

The morphology and systematic position of the Didiereaceae of Madagascar

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ABSTRACT

The Didiereaceae, endemic to the arid south-west of Madagascar is one of the most remarkable plant families in the world. Four genera and 11 species are known, of which 3 have been described by the author: *Decaryia* (1 species), *Alluaudiopsis* (2 spp.), *Alluaudia* (6 spp.) and *Didierea* (2 spp.). The species show different growth forms, but their shoot-stem-systems are basically similar; they are all spiny, semi-succulent deciduous shrubs or trees, with a stem (shoot) system differentiated into long-shoots and short-shoots (brachyblasts). The long shoots bear normal leaflets, which soon fall off. In their axils, brachyblasts develop proleptically, which produce two types of leaves (1) thorns which develop proleptically in different numbers (1 in *Alluaudia*, 2 in *Alluaudiopsis marnieriana* and several *Didierea*); (2) leaves which are green, deciduous assimilation organs (2 per brachyblast in *Alluaudia*, several in *Didierea*).

The stem organization is comparable to that of the Cactaceae of the New World. The brachyblasts of the Didiereaceae are homologous to the areoles of the Cactaceae, most obviously to those of the primitive members, the Pereskioideae. The affinities between the two families can be demonstrated by means of grafting. It is possible to graft *Didierea*s onto Pereskioideae and vice versa.

The flower structure of Didiereaceae is very uniform. Flowers are unisexual and dioecious and show affinities to those of the Portulacaceae. The development of the gynoecium, the ovule and the female gametophyte as well as the presence of betalains in the flowers indicate that the Didiereaceae do not belong to the Sapindales as was sometimes assumed, but to the Centrospermae. They should be placed between Portulacaceae and Cactaceae. The ancestors of the Didiereaceae are not known.

RÉSUMÉ

LA MORPHOLOGIE ET LA POSITION SYSTÉMATIQUE DES DIDIÉRÉACÉES DE MADAGASCAR

Les Didiéréacées, endémiques dans le sud-ouest de Madagascar, sont une des familles de plantes les plus remarquables du monde. Quatre genres et onze espèces sont connus, dont trois ont été décrites par l'auteur: *Decaryia* (1 espèce), *Alluaudiopsis* (2 spp.), *Alluaudia* (6 spp.) et *Didierea* (2 spp.). Les espèces montrent des formes biologiques différentes mais leurs systèmes de ramification sont fondamentalement similaires: ce sont tous des arbres ou arbustes décidus, épineux, semi-succulents, avec un système de ramification différencié en rameaux longs et rameaux courts (brachyblastes). Les rameaux longs portent de petites feuilles normales qui tombent très vite. A leur aisselle, des brachyblastes se développent proleptiquement et produisent deux types de feuilles (1) des épines qui se développent proleptiquement en nombres divers (1 chez *Alluaudia*, 2 chez *Alluaudiopsis marnieriana* et plusieurs chez *Didierea*); (2) des feuilles qui sont des organes d'assimilation verts et caducs (2 par brachyblaste chez *Alluaudia* et plusieurs chez *Didierea*).

L'organisation de la tige est comparable à celle des Cactacées du Nouveau Monde. Les brachyblastes des Didiéréacées sont homologues aux aréoles des Cactacées, de manière plus évidente à celles de ses membres primitifs, les Pereskioïdées. Les affinités entre les deux familles peuvent être démontrées au moyen du greffage. Il est possible de greffer des *Didierea* sur des Pereskioïdées et vice-versa.

La structure florale des Didiéréacées est très uniforme. Les fleurs sont unisexuées et dioïques et montrent des affinités avec celles des Portulacacées. Le développement du gynécée, de l'ovule et du gamétophyte femelle aussi bien que la présence de bétalaines dans les fleurs indiquent que les Didiéréacées n'appartiennent pas aux Sapindales comme cela fut quelquefois supposé, mais aux Centrospermae. Elles devraient être placées entre les Portulacacées et les Cactacées. Les ancêtres des Didiéréacées ne sont pas connus.

One of the most remarkable groups of flowering plants are the Madagascan Didiereaceae, one of the seven endemic families of the 'Grand Ile.' They are not only characterized by an unusual morphology, but their precise systematic position has not been finally established. As regards geographical distribution, the members of this small family are restricted to a limited area, viz. the coastal region of the extreme dry south-west of the Island (Fig. 1). We know nothing of their ancestry or affinities, neither in Madagascar itself nor in neighbouring Africa and other parts of the world. In the extreme

south-west, the Didiereaceae are associated with arborescent leafless, more or less succulent Euphorbias such as *Euphorbia enterophora*, *E. stenoclada*, *E. leucadendron*, *E. plagiantha* and others. Together they form a deciduous plant community, known as *Euphorbia-Didiereaceae* Bush (Fig. 2). Four genera of the Didiereaceae with 11 species are presently recognized, three of which have been described by the author. The genera, mostly named after French generals, are the following: *Decaryia* (monotypic: *D. madagascariensis*), *Alluaudiopsis* (two species: *A. fiherenensis* and *A. marnieriana*), *Alluaudia* (six species: *A. procera*, *A. montagnacii*, *A. ascendens*, *A. comosa*, *A. dumosa* and *A. humbertii*) and *Didierea* itself (two species: *D. madagascariensis* and *D. trollii*). All are woody succulents, shrubs or

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FIG. 1.—Distribution of *Euphorbia* - Didiereaceae Bush (hatched) in Madagascar.

trees, up to 15 m high, but the arborescent species pass through a shrubby juvenile stage. The best example showing the different stages is *D. trollii*. Early on the plant forms a 'thicket' of creeping, plagiotropic shoots; with increasing age, one (or more) shoot(s) start to grow upright, forming trunks, which later branch, forming a crown, while the basal branches die off (Fig. 3). Most of the Didiereaceae are of arborescent growth; only *Alluaudiopsis* retains a shrubby growth-form.

All Didiereaceae are spiny plants and show a sharp differentiation between long-shoots and short-shoots (brachyblasts). In other words, the Didiereaceae have the same organization as the primitive Cacti, *Pereskia* and *Peresklopsis*: the short-shoots have an extremely short axis which, in most species, is buried into the cortex; only in *Didierea* is the growing point of the short-shoots elevated on a more or less elongated podarium (Fig. 4), as for example in genus *Leuchtenbergia* of the Cactaceae. The brachyblasts of the Didiereaceae are homologous to the areoles of the Cacti; they develop

proleptically in the axils of normal, but soon deciduous long-shoot leaves; they produce, also proleptically, thorns, which correspond to those of the Cacti (representing transformed leaves); in each growing period the areoles produce leaves as assimilation organs, as can be observed sometimes in the areoles of the primitive Cacti; also, the inflorescences descend from the areoles and an areole can be transformed into a long-shoot. It is surprising that French botanists such as Choux, Perrier de la Bathie and Humbert did not recognize this organization.

The thorns appear in different numbers and positions in the different genera: in *Decaryia* and *Alluaudiopsis marnieriana* there are two thorns in a lateral position occurring as stipules (the same structure exists in *Pereskia aculeata*); in *Alluaudia* (adult plants) only one brachyblast-thorn is formed; it stands in a median position above the areole-growing point; in *Didierea* the thorns are arranged in whorls of mostly four, and the median-basal-one is often elongated.

Differences also exist in the number of the brachyblast-leaves in the different genera. *Alluaudia dumosa* is mostly leafless throughout the year; in the other species the leaves are produced mostly in pairs, and the shortly petioled lamina takes a vertical position, so that a long-shoot, fully covered with leaves, looks very strange (Fig. 5); in *Didierea*, the small and narrow-lanceolate brachyblast-leaves appear in great numbers in the form of rosettes.



FIG. 2.—*Euphorbia* - Didiereaceae Bush with flowering plants of *Alluaudia procera* near Ampanihy, S. W. Madagascar.



FIG. 3.—*Didierea trollii* with several trunks and dying basal branches.

These brachyblast-leaves are the true assimilatory organs; they persist during the rainy season and die off at the beginning of the dry period; but the same areole is able to form new leaves in the next growing season.

It is clear that the primitive-foliaged Cacti and the Didiereaceae show a striking convergence in the organization of their shoots; the inflorescence and flower-structure, however, is quite different in the two families. This may be the reason that the Didiereaceae were not considered as belonging to the Centrospermales, but rather to the Sapindales.

The flowers of the Didiereaceae seldom appear singly: they are arranged in more or less richly branched inflorescences; they appear instead of leaves in a lateral position along the long-shoots, i.e. an areole growing-point can become fertile and produce an inflorescence instead of leaves. In principle, the inflorescences of all species are monotelous synflorescences (in the sense of Troll); the abortion of the terminal flowers of the partial inflorescences leads to so called 'Rumpf-synflorescences' (Troll). *Didierea*, *Alluaudiopsis marnieriana* (Fig. 6) and *Alluaudia comosa* have extremely reduced inflorescences: only the terminal flower of a dichasium is developed, so that a whole paracladium simulates a single flower. We call these reduced partial inflorescences 'monades'; in *Didierea* many of them appear in one areole at the same time, so that a branch, at flowering-time, is profusely covered with opened flowers (Fig. 7). The length of the synflorescence axis is variable: in most of the *Alluaudia* species it is well developed and can reach a length up to 15 cm; in *Alluaudia comosa*, *Alluaudiopsis marnieriana* and *Didierea* the axis is so short that the flower-buds are hidden in the groove of the areole. The flowers of all Didiereaceae are dioecious and haplochlamydic. The four tepals are surrounded at the base by two often keeled bracts, which form a kind of involucre. In the female

flowers they enlarge during embryogenesis and serve to distribute the small nut-fruits by wind.

Mostly the Didiereaceae is considered as belonging to the Sapindales. The male flowers have a variable number (6–10) of stamens; the filaments are united at their base to a ring, which produces secretory tissue on its inner side; the pistil is

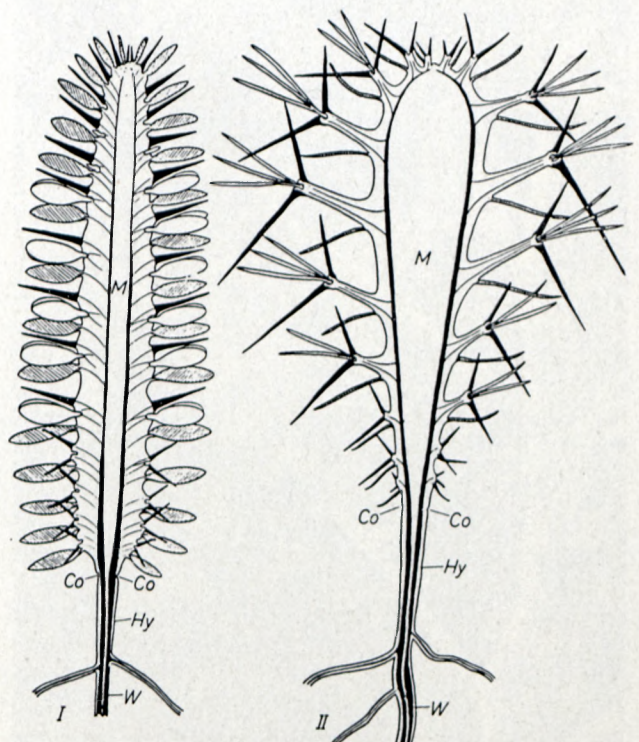


FIG. 4.—Growth form of young plants of *Alluaudia procera* (I) and *Didierea madagascariensis* (II). The leaves of the short-shoots (brachyblasts) are unhatched and those of the long-shoots, hatched. W, main root; Hy, hypocotyl; Co, cotyledons; M, pith.

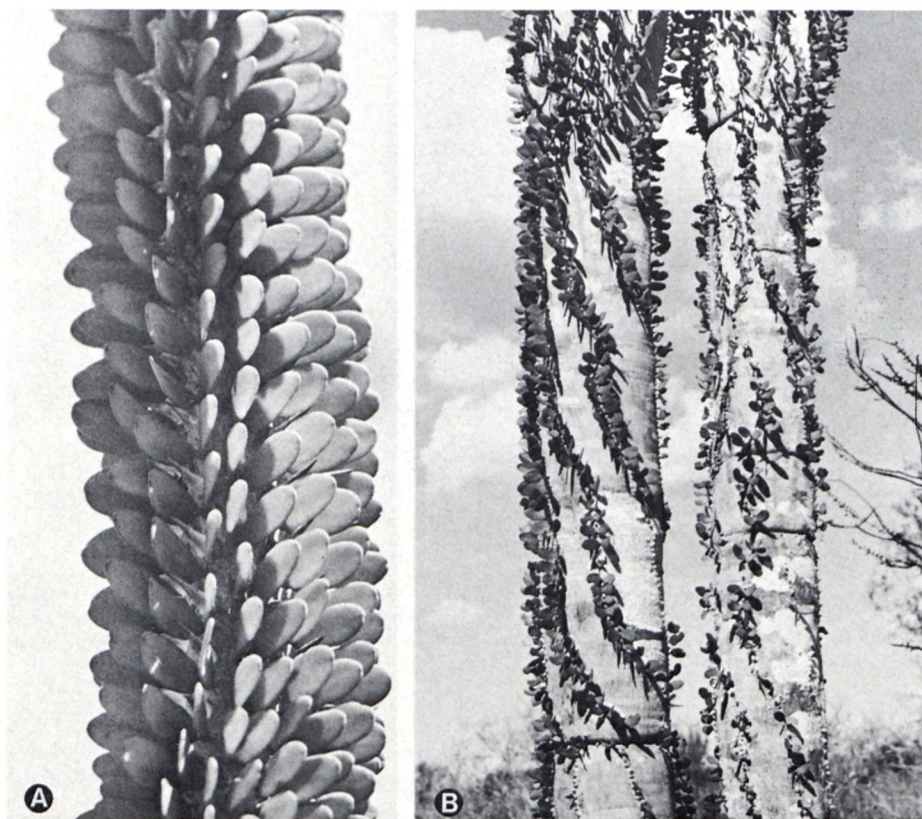


FIG. 5.—*Alluaudia procera*. Stems (a) and long-shoot (b) with the leaves of the brachyblasts. Each growing point produces two vertical leaves.

atrophied and sterile; in the female flowers the stamens are reduced to staminodes; the gynoeceum is trimerous, but only the medium-adaxial carpel is fertile and bears one hemicyampylotropous ovule.



FIG. 6.—*Alluaudiopsis marnieriana*. Branches with male (a) and female (b) flowers.

This is bitegmic, and between both integuments, a small split, a special peculiarity of the ovules of the Centrospermae, can be observed. Embryogenesis is of the *Chenopodium*-type; the embryo is campylotropous and embedded in a thin tissue of perisperm.

The systematic position of the Didiereaceae was, for a long time, unclear, but our morphological, anatomical, embryological and biochemical investigations have shown that the Didiereaceae belong, without doubt, to the Centrospermae; the discovery of *Alluaudiopsis marnieriana* by the author provided important proof of this hypothesis. It is the only member of the Didiereaceae with carmine red tepals; in all the other species only the filaments and the well-developed stigmas are red-carmine in colour, but this red colour, as Reznik confirmed, is not caused by normal anthocyanins, but by red betaine, a plant colour-substance, which has so far only been found in families of the Centrospermae. This character is one of the main reasons for placing the Didiereaceae in the Centrospermae. The Didiereaceae is a distinct family within the tribe Centrospermae and has relationships with the Portulacaceae and Basellaceae as well as the Cactaceae and Nyctaginaceae. Therefore, we can consider the spiny Didiereaceae as the Cacti of the Old World; both groups have the same organization of their vegetative organs, i.e. differentiation into brachyblasts (= areoles) and long-shoots, and also show reduction of the long-shoot-leaves and the formation of leaf-thorns. Moreover, it is possible to graft Didiereaceae onto Cacti and vice versa a further proof, in our opinion, of the relationship of these two plant-groups.

Unfortunately, we know nothing of the phylogeny of the Didiereaceae. We have not yet found

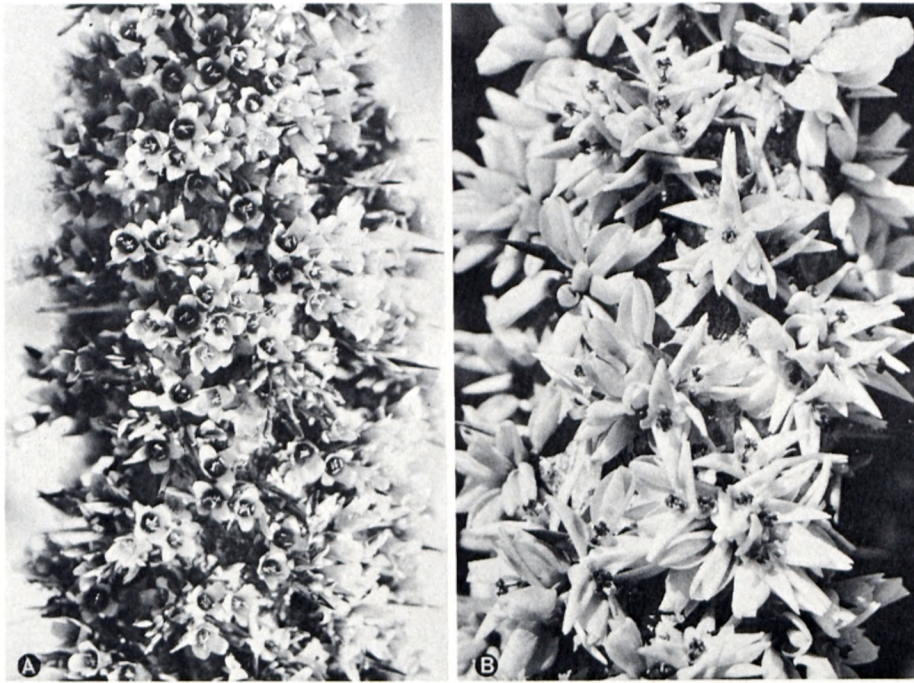


FIG. 7.—*Didierea madagascariensis*. Long-shoot with male flowers (a) and female flowers (b).

plants either in Madagascar itself or in neighbouring Africa and Asia, in which the ancestry of the Didiereaceae could be traced. The family has developed after the isolation of the island from the continent; it is possible that, before the massive

destruction of primary vegetation in Madagascar, plants existed which could be regarded as ancestors of this interesting plant group. Unfortunately, no fossils have been found to help elucidate the phylogeny of the Didiereaceae.

