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Phylogeny and Taxonomy of  
Subfamily Zygothylloideae  
(Zygothyllaceae) with Special  
Reference to the Genus *Fagonia*

BY

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## Abstract

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Members of Zygophylloideae are shrubs, shrublets and herbs of arid and semiarid areas of almost all continents, and many of the species are major components of the vegetation in their areas of distribution. A phylogenetic analysis of Zygophylloideae based on noncoding *trnL* plastid DNA sequences and morphological data, indicates that the currently recognised genera *Augea*, *Tetraena*, and *Fagonia*, are embedded in *Zygophyllum*. A new generic classification based on six monophyletic and morphologically distinctive entities is proposed here: *Augea*, *Fagonia*, *Melocarpum*, *Roepera*, *Tetraena* and *Zygophyllum*.

The taxonomy of the genus *Fagonia* is revised in detail. A key to the 34 species recognised is presented, as well as descriptions and distribution maps for each species. Five new species are described and illustrated, *F. densispina*, *F. gypsophila* and *F. latistipulata* from Somalia, and *F. hadramautica* and *F. mahrana* from the southern part of the Arabian Peninsula. Of the accepted species, 26 are restricted to the Old World and eight to the New World. The names of all four species of *Fagonia* currently on the IUCN Red List of Threatened Plants are put into synonymy. Instead, eight other species are proposed for the list.

Relationships within *Fagonia* are inferred from analysis of plastid *trnL* intron and nuclear ribosomal ITS sequences. The phylogenetic analysis is performed using parsimony and Bayesian model averaging. All species of *Fagonia* in the Old World, except *F. cretica*, form a weakly supported clade, and all *Fagonia* species of the New World, except *F. scoparia*, form a second, well supported clade, sister to the Old World clade. *Fagonia scoparia*, endemic to northeastern Mexico is sister to all other *Fagonia* species. Vicariance-dispersal analysis indicated that the occurrences of *Fagonia* in South America and southern Africa are due to dispersals, and that the ancestor of *Fagonia* had a distribution in agreement with the boreotropics hypothesis.

**Keywords:** Phylogeny, Taxonomy, Zygophylloideae, *Fagonia*, Biogeography

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## List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

- I B.-A. Beier, M. W. Chase & M. Thulin. 2003. Phylogenetic relationships and taxonomy of subfamily Zygophylloideae (Zygophyllaceae) based on molecular and morphological data. *Pl. Syst. Evol.* 240: 10-39.
- II B.-A. Beier. 2001. Two new unifoliolate species of *Fagonia* (Zygophyllaceae) from the Horn of Africa region, and the resurrection of *F. subinermis* from Iran. *Nord. J. Bot.* 21: 449-455.
- III B.-A. Beier. A revision of *Fagonia* (Zygophyllaceae). *Systematics and Biodiversity* (submitted)
- IV B.-A. Beier, J. A. A. Nylander, M. W. Chase & M. Thulin. Phylogenetic relationships and biogeography of the desert plant genus *Fagonia* (Zygophyllaceae), inferred by parsimony and Bayesian model averaging. *Molecular Phylogenetics and Evolution* (submitted)

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Papers I and IV were written by the first author, and comments and suggestions were given by co-authors. The papers were also planned in cooperation with the co-authors. The first author is responsible for all the morphological and molecular work, with the exception of loading and running the sequencer. The first author also conducted the parsimony and biogeographical analyses, whereas the analysis of Bayesian model averaging was designed, described and presented by the second author in paper IV.

**Important note.** Paper III of this thesis is a manuscript that contains the descriptions of three new species. This paper has been submitted for publication elsewhere, and in order to make clear that the names of these new species are not validly published in this thesis the Latin diagnoses necessary according to the International Code of Botanical Nomenclature<sup>1</sup> are omitted.

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## PREFACE

The total number of known flowering plants has been estimated to be between 223 300 and 422 100, and at least 34 000 species are estimated to be still undescribed<sup>2,3,4</sup>. On average c. 2 000 species new to science have been described each year during the last decade, and the discovery of new species is continuing unabated<sup>2</sup>. The undescribed species will be discovered during fieldwork, but also in the collections of the c. 3 100 different herbaria holding around 300 million sheets<sup>5</sup>. Although the majority of the species of flowering plants have been described, the information about them is widely scattered, differs much regarding quality, and is in some cases only available with difficulty. The fact that the estimated number of known flowering plants varies so greatly is an illustration of how much systematic and taxonomic work is needed to get the already described species in order. In paper I a new formal generic taxonomy of *Zygophylloideae* is proposed, and in paper III a complete taxonomic revision of *Fagonia* is presented. This is a small step towards increased order in the 457 families of flowering plants<sup>15</sup>.

The demand for accurate knowledge about biodiversity has increased considerably following a growing awareness about the biodiversity crisis, and the resulting Convention on Biological Diversity. In the third paper I have shown that all species of *Fagonia* currently on the IUCN Red List of threatened species are synonyms of more or less common species. Instead eight other species of *Fagonia* are categorized as vulnerable according to the criteria of the IUCN Red List.

The many new methods and tools that have been taken into use in various fields of evolutionary biology, has opened up for many new and exciting questions<sup>6,7,8,9</sup>. It is now, for example, possible to explore the history of geographical distributions and morphological traits. Another advantage of these new methods is the much greater possibility to name organisms in a manner that more accurately reflects their relationships, than previously.

In paper IV an analysis of the remarkably disjunct distribution of *Fagonia*, spanning four continents, is presented using new methods and tools for phylogenetic and biogeographic analysis. Further studies in *Zygophylloideae*, using these only relatively recently available methods, will likely reveal how this subfamily became such an important component of the vegetation in arid areas.

## INTRODUCTION

### *Circumscription of Zygothylloideae*

Zygothylloaceae, in the classification by Sheahan & Chase<sup>10</sup>, 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 a position within the eurosid I clade<sup>12,13,14,15</sup>. The largest subfamily in Zygothylloaceae is Zygothylloideae, with about 185 species of shrubs, subshrubs and herbs grouped into four genera, *Fagonia* and *Zygothylum*, and the monotypic *Augea* and *Tetraena*. In previous classifications of Zygothylloaceae<sup>16,17</sup> a much wider circumscription of Zygothylloideae was used.

### *The polyphyletic genus Zygothylum*

Some authors have questioned the monophyly of the large and morphologically diverse *Zygothylum*<sup>10,11,18,19</sup>, but the genus, as understood and circumscribed by Engler<sup>16</sup>, has also been accepted by several authors<sup>20,21,22,23</sup>. To accommodate the large range of variation, Engler<sup>16</sup> subdivided *Zygothylum* into 17 sections, whereas Van Huyssteen<sup>21</sup> proposed a classification into two subgenera and 13 sections, mainly on the basis of fruit and filament characters.

In 2000 Sheahan and Chase<sup>11</sup> published a study based on *rbcL* and *trnL-F* sequences from 36 members of Zygothylloaceae. In that study Zygothylloideae were strongly supported as monophyletic, whereas *Zygothylum* was polyphyletic with *Augea*, *Fagonia* and *Tetraena* embedded within it. The main groupings are the same in the *rbcL* and the *trnL-F* analyses, but the branching order within Zygothylloideae differed considerably between the two 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 weakly supported as sister to the clade with *Fagonia* and the two species of *Zygothylum* mentioned above. Three species of *Zygothylum* from South Africa come out in a strongly supported clade as sister to three Australian species. The type of *Zygothylum*, *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 four species distributed in Africa and southwestern Asia. The results obtained by Sheahan and Chase<sup>11</sup> clearly indicated that the generic classification within Zygothylloideae needs reconsideration.

### *Systematics of Fagonia*

The relationships between species of *Fagonia* have been subjected to only a few studies. Ozenda and Quézel<sup>24</sup> grouped the North African *Fagonia* species into four “natural groups”, and later El Hadidi<sup>25</sup> proposed a modified scheme subdividing *Fagonia* into four complexes. The species of the New World were hypothesized to be associated with one of the complexes. El Hadidi<sup>25</sup> also recognized that three groups of *Fagonia* species with short stipules and 3-foliolate leaves are more closely related to each other than to the group of species with long stipules and 1- to 3-foliolate leaves. To summarize, the “natural groups” presented by Ozenda and Quézel<sup>24</sup> and El Hadidi<sup>25</sup> were based on vague criteria and included only the Old World species, and a modern phylogenetic analysis of both New and Old World species of *Fagonia* is clearly needed.

### *Taxonomy of Fagonia*

The delimitation of species in *Fagonia* is known for being notoriously difficult, and more than 160 names have been published since 1753 when Linnaeus erected the genus in *Species Plantarum*. Linnaeus recognized three species: *F. arabica*, *F. cretica* and *F. hispanica*.

Different opinions about the species limits in the genus can be illustrated by Anderson<sup>26</sup>, who in 1860 lumped all the 25 species, until then described, into a single variable species, *F. cretica*. Later, in 1868, Oliver<sup>27</sup> published a similar treatment, where all the species then known from tropical Africa were included in *F. cretica*. However, the treatments of *Fagonia* in the Old World by de Candolle<sup>28</sup> (1824) and Boissier<sup>29</sup> (1867) differed widely, with ten species recognized by de Candolle and 14 by Boissier. The treatments by de Candolle and Boissier have been followed to a large extent by subsequent authors and most of their taxa have until now been widely accepted<sup>19,30,31,32</sup>, although often with different circumscriptions.

There has also been controversy concerning the species limits of *Fagonia* in America. Bentham<sup>33</sup> and Standley<sup>34</sup> separated the North and South American species from each other in contrast to Johnston<sup>35</sup>, who treated *F. chilensis* in a wider sense, with a distribution in both South and North America. In the latest treatments of the species of *Fagonia* in the New World one South American and eight North American species are accepted<sup>34,36,37</sup>.

The problems presented above and the conflicting species delimitations published in the different regional treatments of the genus<sup>19,25,32,36,38,39,40,41,42</sup>, clearly point to the necessity of a worldwide revision of *Fagonia*. This has not been undertaken since 1860<sup>26,27</sup>, which probably accounts for some of the confusion regarding the taxonomy of the genus.

### *Biogeography of Fagonia*

The genus *Fagonia* has a remarkably disjunct distribution covering arid areas of the New and Old World (Fig. 1). It is found in Mexico, southwestern USA, Chile, and Peru in the New World, whereas in the Old World it is known from southern Africa, parts of Macaronesia, North Africa south to the Sahel regional transition zone, and the southernmost parts of Europe, including many of the Mediterranean islands. *Fagonia* is also known from the Horn of Africa region, western Asia, and the Arabian Peninsula east to Afghanistan and western India. Different species of *Fagonia* are restricted to distinct regions in the Old or New World. Areas rich in endemic species of *Fagonia* are: Baja California with six species, and the Horn of Africa region (including southern Yemen and Oman), with eight species.

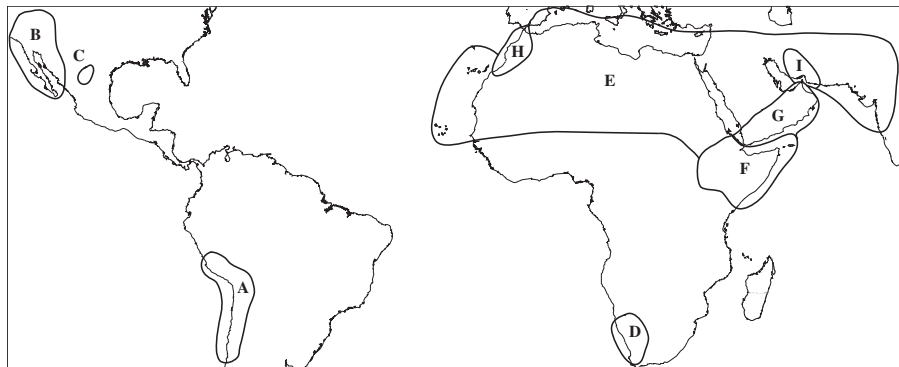


Fig. 1. Distribution map of *Fagonia* with the nine areas of endemism: A=South America, B=North America, C=Northeastern Mexico, D=Southern Africa, E=Saharo-Sind including parts of Macaronesia, F=Horn of Africa region, G=Yemen and Oman, H=Southwestern Morocco and I=Southern Iran.

The disjunct distribution of *Fagonia* has been explained by several different hypotheses. Engler<sup>43,44</sup> proposed that the New World localities of *Fagonia* had been established by seeds of *F. cretica* introduced by cargo ships from the Iberian peninsula and that *Fagonia* was a truly Old World genus. Johnston<sup>45</sup> explained the distribution of *Fagonia* as remnants of a widespread early Tertiary desert flora. Axelrod<sup>46</sup> initially considered the distribution as a result of a break-up of the range of a common pantropical Tertiary ancestor and subsequent speciation. Later Axelrod<sup>47</sup> considered the distribution as being remnant of the dry flora that inhabited Gondwanaland prior to its break-up during the Cretaceous, whereas Stebbins and Day<sup>48</sup> considered that the distribution was a result of a pre-Tertiary migration from the Old to the New World via the Bering land bridge. Porter<sup>49</sup> believed in a combination of sea-floor spreading and long-distance dispersal from east to west during the early Tertiary, when the continents of the Old and New

Worlds were much closer than at present. To sum up, several hypotheses of the historical biogeography of *Fagonia* have been put forward, all on more or less loose grounds and without being based on a phylogeny of *Fagonia*.

## METHODS

### *Morphological methods*

I collected morphological data by studying herbarium specimens from ALF, ATH, B, BM, BR, C, CAS, DS, E, FI, FT, G, GH, GOET, HBG, HUH, HUI, K, KUH, L, M, MA, MO, MPU, MSB, NBG, NY, P, PR, PRC, RSA, S, SD, TARI, TCD, TUC, UC, UPS, US, W, WU and Z (acronyms according to Holmgren et al.<sup>50</sup>). I have also studied several species in the field during collecting trips to Mexico, South Africa, Spain and Yemen. In order to study flower and fruit characters material was softened in boiling water with a small amount of detergent added. Examination and measurement of softened plant parts was made under a dissection microscope, typically under 12 to 25 times magnification. Some small plant parts, e.g. cross-sections of seeds, were studied under a light microscope. Pollen grains were subjected to acetolysis<sup>51</sup> and studied by light microscopy and scanning electron microscopy (SEM). Seeds were also studied by SEM after being prepared according to the protocol in Ismail and El-Ghazaly<sup>52</sup>, involving a treatment with 10% HCl after being soaked in water. The circumscription of species in paper II and III is based on a morphological species concept. This concept can be summarized as follows: “Species are the smallest groups that are consistently and persistently distinct and distinguishable by ordinary means”, and implies that discontinuities in the morphological variation are used in the circumscription of species<sup>52a</sup>.

### *Molecular methods*

Plastid *trnL* intron and/or nuclear ribosomal internal transcribed spacer (ITS) sequences, including the 5.8S gene, were used in the studies presented here. The choice of sequences used are based on published results presented by Sheahan & Chase and Soltis & Soltis<sup>10,11,53</sup>, which indicated that these regions would contain an appropriate amount of variation for inferring phylogenetic relationships in the groups studied. Using both plastid and nuclear markers can lower the risk of inferring an incorrect species phylogeny. By the use of ITS it is at least theoretically possible to detect chloroplast capture, which could have happened in a hybridization event<sup>52</sup>.

Species of Zygothylloideae included in the analyses in paper I were selected to cover morphological and geographical variation within the subfamily. The 34 species of *Zygothylloideae* sensu lato included, represent 12 of the 17 sections recognised by Engler<sup>16</sup> and 10 of the 13 sections recognised by Van Huyssteen<sup>21</sup>. In total 24% of the species in the subfamily were sampled. The sampling of *Fagonia* in paper IV is nearly complete, and only two species, *F. densispina* (newly described) and *F. californica* (closely related to *F. laevis*), are missing from the analyses. Six of the widely distributed and variable species are sampled with more than one specimen in the analysis in order to increase the possibility of detecting lineage sorting and hybridization<sup>52</sup>. DNA extraction and purification was carried out using standard procedures<sup>54,55</sup>. The *trnL* intron and ITS were amplified and sequenced according to published protocols<sup>56,57,58,59,60</sup>. Alignment of the data set was performed manually following the guidelines of Kelchner<sup>61</sup>.

#### *Phylogenetic methods*

The parsimony analyses and the calculation of bootstrap percentages (BP) were made using PAUP\* 4.0b10<sup>62</sup>. The morphological as well as the different molecular data sets were analyzed separately and in combination in the studies. The choice of outgroup in paper I is based on Sheahan and Chase<sup>10,11</sup> and the choice of outgroup in paper IV is based on Beier et al.<sup>60</sup>. Bayesian model averaging is used to infer model-based phylogenies of *Fagonia* in paper IV.

#### *Analysis of biogeography*

The historical biogeography of *Fagonia* was explored by dispersal-vicariance analysis using DIVA v. 1.1<sup>63</sup>. The distributions of species were subdivided into nine areas of endemism. An area of endemism is here defined as a geographic region with at least two species that exhibit distributional congruence, following Harold and Moor<sup>64</sup>. Exceptions from this definition were made in two cases of very isolated occurrences of single endemics. The areas are as follows: A) South America, consisting of Chile and Peru, B) North America consisting of Baja California, Mexico, and southwestern USA, C) northeastern Mexico consisting of the region of Coahuila, D) southern Africa, consisting of Botswana, Namibia, and South Africa, E) the Saharo-Sindian region including the Mediterranean region from Morocco in the west to India in the east, south to c. 15° N in the Sahel regional transition zone and north to southern Italy and Spain, and Macaronesia except the Azores, F) the Horn of Africa region consisting of Djibouti, eastern Eritrea, eastern Ethiopia, northeastern Kenya, Socotra and Somalia, G) southern Arabia consisting of continental Yemen and Oman, H) southwestern Morocco, and I) southern Iran.

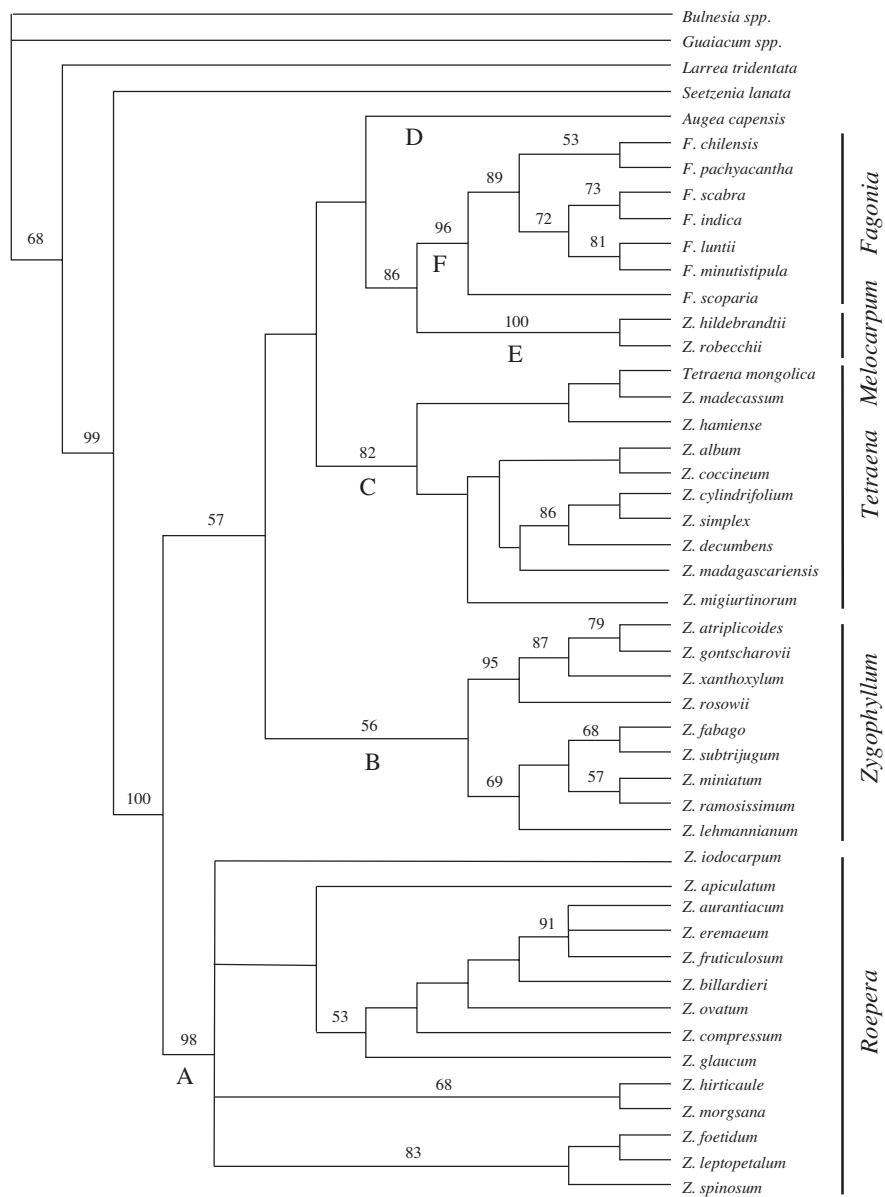
## RESULTS

### *Phylogenetic relationships and taxonomy of subfamily Zygophylloideae (Paper I)*

The results in this study were based on a morphological and a molecular data set. In the preparation of the morphological data set, stipules were found in all examined taxa, including *Augea*, which has been reported to lack stipules<sup>16,65,66,67</sup>. Also, the reported absence of endosperm in the seeds of *Augea*<sup>10,16,67</sup>, and *Tetraena mongolica*<sup>10,68</sup> is not consistent; some seeds have an endosperm, and others lack it in both these taxa.

A parsimony analysis of the combined morphological and *trnL* data set generated 1570 shortest trees (ST) of 691 steps with consistency index (CI) of 0.70 and retention index (RI) of 0.79. The topology of the consensus tree shows the same main groups as in the analysis of the data set with molecular data only (topology not shown), but differs with respect to the internal resolution within five of the six main groups. Also, bootstrap percentages (BP) differ in four of the six main clades between the molecular and the combined data set. Parsimony analysis of the morphological data resulted in an almost unresolved topology in the consensus tree (not shown). The only clades with a BP above 50 were those corresponding to clade E and F. The combined consensus tree is shown in Fig. 2, 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 several characters: aril covering the hilum, sepals persistent in fruit (with a parallelism in *Augea* and some species of *Fagonia*), a papillate disc, and an outer testa with helical threads (with a parallelism in *Augea*).



**Fig. 2.** Strict consensus tree based on a combined data set of molecular and morphological characters. Figures above nodes are BP and letters A to F denote groups discussed.

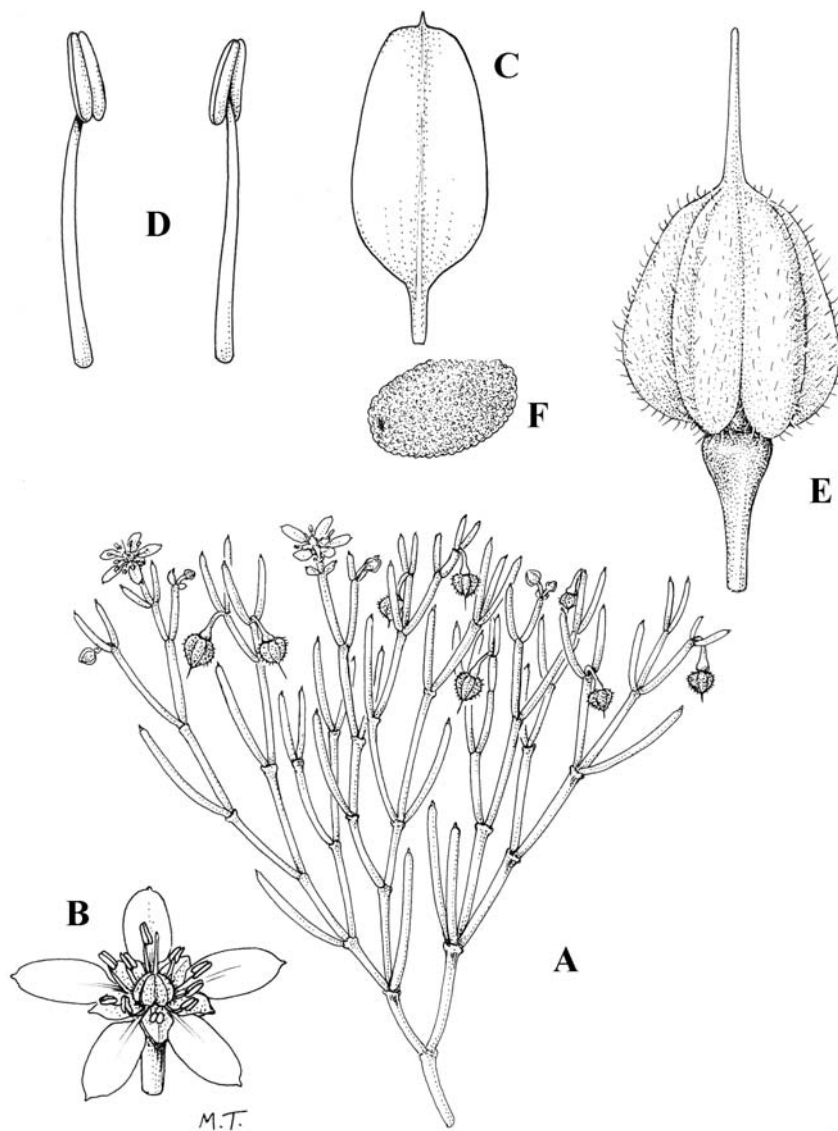
A clade (B) comprising all the Asian species of *Zygophyllum* included in this study and the type of the genus, *Z. fabago*, is weakly supported (BP 56) and has two subgroups (BP 96 and 68). An outer testa with funnel- or rod-like structures (with a parallelism in clade C) is a synapomorphy for this

clade. Clade C (BP 82) comprises *Tetraena mongolica*, and the rest of the *Zygophyllum* species in this study, including species from Madagascar, South Africa, northern Africa and the southwesternmost parts of Asia. Synapomorphies for clade C are schizocarpic fruits (with parallelisms in *Augea*, *Z. aurantiacum*, *Z. eremaeum* and *Z. fruticosum*) and an 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, with the two species of *Z.* sect. *Melocarpum*, is well supported as sister to clade F (BP 100). 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* in clade B) 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 91). *Fagonia scoparia* from Mexico is sister to all other taxa. Synapomorphies for clade F are entirely free stipules (a reversal), spinescent or pointed stipules and obconical capsules.

#### *A revision of Fagonia (Paper II & III)*

The morphology of the genus *Fagonia* is discussed. All species were shown to have leaves, including *F. scoparia*, which has been described as leafless<sup>34,69</sup>. Thirty-four species are recognized, and the genus has a disjunct distribution in arid areas of the New and Old World. Of the accepted species, 26 are restricted to the Old World and eight to the New World. Most of the Old World species are confined to the Saharo-Sindian region, with two extending to parts of Macaronesia. Eight species are endemic to the Somalia-Masai region, and two are restricted to southern Africa. In the New World four species are endemic to Baja California, two to northern Baja California and adjacent parts of southwestern USA, one to the province of Coahuila in northeastern Mexico, and one to Chile and Peru. In total 167 names are accounted for; lectotypes are selected for 33 names, and two names are neotypified. Five new species are described and illustrated, *F. densispina*, *F. gypsophila* (Fig. 3) and *F. latistipulata* from Somalia, and *F. hadramautica* and *F. mahrana* (front page) from Yemen. The names of all four species of *Fagonia* currently on the IUCN Red List of Threatened Plants are put into synonymy.

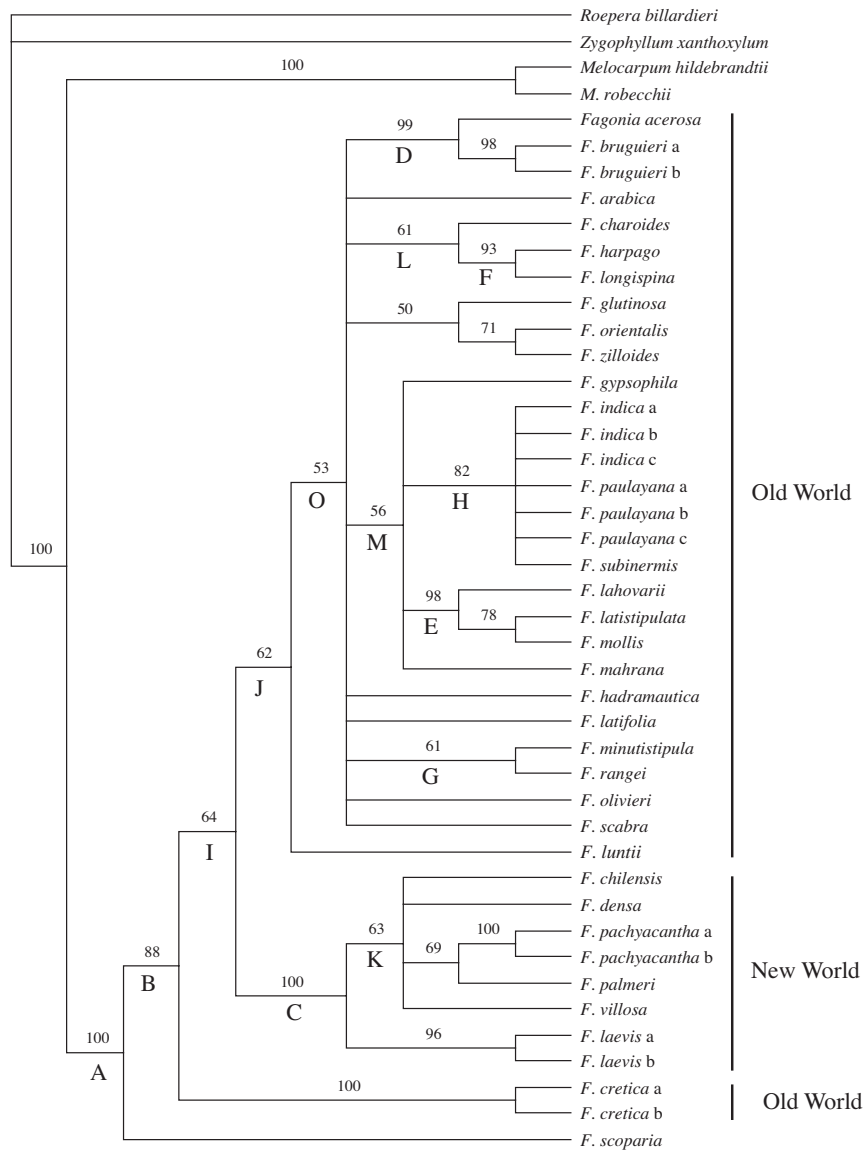


**Fig. 3.** *Fagonia gypsophila* Beier & Thulin. A: Branch, x 1. -B: Flower, x 3. - C: Petal, x 9. - D: Stamens in front and back view, x 15. - E: Capsule, x 9. - F: Seed, x 15. Drawn by Margaret Tebbs. Reproduced with kind permission of Nord. J. Bot.

*Phylogenetic relationships and biogeography of Fagonia (Paper IV)*

The analyses of the phylogenetic relationships of *Fagonia* corroborated the results of Paper 1<sup>60</sup>. *Fagonia scoparia* from Mexico is sister to all other species of *Fagonia* and the rest of the species from the New World form a

sister clade to all Old World species except *F. cretica*. Analysis of the combined matrix, including ITS and *trnL*, produced 2918 trees of 703 steps with CI of 0.58 (excluding uninformative characters) and RI of 0.75. The strict consensus tree is shown with BP in Fig. 4.



**Fig. 4.** Strict consensus tree based on a combined data set of *trnL* and ITS, with bootstrap percentages indicated above the branches.

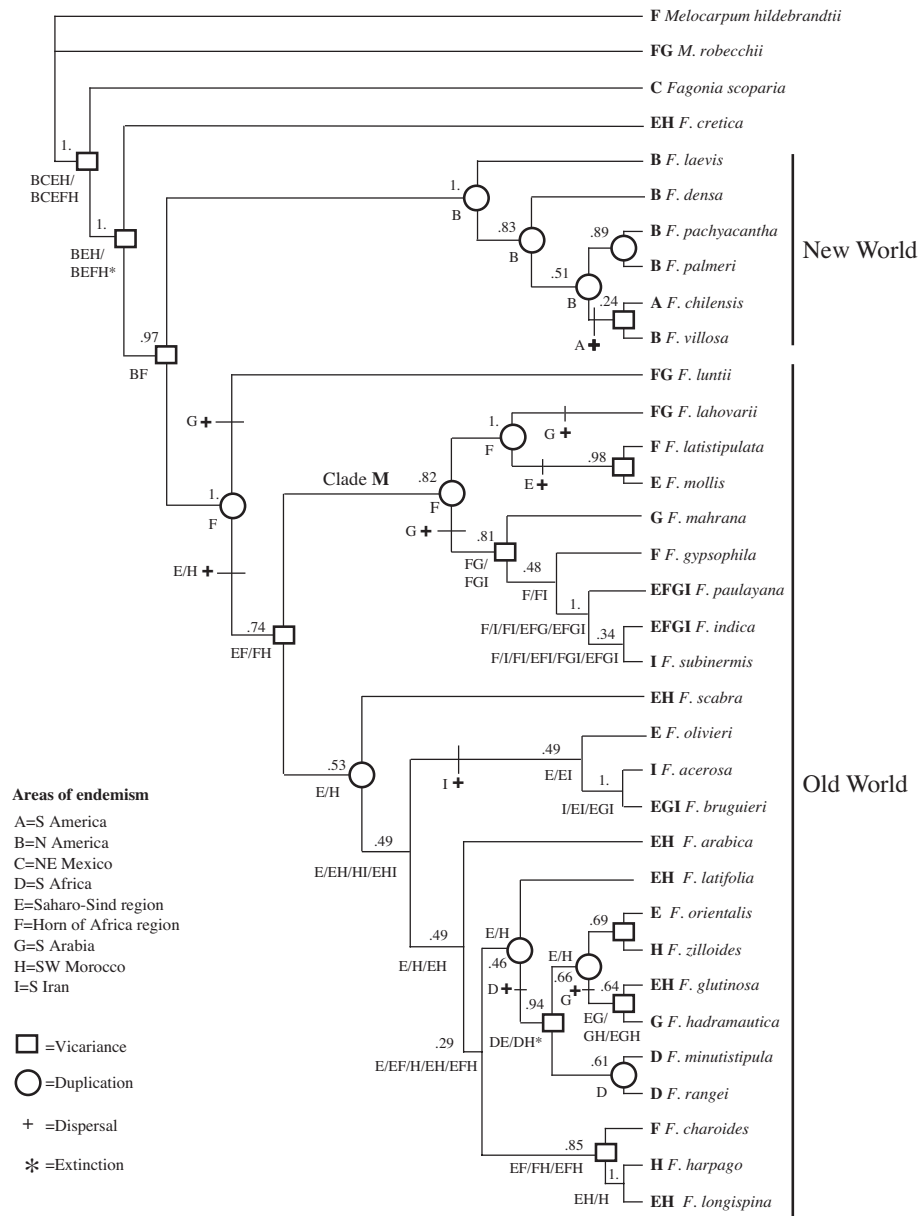
The topology of the consensus tree of the combined data set shows the same eight clades, A-H, as in the analysis of ITS only (result not shown), whereas the topology of *trnL* only supported clades A, B and C (result not shown). The consensus tree from the combined analysis also has a better resolution than the consensus trees from the single data set analyses. The following clades were only detected in the consensus tree from the combined analysis: *Fagonia cretica*, with a distribution from the Cape Verde Islands to southern Europe and North Africa east to Egypt, is weakly supported as sister to the rest of clade B (BP 64; clade I). Clade C, with all the New World species except *F. scoparia*, is weakly supported as sister to a clade with all the Old World species except *F. cretica* (BP 62; clade J). North American *F. laevis* is weakly supported (BP 63; clade K) as sister to the rest of the New World species in clade C, nesting the South American *F. chilensis* within the North American species. Also, *F. charoides*, endemic to Somalia, is weakly supported (BP 68; clade L) as sister to *F. harpago* in Morocco and *F. longispina* in Morocco and Algeria (clade F).

The vicariance-dispersal analysis (DIVA) required 28 dispersal events, and the ancestor of *Fagonia* is given two alternative ancestral distributions in the analysis (Fig. 5.): 1) North America (B), northeastern Mexico (C), Saharo-Sind (E) with the bordering area of southwestern Morocco (H), or 2) the same area, but including the of Horn of Africa (F). These alternative distributions of the ancestor of *Fagonia* indicate that it had a range agreeing with the boreotropics hypothesis<sup>70,71,72</sup>.

The ancestor to all species of *Fagonia* except *F. scoparia* is also given two alternative ancestral distributions: North America (B), Saharo-Sind (E) with the bordering area of Morocco (H), or the same area plus the Horn of Africa. Vicariance separated the ancestor of all *Fagonia* species, except *F. cretica* and *F. scoparia*, to North America (B) and to the Horn of Africa region (F). Considering, that vicariance took place between two areas not adjoined; North America (B), and Horn of Africa (F), extinction is inferred at this node. All the New World species of *Fagonia* are indicated to be a result of duplications, i.e. successive speciations within the area, with the exception of *F. chilensis* in South America, which is conceived as evolved after dispersal of the ancestor from North America.

The ancestor of all species of the Old World, except *F. cretica*, was endemic to the Horn of Africa (F), from where dispersal to Saharo-Sind (E) or southwestern Morocco (H), and southern Arabia (G) took place. The ancestor of all species of the Old World, except *F. cretica* and *F. luntii*, had a wide distribution covering the Horn of Africa (F) and Saharo-Sind (E), or the Horn of Africa (F) and southwestern Morocco. However, this node is not

well supported (Fig. 4 & 5). Some of the terminal nodes seem to be results of relatively recent dispersals to Saharo-Sind (E) and southern Arabia (G), and narrow endemics such as *F. hadramautica* are indicated to have evolved after recent dispersals.



**Fig. 5.** The inferred historical distribution of *Fagonia*, using DIVA. Equally optimal distributions are separated by slash (/).

## DISCUSSION

In paper I it is shown that the current generic subdivision of Zygothylloideae obviously cannot be maintained because *Fagonia*, *Augea* and *Tetraena* are all embedded within *Zygothylum*. A possible solution could be to treat the whole subfamily as a single genus, for which the Linnaean names *Zygothylum* 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 in the results section (Fig. 2). With this approach, the distinctive genera *Fagonia* and *Augea* can be kept with their current circumscriptions, the circumscription of *Zygothylum* would be reduced to the species in clade B and their relatives not included in this study, *Tetraena* would be extended to include all the species in clade C and their relatives, the generic name *Roepera* could be resurrected for the species in clade A and their relatives, and a new generic name, *Melocarpum*, would be given to clade E.

The latter approach above is advocated in paper I 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 *Zygothylum* sensu lato (including all of Zygothylloideae), 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<sup>11</sup>.

The mix of characters in *Augea* (clade D), such as outer testa with helical threads (found 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 *Zygothylum* clade, with one well and one moderately supported subclade 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.

In paper III the revision of *Fagonia* corroborates the view that species do not evolve in order to be easily recognized by us. Many species of *Fagonia* are indeed difficult to identify and delimit and the large number of published names, c. 167 since 1753, bears witness to this. This revision also demonstrates the importance of publishing global revisions and not only

regional treatments. Many of the synonymous names listed here have been published because the full range of variation of many species has not been properly appreciated.

In paper IV the hypothesis that the Tertiary north Atlantic land bridge had a significant influence on the development of modern continental biotas<sup>70,71,72</sup>, including that of Africa and North America, is further strengthened. The Tertiary north Atlantic land bridge is hypothesised to be the historical reason why the distribution of *Fagonia* is largely confined to North America and northern Africa including the Horn of Africa.

The explanation of Stebbins and Day<sup>48</sup>, that the distribution of *Fagonia* is a result of a pre-Tertiary migration from the Old to the New World via the Bering land bridge is here viewed as much less likely. This is because the climate was less favourable in the Bering area for thermophilic taxa, and the geographical gap between Baja California and India is much larger than that between Baja California and northwestern Africa. Long-distance dispersal crossing the Atlantic from Africa to South America as suggested by Raven and Axelrod<sup>73</sup> and Porter<sup>49</sup> is not supported by the results presented here. Also, Engler's<sup>43,44</sup> idea about anthropogenic dispersal from the Old World to the New World is highly unlikely as all the New World species differ considerably from the Old World species with respect to molecular data.

The schemes of relationships and classifications presented by Ozenda & Quézel<sup>24</sup> and El Hadidi<sup>74</sup> (1966) are not supported by the results in paper IV. For example, *F. cretica* and *F. orientalis* (as "*F. flamandii*") were placed as sister taxa in their classification, as were *F. arabica* and *F. zilloides*. These relationships are not supported by our results. *Fagonia cretica* is sister to all *Fagonia* species except *F. scoparia*, and *F. zilloides* is sister to *F. orientalis*. The subsequent classifications by El Hadidi<sup>25,75</sup> are also not supported by paper IV.

## CONCLUDING REMARKS

A better taxonomic and nomenclatural order is now brought to Zygophylloideae, and to *Fagonia*, although many problems certainly remain. It is hoped that the identification of species of *Fagonia* will be easier and more consistent from now on. The increased knowledge of the taxonomy of *Fagonia* points to the necessity of major changes in the IUCN Red List for this genus. The four species on the list today have been synonymized, and instead, eight other species are proposed to be included on the list in the category of vulnerable. The formerly monotypic genus *Tetraena*, endemic to

China, has been treated as an especially interesting taxon from a conservation point of view. Not being a member of a monotypic genus anymore does not make this geographically restricted species less interesting, but it signals that much caution is needed if monotypic genera are to be given a special status.

In paper IV it is shown that a reasonably well-supported phylogeny can offer data for analyses giving new insights into historical biogeography. The remarkably disjunct distribution of *Fagonia* is here explained by an ancestral distribution in agreement with the boreotropics hypothesis, and the occurrences of *Fagonia* in South America and southern Africa are explained as dispersals.

## SAMMANFATTNING

Systematik och taxonomi är grunden för att kommunikation om växter, djur och andra organismer ska kunna ske på ett meningsfullt sätt. Regelverket som bestämmer hur olika organismer ska namnsättas är av fundamental betydelse för att denna kommunikation ska kunna upprätthållas på ett väl fungerade sätt.

Zygophylloideae tillhör en av de växtgrupper där systematiken och taxonomin länge varit osäker. Detta har bland annat inneburit att det varit oklart vilka släkten och hur många arter gruppen egentligen innehåller. Zygophylloideae består av arter som ofta dominerar vegetationen i jordens torrområden; inga arter förekommer i Sverige. Eftersom gruppen är så ekologiskt betydelsefull finns det ett särskilt intresse av att klara ut vilka arter som den egentligen består av. Därtill är det intressant att försöka förstå hur gruppen har spritt sig till så många av jordens torrområden.

I avhandlingens första artikel avgränsas naturliga släkten i Zygophylloideae, det vill säga sådana släkten som består av arter vilka är varandras närmaste släktingar. Avgränsningarna är gjorda dels med hjälp av morfologiska karaktärer, dels med hjälp av data från sekvenser från växternas DNA och resultatet är att sex släkten kunde urskiljas: *Augea*, *Fagonia*, *Melocarpum*, *Roepera*, *Tetraena* och *Zygophyllum*. Ett av släktena, *Melocarpum*, är nygjort och består av mer än meterhöga buskar som har sin huvudutbredning i Somalia och Yemen.

I avhandlingens andra och tredje artikel avgränsas arterna i släktet *Fagonia*. Lika lätt som det är att känna igen släktet *Fagonia* lika svårt är det att känna igen släktets olika arter. *Fagonia* utgörs vanligen av upp till 30 cm höga och torniga buskar med violetta blommor. Det har skrivits hundratals artiklar om släktet och över 160 olika arter, underarter, varieteter och former

har beskrivits. Med hjälp av stora mängder insamlat material bestående av tusentals herbarieark från sammanlagt 42 olika herbarier samt egna insamlingar har jag genomfört en heltäckande revision av släktet. *Fagonia* består nu av 34 arter varav fem är nya för vetenskapen: *F. densispina*, *F. gypsophila* och *F. latistipulata* från Somalia, samt *F. hadramautica* och *F. mahrana* från Arabiska halvön. Ett resultat av revisionen är att samtliga arter av släktet som för närvarande är upptagna på Internationella naturvårdsunionens (IUCN) lista över hotade eller sårbara växter (Red List of Threatened Species) visat sig vara synonymer till mer eller mindre vanliga arter. Istället har åtta andra arter visat sig uppfylla kriterierna för sårbara arter och ett ändringsförslag är insänt till IUCN.

I avhandlingens fjärde artikel utreds släktskapen mellan de olika *Fagonia*-arterna. Ett av syftena med detta är att få data som skulle göra det möjligt att utforska historien om släktets mycket vidsträckta utbredning över fyra kontinenter. *Fagonia* förekommer i Sydamerika och Nordamerika, i södra Afrika, Nordafrika, Afrikas horn, sydligaste Europa samt i västra Asien inkluderande Arabiska halvön och västra Indien. Resultatet av de genomförda analyserna indikerar att släktet vid uppkomsten hade en utbredning som förmodligen sträckte sig över ett område som idag motsvaras av östra USA och centrala Europa. Detta område var mer eller mindre väl sammanknutet av en nordatlantisk landbrygga som existerade fram till för åtminstone 40 miljoner år sedan. Förekomsterna av *Fagonia* i Sydamerika och södra Afrika har sannolikt uppkommit genom spridning vid betydligt senare tillfällen, efter att släktet delats upp i en amerikansk och en afrikansk/europeisk gren.

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