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## Some trends in the evolution of the Mesembryanthemaceae

H.-D. IHLENFELDT

### SUMMARY

The apparently eminent rôle of neotenic phenomena, in a very broad sense, in the evolution of this family is discussed in some detail and illustrated by a number of examples.

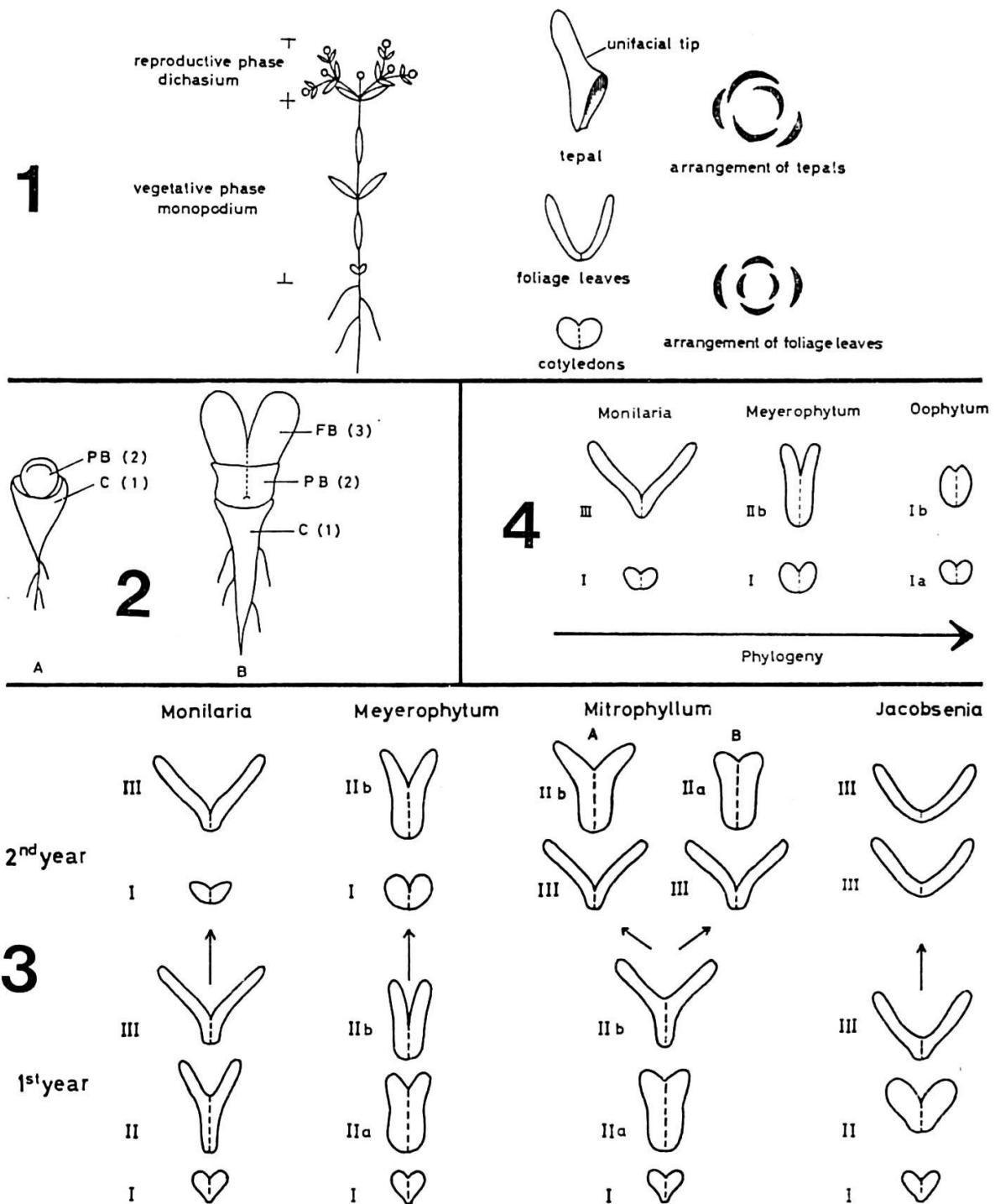
### RÉSUMÉ

Le rôle important que jouent les phénomènes néoténiques au sein de cette famille est discuté.

The present system of the family *Mesembryanthemaceae*, outlined by Schwantes in 1947 and amended by several authors (Ihlenfeldt & Straka, 1962; Ihlenfeldt & al., 1960, 1962) is still far from reflecting evolution in this family. This is due to the lack of information on the mechanisms of evolution and on the evolutionary trends in this family.

More than 2000 described species of this family—far too many as we think—present a broad variety of different habits: upright growing little shrubs with succulent leaves, annuals spreading on the ground, and dwarf forms that produce but one pair of highly succulent leaves every year. In contrast to the different habits, the basic morphological structure of this family is rather uniform (Fig. 1): the vegetative phase of plants belonging to this family, consists of a monopodial system of stems, starting with a pair of short and almost entirely connate cotyledons, and going on with long foliage leaves only connate at the base in decussate arrangement. The reproductive phase consists of a dichasium: the flowers are normally composed of five tepals in helical arrangement that represent a third basic type of leaves with a large unifacial portion at the tip and a broad sheath, of an androecium whose five primordia undergo a centrifugal dédoublement thus producing numerous fertile stamens and numerous sterile petal-like staminodes, and of five carpels alternating with the primordia of the stamens. The carpels are more or less sunk into a cup-like structure (receptacle) which appears to be a derivative of the stem.

The main evolutionary trends and progressions in this family have been reviewed by Ihlenfeldt (1960). Although recent studies in some groups of this family make some



amendments necessary, in this paper I only intend to direct attention to a number of phenomena or processes that obviously play an eminent rôle in the evolution of this family. These phenomena can be called neotenic phenomena in a very broad sense. The theoretical background has already been discussed earlier (Ihlenfeldt, 1971). The following examples, which will be on the genus level (another example on the species level is given in Hartmann, 1975; see below pp. 255-261), are bound to demonstrate how these phenomena work and how, taken into consideration, they help to reconstruct the phylogeny of this family.

The first example is a case of neoteny in the strict sense or, in terms of ontogeny, a case of terminal abbreviation of the vegetative phase. Schwantes (1957) was the first to guess that neotenic processes might be involved in the evolution of certain groups of the *Mesembryanthemaceae*, when speculating that *Lithops* N. E. Br. might be "juvenile stages (of *Schwantesia* Dinter) capable of flowering" (p. 240). The same relations obviously exist between the two genera *Maughaniella* L. Bolus and *Diplosoma* Schwantes, both members of the subtribe *Mitrophyllinae* of the subfamily *Ruschioideae*. This interesting subtribe, as it is delimitated up to the present, is characterized by the heterophyllous condition of leaf sequence.

The monotypic genus *Maughaniella* forms very tiny, upright growing plants. Two pairs of leaves appear every rainy season: the first one being very short, almost entirely laterally connate and only shortlived, the second one being much longer and connate for about half the length (Plate I, A & B). The monotypic genus *Diplosoma* forms tiny plants too; the first pair of leaves of the rainy season is very short, almost entirely connate and remains hidden in the remnants of the leaves of the last year, the second pair is long and asymmetrically connate at the base and spreading on the ground (Plate I, C). But the seedling of *Diplosoma* produces leaves that stand upright and are very similar to those of *Maughaniella* (Fig. 2; Plate I, E). The first pair of spreading leaves appears in the second year of life, the asymmetrically connate spreading type for the first time in the year following the first formation of a flower.

The morphological diagram (Fig. 1) may be interpreted as a basic morphological program with, for instance, a definite sequence of leaves: cotyledons (very short and almost entirely connate); foliage leaves (long, only connate at the base); tepals (small, long unifacial tip and broad sheath). From frequent aberrations that occur under conditions of cultivation, one can conclude that it is possible to imagine this program as being continuously proceeding, that means containing the information to induce any conceivable intermediate form between those three basic types of leaves

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Fig. 1. — Diagram showing the basic morphological organization of the *Mesembryanthemaceae*.

Fig. 2. — Development of the seedling in *Diplosoma*. A: A very early stage showing the pair of cotyledons (C) and the first pair of foliage leaves (PB) which are very short and laterally connate for all their length.—B: A later stage, the first pair of foliage leaves having already withered and the second pair of foliage leaves (the last pair of the first year of life) being fully developed; it consists of relatively long leaves connate for about half their length. Compare also Plate I, E.

Fig. 3. — Diagram of leaf sequences in *Monilaria*, *Meyerophytum*, *Mitrophyllum* and *Jacobsenia*. The arrows mark the resting period. For detailed information compare text on pp. 252 f.

Fig. 4. — Diagram of leaf sequences in *Monilaria*, *Meyerophytum* and *Oophytum*, demonstrating the increasing terminal abbreviation of the leaf sequence.

that have been pictured in the diagram. The type that definitely appears, depends on the point of time of its induction.

A more complicated example is represented by the genera *Monilaria* (Schwantes) Schwantes, *Meyerophytum* Schwantes and *Mitrophyllum* Schwantes, members of the *Mitrophyllinae* as well.

The species of the genus *Monilaria* form little shrublets up to 20 cm high which have thickened, relatively short ("moniliform", hence the name of the genus) internodes. The first pair of leaves to become visible from outside in the beginning of the rainy season consists of very short, nearly hemispheric leaves that are laterally connate for nearly all their length. This pair of leaves is rather shortlived, and it is soon followed by another pair of leaves that are long and connate only at the very base (Fig. 3).

In *Meyerophytum*, little shrublets as well, the first pair of leaves to appear in the beginning of the rainy season is very similar to that of *Monilaria*: short leaves connate for nearly all their length. The second pair consists of relatively long leaves, but in contrast to *Monilaria* these leaves are connate for a considerable part of their length, at least for one third (Fig. 3).

The species of *Mitrophyllum* form shrublets up to 1 m high. The first pair of leaves to appear in the beginning of the rainy season, consists of long leaves only connate at the very base, thus resembling the second pair of *Monilaria*. Later on, a second pair is formed whose leaves are relatively long and connate at least for half their length, thus resembling the second pair in *Meyerophytum* (Fig. 3).

Which are the phylogenetic relations among these three genera? The clue is given by the genus *Jacobsenia* L. Bolus, hitherto not a member of the *Mitrophyllinae*. But already in 1957 Schwantes filed *Jacobsenia* very close to *Mitrophyllum*, obviously because this genus is very similar to *Mitrophyllum* in its habit. But *Jacobsenia* lacks the typical characteristic of the *Mitrophyllinae*, namely the heterophyllous condition of leaf sequence. *Jacobsenia* normally develops but two pairs of leaves every year, thus strikingly resembling the *Mitrophyllinae*, but the two leaf pairs are equal in size and shape; they are long and only connate at the very base, thus resembling the second pair of *Monilaria* and the first pair of *Mitrophyllum* (Fig. 3).

Studying the development of the seedlings of these four genera, the relations among these four genera become clear. During the first year of life *Jacobsenia* normally produces—as the other three genera do—three pairs of leaves, which are different in size and shape: the first pair (the cotyledons) very short and laterally almost entirely connate, a third pair long and connate only at the very base (thus representing the normal foliage type of the *Mesembryanthemaceae*) and a second pair of an intermediate type which is relatively long but connate for a considerable part of its length. During the first year of life the seedlings of *Monilaria* produce three pairs of leaves whose morphological types are very similar to those of *Jacobsenia*. But whereas in the next rainy season *Jacobsenia* goes on producing leaves of the third type (foliage leaf type), in *Monilaria* the program that induces the leaf types, is switched back at the end of the first vegetation period and starts in the second year of life again from the beginning. The first pair of leaves to appear in the next rainy season again very much resembles the morphological type of the cotyledons, but the second pair already represents the type of the third pair of leaves of the first year (foliage leaf

type). That means: starting with the second year of life, in *Monilaria* there is a permanent ontogenetic abbreviation in the middle of the original leaf sequence compared with the first year of life.

In *Meyerophytum* things are very similar. In the end of the rainy season the morphological program is switched back as in *Monilaria*. The only difference is, that during the first and the following years the program is a little bit slow so that the third morphological type of leaves (foliage leaf) is never reached. Compared with the leaf sequence of *Jacobsenia* in the first year of life, there is in *Meyerophytum* a permanent terminal abbreviation of the leaf sequence (Fig. 3).

In *Mitrophyllum* too the program is slow during the first year of life, the third type (foliage leaf) is formed only in the beginning of the second year. The switching back of the program takes place in the middle of the rainy season, and so it does in the following years (Fig. 3). Moreover it is not switched back totally, but it always starts with the intermediate type (II in Fig. 3). In terms of ontogeny there is a permanent abbreviation in the beginning of the leaf sequence (basal abbreviation).

Thus we can conclude: the three genera *Monilaria*, *Meyerophytum* and *Mitrophyllum* evolved from *Jacobsenia* on different lines by two evolutionary processes: repetition of the leaf sequence of the first year of life (the switching back taking place at different points of time) and elimination of one of the possible three leaf types of the seedling.

Comparing the leaf sequence of *Monilaria* with that of *Meyerophytum* where the normal foliage type is never reached, neither in the first year nor in the following years, one can ask whether there might exist a genus, in which the morphological program is even slower, that means that only leaves of the cotyledon-like type are produced (Fig. 4). There are certain conditions which this genus X ought to fulfil: the genus should develop two pairs of leaves every year, which could possibly be a little bit heterophyllous, should have a certain type of capsule, certain idioblasts in the epidermis and it should occur in the area in which the *Mitrophyllinae* have their habitat. This genus does exist, its name is *Oophytum* N. E. Brown, hitherto classified together with the well-known genus *Conophytum* N. E. Brown under the *Conophytinae* (Plate I, E). *Conophytum* produces only one pair of leaves every year except when developing a flower, then there is an additional pair of bracts. In *Oophytum* the second pair of leaves is formed independently from whether a flower is formed or not, thus the second pair of leaves cannot be interpreted as bracts. In our opinion *Oophytum* is a highly evolved—that means highly reduced or neotenic—member of the *Mitrophyllinae*.

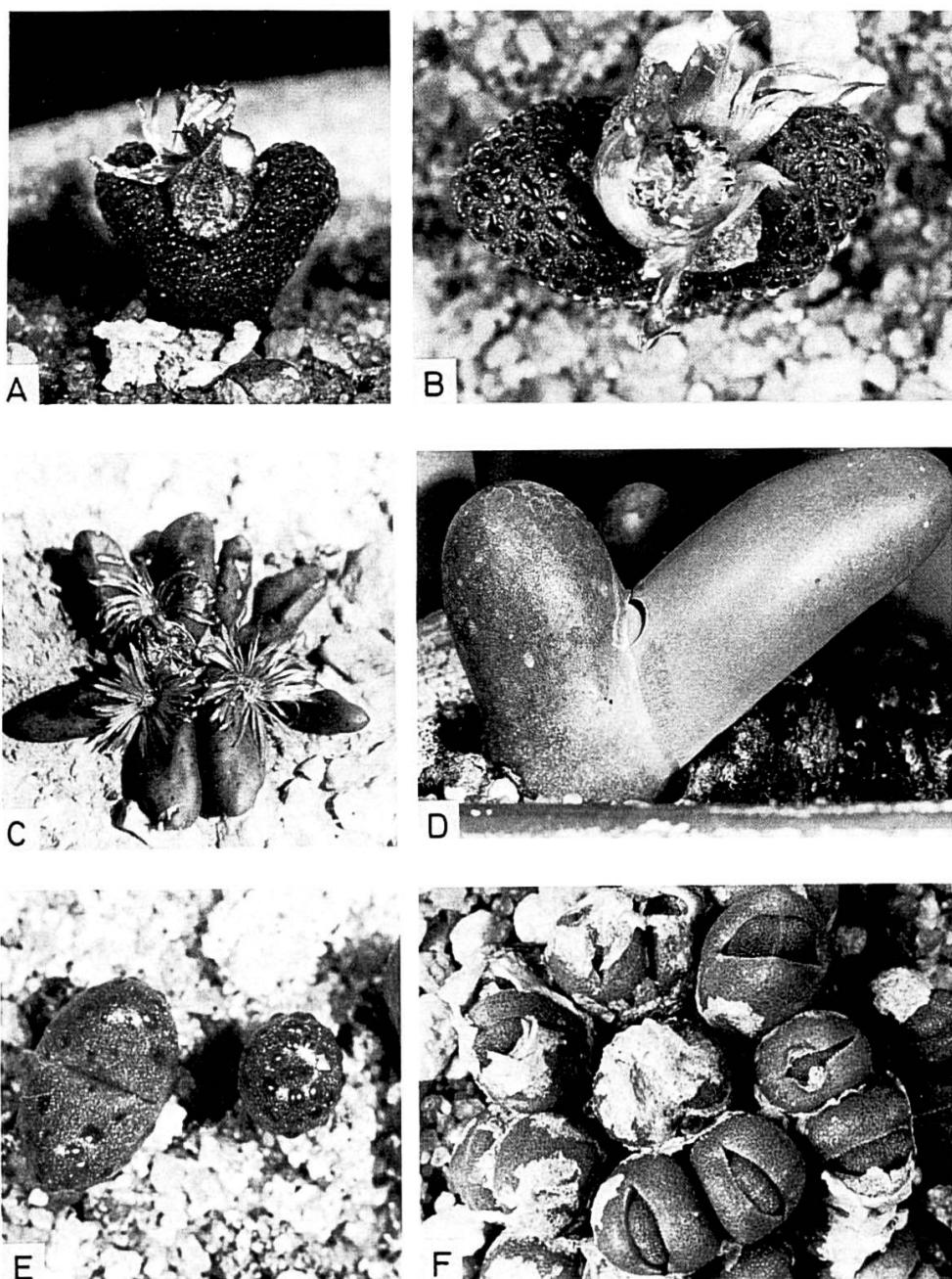
Until now ontogenetic abbreviations and repetitions of ontogenetic programs have been discussed. The being slow of the program that induces the type of leaves in *Meyerophytum*, *Mitrophyllum* and *Oophytum* leads to the third type of ontogenetic processes: alterations in time correlation of morphological subprograms. A considerable number of cases, in which this most interesting neotenic phenomenon is involved, have been studied during the last years, only one very extreme case will be demonstrated here. It has already been mentioned that beside the cotyledon type and the foliage type, there exists a third basic leaf type, the tepal type with a broad sheath and a unifacial tip. It has already been mentioned, too, that the appearance of this type normally is combined with a change of leaf arrangement. In the subfamily

*Mesembryanthemoideae* which, as we now believe, has very close relationships with the *Mitrophyllinae*, there is a very odd and puzzling genus: *Dactylopsis* N. E. Brown. Plants of this genus have "cylindrical" (more exactly: unifacial) leaves the arrangement of which is alternate (Plate I, D). These unifacial foliage leaves in reality are huge tepals functioning as foliage leaves; or in terms of ontogeny: the subprogram that induces the normal form of tepals is early and superposes the program that induces the normal foliage leaves of the vegetative phase thus creating a "hybrid" form between foliage leaf and tepal.

Wherever we study the morphology of the *Mesembryanthemaceae* more intensively, we find neotenic processes as described above at work. We have the impression that these processes are among the most important mechanisms of evolution in this family, if they are not even the most important ones.

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A, B: flowering specimens of *Maughaniella luckhoffii* (L. Bolus) L. Bolus. The first pair of leaves of the season has already withered. (A, ca. 0.75 x nat. size; B, ca. 1.5 x nat. size.)

C, *Diplosoma retroversum* (Kensit) Schwantes. In the centre of the plant there is an old capsule formed in the last year. This specimen has produced four stems, each of them with a pair of long leaves (the second pair of the season), asymmetrically connate at the base and spreading on the ground. (Ca. 0.4 x nat. size.)

D, *Dactylopsis digitata* (Ait.) N. E. Brown. The plant shows two foliage leaves in alternate arrangement and a third leaf just emerging from the sheath of the second leaf. Note the huge unifacial portion of the leaves. (Ca. 0.5 x nat. size.)

E, seedlings of *Diplosoma retroversum*. The seedling on the right hand side shows the first pair of foliage leaves (the cotyledons have already withered), the seedling on the left hand side the second pair of foliage leaves. Compare also Fig. 2 of the text. Ca. 2 x nat. size.

F, *Oophytum nanum* (Schltr.) L. Bolus. An old specimen in the beginning of the rainy season. The first pairs of leaves are fully developed, the second pairs are just emerging from the central slit of the first pairs. (Ca. 0.5 x nat. size.)