	0	0	0	a	1	a	0	-	-	-	-	a	1	c	1	0	1	2	1	1	-	-
Larrea	1	0	1	0	1	0	1	1	1	0	0	1	0	0	1	0	1	0	1	1	0	1	0	3	1	2	1	3	2	2	1	1	1	-
Seetzenia	1	0	1	0	2	0	1	0	0	0	0	0	0	1	-	-	-	2	0	-	-	-	-	1	1	1	1	2	2	1	1	1	1	-
Augea capensis	1	1	1	1	0	1	-	-	1	1	3	0	1	1	2	0	2	0	1	0	1	1	0	1	-	3	1	2	2	0	0	1	1	-
Fagonia chilensis	1	0	0	0	2	0	0	0	0	0	g	0	0	a	0	0	0	0	0	-	-	-	-	b	1	2	0	1	2	0	1	1	1	-
F. cretica	1	0	0	0	2	0	0	0	0	0	j	0	0	0	0	0	a	0	0	-	-	-	-	0	1	2	0	1	2	0	1	1	1	-
F. indica	1	0	0	0	0	a	0	0	0	0	g	0	1	0	0	0	a	0	0	-	-	-	-	0	1	2	0	1	2	0	1	1	1	-
F. luntii	1	0	0	0	0	0	0	0	0	a	g	0	0	0	0	0	0	0	0	-	-	-	-	b	1	2	0	1	2	0	1	1	1	-
F. minutistipula	1	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	a	0	0	-	-	-	-	b	1	2	0	1	2	0	1	1	1	-
F. pachyacantha	1	0	0	0	2	0	0	0	0	0	2	0	0	1	0	0	a	0	0	-	-	-	-	b	1	2	0	1	2	0	1	1	1	-
F. scoparia	1	0	0	0	0	1	-	-	?	0	3	0	1	1	0	0	0	0	0	-	-	-	-	0	1	2	0	1	2	0	1	1	1	-
Tetraena mongolica	0	1	1	0	1	0	0	0	1	0	1	0	0	0	d	1	0	1	1	1	1	1	0	0	1	1	1	-	1	0	1	0	1	-
Zygophyllum album	1	1	1	1	1	0	1	0	1	1	a	1	0	0	2	0	1	0	1	1	1	0	0	0	1	2	1	0	2	0	1	0	1	-
Z. apiculatum	1	1	1	0	1	0	0	0	1	a	3	0	1	1	1	0	1	0	1	1	0	1	0	1	0	2	0	0	0	0	0	1	0	0
Z. atriplicoides	0	1	1	0	0	1	-	-	1	a	1	1	0	0	1	0	1	0	1	1	?	1	0	1	1	d	0	3	1	0	1	0	0	1
Z. aurantiacum	1	1	1	0	1	a	0	1	1	a	3	0	1	1	1	1	1	1	0	-	-	-	-	1	0	1	1	g	0	0	0	1	0	0
Z. billardieri	1	1	1	0	1	0	0	1	1	0	3	0	1	1	1	1	1	1	0	-	-	-	-	1	0	1	0	0	2	0	0	1	0	0
Z. coccineum	1	1	1	1	1	0	1	0	1	1	k	1	0	1	f	0	1	0	1	1	0	0	0	0	1	2	1	2	2	0	1	0	1	-
Z. compressum	1	1	1	0	1	0	0	1	1	a	3	0	1	1	1	1	1	1	1	1	0	1	0	1	0	0	0	b	2	0	0	1	0	0
Z. cylindrifolium	1	1	1	1	a	0	1	0	1	1	3	1	0	1	2	0	1	0	1	0	0	0	0	1	1	2	1	0	2	0	1	0	1	-
Z. decumbens	1	1	1	0	a	0	1	0	1	1	3	1	0	1	2	0	1	0	1	0	1	0	0	a	1	2	1	0	2	0	1	0	1	-
Z. eremaeum	1	1	1	0	1	0	0	1	1	0	3	0	1	1	1	1	a	1	0	-	-	-	-	1	0	1	1	3	0	0	0	1	0	0
Z. fabago	1	1	1	0	1	0	0	0	1	a	3	1	0	1	h	0	1	0	1	1	0	1	0	1	1	2	0	2	2	0	1	0	1	-
Z. foetidum	1	1	1	0	1	0	1	0	1	1	3	0	1	a	e	0	1	0	1	1	0	1	1	1	0	2	0	g	2	0	0	1	0	0
Z. fruticulosum	1	1	1	0	1	0	0	1	1	a	3	0	1	1	1	1	1	1	0	-	-	-	-	1	0	1	1	g	1	0	0	1	0	0
Z. glaucum	1	1	1	0	1	0	0	0	1	1	3	0	1	1	1	1	1	1	1	1	0	1	0	1	0	1	0	2	2	0	0	1	0	0
Z. gontscharovii	0	1	1	0	0	1	-	-	1	1	1	a	0	0	d	1	1	1	1	1	0	1	0	a	1	1	0	3	1	0	1	0	1	-

Table 3 (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Z. hamiense	1	1	1	1	a	0	0	0	1	1	a	0	0	0	1	0	1	0	1	1	1	1	0	0	1	2	1	2	2	0	1	0	1	-
Z. hildebrandtii	1	1	1	0	0	1	-	-	0	1	3	1	0	1	0	0	1	0	0	-	-	-	-	1	1	2	0	4	2	0	1	1	0	1
Z. hirticaule	1	1	1	0	1	1	-	-	1	1	3	0	1	0	1	0	0	0	1	1	0	1	1	0	0	2	0	2	1	0	0	1	0	0
Z. iodocarpum	1	1	1	0	1	0	0	0	1	d	3	0	1	1	1	0	1	0	1	1	0	0	0	1	0	2	0	2	2	0	0	1	0	0
Z. lehmannianum	1	1	1	0	3	0	0	0	1	1	3	1	0	1	1	0	1	0	1	1	0	1	0	1	1	2	0	2	2	0	1	0	1	-
Z. leptopetalum	1	1	1	0	1	0	1	0	1	0	k	?	1	a	g	0	1	0	1	1	0	1	1	1	0	2	0	2	2	0	0	1	0	0
Z. madagascariensis	1	1	1	1	1	0	1	0	1	1	0	1	0	1	d	0	0	0	1	0	1	0	0	1	1	2	1	2	2	0	1	0	1	-
Z. madecassum	1	1	1	0	1	0	1	0	1	1	a	0	0	0	2	a	1	0	1	0	1	0	0	0	1	c	1	2	1	0	1	0	1	-
Z. migiurtinorum	1	1	1	1	1	0	1	0	1	1	3	1	0	1	2	0	1	0	1	1	0	1	0	1	1	2	1	0	2	0	1	0	1	-
Z. miniatum	1	1	1	0	e	0	0	0	1	0	3	1	0	1	g	0	1	0	1	1	1	1	0	1	1	1	0	2	2	0	1	0	1	-
Z. morgsana	1	1	1	0	1	0	1	0	1	1	3	?	1	0	1	1	1	1	1	1	0	1	0	1	0	1	0	g	1	0	0	1	0	0
Z. ovatum	1	1	1	0	1	0	0	1	1	d	3	0	1	1	2	1	1	1	0	-	-	-	-	1	0	1	0	2	2	0	0	1	0	0
Z. ramosissimum	1	1	1	0	1	0	0	0	1	0	3	1	0	1	g	0	1	0	1	1	1	1	0	1	1	2	0	i	2	0	1	0	1	-
Z. robecchii	1	1	1	0	0	1	-	-	0	1	3	1	0	1	0	0	1	0	0	-	-	-	-	1	1	2	0	4	2	0	1	1	0	1
Z. rosowii	?	1	1	0	1	0	0	0	1	1	3	1	0	1	i	0	1	0	1	1	0	1	0	1	1	2	0	2	2	0	1	0	1	-
Z. simplex	1	1	1	1	0	1	-	-	1	1	3	1	0	1	1	0	1	0	1	0	1	0	0	1	1	2	1	0	2	0	1	0	1	-
Z. spinosum	1	1	1	1	1	1	-	-	1	1	3	a	1	1	f	0	1	0	1	1	a	1	0	1	0	2	0	2	2	0	0	1	0	0
Z. subtrijugum	1	1	1	0	g	0	0	0	1	1	3	1	0	1	b	0	1	0	1	1	0	1	0	1	1	2	0	2	2	0	1	0	1	-
Z. xanthoxylum	0	1	1	0	1	0	1	0	1	1	3	1	0	1	1	1	1	1	1	1	0	1	0	1	1	a	0	3	1	0	1	0	1	-

Spjut (1994), but we regard it here as probably derived from a loculicidal condition. A loculicidal capsule is found in almost all Australian species of *Zygophyllum*, all South African species of *Z.* subgen. *Zygophyllum* sensu Van Zyl (2000), most Asian *Zygophyllum* species, and *Z.* sect. *Melocarpum*. In contrast to Engler (1931), we also interpret *Fagonia* as having loculicidal capsules because seeds are shed from each locule before the fruits fall off.

(2) Schizocarp. This type of fruit has a septicidal dehiscence into separate mericarps. The mericarps may later open along a dorsal suture. The fruit can be winged or succulent and fleshy before maturing. Fruits described as indehiscent are found in this group as are those classified as septicidal. The schizocarp is a characteristic of *Augea*, *Tetraena*, a few Australian *Zygophyllum* species with winged fruits, all South African species of *Z.* subgen. *Agrophyllum* sensu Van Zyl (2000), as well as all species of *Zygophyllum* from North Africa and Madagascar and a few species from Asia.

Seeds: An aril covering the hilum (character 33) is found in many species of Z*ygophyllum* sensu lato. However, for some South African species mature seeds have not been available, and the coding of this character has therefore sometimes been based on information from the literature. Arillate seeds are characteristic of *Z.* subgen. *Zygophyllum* sensu Van Zyl (2000) and associated with myrmecochorous dispersal (Bond and Slingsby 1983). Arillate seeds of a similar type, formed from a long narrow funicle, are also found in Australian species of *Zygophyllum*. A different type of aril (character 34), formed from a short and conspicuously widened funicle, is found in *Z.* sect. *Melocarpum* and some Asian species of *Zygophyllum*.

The reported absence of endosperm in the seeds of *Augea* (e.g. Engler 1931, Sheahan and Chase 1996, Ronse Decraene et al.1996, Mabberley 1997) and *Tetraena mongolica* (Ying et al. 1993, Sheahan and Chase 1996) is not consistent; some seeds have an endosperm, and others lack it. Because all species included in the study have endospermous seeds, this character has not been used in our analysis.

The outermost cell-layer of the testa of all the studied species of Zygophylloideae is more or less smooth when dry and mucilaginous when wet. The amount of transparent mucilage produced varies as well as the degree of adhesiveness. Mucilage is also produced by *Seetzenia* in the outgroup, but there it is found beneath the outermost layer that is leathery in dry condition. Also, the soaked seeds of *Seetzenia* become much stickier than those of any other taxa included in this study. According to Engler (1931), three species of *Bulnesia* have almost the same structure in the exotesta as some species of *Zygophyllum*. We have not been able to detect this structure in our study, and *Bulnesia* is therefore coded as missing mucilage.

In many of the species of Zygophylloideae, various characteristic structures appear in the mucilaginous outer testa. Seeds of 39 members of Zygophylloideae were therefore studied by scanning electron microscopy (SEM) and transmission electron microscopy (TEM). To remove mucilage the seeds were prepared according to the protocol in Ismail and El-Ghazaly (1990), involving a treatment with 10% HCl after being soaked in water. The images were generated for all 39 species by SEM (Philips XL 30) and in a video graphic printer (Sony UP-860 CE). The helical structures of the seeds of *Augea* and two *Zygophyllum* species were further analysed using TEM. The TEM slides were prepared after fixation in 2.5% glutaraldehyde solution over night, followed by a wash in buffer, and fixation in 1% OsO_4 for two hours at +4 °C. The samples were then washed three times for 10 minutes in a buffer and dehydrated in an ethanol series: 20%, 50% respectively 70% ethanol for 20 minutes followed by 80%, 90% respectively 95% over night. This was followed by dehydration in 100% ethanol 2×20 min. The seeds were then kept in acetone for 20 minutes. Infiltration was done by a resin-aceton 1:1 solution over night followed by infiltration in clean resin over night. The samples were embedded in epoxy, TAAB 812 (TAAB Industries Ltd.). A LKB microtome was used to produce the TEM slides and a Philips CM 10 to view the slides. The different main types of outer testa are illustrated in Fig. 1. The results indicate that the outer testa of all species included in Zygophylloideae can be divided into three groups as follows:

(1) An outer testa consisting of cells forming a uniform layer of mucilage without internal structure, which is found in all studies species of *Fagonia*, and in *Zygophyllum hildebrandtii* and *Z. robecchii*. The mucilage layer was in

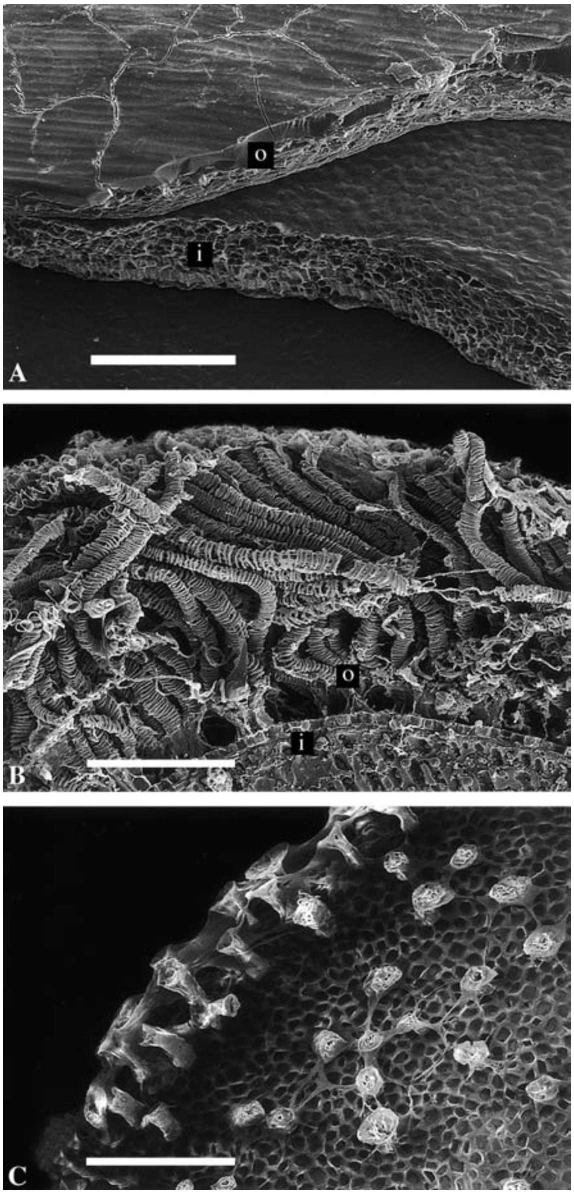


Fig. 1. The three types of testa found in Zygophylloideae after HCl treatment. Scale bars = 0.0035 mm. A. *Fagonia laevis* Standl. Combined surface view and t/s showing outer (o) and inner (i) testa without funnels or helical threads. B. *Zygophyllum iodocarpum*. Outer and inner testa in t/s, showing helical threads in outer testa. Each helical thread is produced by one cell. C. *Zygophyllum migiurtinorum*. Surface view of outer and inner testa. Outer testa with funnel-like structures produced by some of the cells and remnants of mucilage in-between. Inner testa showing reticulate pattern

these taxa not or little affected by the HCl treatment.

(2) An outer testa consisting of mucilage cells with an internal structure of helical threads, which is found in *Augea*, all Australian species of *Zygophyllum*, and the South African species of *Z.* subgen. *Zygophyllum* sensu Van Zyl (2000).
(3) An outer testa with mucilage cells with internal funnel- or rod-like structures, which is found in *Tetraena*, the Asian, North African and Madagascan species of *Zygophyllum*, and the South African species of *Z.* subgen. *Agrophyllum* sensu Van Zyl (2000).

The helical threads in the outer testa of type (2) cannot be seen unless the seeds are soaked in water. They often also remain visible when seeds dry out after soaking. The funnel- or rod-like structure of type (3) can sometimes be seen also in dry seeds under a dissecting microscope but are more easily observed after soaking. The adaptive significance of these structures is unknown.

Molecular data. Plastid *trn*L sequences for 48 species were collected and used in our analysis (Table 1). DNA was extracted using a modification of the CTAB method of Doyle and Doyle (1987). The DNA from silica dried material was precipitated in ethanol and purified using the QIAquick purification kit following the manufacturer's protocol (Qiagen Ltd). The DNA from herbarium material was precipitated in isopropanol, following the recommendations of Fay et al., (1998), and purified on a cesium chloride/ethidium bromide gradient (1.55g ml^{-1}).

PCR was carried out using the c and d primers of Taberlet et al. (1991). Sequencing of the region between *trn*L (UAA)3′ exon and *trn*F (GAA), covered by the e and f primer, proved to be impossible for many of the taxa due to long homopolymer regions (A or T) causing Taq to make many mistakes and drop bases, leading to electropherograms that were difficult to edit with confidence. Published *trn*L-F sequences (Sheahan and Chase 2000) of taxa in Zygophylloideae indicated that this region does not contain much useful information since these homopolymer regions are interspersed with highly conserved portions.

The amplified products were purified using the QIAquick purification kit (Qiagen Ltd) following the manufacturer's protocol. Cycle sequencing was done using the Dye Terminator Cycle Sequencing kit (Applied Biosystems Inc.). The protocol of the manufacturer was followed with the exception of the dye concentration, which was reduced to 1 μl in a reaction volume of 10 μl buffer. The reactions were run on an ABI 377 automated sequencer. The electropherograms were edited and assembled in Sequencner 3.1 (Gene Code Inc.).

Alignment of the data set was done manually following the guidelines of Kelcher (2000). Gaps were inserted so as to keep the number of the total changes (insertions/deletions and substitutions) to a minimum. Substitutions and indels we treated as equally probable events. Underlying patterns, usually repeating events, were taken into account when aligning. The alignment is available on request from B-AB and MWC.

Phylogenetic analysis. The data matrices were analysed using the parsimony options of PAUP* 4.0b10 (Swofford 2002), which treats inapplicable, unknown or missing and gap character states as missing data. All characters were given equal weight and treated as unordered (Fitch parsimony; Fitch 1971).

The data sets were analysed in two steps: 10 000 replicates of random addition sequence were run with TBR branch swapping, holding ten trees per step during stepwise addition and with MulTrees on. The shortest trees collected in the first analysis were used as starting trees in a second search in which we used TBR branch swapping with MulTrees on.

Clade support was calculated with 10000 bootstrap replicates in PAUP* 4.0b10 (Swofford 2002) using TBR branch swapping with simple addition and MulTrees off. In this study we consider clades with bootstrap values from 50% up to 60% as weakly, from 61% up to 80% as moderately, and above 80% as well supported.

The two data sets were analysed separately and in combination. The combined data set was analysed by the same procedure as the two separate sets.

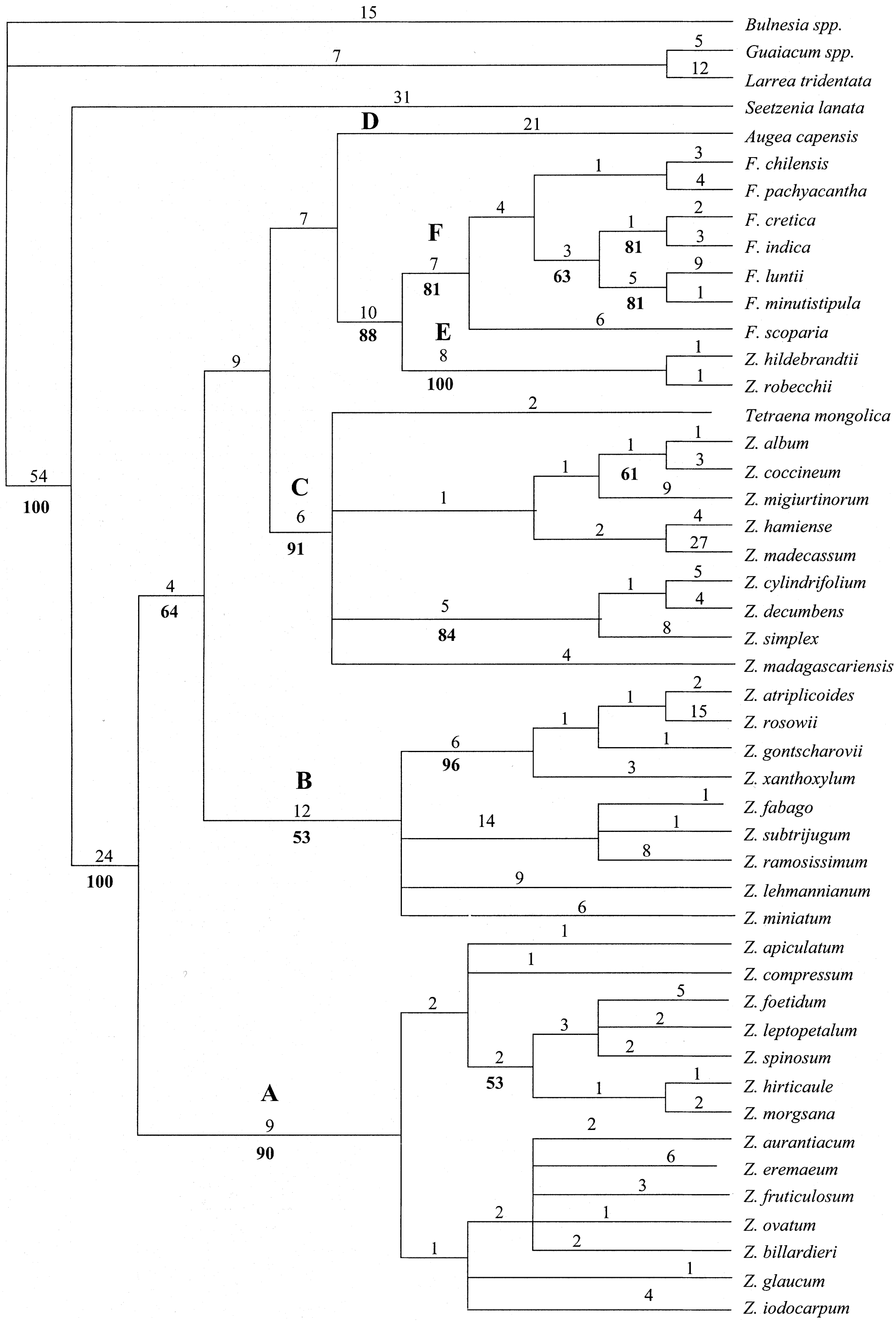
Results

Molecular data. The aligned matrix was 671 bp long, of which 402 positions were constant and 126 (19%) potentially parsimony informative. The analysis produced 17586 maximally parsimonious trees (MPT's) of 454 steps with a consistency index (CI) of 0.78 (excluding uninformative characters) and a retention index (RI) of 0.85. One of the shortest trees (the first one found) is shown in Fig. 2; branch lengths (ACCTRAN optimisation) are indicated above the branches and bootstrap percentages (BP) below. The topology of the consensus tree shows six main groups, denoted with letters A–F in Fig. 2.

Augea, *Fagonia* and *Tetraena* are nested within *Zygophyllum* sensu lato in all shortest trees. All Australian species of *Zygophyllum* and all South African species of *Z.* subgen. *Zygophyllum* form a clade (BP 90; clade A) sister to the rest of Zygophylloideae. The rest of Zygophylloideae form a clade (BP 64) with all the Asian species of *Zygophyllum* (including the type of the genus, *Z. fabago*) forming one clade (BP 53; clade B). A second clade (BP 91; clade C) is formed by *Z. album*, *Z. coccineum*, *Z. decumbens*, *Z. simplex*, *Z. hamiense* and *Z. migiurtinorum*, which occur mainly in northern Africa and Arabia, *Z. madecassum* and *Z. madagascariense* (= *Z. depauperatum*) from Madagascar, the South African species *Z. cylindrifolium* of *Z.* subgen. *Agrophyllum* and *Tetraena mongolica*. All the species of *Fagonia* (including the type of genus, *F. cretica*; clade F, BP 81) and two *Zygophyllum* species, *Z. hildebrandtii* and *Z. robecchii* of *Z.* sect. *Melocarpum* (clade E, BP 100), and *Augea* (clade D) are found in the third clade (BP < 50). The clade with *Fagonia* and *Z.* sect. *Melocarpum* has BP 88.

Morphological data. In the cladistic analysis based on the morphological data only, 4747 MPT's of 222 steps with CI of 0.59 and RI's of 0.75 were found. One of the MPT's (the first one found) is shown in Fig. 3. The topology was poorly supported, but there were clades corresponding to *Fagonia* (BP 84), *Z.* sect. *Melocarpum* (BP 96) and *Roepera* (BP < 50).

Combined data. An analysis of the combined morphological and molecular data set generated 2027 MPT's of 692 steps with CI of 0.70 and RI of 0.79. The topology of the


Bulnesia spp.
Guaiacum spp.
Larrea tridentata
Seetzenia lanata
D
Augea capensis
F. chilensis
F. pachyacantha
F. cretica
F. indica
F. luntii
F. minutistipula
F
F. scoparia
E
Z. hildebrandtii
Z. robecchii
Tetraena mongolica
Z. album
Z. coccineum
Z. migiurtinorum
C
Z. hamiense
Z. madecassum
Z. cylindrifolium
Z. decumbens
Z. simplex
Z. madagascariensis
Z. atriplicoides
Z. rosowii
Z. gontscharovii
Z. xanthoxylum
B
Z. fabago
Z. subtrijugum
Z. ramosissimum
Z. lehmannianum
Z. miniatum
Z. apiculatum
Z. compressum
Z. foetidum
Z. leptopetalum
Z. spinosum
Z. hirticaule
Z. morgsana
A
Z. aurantiacum
Z. eremaeum
Z. fruticulosum
Z. ovatum
Z. billardieri
Z. glaucum
Z. iodocarpum

consensus tree shows the same main groups as in the analysis of the molecular data set but differs with respect to the internal resolution within five of the six main groups. The bootstrap percentages differ in four of the six main clades from the molecular data set. One of the MPT (the first one found) is shown in Fig. 4, with the six main groups denoted with the letters A–F.

Zygophylloideae form a well-supported clade (BP 100). An outer testa of a single layer of mucilage-producing cells, more or less fused stipules (with a reversal in *Fagonia*) and loculicidal capsules (with reversals in *Tetraena*, *Augea*, and some species of *Zygophyllum*) are morphological synapomorphies for this clade.

The well-supported clade A (BP 98), including all Australian species of *Zygophyllum* and all South African species of *Z.* subgen. *Zygophyllum*, is weakly supported as sister to the rest of Zygophylloideae (BP 57). Clade A is supported by the characters aril covering the hilum, sepals persistent in fruit (with a parallelism in *Augea* and a few species of *Fagonia*), a papillate disc, and an outer testa with helical threads (also with a parallelism in *Augea*).

A clade (B) comprising all the Asian species of *Zygophyllum* in our study and the type of the genus, *Z. fabago*, is weakly supported (BP 56) and has two subgroups (BP 95 and 69). An outer testa with funnel- or rod-like structures (with a parallelism in clade C) and leaflets four or more (found in some species only) are synapomorphies for this clade.

Clade C (BP 82) comprises *Tetraena mongolica*, the mainly northern African/Arabian species *Z. hamiense*, *Z album*, *Z. coccineum*, *Z. migiurtinorum*, *Z. decumbens* and *Z. simplex*, the Madagascan *Z. madecassum* and *Z. madagascariense*, and the South African *Z. cylindrifolium*. Synapomorphies for clade C are schizocarpic fruits (with parallelisms in *Augea*, *Z. aurantiacum*, *Z. eremaeum* and *Z. fruticulosum*) outer testa with funnel- or rod-like structures (with a parallelism in clade B).

Augea, clade D, has a position (BP < 50) as sister to the two species of *Z.* sect. *Melocarpum* plus *Fagonia*. *Augea* has several autapomorphies, e.g. a ten-locular fruit and an urceolate nectar disk with ten subulate teeth. An outer testa with helical threads is a parallelism with clade A, and schizocarpic fruits are a parallelism with clade C.

Clade E (BP 100), with the two species of *Z.* sect. *Melocarpum*, is well supported as sister to clade F (BP 86). Morphological synapomorphies for clades E and F together include presence of petiolules, violet petals and lack of filament appendages (a parallelism also found in some members of clade A). Synapomorphies for clade E are ovoid fruits (a parallelism with *Z. ramosissimum*) and aril formed from a short and conspicuously widened funicle (a parallelism with *Z. atriplicoides*).

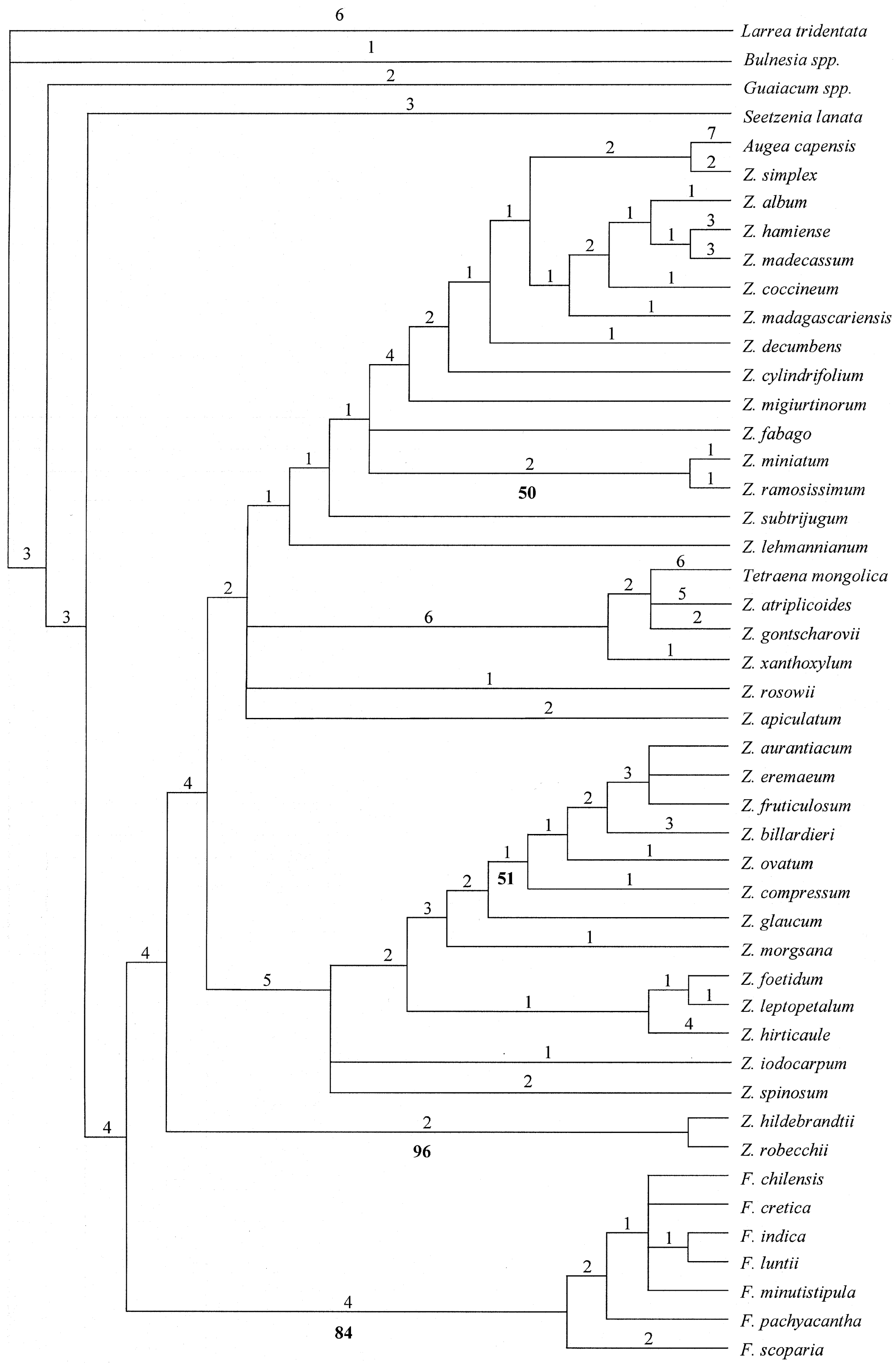
Clade F, with all the species of *Fagonia*, is well supported (BP 96). *F. scoparia* from Mexico is sister to all other taxa, including the type of the genus, *F. cretica*. Synapomorphies for clade F are entirely free stipules (a reversal), spinescent or pointed stipules and obconical capsules.

Discussion

Sheahan and Chase (2000) pointed out that all species of Zygophylloideae share a 192 bp deletion in the *trn*L (UUA) intron. To this we can now add the morphological synapomorphies: a testa with mucilage in the outermost cell-layer, more or less fused stipules (with a reversal in *Fagonia*), and loculicidal capsules (with reversals in some groups, see under results).

The current generic subdivision of Zygophylloideae obviously cannot be maintained because *Fagonia*, *Augea* and *Tetraena* are all embedded within *Zygophyllum*. A possible

Fig. 2. One of 17586 most parsimonious trees from the *trn*L data set. Figures below nodes are BP from 10 000 replicates. Branch lengths are indicated above the branches


Larrea tridentata
Bulnesia spp.
Guaiacum spp.
Seetzenia lanata
Augea capensis
Z. simplex
Z. album
Z. hamiense
Z. madecassum
Z. coccineum
Z. madagascariensis
Z. decumbens
Z. cylindrifolium
Z. migiurtinorum
Z. fabago
Z. miniatum
Z. ramosissimum
50
Z. subtrijugum
Z. lehmannianum
Tetraena mongolica
Z. atriplicoides
Z. gontscharovii
Z. xanthoxylum
Z. rosowii
Z. apiculatum
Z. aurantiacum
Z. eremaeum
Z. fruticulosum
Z. billardieri
Z. ovatum
Z. compressum
51
Z. glaucum
Z. morgsana
Z. foetidum
Z. leptopetalum
Z. hirticaule
Z. iodocarpum
Z. spinosum
Z. hildebrandtii
Z. robecchii
96
F. chilensis
F. cretica
F. indica
F. luntii
F. minutistipula
F. pachyacantha
F. scoparia
84

solution could be to treat the whole subfamily as a single genus, for which the Linnean names *Zygophyllum* and *Fagonia* would have equal priority. However, such a change would be nomenclaturally disruptive because both these names have been used consistently since 1753. Also *Augea* has been in consistent use since 1794 and *Tetraena* since 1889. Lumping these genera would also conceal much systematic and biogeographical information.

An alternative approach would be to base a new generic classification on the clades A–F presented above (Fig. 4). With this approach, the distinctive genera *Fagonia* and *Augea* can be kept with their current circumscriptions, the circumscription of *Zygophyllum* would be reduced to the species in clade B and their relatives, *Tetraena* would be extended to include all the species in clade D and their relatives, the generic name *Roepera* could be resurrected for the species in clade A and their relatives and a new generic name would be given to clade E.

We advocate the latter approach above because, on balance, it gives a less disruptive and more informative classification. All these clades are more easily recognised by morphological characters than would be *Zygophyllum* sensu lato (including all of Zygophylloideae), and they are also to a large extent confined to specific geographical areas. These six clades are also present in all the trees of Sheahan and Chase (2000), although the relative positions of some of them vary between the *trn*L-F tree and that of *rbc*L. The topology of our combined tree (Fig. 4) agrees with the tree based on *trn*L-F data in the study by Sheahan and Chase (2000) regarding the six main clades (A–F) presented here.

The clades A–F are each briefly discussed below with their assigned generic names. For clade E, we propose the name *Melocarpum* based on *Zygophyllum* sect. *Melocarpum*.

Roepera **(clade A).** This clade with all Australian species and a large number of the South African species of *Zygophyllum* is well supported in the molecular and combined analyses. In the combined tree of Sheahan and Chase (2000), this clade was not sister to the rest of Zygophylloideae as in our combined tree but had a weakly supported position as sister to a clade with *Augea*, *Fagonia* and *Melocarpum*. However the tree based on *trn*L-F data presented by Sheahan and Chase agrees with our combined tree in this respect. Six additional South African species, *Z. cordifolium*, *Z. cuneifolium*, *Z. fulvum*, *Z. leucocladum*, *Z. liechtensteinianum* and *Z. "spitskopense"* (unpublished name), were included in a molecular study based on *trn*L-F sequences by Makwarela (2001) and also grouped with species of *Roepera*.

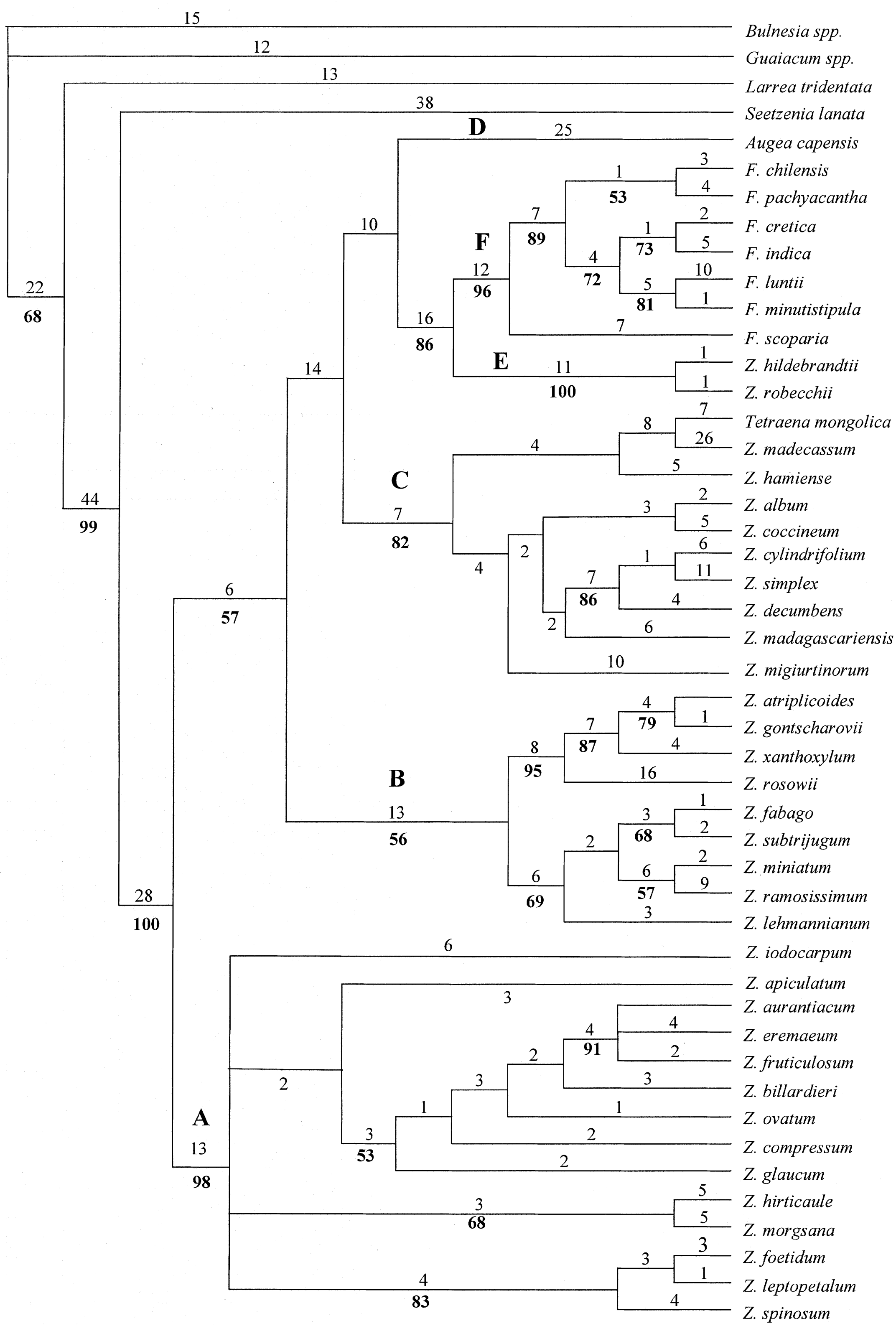
The *Roepera* clade is well supported by morphological characters (see under Results). However, the group was not recognised by Van Huyssteen (1937), who placed, for example, the Australian species *Z. billardieri* and *Z. fruticulosum* in different subgenera within *Zygophyllum*. Van Zyl (2000), on the contrary, grouped the South African species of *Roepera* together on morphological grounds as *Z.* subgen. *Zygophyllum*.

Roepera was originally described to accommodate two Australian species with tetramerous flowers without filament appendages, and the name has been used only a few times in the 19th century. In the expanded sense proposed here, the resurrected genus has around 60 species, most of them with pentamerous flowers but easily recognised by the aril covering the hilum, persistent sepals (a parallelism with *Augea* and a few species of *Fagonia*), a papillate disc, and an outer testa with helical threads (again a parallelism with *Augea*).

Zygophyllum **(clade B).** Sheahan and Chase (2000) sampled only two species from this Asian clade. The nine species included in

◀

Fig. 3. One of 4747 most parsimonious trees from the morphological data set. Figures below nodes are BP from 10000 replicates. Branch lengths are indicated above the branches


Bulnesia spp.
Guaiacum spp.
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F
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F. indica
F. luntii
F. minutistipula
F. scoparia
E
Z. hildebrandtii
Z. robecchii
Tetraena mongolica
Z. madecassum
Z. hamiense
C
Z. album
Z. coccineum
Z. cylindrifolium
Z. simplex
Z. decumbens
Z. madagascariensis
Z. migiurtinorum
Z. atriplicoides
Z. gontscharovii
Z. xanthoxylum
B
Z. rosowii
Z. fabago
Z. subtrijugum
Z. miniatum
Z. ramosissimum
Z. lehmannianum
Z. iodocarpum
Z. apiculatum
Z. aurantiacum
Z. eremaeum
Z. fruticulosum
Z. billardieri
A
Z. ovatum
Z. compressum
Z. glaucum
Z. hirticaule
Z. morgsana
Z. foetidum
Z. leptopetalum
Z. spinosum

our study form a weakly supported clade in the combined tree with two, more strongly supported subclades. The members of this clade have characteristic seeds with an outer testa with funnel- or rod-like structures. Similar seeds are also found in *Tetraena*, but *Zygophyllum* differs from this in having loculicidal capsules (not schizocarps) and is the only genus except *Fagonia* in Zygophylloideae containing species with more than two leaflets per leaf. On morphological grounds, about 50 species can be assigned to the group. Morphological variation within the genus even in this restricted sense is relatively great, and the generic names *Miltianthus* and *Sarcozygium* are based on species from this clade. However, Borissova (1949) placed all members of this clade in *Zygophyllum*, and with the evidence available at present there are no compelling reasons for further subdivision.

Tetraena **(clade C).** Since publication in 1889, *Tetraena* has always been recognised as a monotypic genus, and in some recent publications it was placed in a separate subfamily (Ma and Zhang 1990, Takhtajan 1996). However, in the study by Sheahan and Chase (2000), *Tetraena* was associated with the mainly African/Arabian species *Z. album*, *Z. coccineum*, *Z. cylindrifolium*, *Z. decumbens* and *Z. simplex*. Our study corroborates this association, and the African/Arabian species *Z. hamiense* and *Z. migiurtinorum*, and Madagascan *Z. madagascariense* and *Z. madecassum*, are also shown to belong here. Four South African species included in a molecular study based on *trn*L-F sequences by Makwarela (2001), *Z. tenue*, *Z. retrofractum*, *Z. rigidum* and Z. *microcarpum*, are also members of this clade.

The results indicate that *Tetraena mongolica* is not such an isolated species as has been thought (Ma and Zhang 1990, Takhtajan 1996). Some of the characters that have been put forward as unique for it, such as bicuspidate hairs, tetramerous flowers and tricolporoidate pollen grains, are also found in other members of this clade. The fruit of *Tetraena* looks at first to be different from others of Zygophylloideae, but we interpret the fruit of *Tetraena* to be similar to the fruit of e.g. *Z. longistipulatum*, in which each free, more or less cylindrical locule in the mature fruit is attached by only a minor ventral part.

Chromosome number has also been used as a character to distinguish *Tetraena* from *Zygophyllum* sensu lato. However, recent publications have given different chromosome numbers (Ma and Zhang 1990, Ying et al. 1993), and pending clarification these data are omitted here.

Tetraena now comprises about 40 species. It has, as in *Zygophyllum* sensu stricto, seeds with an outer testa with funnel- or rod-like structures, but the fruits in *Tetraena* are schizocarpic, a character that in Zygophylloideae is otherwise found only in *Augea* and a few Australian species of *Roepera*. On morphological grounds, it seems obvious that all the South African species treated as *Z.* subgen. *Agrophyllum* by Van Zyl (2000) belong to *Tetraena*.

Augea **(clade D).** Several authors have placed *Augea*, with the single species *A. capensis* in South Africa, in a separate subfamily (Schönland 1914, Engler 1931, Oltmann 1971, Takhtajan 1996). However, some of the characters used to support this taxonomy, such as absence of both stipules and endosperm, are incorrect according to our observations. The morphological cladogram of Ronse Decraene et al. (1996) placed *Augea* as sister to *Tribulus*, *Fagonia* and *Zygophyllum*, but this was based on incorrect information. These authors coded *Augea* as being without stipules and endosperm and with a loculicidal capsule. Also, the codings for *Zygophyllum* (sensu lato) are

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Fig. 4. One of 2027 most parsimonious trees based on a combined data set of molecular and morphological characters. Figures below nodes are BP from 10 000 replicates. Branch lengths are indicated above the branches. Letters A to F denote groups discussed

largely incorrect or too generalized. With a corrected coding of the data matrix used by Ronse Decraene et al. (1996), *Augea*, *Fagonia* and *Zygophyllum* come out together.

The inclusion of *Augea* in Zygophylloideae has previously been proposed by, e.g. El Hadidi (1975), Sheahan and Cutler (1993) and Sheahan and Chase (2000). In our study *Augea* is sister to *Fagonia* and *Melocarpum*, which agrees with the result of Sheahan and Chase (2000). However, this position has a BP below 50. The seeds of *Augea*, with helical threads in the outer testa, are remarkably similar to those of *Roepera*, and the persistent sepals are another similarity with this genus. However, *Augea* and *Roepera* never cluster together in the analyses and also differ markedly in several ways. The decacarpellate, schizocarpic fruits of *Augea*, for example, are different from the mostly pentacarpellate, loculicidal capsules of *Roepera*. Our conclusion is that, although *Augea* can be firmly placed within Zygophylloideae, it is still an isolated taxon best treated as a separate genus.

***Melocarpum* (clade E).** The two species *Z. hildebrandtii* and *Z. robecchii*, constituting *Z.* sect. *Melocarpum* and occurring in the Horn of Africa region, form a well supported clade with a stable position as sister to *Fagonia* (clade F). El Hadidi (1978) pointed out the similarity of the two species of *Z.* sect. *Melocarpum* and the unifoliolate species *Fagonia socotrana* and *F. migiurtinorum* (here treated as synonyms of *F. luntii*), and J. B. Gillett subsequently suggested on herbarium labels at K that these four species should be placed together in a new genus. Because *Z.* sect. *Melocarpum* and *F. luntii* do not form an exclusive clade there is no support for this proposal in our study. Instead our results corroborate the suggestion by Thulin (1993) that sect. *Melocarpum* "could probably well be treated as a distinct genus". Morphological characters supporting the recognition of *Melocarpum* are entirely fused stipules, glabrous ovary, ovoid (versus obconical) fruit and seeds with an aril formed from a short, conspicuously widened funicle.

***Fagonia* (clade F).** In Sheahan and Chase (2000), the three species of *Fagonia* included (all from the Old World) formed a well supported clade. Our sample includes three species from the New World, and two of these, *F. chilensis* and *F. pachyacantha*, form a weakly supported clade sister to all four included Old World species. The Mexican species *F. scoparia* is sister to the rest of the genus.

The free and spinescent or pointed stipules in *Fagonia* are unique within Zygophylloideae (somewhat spinescent but more or less fused stipules are found in some South African species of *Roepera*) as are the obconical capsules. An amalgamation of *Fagonia* and *Melocarpum*, the latter with entirely fused, minute and membranous stipules and ovoid capsules, would not violate the principle of monophyly but would blur the circumscription of *Fagonia* that has to our knowledge never been questioned since erection of the genus in 1753.

Concluding remarks. The six clades discussed here are generally well supported and agree with the results of Sheahan and Chase (2000). However, the relative positions of the clades are still uncertain, except for the well-supported sister relationship between *Fagonia* and *Melocarpum*. The mix of characters in *Augea*, such as outer testa with helical threads (found also in *Roepera*) and schizocarpic fruits, otherwise found mainly in *Tetraena*, may indicate a hybrid origin of the genus, a hypothesis that should be further explored. The weakly supported *Zygophyllum* clade, with two well-supported subclades, also needs further study including a larger sample of taxa. The morphological data are shown to be homoplastic and able to resolve only *Fagonia* and *Melocarpum* among the genera that we have chosen to recognise. However, the morphological data have increased resolution in parts of the tree and have added support for some of the clades.

Zygophylloideae has now been given a systematic framework that will enable further studies of, for example, character evolution and biogeographic patterns. The taxonomic consequences of our conclusions are presented in the next section of this paper.

Taxonomy of Zygophylloideae

Zygophylloideae Arn., Encycl. Brit., ed. 7, 5: 104 (1832); Engl. and Prantl, Nat. Pflanzenfam. III, 4: 78 (1890).

Herbs or shrubs, rarely annuals, up to c. 3 m tall. Stems glabrous, pubescent or glandular, terete to ± angular, commonly with ± thickened nodes, sometimes differentiated in short and long shoots. Stipules membranous, herbaceous or spinescent, fused or free. Leaves opposite, simple or 1-, 2-, or sometimes up to 10-foliolate, sessile or petiolate; leaf-blades/leaflets linear to orbicular, terete or flat, often mucronate. Flowers in monochasia, with pedicels. Sepals 4 or 5, ± triangular or oblong, glabrous or pubescent, deciduous or persistent. Petals 4 or 5, clawed, spreading or connivent, white, yellow, orange, red or violate. Stamens 8 or 10; filaments often with basal appendages. Pollen grains tricolporate, reticulate. Disc smooth or papillate. Ovary 4- or 5-locular, rarely 3- or 10-locular, pubescent or glabrous; stigma simple. Fruit a loculicidal capsule or schizocarp. Seeds ± ovate, flat, black or brownish, endospermous; outer testa mucilaginous when wet, often with helical threads or funnel- or rod-like structures; aril sometimes present.

The subfamily, with approximately 180 species in six genera, is found world-wide in warm and arid to semi-arid areas.

Key to the genera

1. Sepals persistent on mature fruit 2
– Sepals not persistent on mature fruit 4
2. Outer testa without helical threads when wet; stipules free, spinescent or pointed .... 6. *Fagonia*
– Outer testa with helical threads visible after wetting; stipules more or less fused, herbaceous or occasionally stiff 3
3. Gynoecium of 4 or 5 carpels; disc not cup-shaped, regularly 8–10 angled, papillate .... 1. *Roepera*
– Gynoecium of 10 carpels; disc cup-shaped with 10 distinct ± lanceolate lobes, not papillate .... 4. *Augea*
4. Filaments with basal appendages; outer testa with internal funnel- or rod-like structures 5
– Filaments without basal appendages; outer testa without internal funnel- or rod-like structures 6
5. Fruit a loculicidal capsule; staminal appendages undivided .... 2. *Zygophyllum*
– Fruit a schizocarp; staminal appendages sometimes split .... 3. *Tetraena*
6. Stipules entirely fused, membranous; fruit ± ovoid, glabrous .... 5. *Melocarpum*
– Stipules free, spinescent or pointed; fruit obconical, pubescent .... 6. *Fagonia*

1. *Roepera* A. Juss in Mem. Mus. Hist. Nat. 12: 454 (1825). *Zygophyllum* sect. *Roepera* (A. Juss.) Engl. in Engler and Prantl, Nat. Pflanzenfam. III, 4: 82 (1890). Lectotype: *R. billardieri* (DC.) G.Don (selected here).

Zygophyllum billardieri and *Z. fruticulosum* were cited as members of *Roepera* in the protologue (Jussieu 1825), but the combinations needed were not made until Don (1831).

Shrubs, subshrubs or herbs, up to c. 3 m tall. Stems glabrous or pubescent with unicellular hairs only. Stipules ± fused, herbaceous or occasionally stiff. Leaves opposite, sessile or petiolate, 1- or 2-foliolate; leaflets obovate, ovate, oblong or linear, flat or terete, sometimes with mucro; rhachis herbaceous or ± spinose. Sepals 4–5, acute-attenuate or rounded-obtuse at the apex, herbaceous, sometimes with membranous margins, glabrous, persistent in fruit. Petals 4–5, ± obovate, pink, yellow, white, orange or white with red veins, basal petal marked in red, brown or yellow, or without basal marking, ± spreading. Stamens 8–10; filaments with undivided appendages, or rarely without appendages. Disc papillate. Ovary 4–5-locular, glabrous or rarely papillose or pubescent. Fruit a loculicidal capsule or rarely a winged schizocarp, obovate, ovate or ± oblong in outline. Outer testa of seeds mucilaginous with an internal structure of helical threads; hilum covered by ± well developed aril.

Genus of approximately 60 species, restricted to warm and arid areas in Australia, Botswana, Namibia and South Africa.

The Australian species (as *Zygophyllum*) have been treated by Barker (1996, 1998), and the southern African species (as *Z.* subgen. *Zygophyllum*) have been revised by Van Zyl (2000). A number of new species provisionally described by Van Zyl (2000) have not yet been validly published, and these are not included in the list of taxa below. Only basionyms are cited, except in a few cases for which additional synonyms not listed in the papers by Barker (1996, 1998) and Van Zyl (2000) are given.

Roepera ammophila (F. Muell.) Beier & Thulin, comb. nov. *Zygophyllum ammophilum* F. Muell. in Linnaea 25: 376 (1853). Australia.

Roepera angustifolia (H. Eichler) Beier & Thulin, comb. nov. *Zygophyllum angustifolium* H. Eichler in Telopea 4: 13 (1990). Australia.

Roepera apiculata (F. Muell.) Beier & Thulin, comb. nov. *Zygophyllum apiculatum* F. Muell. in Linnaea 25: 373 (1853). *Z. terminale* Turcz. in Bull. Soc. Imp. Naturalistes Moscou 31: 437 (1858). Australia.

Roepera aurantiaca Lindl. in Bot. Reg. 24, 105: 57 (1838). *Zygophyllum aurantiacum* (Lindl.) F. Muell. in Linnaea 25: 376 (1853). Australia.

Roepera aurantiaca Lindl. ssp. ***cuneata*** (R.M. Barker) Beier & Thulin, comb. nov. *Zygophyllum aurantiacum* (Lindl.) F. Muell. ssp. *cuneatum* (R.M. Barker) in J. Adelaide Bot. Gard. 17: 163 (1996). Australia.

Roepera aurantiaca Lindl. ssp. ***simplicifolia*** (R.M. Barker) Beier & Thulin, comb. nov. *Zygophyllum aurantiacum* (Lindl.) F. Muell. ssp. *simplicifolium* R.M. Barker in J. Adelaide Bot. Gard. 18: 61 (1996). Australia.

Roepera aurantiaca Lindl. ssp. ***verticillata*** (R.M. Barker) Beier & Thulin, comb. nov. *Zygophyllum aurantiacum* (Lindl.) F. Muell. ssp. *verticillatum* R.M. Barker in J. Adelaide Bot. Gard. 17: 164 (1996). Australia.

Roepera billardieri (DC.) G. Don, Gen. hist. 1: 770 (1831). *Zygophyllum billardieri* DC., Prodr. 1: 705 (1824). Australia.

Roepera botulifolia (Van Zyl) Beier & Thulin, comb. nov. *Zygophyllum botulifolium* Van Zyl in Bothalia 27: 131 (1997). South Africa.

Roepera compressa (J.M. Black) Beier & Thulin, comb. nov. *Zygophyllum compressum* J.M. Black, Fl. S. Austral. 2: 333 (1924). Australia.

Roepera confluens (H. Eichler) Beier & Thulin, comb. nov. *Zygophyllum confluens* H. Eichler in Telopea 4: 14 (1990). Australia.

Roepera cordifolia (L.f.) Beier & Thulin, comb. nov. *Zygophyllum cordifolium* L.f., Suppl. Pl.: 232 (1782). Namibia and South Africa.

Roepera crassissima (Ising) Beier & Thulin, comb. nov. *Zygophyllum crassissimum* Ising in Trans. & Proc. Roy. Soc. South Australia 81: 167 (1958). Australia.

Roepera crenata (F. Muell.) Beier & Thulin, comb. nov. *Zygophyllum crenatum* F. Muell. in Linnaea 25: 374 (1853). Australia.

Roepera cuneifolia (Eckl. & Zeyh.) Beier & Thulin, comb. nov. *Zygophyllum cuneifolium* Eckl. & Zeyh., Enum. Pl. Afric. Austral. 1: 97 (1835). South Africa.

Roepera debilis (Cham.) Beier & Thulin, comb. nov. *Zygophyllum debile* Cham. in Linnaea 5: 46 (1830). South Africa.

Roepera divaricata (Eckl. & Zeyh.) Beier & Thulin, comb. nov. *Zygophyllum divaricatum* Eckl. & Zeyh., Enum. Pl. Afric. Austral. 1: 97 (1835). South Africa.

Roepera eichleri (R.M. Barker) Beier & Thulin, comb. nov. *Zygophyllum eichleri* R.M. Barker in J. Adelaide Bot. Gard. 18: 50 (1998). Australia.

Roepera emarginata (H. Eichler) Beier & Thulin, comb. nov. *Zygophyllum emarginatum* H. Eichler in Telopea 4: 15 (1990). Australia

Roepera eremaea (Diels) Beier & Thulin, comb. nov. *Zygophyllum fruticulosum* DC. var. *eremaeum* Diels in Bot. Jahresber. 35: 315 (1904). Australia.

Roepera flava (R.M. Barker) Beier & Thulin, comb. nov. *Zygophyllum flavum* R.M. Barker in J. Adelaide Bot. Gard. 17: 164 (1996). Australia.

Roepera flexuosa (Eckl. & Zeyh.) Beier & Thulin, comb, nov. *Zygophyllum flexuosum* Eckl. & Zeyh., Enum. P. Afric. Austral. 1: 97 (1835). South Africa.

Roepera foetida (Schrad. & J.C. Wendl.) Beier & Thulin, comb. nov. *Zygophyllum foetidum* Schrad. & J.C. Wendl., Sert. Hannov. 1, 3: 17 (1795). South Africa.

Roepera fruticulosa (DC.) G. Don, Gen. hist. 1: 771 (1831). *Zygophyllum fruticulosum* DC., Prod. 1: 705 (1824). Australia.

Roepera fulva (L.) Beier & Thulin, comb. nov. *Zygophyllum fulvum* L., Sp. P1.: 386 (1753). South Africa.

Roepera fuscata (Van Zyl) Beier & Thulin, comb nov. *Zygophyllum fuscatum* Van Zyl in Bothalia 27: 129 (1997). South Africa.

Roepera glauca (F. Muell.) Beier & Thulin, comb. nov. *Zygophyllum glaucum* F. Muell. in Trans. & Proc. Victorian Inst. Advancem. Sci. 1: 29 (1855). Australia.

Roepera halophila (R.M. Barker) Beier & Thulin, comb. nov. *Zygophyllum halophilum* R.M. Barker in J. Adelaide Bot. Gard. 18: 55 (1998). Australia.

Roepera hirticaulis (Van Zyl) Beier & Thulin, comb. nov. *Zygophyllum hirticaule* Van Zyl in Bothalia 29: 235 (1999). Namibia.

Roepera horrida (Cham.) Beier & Thulin, comb. nov. *Zygophyllum horridum* Cham. in Linnaea 5: 46 (1830). South Africa.

Roepera howittii (F. Muell.) Beier & Thulin, comb. nov. *Zygophyllum howittii* F. Muell. in Fragm. Phyt. Austral. 3: 150 (1863). Australia.

Roepera humillima (M. Koch ex Tate) Beier & Thulin, comb. nov. *Zygophyllum humillimum* M. Koch ex Tate in Trans. & Proc. Roy. Soc. South Australia 24: 207 (1900). Australia.

Roepera hybrida (Tate) Beier & Thulin, comb. nov. *Zygophyllum hybridum* Tate in Trans. & Proc. Roy. Soc. South Australia 23: 291 (1899). Australia.

Roepera incrustata (Sond.) Beier & Thulin, comb. nov. *Zygophyllum incrustatum* Sond. in Harv. & Sond., Fl. Cap. 1: 362 (1860). South Africa.

Roepera iodocarpa (F. Muell.) Beier & Thulin, comb. nov. *Zygophyllum iodocarpum* F. Muell. in Linnaea 25: 372 (1852). Australia.

Roepera kochii (Tate) Beier & Thulin, comb. nov. *Zygophyllum kochii* Tate in Trans. & Proc. Roy. Soc. South Australia 23: 291 (1899). Australia.

Roepera leptopetala (Sond.) Beier & Thulin, comb. nov. *Zygophyllum leptopetalum* Sond. in Harv. & Sond., Fl. Cap. 1: 363 (1860). Namibia and South Africa.

Roepera leucoclada (Diels) Beier & Thulin, comb. nov. *Zygophyllum leucocladum* Diels in Schultze, Aus Namaland und Kalahari: 705 (1907). Namibia and South Africa.

Roepera lichtensteiniana (Cham.) Beier & Thulin, comb. nov. *Zygophyllum lichtensteinianum* Cham. in Linnaea 5: 47 (1830). South Africa.

Roepera lobulata (Benth.) Beier & Thulin, comb. nov. *Zygophyllum iodocarpum* F. Muell. var. *lobulatum* Benth. in. Fl. Austral. 1: 293 (1863). Australia.

Roepera macrocarpon (Retief) Beier & Thulin, comb. nov. *Zygophyllum macrocarpon* Retief in Bothalia 17: 189 (1987). Namibia and South Africa.

Roepera maculata (Aiton) Beier & Thulin, comb. nov. *Zygophyllum maculatum* Aiton in Hort. Kew. 2: 60 (1789). Namibia and South Africa.

Roepera maritima (Eckl. & Zeyh.) Beier & Thulin, comb. nov. *Zygophyllum maritimum* Eckl. & Zeyh., Enum. Pl. Afric. Austral. 1: 96 (1835). South Africa.

Roepera marliesiae (R.M. Barker) Beier & Thulin, comb. nov. *Zygophyllum marliesiae*

R. M. Barker in J. Adelaide Bot. Gard. 18: 63 (1998). Australia.

Roepera microphyllum (L.f.) Beier & Thulin, comb. nov. *Zygophyllum microphyllum* L.f., Suppl. Pl: 232 (1782). Southern Africa.

Roepera morgsana (L.) Beier & Thulin, comb. nov. *Zygophyllum morgsana* L., Sp. P1.: 385 (1753). Namibia and South Africa.

Roepera orbiculata (Welw. ex Oliv.) Beier & Thulin, comb. nov. *Zygophyllum orbiculatum* Welw. ex Oliv. in Fl. Trop. Afr. 1: 285 (1868). Angola.

Roepera ovata (Ewart & J. White) Beier & Thulin, comb. nov. *Zygophyllum ovatum* Ewart & J. White in J. & Proc. Roy. Soc. New South Wales 42: 197 (1908). Australia.

Roepera prismatotheca (F. Muell.) Beier & Thulin, comb. nov. *Zygophyllum prismatothecum* F. Muell. in Linnaea 25: 375 (1853). Australia.

Roepera pubescens (Schinz) Beier & Thulin, comb. nov. *Zygophyllum pubescents* Schinz in Bull. Herb. Boissier Sér. 2, 8: 631 (1908). Southern Africa.

Roepera pygmaea (Eckl. & Zeyh.) Beier & Thulin, comb. nov. *Zygophyllum pygmaeum* Eckl. & Zeyh., Enum. P1. Afric. Austral. 1: 97 (1835). South Africa.

Roepera reticulata (R.M. Barker) Beier & Thulin, comb. nov. *Zygophyllum reticulatum* R. M. Barker in J. Adelaide Bot. Gard. 18: 57 (1998). Australia.

Roepera retivalvis (Domin) Beier & Thulin, comb. nov. *Zygophyllum retivalve* Domin in Biblioth. Bot. 89: 281 (1926). Australia.

Roepera rogersii (Compton) Beier & Thulin, comb. nov. *Zygophyllum rogersii* Compton in Trans. Roy. Soc. South Africa 19: 296 (1931). South Africa.

Roepera rowelliae (R.M. Barker) Beier & Thulin, comb. nov. *Zygophyllum rowelliae* R. M. Barker in J. Adelaide Bot. Gard. 18: 53 (1998). Australia.

Roepera schreiberi (Merxm. & Giess) Beier & Thulin, comb. nov. *Zygophyllum schreiberi* Merxm. & Giess in Mitt. Bot. Staatssamml. München 2: 447 (1974). Namibia and South Africa.

Roepera sessilifolia (L.) Beier & Thulin, comb. nov. *Zygophyllum sessilifolium* L., Sp. P1.: 385 (1753). South Africa.

Roepera similis (H. Eichler) Beier & Thulin, comb. nov. *Zygophyllum simile* H. Eichler in Telopea 4: 15 (1990). Australia.

Roepera sphaerocarpa (Schltr. ex Van Huysst.) Beier & Thulin, comb. nov. *Zygophyllum sphaerocarpum* Schltr. ex Van Huysst., Morph. -syst. Stud. Zygoph. Afr.: 73 (1937). South Africa.

Roepera spinosa (L.) Beier & Thulin, comb. nov. *Zygophyllum spinosum* L., Sp. P1: 386 (1753). South Africa.

Roepera teretifolia (Schltr.) Beier & Thulin, comb. nov. *Zygophyllum teretifolium* Schltr. in Engl. Jahrb. 27: 159 (1900). South Africa.

Roepera tesquorum (J.M. Black) Beier & Thulin, comb. nov. *Zygophyllum tesquorum* J. M. Black in Fl. S. Austral. 2: 334 (1924). Australia.

Roepera tetraptera (R.M. Barker) Beier & Thulin, comb. nov. *Zygophyllum tetrapterum* R. M. Barker in J. Adelaide Bot. Gard. 17: 164 (1996). Australia.

2. *Zygophyllum* L., Sp. P1. 1: 386 (1753). Lectotype: *Z. fabago* L. (Hitchcock and Greene, Nomencl. Prop. Brit. Bot.: 153, 1929).

Sarcozygium Bunge in Linnaea 17: 7 (1843). Type: *S. xanthoxylum* Bunge.

Miltianthus Bunge in Arbeiten Naturf. Vereins Riga 1: 197 (1847). Type: *M. portulacoides* (Cham.) Bunge.

Shrubs, subshrubs or herbs, up to c. 2 m tall. Stems glabrous or pubescent, with unicellular, 2- or 3-armed trichomes. Stipules ± fused, herbaceous or membranous. Leaves opposite, sometimes on short shoots and then seemingly alternate, sessile or petiolate, simple or 1–10-foliolate; leaf-blades/leaflets flat or terete, orbicular, ovate, obovate, oblong or linear, sometimes with soft mucro; rhachis herbaceous. Sepals 4–5, acute-attenuate or rounded-obtuse at the apex, herbaceous or ± succulent, glabrous or pubescent, deciduous. Petals 4–5, ± obovate, white, yellow or pale orange, ± connivent. Stamens 8–10; filaments with undivided basal appendages. Disc smooth. Ovary 3–5-locular, glabrous or hairy. Fruit a loculicidal capsule, ± oblong, ovate or obovate in outline; endo- and exocarp sometimes extending as wings. Outer testa of seeds mucilaginous with internal funnel- or rod-like structures; aril formed from a short and conspicuously widened funicle sometimes present.

Genus of some 50 species in the Middle East and east to Central Asia, Iran and China.

Most of the species have been treated in the papers by Popov (1925, 1926), Borissova (1949) and Grubov (1998). Species delimitation sometimes differs between authors, and the list below comprises some taxa that may be of doubtful status. Synonyms are not listed, except in a few cases. Infraspecific names are omitted.

Zygophyllum atriplicoides Fisch. & C.A. Mey., Zygophyllaceae: 12 (1834). Central Asia, Iran, Pakistan and Armenia.

Zygophyllum balchaschense Boriss., Fl. USSR 14: 725 (1949). Kazahkstan.

Zygophyllum betpakdalense Golosk. & Semiotr. in Izv. Akad. Nauk Kazahsk. SSR, Ser. Bot. Pocvov 1: 73 (1960). Kazahkstan.

Zygophyllum borissovae Beier & Thulin, nom. nov. *Z. microcarpum* Boriss., Fl. USSR 14: 724 (1949), nom. illegit., non Licht. ex Cham. in. Linnaea 5: 46 (1830). Kazahkstan.

Zygophyllum brachypterum Kar. & Kir. in Bull. Soc. Imp. Naturalistes. Moscou 14: 397 (1841). Central Asia.

Zygophyllum budunense Semiotr. in. Bot. Mater. Gerb. Inst. Bot. Akad. Nauk Kazahsk. SSR 3: 19 (1965). Kazakhstan.

Zygophyllum cuspidatum Boriss., Fl. USSR 14: 726 (1949). Central Asia.

Zygophyllum darvasicum Boriss., Fl. USSR 14: 729 (1949). Central Asia.

Zygophyllum dielsianum (Popov) Popov in Schedis ad Herb. Fl. As. Med. Fasc. 18: 75 (1928). Central Asia.

Zygophyllum eichwaldii C.A. Mey., Eichw. Pl. nov.: 15 (1831). Central Asia.

Zygophyllum englerianum (Popov) Popov, Fl. Uzbekistan 4: 57 (1959). Central Asia.

Zygophyllum eurypterum Boiss. & Buhse, Aufzähl. Transkauk. Pflanz.: 49 (1860). Central Asia, Iran and Afghanistan.

Zygophyllum fabago L., Sp. Pl.: 385 (1753). Middle East, Central Asia and South-eastern Europe (introduced elsewhere in Europe, in North Africa, and in America).

Zygophyllum fabagoides Popov in Bjull. Sredne-Aziatsk. Gosud. Univ. 11: 113 (1925). Central Asia.

Zygophyllum ferganense (Drobow) Boriss., Fl. USSR 14: 187 (1949). Central Asia.

Zygophyllum furcatum C.A. Mey. in. Ledeb., Fl. Altaic. 2: 106 (1830). Central Asia.

Zygophyllum gobicum Maxim., Enum. pl. Mongolia 1: 125 (1889). Kazakhstan and Mongolia.

Zygophyllum gontscharovii Boriss. Fl. USSR 14: 729 (1949). Iran, Central Asia.

Zygophyllum heterocladum Rech.f. & Patzak in Kongel. Danske Vidensk. Selsk., Biol. Skrift. 13,4: 15 (1963). Afghanistan.

Zygophyllum iliense Popov in Bjull. Sredne-Aziatsk. Gosud. Univ. 12: 112 (1926). Central Asia.

Zygophyllum kansuense Y.X. Liou in Acta Phytotax. Sin. 18: 484 (1980). China.

Zygophyllum karatavicum Boriss., Fl. USSR 14: 726 (1949). Central Asia.

Zygophyllum kaschgaricum Boriss., Fl. USSR 14: 728 (1949). Central Asia.

Zygophyllum kegense Boriss., Fl. USSR 14: 727 (1949). Central Asia.

Zygophyllum kopalense Boriss., Fl. USSR 14: 726 (1949). Kazakhstan.

Zygophyllum latifolium Schrenk in Bull. Phys.-Math. Acad. Petersb. 2: 198 (1844). Kazakhstan.

Zygophyllum lehmannianum Bunge in Arbeiten Naturf. Vereins Riga 1: 202 (1847). Central Asia.

Zygophyllum loczyi Kantiz, P1. Exped. Szechenyi As. centr. lect.: 13 (1891). Kazakhstan and Mongolia.

Zygophyllum macrophyllum Regel & Schmalh. in Izv. Obsc. Ljubit. Estestv. Antrop. Etnogra 34, 2: 16 (1882).

Z. portulacoides Cham. in Linnaea 5: 50 (1830), nom. illegit., non Forssk. *Miltianthus portulacoides* (Cham.) Bunge in Arb. Naturf. Ver. Riga 1: 197 (1847), nom. illegit. Central Asia and Afghanistan.

Zygophyllum macropodum Boriss., Fl. USSR 14: 556 (1949). Central Asia.

Zygophyllum macropterum C.A. Mey. in Ledeb., Fl. Altaic. 2: 102 (1830). Central Asia.

Zygophyllum megacarpum Boriss., Fl. USSR 14: 730 (1949). Central Asia.

Zygophyllum melongena Bunge in Ledeb., Fl. Altaic. 2: 104 (1830). Central Asia.

Zygophyllum miniatum Cham. & Schlecht. in Linnaea 5: 49 (1830). Central Asia.

Zygophyllum mucronatum Maxim. in Bull. Acad. Petersb. 11: 175 (1883). China, Mongolia.

Zygophyllum neglectum Grubov, Opred. Sosud. Rast. Mongolii: 176 (1982). Mongolia.

Zygophyllum obliquum Popov in Bjull. Sredne-Aziatsk. Gosud. Univ. 11: 113 (1925). Central Asia.

Zygophyllum ovigerum Fisch. & C.A. Mey. ex Bunge, Rel. Lehm.: 236 (1851).

Zygophyllum oxianum Boriss. in Fl. of the USSR 14: 555 (1949). Central Asia.

Zygophyllum oxycarpum Popov in Bjull. Sredne-Aziatsk. Gosud. Univ. 12: 112 (1926). Central Asia.

Zygophyllum pamiricum Grubov in Novosti. Sist. Vyssh. Rast. 31: 175 (1998). Central Asia.

Zygophyllum potaninii Maxim. in. Bull. Acad. Imp. Sci. Saint-Petersbourg 11: 448 (1881). Central Asia.

Zygophyllum pterocarpum Bunge in Ledeb., Fl. Altaica 2: 103 (1830). Central Asia.

Zygophyllum ramosissimum Popov in Bjull. Sredne-Aziatsk. Gosud. Univ. 11: 115 (1925). Central Asia.

Zygophyllum rosowii Bunge in Linnaea 17: 5 (1843). Central Asia.

Zygophyllum sinkiangense Y.-X. Liou in Acta Phytotax. Sin. 18: 484 (1980). China.

Zygophyllum stenopterum Schrenk in Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Petersbourg 3: 308 (1845). Central Asia.

Zygophyllum subtrijugum C.A. Mey. in Ledeb., F1. Altaica 2: 105 (1830). Central Asia.

Zygophyllum taldykurganicum Boriss., Fl. USSR 14: 727 (1949). Kazakhstan.

Zygophyllum turcomanicum Fisch. & C.A. Mey. in Bull. Soc. Imp. Naturalistes Moscou 12: 149 (1839). Central Asia.

Zygophyllum xanthoxylum (Bunge) Engl. in Engl. & Prantl, Nat. Pflanzenfam. III, 4: 81 (1890). *Sarcozygium xanthoxylum* Bunge in Linnaea 17: 7 (1843). Mongolia.

3. *Tetraena* Maxim in Enum. Pl. Mongolia 1: 129 (1889). Type: *T. mongolica* Maxim.

Zygophyllum subgen. *Agrophyllum* Endl., Genera Plantarum: 1164 (1841). Type: not selected.

Petrusia Baill. in Bull. Mens. Soc. Linn. Paris 35: 273 (1881). Type: *P. madagascariensis* Baill.

The generic name *Agophyllum* Necker (1790), which was intended for species in this group, was not validly published (ICBN, Art. 32.8).

Shrubs, subshrubs or herbs, up to c. 1.5 m tall. Stems glabrous or pubescent, with unicellular 2- or 3-armed trichomes. Stipules ± fused, herbaceous or membranous. Leaves opposite, sometimes on short shoots and then seemingly alternate, sessile or petiolate, simple, 1- or 2-foliolate; leaflets flat or terete, orbicular, ovate, obovate, oblong or linear, sometimes with soft mucro; rhachis herbaceous. Sepals 5, rarely 4, acute-attenuate or rounded-obtuse at the apex, herbaceous or succulent, glabrous or pubescent, sometimes with membranous margin, deciduous. Petals 5, rarely 4, ± obovate, white, yellow or pale orange, ± connivent or rarely spreading. Stamens 10; filaments with undivided or split basal appendages. Disc smooth. Ovary 3-5-locular, glabrous or hairy. Fruit a schizocarp, obovate, orbicular, ovate or ± oblong in outline, mericarps opening septicidally or indehiscent, rarely with locules separated and almost free; endo- and exocarp sometimes extending as wings. Outer testa of seeds mucilaginous with internal funnel- or rod-like structures.

Genus of some 40 species with a distribution stretching from the Canary Islands and South Africa to China. The species in southern Africa were treated in detail (as *Z.* subgen. *Agrophyllum*) by Van Zyl (2000). Other accounts of various species have been published by Borissova (1949), Ozenda (1958), Humbert (1952), El Hadidi (1977), Thulin (1993), Ying et al. (1993) and Boulos (2000). A number of new species provisionally described by Van Zyl (2000) have not been validly published, and these are not included in the list of taxa below. In most cases only basionyms are cited, but some new synonyms are included as well as some that are needed for clarity.

Tetraena aegyptia (A.I. Hosny) Beier & Thulin, comb. nov. *Zygophyllum aegyptium* A.I. Hosny in Bot. Notiser 130: 467 (1977). North Africa and Cyprus.

Tetraena alba (L.f.) Beier & Thulin, comb. nov. *Zygophyllum album* L.f., Pl. Rar. Hort. Upsal.: 11, t. 6 (1762). Arabian Peninsula, Iran, Pakistan, northern and north-eastern Africa, Middle East, Cyprus, Greece and Spain.

Tetraena applanata (Van Zyl) Beier & Thulin, comb. nov. *Zygophyllum applanatum* Van Zyl in Bothalia 29: 233 (1999). Namibia.

Tetraena bucharica (B. Fedtsch.) Beier & Thulin, comb. nov. *Zygophyllum bucharicum* B. Fedtsch. in. Izv. Glavn. Bot. Sada. RSFSR 18: 13 (1918). Central Asia.

Tetraena chrysopteron (Retief) Beier & Thulin, comb. nov. *Zygophyllum chrysopteron* Retief in Bothalia 21: 55 (1991). Southern Africa.

Tetraena clavata (Schltr. & Diels) Beier & Thulin, comb. nov. *Zygophyllum clavatum* Schltr. & Diels in Schultze, Aus Namaland und Kalahari: 705 (1907). South Africa and Namibia.

Tetraena coccinea (L.) Beier & Thulin, comb. nov. *Zygophyllum coccineum* L., Sp. P1.: 386 (1753). Northern and north-eastern Africa, Arabian Peninsula and Iran.

Tetraena cornuta (Coss.) Beier & Thulin, comb. nov. *Zygophyllum cornutum* Coss. in Bull. Soc. Bot. France 2: 364 (1855). North Africa.

Tetraena cylindrifolia (Schinz) Beier & Thulin, comb. nov. *Zygophyllum cylindrifolium* Schinz in Bull. Herb. Boissier Sér. 2, 8: 631 (1908). Namibia.

Tetraena decumbens (Delile) Beier & Thulin, comb. nov. *Zygophyllum decumbens* Delile in Descr. Egypte, Hist. nat. 2: 221 (1813). Northern and north-eastern Africa, South Africa, and Arabian Peninsula.

Tetraena dumosa (Boiss.) Beier & Thulin, comb. nov. *Zygophyllum dumosum* Boiss., Diagn. Pl. Orient. 1, 8: 125 (1849). Middle East.

Tetraena fontanesii (Webb & Berthel.) Beier & Thulin, comb. nov. *Zygophyllum fontanesii* Webb & Berthel., Hist. Nat. Iles Canaries 1: 17 (1835). Canary Islands, Cape Verde Islands and North Africa.

Tetraena gaetula (Emb. & Maire) Beier & Thulin, comb. nov. *Zygophyllum gaetulum* Emb. & Maire in Bull. Soc. Hist. Nat. Afrique N. 14: 36 (1928).

Z. ifniense Caball. in Trab. Mus. Nac. Ci. Nat., Ser. Bot. 30: 22 (1935). North Africa.

Tetraena gaetula (Emb. & Maire) Beier & Thulin spp. **waterlotii** (Maire) Beier & Thulin, comb. nov. *Zygophyllum waterlotii* Maire in Bull. Soc. Hist. Nat. Afrique N. 28: 348 (1937). *Z. gaetulum* Emb. & Maire ssp. *waterlotii* (Maire) A. Dobignard, F. Jacquemoud & D. Jordan in Candollea 47: 415 (1992). Western Sahara, Mauretania and Senegal.

Tetraena geslinii (Coss.) Beier & Thulin, comb. nov. *Zygophyllum geslinii* Coss. in Bull. Soc. Bot. France 3: 705 (1856). North Africa.

Tetraena giessii (Merxm. & A. Schreib.) Beier & Thulin, comb. nov. *Zygophyllum giessii* Merxm. & A. Schreib. in Mitt. Bot. Staatssamml. München 2: 449 (1974). Namibia.

Tetraena hamiensis (Schweinf.) Beier & Thulin, comb. nov. *Zygophyllum hamiense* Schweinf. in Bull. Herb. Boissier. 7, Appendix 2: 277 (1899). Iran, Arabian Peninsula and Somalia.

Tetraena longicapsularis (Schinz) Beier & Thulin, comb. nov. *Zygophyllum longicapsulare* Schinz in Verh. Bot. Vereins Prov. Brandenburg 29: 55 (1888). Namibia.

Tetraena longistipula (Schinz) Beier & Thulin, comb. nov. *Zygophyllum longistipulatum* Schinz in Verh. Bot. Vereins Prov. Brandenburg 29: 56 (1888). Namibia.

Tetraena madagascariensis (Baill.) Beier & Thulin, comb. nov. *Petrusia madagascariensis* Baill. in Bull. Mens. Soc. Linn. Paris 35: 273 (1881). *Zygophyllum madagascariens* (Baill.) Stauffer in Ber. Schweiz. Bot. Ges. 66: 273 (1956).

Z. depauperatum Drake in Bull. Mus. Hist. Nat. Par. 9: 38 (1903). Madagascar.

Tetraena madecassa (H. Perrier) Beier & Thulin, comb. nov. *Zygophyllum madecassum* H. Perrier in Bull. Mus. Hist. Nat. Paris 2, 22: 284 (1950). Madagascar.

Tetraena mandavillei (Hadidi) Beier & Thulin, comb. nov. *Zygophyllum mandavillei* Hadidi in Publ. Cairo Univ. Herb. 78: 327 (1977). Saudi Arabia.

Tetraena microcarpa (Licht. ex Cham.) Beier & Thulin, comb. nov. *Zygophyllum microcarpum* Licht. ex Cham. in Linnaea 5: 46 (1830). Southern Africa.

Tetraena migahidii (Hadidi) Beier & Thulin, comb. nov. *Zygophyllum migahidii* Hadidi in Publ. Cairo Univ. Herb. 78: 328 (1977). Saudi Arabia.

Tetraena migiurtinorum (Chiov.) Beier & Thulin, comb. nov. *Zygophyllum migiurtinorum* Chiov., F1. Somala: 111 (1929).

Z. smithii Hadidi in Kew Bull. 35: 336 (1980). Yemen, Oman, and Somalia.

Tetraena mongolica Maxim., Enum. Pl. Mongolia 1: 129 (1889). China.

Tetraena prismatica (Chiov.) Beier & Thulin, comb. nov. *Zygophyllum prismaticum* Chiov., F1. Somala: 111 (1929). Somalia.

Tetraena prismatocarpa (Sond.) Beier & Thulin, comb. nov. *Zygophyllum prismatocarpum* Sond. in Harv. & Sond., Fl. Cap. 1: 357 (1860). South Africa.

Tetraena pterocaulis (Van Zyl) Beier & Thulin, comb. nov. *Zygophyllum pterocaule* Van Zyl in Bothalia 29: 231 (1999). Namibia and South Africa.

Tetraena qatarensis (Hadidi) Beier & Thulin, comb. nov. *Zygophyllum qatarense* Hadidi in Webbia 32: 394 (1978). Arabian Peninsula.

Tetraena retrofracta (Thunb.) Beier & Thulin, comb. nov. *Zygophyllum retrofractum* Thunb., Prod. Fl. Cap. 1: 80 (1794). Southern Africa.

Tetraena rigida (Schinz) Beier & Thulin, comb. nov. *Zygophyllum rigidum* Schinz in Verh. Bot. Vereins Prov. Brandenburg 29: 55 (1888). Namibia and South Africa.

Tetraena simplex (L.) Beier & Thulin, comb. nov. *Zygophyllum simplex* L., Mant. Pl. 1: 68 (1767).

Z. portulacoides Forssk., Fl. Aegypt. Arab.: 88 (1775). Northern and north-eastern Africa, Tchad, Niger, South Africa, Namibia, Angola, Cape Verde Islands, Madagascar, Arabian Peninsula, India and Pakistan.

Tetraena somalensis (Hadidi) Beier & Thulin, comb. nov. *Zygophyllum somalense* Hadidi in Kew Bull. 33: 121 (1978). Somalia.

Tetraena stapfii (Schinz) Beier & Thulin, comb. nov. *Zygophyllum stapfii* Schinz in Verh. Bot. Vereins. Prov. Brandenburg 29: 57 (1888). Namibia.

Tetraena tenuis (Glover) Beier & Thulin, comb. nov. *Zygophyllum tenue* Glover in Ann. S. African Mus 9: 172 (1913). Southern Africa.

4. Augea Thunb., Prodr. Fl. Cap. 1: 80 (1794). Type: *A. capensis* Thunb.
Succulent subshrub or herb up to c. 45 cm tall. Stems glabrous. Stipules minute, membranous, ± fused, soon deciduous. Leaves opposite, sessile, simple, terete, ± oblong, connate, with or without mucro. Sepals 5, glabrous, ± succulent, acute-attenuate at the apex, persistent in fruit. Petals 5, deeply split into 3 linear lobes, white. Stamens 10; filaments with split basal appendages. Disc cup-shaped with 10 distinct ± lanceolate lobes. Ovary 10-locular, glabrous. Fruit a schizocarp, ± oblong in outline. Outer testa of seeds mucilaginous with an internal structure of helical threads.

Monotypic genus endemic to South Africa and Namibia. Accounts of *Augea* have been published by, e.g. Schönland (1914), Engler (1931) and Takhtajan (1996).

5. *Melocarpum* (Engl.) Beier & Thulin, comb. nov. *Zygophyllum* sect. *Melocarpum* Engl., Abh. Königl. Akad. Wiss. Berlin, 2: 13 (1896). Lectotype: *M. hildebrandtii* Engl. (selected here).

No species names were validly published in the protologue of *Z.* sect. *Melocarpum*, but *Z. hildebrandtii* and *Z. robecchii* were published simultaneously by Engler (1897).

Shrubs subshrubs up to c. 1.5 m tall. Stems glabrous. Leaves opposite, 1-foliolate, flat, orbicular, obovate, or ovate, without petiole but with a short petiolule. Stipules entirely fused, minute. Sepals 5, acute-attenuate at the apex, glabrous, with membranous margin, herbaceous, deciduous. Petals 5, ± obovate, voilet, spreading. Stamens 10; filaments without basal appendages. Disc smooth. Ovary 5-locular, glabrous. Fruit a loculicidal capsule, 5-angled, ± ovoid; exocarp with raphids. Outer testa of seeds mucilaginous and without internal structures; hilum almost as long as seed; aril present, formed from a short conspicuously widened funicle.

Genus of two species confined to the Horn of Africa region. Accounts of the species are found in El Hadidi (1978) and Thulin (1993).

Melocarpum hildebrandtii (Engl.) Beier & Thulin, comb. nov. *Zygophyllum hildebrandtii* Engl. in Ann. Ist. Bot. Roma 7: 15 (1897). Somalia.

Melocarpum robecchii (Engl.) Beier & Thulin, comb. nov. *Zygophyllum robecchii* Engl. in Ann. Ist. Bot. Roma 7: 14 (1897).

Fagonia heinii O. Schwartz in Mitt. Inst. Allg. Bot. Hamburg 10: 121 (1939). Ethiopia, Somalia, Yemen and Oman.

6. *Fagonia L.*, Sp. Pl. 1: 386 (1753). Lectotype: *F. cretica* L. (Vail and Rydb., N. Amer. Fl. 25: 104, 1910).

Shrubs, subshrubs or herbs, up to c. 60 cm tall. Stems glabrous, pubescent or glandular. Leaves opposite, simple, 1-, 2- or 3-foliolate, or rarely up to 7-foliolate; leaflets linear to broadly ovate or obovate, rarely scale-like, usually with mucro, with or without petiole, generally with petiolule. Stipules free, spinescent or rarely pointed and minute. Sepals 5, acute-attenuate at the apex, glabrous, pubescent or glandular, ± herbaceous, sometimes with membranous margin, deciduous or persistent. Petals 5, ± obovate, purple or violet, spreading. Stamens 10; filaments without basal appendages. Disc smooth. Ovary 5-locular, glandular and pubescent. Fruit a loculicidal capsule, deeply 5-angled, ± obconical. Outer testa of seeds mucilaginous without internal structures; hilum much shorter than seed; aril absent.

Genus of approximately 30 species with a disjunct distribution in desert areas of Chile, Mexico, Peru and south-western USA in the New World and in the Old World from the Canary Islands and Cape Verde Islands in the west to Afghanistan and India in the east and to South Africa in the south. The genus is not found in Australia. Accounts of various parts of the genus have been published by Engler (1931), El Hadidi (1973, 1978), Porter (1963), Thulin (1993) and Wiggins (1980). No list of species is given here, but a detailed account of the genus will be presented in a forthcoming revision by B.-A. Beier.

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