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Zygophyllaceae in Africa

M. N. EL HADIDI

SUMMARY

The author gives an outline of a revision of the family *Zygophyllaceae*. The following taxa are proposed to be raised to family level: *Nitraria* (*Nitrariaceae*), *Balanites* (*Balanitaceae*), *Tribuleae* (*Tribulaceae*). *Peganum* and *Tetradiclis* should not be considered as belonging to *Zygophyllaceae*. *Seetzenia* is proposed to be placed in the subtribe *Seetzeniinae*, and *Augea* in *Zygophyllinae* of *Zygophyllaceae*. *Zygophyllaceae* s. str. is considered to include Old World genera with opposite, stipulate, usually compound leaves, capsular fruits and endospermic seeds.

RÉSUMÉ

L'auteur présente un résumé d'une révision de la famille des Zygophyllacées. Il propose d'élever au rang de famille les taxons suivants: *Nitraria* (*Nitrariaceae*), *Balanites* (*Balanitaceae*), *Tribuleae* (*Tribulaceae*). *Peganum* et *Tetradiclis* ne sont pas considérés comme des Zygophyllacées. *Seetzenia* devrait être placé dans la sous-tribu des *Seetzeniinae*, ainsi que *Augea* dans la sous-tribu des *Zygophyllinae* de la famille des Zygophyllacées. *Zygophyllaceae* s. str. comprendra ainsi les genres de l'Ancien Monde à feuilles stipulées, composées et opposées, à fruits en capsule et à graines albuminées.

Zygophyllaceae R. Br. (s. l.) is one of the families of common occurrence in the arid zones of the Old World, particularly in Africa. Some 120 species are known to occur on this continent and constitute about two thirds of the species of this family.

A critical revision of the species of *Zygophyllaceae* in Africa is now in progress. In this respect, an outline of such a revision is briefly discussed as follows.

1. Engler (1931) divided the family *Zygophyllaceae* into seven subfamilies, the first five of which are characterized by their capsular or splitted fruits while the last two subfamilies have a drupaceous, edible fruit. Among the representatives of *Zygophyllaceae* with capsular or splitted fruits, the species of the subfamilies *Peganoideae*, *Tetradiclidoideae* and *Chitonioideae* are characterized by their alternate leaves while those of *Augeoideae* and *Zygophylloideae* are opposite. According to Takhtajan (1959), Engler's *Zygophyllaceae* includes extreme characters which are in favour of the earlier treatment of *Nitrarioideae* and *Balanitoideae* as distinct families, *Nitrariaceae* Lindl. and *Balanitaceae* Endlich. respectively. On the other hand, Hutchinson

(1967: 613) considered *Zygophyllaceae* as a very homogeneous (natural) family. He found it unnecessary to divide the 24 genera (without *Balanites* Delile) into six subfamilies (excluding *Balanitoideae* Engl.) eight tribes and four subtribes as established by Engler (1931). Hutchinson (op. c.) used the leaf characters (nature and arrangement) to distinguish between the genera, and he regarded the fruit characters as supplementary. Hutchinson admitted, however, that about half of the genera have alternate leaves and, besides the simple-leaved (primitive) genera, there are others (more advanced) with compound leaves. Such extremes can hardly be considered as constituents of a homogeneous or natural family.

This may raise the following question: what plants belong actually to the *Zygophyllaceae*? *Zygophyllaceae* is typified by *Zygophyllum* L. which is characterized by its opposite, mostly 2-foliate leaves, and a capsular fruit. In this respect, it may be noticed that Engler (1931), when arranging his seven subfamilies of *Zygophyllaceae*, placed the most typical subfamilies (with opposite leaves and capsular fruits), viz. *Augeoideae* and *Zygophylloideae* in the middle as the fourth and fifth subfamilies. The three preceding subfamilies represent an extreme with alternate leaves, while the two succeeding subfamilies represent another extreme with drupaceous fruits. The sequence of order of the seven subfamilies may show that Engler recognized the apparent diversity of characters among the *Zygophyllaceae*. This was also clear in his discussion (cf. Engler, 1931: 150) on the interrelationships between the genera of *Zygophyllaceae*, in particular *Peganum* and *Tetradiclis*.

It is therefore advisable to take the above-mentioned facts into consideration when discussing the interrelationships between the different genera which are accepted up to the present to belong to this family. Those facts also support the treatment of *Nitraria* L. and *Balanites* Del. as distinct families, viz. *Nitrariaceae* Lindl. and *Balanitaceae* Endlich. respectively. Both families differ essentially from the other *Zygophyllaceae* by their drupaceous fruits, exstipulate leaves and axillary spines.

2. *Peganum* L. (subfamily *Peganoideae* Engl.) is represented all over the North African Sahara by *Peganum harmala* L. var. *harmala* which is believed to be the ancestor of the other taxa occurring in Central and Northern Asia. Among these is the monotypic *Malacocarpus crithmifolius* (Retz.) Fischer & C. A. Mey. of the eastern regions of the Caspian Sea. *Peganum* and *Malacocarpus* are characterized by their alternate, simple and lobate leaves. In this respect, they differ from most of the *Zygophyllaceae* which have opposite leaves. A similar case is that of the monotypic *Tetradiclis* Stev. (subfamily *Tetradiclidoideae* Engl.). *Tetradiclis tenella* (Ehrenb.) Litw. is a tiny succulent plant with alternate simple, lobate leaves. It is known to occur in the salty marshes of Northern Africa and eastwards in Central Asia. Bentham & Hooker (1862) classified *Peganum* L. and *Tetradiclis* Stev. under the family *Rutaceae* while Engler (1931) regarded them as constituting two distinct subfamilies (*Peganoideae* and *Tetradiclidoideae*) of *Zygophyllaceae*. In this relation, Engler (op. c.: 150) wrote: "Da die typischen Zygophyllaceen von den typischen, an Gattungen reicheren Rutaceen durch das Fehlen der Ölbehälter sich unterscheiden, hielt ich es für richtig, die Gattungen *Peganum* und *Tetradiclis*, welche der Ölbehälter entbehren und keinerlei Anhaltspunkte zur irgend welcher engeren Verknüpfung mit den Rutaceen, darbieten, den *Zygophylloideae* als Vertreter koordinierter Unterfamilien

anzuschliessen. Sie sind ebensowenig wie die *Chitonioideae*, *Nitrarioideae* und *Balani-toideae* mit den Simarubaceen zu verbinden und können auch nicht den typischen *Zygophylloideae* subordiniert werden". It is obvious that Engler placed these two genera among *Zygophyllaceae* because of the absence of oil glands which are characteristic of the representatives of *Rutaceae*. He admitted that they can not be classified among the typical *Zygophylloideae*, and can only be regarded as representatives of co-ordinative subfamilies of *Zygophyllaceae*. Phytochemical studies (Saleh & El Hadidi, MS.), have revealed the presence of certain compounds in these genera which are not of common occurrence among the other genera of *Zygophyllaceae*. This fact, besides the other morphological differences are in favour of keeping both of *Peganum* L. and *Tetradiclis* Stev. apart from the *Zygophyllaceae*.

The monogeneric *Morkillia* Rose & Painter (= *Chitonia* Moç. & Sessé) which constitutes the subfamily *Chitonioideae* Engl. deserves a special study. *Morkillia* is characterized by its alternate, compound, imparipinnate leaves and is represented by two species of very limited distribution (Mexico).

3. Apart from the above-mentioned, almost monogeneric taxa of *Peganoideae*, *Tetradiclidoideae* and *Chitonioideae*, we come to the main part of Engler's *Zygophyllaceae* where species are characterized by their opposite leaves and where the subfamilies *Augeoideae* and *Zygophylloideae* belong. The first subfamily is represented by the monogeneric and monotypic S African *Augea* Thunb. which approaches in characters the succulent species of *Zygophyllum*. *Zygophylloideae* was divided by Engler (1931) into two tribes, viz. *Zygophylleae* Engl. (seeds endospermic) and *Tribuleae* Engl. (seeds non-endospermic). *Zygophylleae* is represented in Africa by about 90 species which belong to *Fagonia* L., *Seetzenia* R. Br. and *Zygophyllum* L. The first two genera constitute the subtribe *Fagoniinae* Engl. and are known from the arid regions of Africa, Arabia, W. India and Pakistan. *Zygophyllum* L. is the only genus of the subtribe *Zygophyllinae* Engl. which occurs in the Old World. The other genera of this subtribe (about 8) are N or S American trees or shrubs which approach the Acacias in habit. In this respect they differ from the shrubby or herbaceous succulent species of *Zygophyllum*. The possible relationships between these American genera and the Old World *Zygophyllum* requires a further study.

A monographic study on the genus *Fagonia* L. in the Old World is now being prepared. This reveals the presence of 27 species in Africa, which is the highest number known on any continent. Fourteen of these species are only known from Africa, twelve of which are endemic in certain parts of the Sahara, in coastal regions of Somalia and the Cape Province. Only four *Fagonia* species, viz. *F. glutinosa* Delile, *F. arabica* L., *F. indica* Burm. f., and *F. bruguieri* DC. can be regarded as widely spread taxa which are also known from the western deserts of Asia and the Indian subcontinent.

Noteworthy is a group of E African species which seems to play an important rôle in the phylogeny of this genus: *F. charoides* Chiov., *F. schweinfurthii* Hadidi and *F. migurtinia* Hadidi. *F. schweinfurthii*, the basic taxon of the *F. indica*-complex, seems to have its centre of origin in the Ethiopian highlands. This taxon was described earlier by Schweinfurth (1899) as *F. bruguieri* DC. var. *ehrenbergerii* Schweinf. In some characters it approaches *F. kassasii* Hadidi which is the basic species of the

F. bruguieri-complex, known from the highlands along the Red Sea in S Egypt and N Sudan. This may point to a common origin of the two complexes along the East African highlands. Both complexes comprise species which are widely spread through the Saharo-Sindian desert belt (El Hadidi, 1972).

F. charoides Chiov., which is endemic in the coastal region of Somalia (Migurtinia), represents one of the peculiar extremes of this genus: its leaflets are cylindrical, needle-like and resemble the spiny stipules. However, it shares most of its characters with the species of the *F. arabica*-complex. On the other hand, *F. charoides* approaches *F. thebaica* Boiss. var. *thebaica* in the leaf characters. The latter taxon is the basic one for the *F. thebaica*-complex and is characterized by its cylindrical leaflets which are not, however, spiny. The close resemblance of *F. charoides* with the species of the *F. arabica*- and *F. thebaica*-complexes may, therefore, favour a common origin of these taxa.

F. migurtinia Hadidi, also an endemic species of the coastal region of Somalia (Migurtinia), represents another extreme. Here, the spiny stipules are completely absent and the leaves are simple. It approaches in habit two *Zygophyllum* species which occur in this region, viz. *Z. hildebrandtii* Engl. and *Z. robechii* Engl. These two *Zygophyllum* species have characters in common with *Fagonia* (ovoid, 5-lobed, loculicidal capsule, absence of basal staminal appendages), *Z. robechii* being described as *Fagonia heinii* Schwartz (cf. El Hadidi, 1973: 277). It may be assumed that a certain link exists between *Fagonia* and *Zygophyllum* through these closely allied, simple-leaved species of both genera. The flavonoids of both genera (Saleh & El Hadidi, MS.) seem to indicate a certain relationship between them.

F. latifolia Del., which is endemic in the Egyptian deserts, seems to be the ancestor of a group of *Fagonia* species which are mainly North African. These species which belong to the *F. isotricha*-, *glutinosa*-, and *sinaica*-complexes are characterized by their shorter stipular spines (shorter than the petioles) and predominantly 3-foliate leaves. It has already been shown (El Hadidi, 1974) that the basic species of these three complexes are polymorphic and that they are related to each other by inter-specific taxa. This is in favour of a common ancestor which is believed to be *F. latifolia* Del. The latter species belongs to the *F. isotricha*-complex which also includes the endemic Cape Province species *F. capensis* Hadidi. *F. isotricha* Murbeck may be regarded as the most widespread *Fagonia* species in Africa. It is known from the Sahara, E Africa and the Cape Province. The same is true for *F. sinaica* Boiss. which is not, however, recorded from E Africa but seems to be overlooked. Species of the *F. glutinosa*-complex are only restricted to N Africa. *F. glutinosa* Del. extends eastwards through the Saharo-Sindian desert belt by some infra specific taxa.

Fagonia L. and the monotypic *Seetzenia* R. Br. do not seem to be closely related as may be thought from the way of treating both of them under the subtribe *Fagoniinae* Engler. The two genera differ from each other in the following characters: presence or absence of corolla, nature of the endocarp, existence or non-existence of endosperm. Flavonoids of *Seetzenia* differ from those of *Fagonia* and seem to indicate that *Seetzenia* is more primitive than *Fagonia* (Saleh & El Hadidi, MS.). This may be in favour of treating *Seetzenia* as constituting a distinct subtribe, the *Seetzeniinae* Hadidi.

Zygophyllum L., the largest genus of the family, includes about 80 species, which vary considerably in their characters. This may explain the various treatment of the

genus by different authors. At least five genera were described which match, in a wider sense, with *Zygophyllum* in characters.

Van Huyssteen (1937), in her comprehensive revision of *Zygophyllum* with a special reference to the African species, proposed a system for the classification of this genus. She included the following, previously described genera, viz. *Roepera* A. Juss., *Sarcozygium* Bunge, *Milianthus* Bunge, and *Helimiphyllum* A. Boriss., as sections of *Zygophyllum* L. The genus is subdivided into two subgenera, namely *Agrophyllum* Endlich. and *Zygophyllotypus* v. Huyss., which differ from each other with regard to the nature of the staminal appendages and the type of dehiscence of the capsule.

According to Van Huyssteen (op. c.) 65 *Zygophyllum* species occur in Africa. Recent revisions have confirmed the presence of 20 species in North and East Tropical Africa (Ozenda & Quézel, 1956; El Hadidi, 1975a, b). A similar number is also known from S and SW Africa (Schreiber, 1963; 1966). Most of these species have a limited geographical distribution area and are confined, with the exception of *Z. simplex* L. f., to two main African zones, viz. NE African zone and SW-S African zone. This seems to be related with the developmental history of the genus. The subgenus *Agrophyllum* Endlich., the oldest one and most confined to Africa, was regarded by Engler (1896) to comprise the ancestral taxa of the genus *Zygophyllum*. Among these, some species of the section *Bipartita* v. Huyss., viz. *Z. simplex* L. f. and *Z. decumbens* Delile, were supposed to have given origin to the other taxa of this subgenus which occur in E and S Africa. Both species are mainly N African, although *Z. simplex* is widespread and certainly the most widespread species of the genus. It is a polymorphic species which is known all over the African continent and which continues eastwards through Tropical Arabia to the Indian subcontinent. Van Huyssteen (op. c.) believed that this species acts as a link between the North and South African species of the section *Bipartita*.

Z. album L. f. is another polymorphic N African species which seems to be the ancestor of the taxa of the section *Mediterranea* Engl. which are widely spread through the Saharo-Sindian desert belt.

Zygophyllotypus v. Huyss., the more advanced and rather widely spread subgenus, seems to be heterogeneous. Its geographical distribution is disjunctive. Engler (1896) suggested a N African origin of the ancestors of this subgenus. In one direction, some of the ancestral forms gave origin to the species of the Asiatic sections *Fabago* Endlich., *Sarcozygium* (Bunge) Engler, and *Halimiphyllum* Engler. In two other directions, other ancestors gave origin to the species of the section *Melocarpa* Engler and to the species belonging to the W and S African sections *Paradoxa* v. Huyss., *Grandifolia* Engler, and *Capensia* Engler respectively.

The present author believes that at least the subgenus *Zygophyllotypus* is heterogeneous with regard to its origin. Besides the typical species of the section *Fabago* (the type of *Zygophyllum* is *Z. fabago* L.), it also includes species (sections: *Sarcozygium*, *Halimiphyllum*, *Roepera*, *Milianthus*, etc.) which are regarded by several authors to constitute distinct genera.

A future treatment of this genus should primarily discuss the interrelationships between the different taxa within their areas of distribution. This would lead to a better understanding and a more natural delimitation of the genus.

Among the taxa which are worth considering on a generic level are the species belonging to the section *Melocarpa* Engler. They differ from all the other species of *Zygophyllum* by the absence of basal staminal appendages. The capsule resembles that of *Seetzenia*, while the leaves are similar to those of certain *Fagonia* species, such as *F. socotrana* (Balf. f.) Schweinf. and *F. migurtinia* Hadidi, which are only known from areas where species of *Melocarpa* occur. It was mentioned earlier, that species of *Melocarpa* may constitute a link between *Fagonia* and *Zygophyllum*.

The monotypic *Augea capensis* Thunb. from the dry regions of S Africa is an annual, fleshy herb which approaches the *Zygophyllum* species in most of its characters. This taxon was treated by Engler (1931), on the basis of its 10-locular ovary, under the monogeneric tribe *Augeae* Engl. of the subfamily *Augeoideae* Engl. This character is, however, rather insufficient as the ground of treating *Augea* as a distinct tribe and even subfamily. Engler (op. c.) included it, however, in one and the same subtribe, *Tribulinae* Engl., genera with a 5-locular ovary (*Tribulus*, *Kelleronia*) and others with a 10-12-locular ovary (*Kallstroemia*).

Thus *Augea* Thunb. being closely allied to *Zygophyllum* ought to be classified among the other genera of the subtribe *Zygophyllinae* Engl.

4. The tribe *Tribuleae* Engler of the subfamily *Zygophylloideae* Engler comprises five genera which show clear natural affinities. Of these: *Neoluederitzia* Schinz, *Sisyndite* E. Mey. ex Sond. & Harv., and *Kelleronia* Schinz are only known from Africa, while *Tribulus* L. is rather widely spread. *Kallstroemia* Scop. is Australian.

Tribuleae differs from *Zygophylleae* in several respects. In *Tribuleae*, the leaves are predominantly pinnate and are alternate in three genera (*Neoluederitzia*, *Sisyndite* and *Kelleronia*). The fruit splits into cocci (capsule in *Zygophylleae*) and the seeds are without endosperm (endospermic in *Zygophylleae*). In addition, phytochemical studies (Saleh & El Hadidi, MS.) indicate a slight divergence in the flavonoid pattern from that of the *Zygophyllum* species.

These differences are in favour of treating *Tribuleae* Engl. as a distinct family, *Tribulaceae* Hadidi.

5. *Zygophyllaceae* (s. str.) comprises accordingly a group of naturally allied taxa which seem to have their centre of origin in the N African Sahara and the E African highlands. The arid zones of SW and S Africa constitute another centre of origin for the taxa which are restricted to these regions.

Thus, *Zygophyllaceae* (s. str.) comprises shrubby plants (rarely herbs) with opposite, stipulate, (simple or) usually pinnate leaves. The flowers are 4-5-merous, petals are rarely absent; stamens 1-2 times as many as the petals, filaments nude or appendaged at the base; ovary 4-5- rarely 2-12-locular, often angular or winged; fruit a loculicidal or septicidal capsule. Seeds with endosperm. The family includes primarily the S African *Augea* Thunb. and the other genera of *Zygophylleae* Engler which are known from the Old World.

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