

THE VASCULAR PATTERN IN THE FLOWER OF SOME MESEMBRYANTHEMACEAE: APTENIA CORDIFOLIA AND DOROTHEANTHUS BELLIDIFORMIS

The effect of an ontogenetical shifting on the vascular pattern and vascular conservatism.

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SUMMARY

1. The vascular pattern in the flower at various stages of maturity of *Aptenia cordifolia* and *Dorotheanthus bellidiformis* is examined.
2. The vascular pattern of *Dorotheanthus* has been compared with that of *Aptenia*: typologically, *Dorotheanthus* is derived from *Aptenia*.
3. The vascular pattern of *Aptenia* has been compared with the observations of Ihlenfeldt: the differences are probably due to the use of different methods.
4. The vascular pattern in the 'ovary wall' of *Aptenia* has been compared with that in the outer floral whorls of *Melandrium rubrum* (*Caryophyllaceae*): it is necessary to postpone the decision as to which type of inferior ovary is present in *Aptenia* and *Dorotheanthus* until more evidence is available.

1. INTRODUCTION

The *Mesembryanthemaceae* (order *Centrospermae*) are indigenous to South Africa and show more or less succulence. The flowers are characterized by (Ihlenfeldt, Schwantes & Straka, 1962): 1) a calyx with 4—6 sepals, mostly of unequal size; 2) several whorls of petaloid staminodes and stamens; 3) a plurilocular, semi-inferior to inferior, syncarpous ovary, compounded of 3—23 carpels; 4) mostly many ovules, attached to the placenta by a very long funicle; and 5) characteristic loculicide, hygrochastic capsules.

The sub-families of the *Mesembryanthemaceae* used to be classified in the family *Aizoaceae* (= *Ficoidaceae*) (e.g. Eckardt, 1964). However, according to Ihlenfeldt & Straka (1961), they have to be treated as a separate family.

The *Mesembryanthemaceae* can be divided into two groups according to the placentation, and into four subfamilies, as follows:

group A: axile placentation.

1. *Mesembryanthemoideae* sensu Ihl., Schw. et Str. (syn. with *Aptenioideae* Schwant.).
2. *Hymenogynioideae* Schwant.
3. *Caryotophoroideae* Ihl., Schw. et Str.

group B: basal to pseudo-parietal placentation.

4. *Ruschioideae* Schwant.

The members of group A are supposed to be more primitive than those of group B. Very young stages of both types are identical, and have axile placentation (Ihlenfeldt, 1961). In the genera of the *Ruschioideae* the placentation shifts ontogenetically from axile to basal or parietal (already noted by Huber, 1924). This shifting is the result of changes in relative growth rates in the ovary. These changes in relative growth rates have been known for a very long time, and Buxbaum (1951) illustrated them in the *Mesembryanthemaceae* (his fig. 27). This means that, on the basis of the carpel concept, it is incorrect to use the term parietal to describe placentation in the *Ruschioideae*. It should be interpreted as being axile, but is still called pseudo-parietal.

In a study on the *Mesembryanthemaceae*, Ihlenfeldt (1961) made a comparison between the vascular patterns in ovaries with diverse types of placentation. Although in his study some very complicated vascular patterns (e.g. *Dorotheanthus*) were not completely elucidated, Ihlenfeldt concluded that the various vascular patterns can be reduced to a common groundplan; and that, with regard to the vascular pattern, the subfamily *Ruschioideae* should be considered to be more derived than the subfamily *Mesembryanthemoideae*.

On account of the foregoing it was decided to examine the effect of ontogenetical shifting on vascularisation. For that purpose the vascular pattern in a flower with pseudo-parietal placentation will be compared with the vascular pattern in a flower with axile placentation. As an example of the latter the flower of *Aptenia cordifolia* (L.f.) Schwant. (subfamily *Mesembryanthemoideae*) will be examined. Preparatory studies demonstrated, that the vascular pattern of *Dorotheanthus* is much more complicated than appears from the study of Ihlenfeldt (1961). So as an example of the group with pseudo-parietal placentation the flower of *Dorotheanthus bellidiformis* (Burm.f.) N. E. Br. (subfamily *Ruschioideae*) will be examined.

2. MATERIALS AND METHODS

From plants, cultivated in Hortus de Wolf, Haren (Gr.), flowers at various stages of maturity (buds, flowers, and fruits) were collected, and preserved in ethyl-alcohol 70% or FPA 70%. Examination was carried out on complete flowers and on sections of flowers.

2.1. Complete flowers.

1. Preserved specimens were bleached with NaOH and the lignified elements in the vascular bundles stained with basic fuchsin (Fuchs, 1963).

2. Preserved specimens were bleached with lactic acid and the vascular bundles (phloem and xylem) stained with lacmoid (Aloni & Sachs, 1973).

2.2. Sections of flowers.

Preserved specimens were embedded in paraplast according to the standard technique, via TBA-dehydration. The thickness of the transverse and longitudinal sections was 7 μ . The sections were stained with astra blue-auramine-safranine (Maász & Vágás, 1963).

3. OBSERVATIONS

3.1. *Aptenia cordifolia* is tetramerous, it has sepals of unequal size, two bigger and two smaller ones. The ovary, with four locules and four complete septa, is inferior in the young flower, in the ripened fruit it is semi-inferior. Placentation is axile.

3.1.1. Vascular architecture (fig. 1 and 3).

In the pedicel four vascular bundles, called primary bundles, occur in one circle (A, fig. 1-1). They ascend in the ovary wall¹⁾ in between the septa. Two of them do not branch and supply the central portions of the two bigger sepals. The other two bundles A give off two bundles each (B, fig. 1-2), and ascend towards the smaller sepals.

The four bundles B are situated inside the circle of primary bundles, and give off three bundles each in the floral base (C_1 and C_2 , fig. 1-3; B', fig. 1-4). The bundles C_1 and C_2 form a commissure C (fig. 1-3). The bundles B and B' ascend in the ovary wall in the septal radii. On the level of the hypanthium rim the bundles B split up, form a commissure with the bundles A, and supply the lateral portions of the sepals (fig. 1-9, 10). The bundles B' form a commissure, which gives rise to many bundles, supplying the staminodes and stamens (fig. 1-8, 9, 10).

Commissure C gives rise to four bundles which ascend in the radii of the bundles A ($C_{1,2}$, fig. 1-4). Higher up the bundles $C_{1,2}$ split into three bundles each (fig. 1-8), the central one (C_3) enters finally into the style. The styles are situated in between the septa, with one vascular bundle each (C_3 , fig. 1-10). The other two bundles, branching several times, form a plexus in the roof of the ovarian cavity ($C_{1,2}$, fig. 1-9). This plexus gives rise to some bundles, descending in the septal radii, ending blindly in the lower part of the ovary (C', fig. 1-7).

Commissure C gives rise to another eight bundles (D, fig. 1-4). The two bundles D at both sides of one bundle B fuse and run centripetally in the septal radius into the central column (fig. 1-4,5). In the central column these four bundles D ascend, still in the septal radii (fig. 1-6), giving off some branches in the upper half of the ovary (E, fig. 1-7) supplying the placentae. So each bundle D gives off some bundles E into the placentae in the two adjacent locules. (A placenta is a narrow strip of tissue on the central column, the borders projecting into the locule. There are two rows of ovules on it.) Furthermore, in the placenta there are two conspicuous parallel bundles, that are joined to each other by fusion or are connected by small branches. The placentary bundles are connected with the bundles E (fig. 1-7). The vascular supply in the funicles is derived from the placentary bundles. High up in the central column the bundles D split and unite with the placentary bundles.

Generally, there is not much variation in the vascular architecture in various flowers. A representative pattern can therefore be constructed; it is represented in a three-dimensional model in fig. 3.

1) Since there is no unanimity in the definition of the terms 'ovary wall' and 'hypanthium' (see e.g. Eames, 1961; Leins, 1972; Leins, Merxmüller and Sattler, 1972; Puri, 1951, 1952), in the present study the term 'ovary wall' is used to indicate the total wall outside the ovarian cavity.

3.1.2. Orientation of the vascular bundles.

In the centripetally running part of bundle D, xylem is turned downwards, the centrally ascending part is orientated normally. The bundles E are half inverted. In the bundles E, innervating one placenta, the xylem strands are turned towards each other. The bundles in the placenta seem to be amphicribal. The remaining bundles A, B, and C have normal orientation.

3.2. *Dorotheanthus bellidiformis* is pentamerous, it has sepals of equal size. The inferior ovary has five locules and five complete septa. Placentation is pseudo-parietal.

3.2.1. Vascular architecture (fig. 2 and 4).

In the pedicel ten vascular bundles, called primary bundles, occur in one circle (A and B, fig. 2-1). The bundles A ascend in the ovary wall in between the septa, without branching, and supply the central portions of the sepals.

In the floral base, or sometimes at a higher level, the bundles B give off two bundles each (C_1 and C_2 , fig. 2-2, 3, 4, 5). Then the bundles B ascend in the ovary wall in the septal radii, giving off another bundle in the upper half of the ovary (B' , fig. 2-7). On the level of the hypanthium rim the bundles B split (fig. 2-7), form a commissure with the bundles A (fig. 2-8, 9), and supply the lateral portions of the sepals. The bundles B' form a commissure which gives rise to many bundles, supplying the staminodes and stamens (fig. 2-9, 10).

The bundles C_1 and C_2 ascend, changing their positions from the septal radius to the radius of bundle A, and come to lie inside the circle of ten primary bundles A and B (fig. 2-6, 7). The bundles C_1 and C_2 branch many times and form a plexus in the roof of the ovarian cavity ($C_{1,2}$, fig. 2-8, 9). This plexus gives rise to the styler bundles. The styles are situated between the septa, with two vascular bundles each ($C_{1,2}$, fig. 2-10). In the upper half of the ovary the bundles C_1 and C_2 give off one bundle each (D, fig. 2-6, 7).

The bundles D make a sharp reverse turn. Two bundles D fuse in the septal radius and descend (fig. 2-5, 6). In the floral base these compound bundles D run centripetally into the central column (fig. 2-2, 3), ascend, and end blindly half way up the ovary. The descending part of bundle D gives off various bundles (E, fig. 2-5, 6, 7) which branch and connect with the bundles in the placentae in the two adjacent locules. In the placenta there is a random network of vascular bundles, giving rise to the bundles in the funicles.

In the central column another five bundles occur, alternating with the septa (F, fig. 2-4, 5, 6). Between the bundles D and F there are several connecting branches, so together they build a cylindrical vascular plexus. The bundles F end blindly at a level half way up the ovary; in the floral base they run horizontally, supplying the basal portions of the placentae (F, fig. 2-3, 4). (A placenta is spread over the lower part of the central column, the bottom of the ovary, and the ovary wall, so forming a triangle. The horizontal portion is convex, because of the presence of a thickening in the bottom of the locule. There are many ovules attached to the placenta in an undefined pattern.)

The details of the vascular architecture can be very variable, not only in different flowers, but even in different compartments of the same ovary, particularly with regard to the bundles D, E, and F. Even so a fairly representative pattern can be constructed, and it is represented in a three-dimensional model in fig. 4.

3.2.2. Orientation of the vascular bundles.

In the roof of the ovarian cavity the bundles $C_{1,2}$ are half-inverted: in the bundles supplying the roof of one locule, the xylem strands are turned towards each other. The

two bundles in the style are half-inverted in the same way. The descending part of bundle D is inverted, in the centripetally running part the xylem is turned downwards, the centrally ascending part is orientated normally. The orientation of the bundles in the placenta could not be defined. The remaining bundles A, B, C₁, and C₂ have normal orientation.

4. DISCUSSION

Examination of flowers, prepared according to the method described in 2.1.1., makes it possible to construct a three-dimensional model of the vascular architecture in the flower. A drawback of this method is that only lignified elements are stained and that young bundles not yet lignified are not visible. This is especially important in the young stages, in which, moreover, not all vascular bundles have yet developed. However, this limitation can have its advantages when studying flowers with a very complicated vascular pattern (e.g. *Dorotheanthus*), because it is possible, in those cases, to start by making a very simplified model based on the juvenile vascularisation and to gradually fill in the details as the older stages are examined. Since, by using method 2.1.1., only lignified material is visible, method 2.1.2. has to be used to supply more details of the vascular pattern. Even then it is possible that the smallest bundles are overlooked, so that the final details must be elucidated by means of serial transverse and longitudinal sections. It is not possible, however, to construct a three-dimensional model of vascularisation on the basis of serial sections alone. In *Dorotheanthus*, for example, it is not clear from sections how many main vascular bundles are present in the central column because of the presence of connecting bundles. By examining cleared whole flowers it is quite evident that there are ten bundles, five in the septal radii (D) and five alternating with them (F). It is necessary to examine sections to establish the orientation of the bundles.

4.1. Comparison between the vascular patterns of *Aptenia cordifolia* and *Dorotheanthus bellidiformis*.

The similarities are as follows:

1. The bundles A enter the sepals as their midveins and give off no branches to the inner floral whorls.
2. The bundles B supply the lateral portions of the sepals and give off some branches
 - a. to the stamens and staminodes: the bundles B', forming a commissure;
 - b. to the ovary wall: the bundles C₁ and C₂, forming a plexus in the roof of the ovarian cavity and supplying the styles. For the sake of convenience the complex of C bundles (the whole complex of respectively C₁+C₂+C₃ in *Aptenia* and C₁+C₂ in *Dorotheanthus*) is named the dorsal carpellary bundle, without implicating the classic carpel theory.
3. The bundles D branch off from the bundles C₁ and C₂. Two bundles D fuse in the septal radius and then give off some branches to the placentae in the two adjacent locules. For the sake of convenience the bundle D is named the commissural ventral carpellary bundle, again without implicating the classic carpel theory.

The differences are as follows:

bundle	<i>Aptenia</i>	<i>Dorotheanthus</i>
B	branches off from A in the pedicel.	is a primary bundle.
B'	branches off from B in the floral base.	branches off from B on the level of the hypanthium rim.

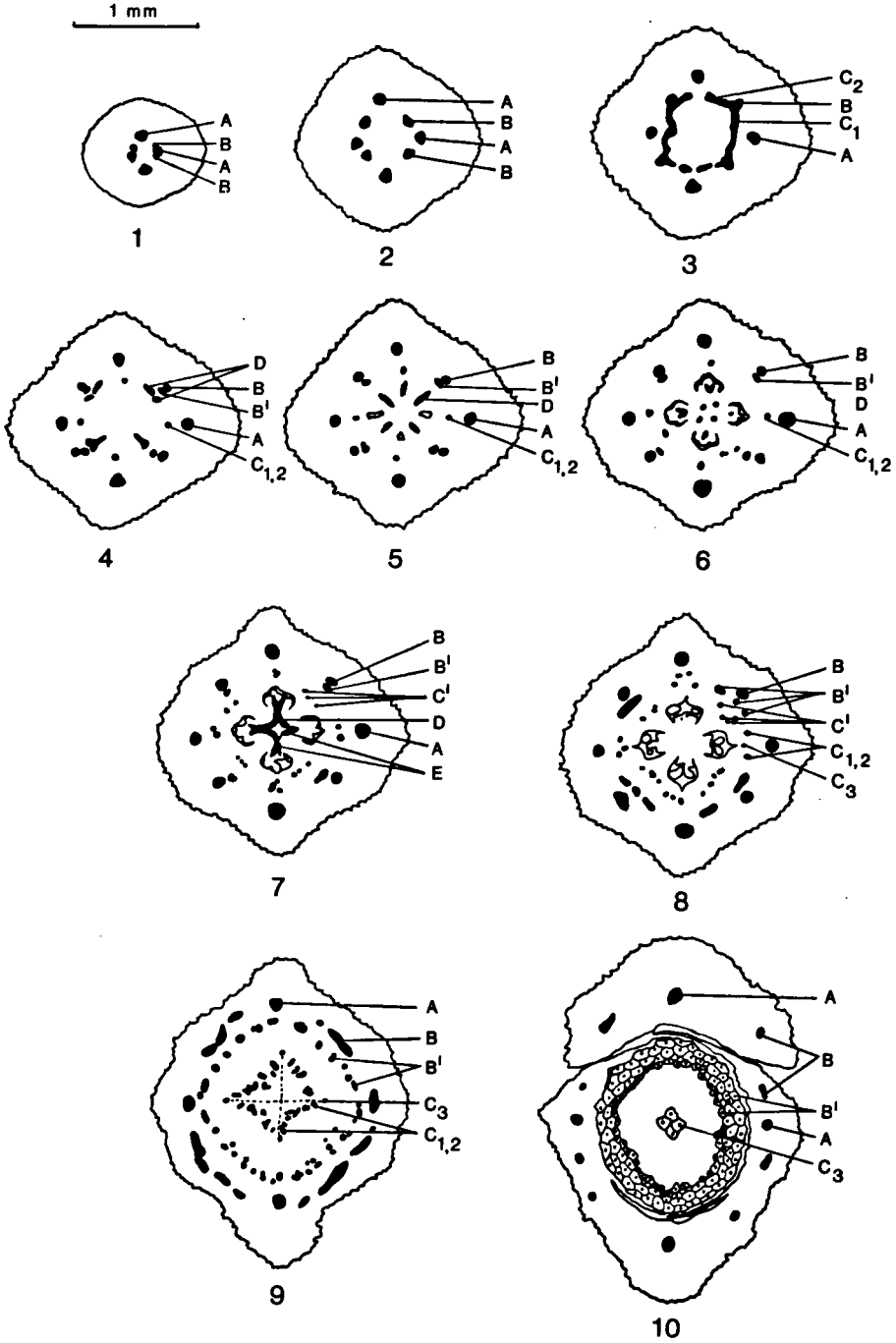


Fig. 1. *Aptenia cordifolia*. Some transverse sections. 1: pedicel; 10: top.

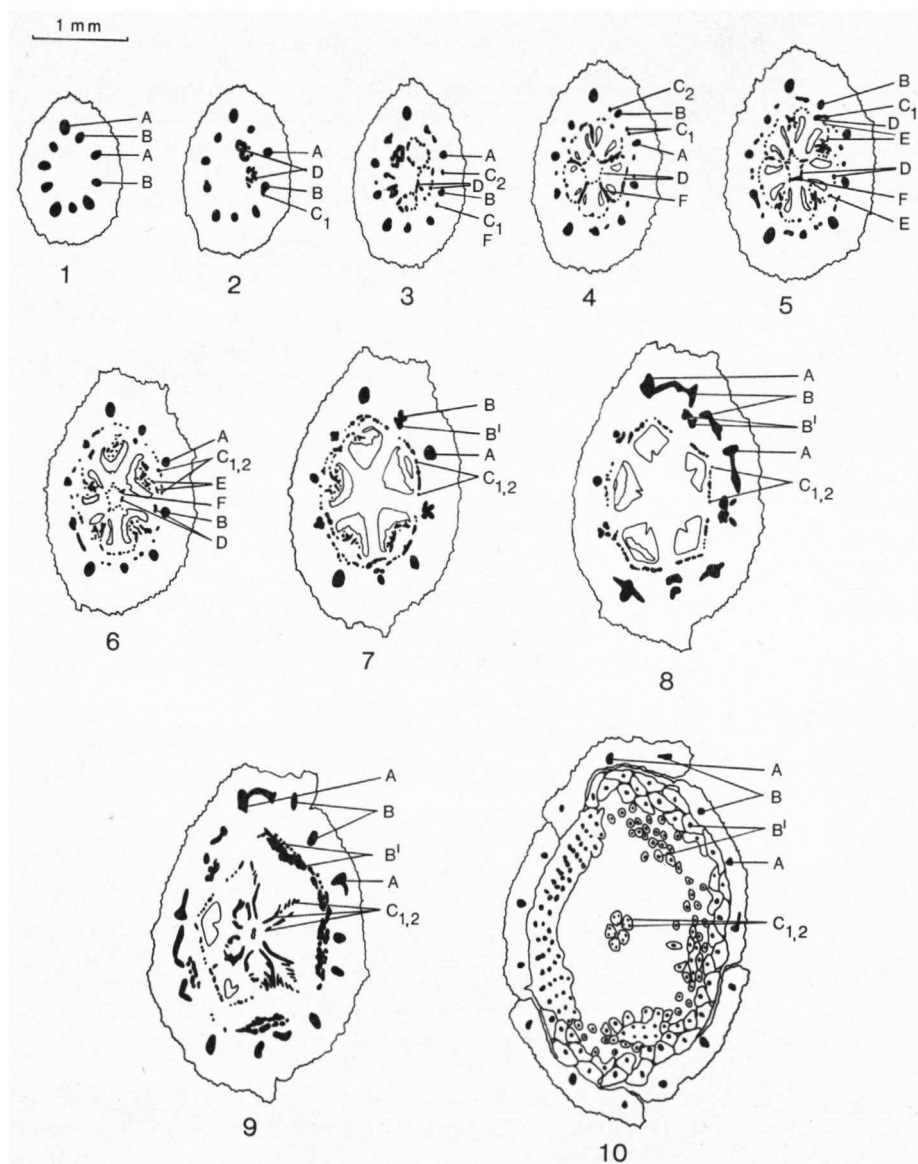


Fig. 2. *Dorotheanthus bellidiformis*. Some transverse sections. 1: pedicel; 10: top.

bundle	<i>Aptenia</i>	<i>Dorotheanthus</i>
C	C ₁ and C ₂ form a commissure C in the floral base, giving rise to the bundles C _{1,2} , ascending in the radii of the bundles A; the bundle C _{1,2} splits in the upper half of the ovary into three: the central one (C ₃) supplying the style, the other two forming a plexus in the roof of the ovarian cavity; from this plexus some branches C' descend in the septal radii, ending blindly.	C ₁ and C ₂ , not forming a commissure in the floral base, ascend separately in the radius of bundle A; the bundles C ₁ and C ₂ unite in the upper half of the ovary and form a plexus in the roof of the ovarian cavity, supplying the styles, each with two vascular bundles.
D	branch off from C ₁ and C ₂ at the level of the floral base; unite high up in the central column with the placental bundles.	branch off from C ₁ and C ₂ in the upper half of the ovary; end blindly half way up the central column; form a cylindrical plexus with the bundles F in the central column.
E	branch little.	branch frequently.
F	not present.	present, supplying the basal portions of the placenta.
placental bundles	two conspicuous parallel bundles.	a random network of bundles.

The present study shows that the bundles B and B' ascend separately, in *Aptenia* from the floral base, and in *Dorotheanthus* from the level of the hypanthium rim. So one is tempted to think that in *Dorotheanthus* there is adnation between the bundles B and B'. However, the shifting of the placentation in *Dorotheanthus* is the result of differences in relative growth rates in various parts of the ovary (Buxbaum, 1951, his fig. 27). The present study shows that:

- The bundles C₁ and C₂ branch off from B in the ovary base, both in *Aptenia* and in *Dorotheanthus*.
- The bundles D branch off from C₁ and C₂, in *Aptenia* about half way between the origin and the fusion of the bundles C₁ and C₂, in *Dorotheanthus* near the fusion of the bundles C₁ and C₂.

From this it can be inferred that the fusion of the bundles B and B' in *Dorotheanthus* cannot be understood as adnation, but is the result of intercalary growth in the ovary wall between the origin of the bundles C₁ and C₂ and the origin of the bundles B'.

At present there is no evidence as to how the bundle F in *Dorotheanthus* should be interpreted. It doesn't occur in *Aptenia*, but contributes to the vascular supply of the placenta in *Dorotheanthus*. Three possibilities can be suggested:

- Bundle F is equivalent to bundle E. Bundle F does in fact supply the placenta, like E, but doesn't originate from bundle D, as does E.
- Bundle F is equivalent to bundle D. In the central column there is no difference between the bundles D and F, either in size, or in course and orientation. However, bundle D

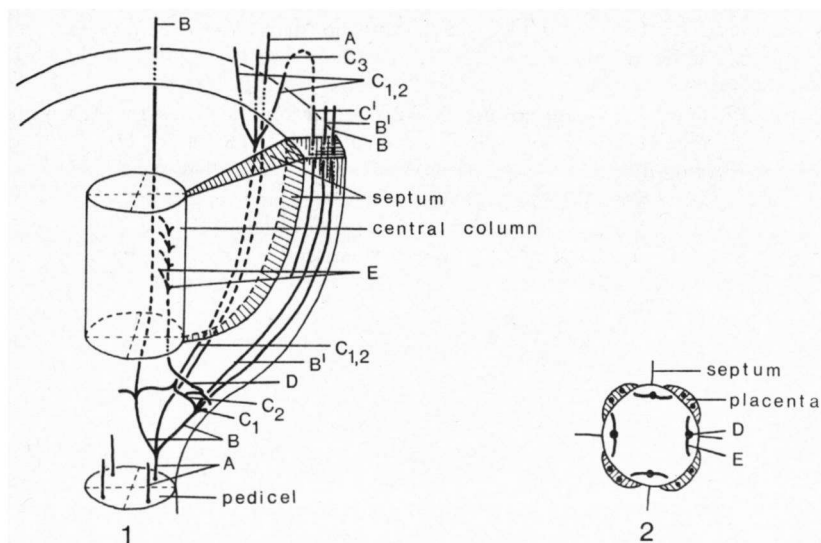


Fig. 3. *Aptenia cordifolia*. 1: Three-dimensional model of the vascular architecture in the flower. 2: Schematic transverse section through the upper half of the central column.

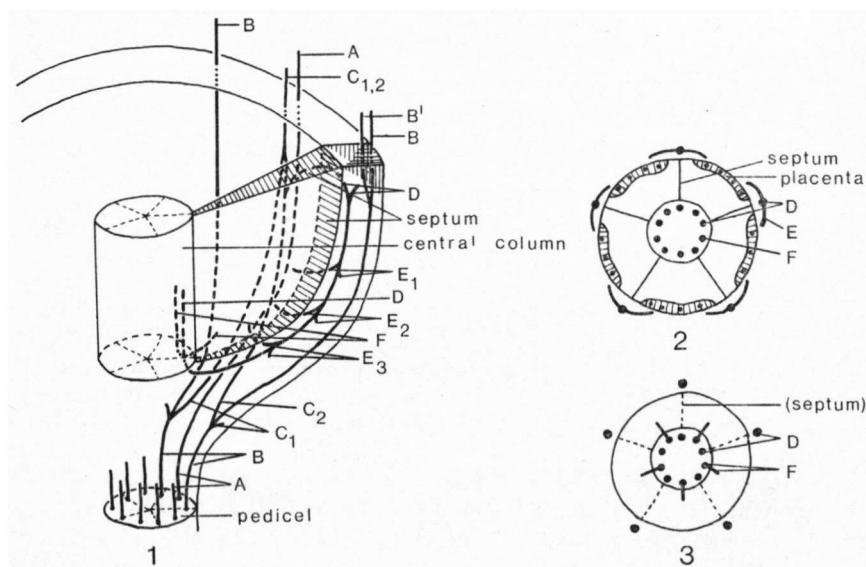


Fig. 4. *Dorotheanthus bellidiformis*. 1: Three-dimensional model of the vascular architecture in the flower. 2: Schematic transverse section through the ovary base. 3: Schematic transverse section through the lower half of the ovary.

branches off from bundle C_1 or C_2 and is situated in the septal radius, while bundle F has no connections with bundle C_1 or C_2 and alternates with the septa. In fact, in the bottom of the ovary bundle F supplies the placenta directly, while bundle D gives off placental bundles (E).

- c. Bundle F is not equivalent to any other vascular bundle. Like the other placental vascular bundles (D and E), bundle F is present in all stages of maturity, so it doesn't develop secondarily.

Probably further studies on some other species will elucidate this problem.

The results of this study demonstrate that the vascular pattern in the pseudo-parietal placentation of *Dorotheanthus* can be interpreted as derived from that in the axile placentation of *Aptenia* by a shifting in the ovary wall. As the flowers examined were not young enough, in this study the ontogenetical shifting has not been investigated (e.g. Huber, 1924; Ihlenfeldt, 1961).

4.2. Comparison with observations of Ihlenfeldt.

Ihlenfeldt (1961) suggested two types of vascular pattern for the *Mesembryanthemoideae*. *Aptenia* served as a representative example of the subfamily *Mesembryanthemoideae* (syn. with *Aptenioideae*), *Delosperma* of the subfamily *Ruschioideae*. These patterns show dissimilarities in several respects with the results of the present study.

4.2.1. *Mesembryanthemoideae*: *Aptenia*.

1. Ihlenfeldt doesn't mention the dorsal carpellary bundle complex $C_1-C_2-C_3$, ascending in the radius of bundle A (BB)¹⁾. He says (p. 43): 'Der Dorsalmedianus, der an der Aussenwand des Fruchtknotens aufsteigen müsste, ist offenbar unterdrückt oder nur so schwach ausgebildet, dass er sich aus der Vielzahl der kleinen zusätzlichen Gefäße nicht heraushebt.'
2. Ihlenfeldt indicates a commissure (K_2) between the bundles (L). In his figures of transverse sections (Abb. 6, fig. 5) this commissure is situated in the central column, in the longitudinal section (Abb. 6, fig. 15) it is situated in the ovary base. Bundle (L) is absorbed in this commissure. In the present study the bundle (L) is interpreted as the ventral bundle D. This bundle D ascends to the top of the central column. The commissure (K_2) has not been observed in the present study. Indeed all bundles E start branching off at the same level in the central column (fig. 1-7), and seem to form a commissure.
3. Ihlenfeldt describes his ventral carpellary bundle (VM) as alternating with a septum. In his figures of transverse sections (Abb. 6, fig. 6, 7) this bundle is found only in the central column and arises at a point where the placenta with two vascular bundles is already present. In *Aptenia* the present author did not observe a vascular bundle in the central column alternating with a septum. The ventral vascular bundle D is situated in the central column in the septal radius. Ihlenfeldt's bundle (VM) is, in the present study, interpreted as a bundle E, branching off from the ventral bundle D (L). In the figure of the longitudinal section (Ihlenfeldt, Abb. 6, fig. 15) the bundle (VM) is found only in the placenta and arises in the floral base. In *Aptenia* the present author observed two conspicuous parallel bundles in the placenta, as is also indicated in the transverse sections of Ihlenfeldt. In the present study Ihlenfeldt's bundle (VM) is interpreted as a placentary bundle.

¹⁾ In brackets are the characters used by Ihlenfeldt for the corresponding bundles in the present study.

The present study agreed with Ihlenfeldt's figures of the transverse sections of the *Mesembryanthemoideae*. However, his figure of the longitudinal section doesn't agree with his figures of transverse sections, nor with the results of the present study. The differences in interpretation of Ihlenfeldt and the present author concerning *Aptenia* (*Mesembryanthemoideae*) are probably due to the fact that Ihlenfeldt based his study on sections only.

4.2.2. *Ruschioideae: Dorotheanthus*.

A comparison between the vascular pattern of *Delosperma*, as an example of the *Ruschioideae* in the study of Ihlenfeldt, and that of *Dorotheanthus* in the present study, is not made at this moment. There are so many differences, both between the results of Ihlenfeldt and the present author concerning *Dorotheanthus*, and between the vascular patterns of the two species, that comparison is impossible without further examination of *Delosperma*.

4.3. Comparison with other *Centrospermae*.

Moeliono (1970) concluded, on the basis of his own study and on the illustrations of e.g. Ihlenfeldt (1961), that in the ovary of the *Mesembryanthemaceae* a placental vascular pattern is found similar to that in the ovary of the *Caryophyllaceae*. Before verifying this conclusion, two remarks must be made:

- a. As is demonstrated above, some of the illustrations of Ihlenfeldt are inconsistent with the observations in the present study. Moreover, examination of some other genera of the *Mesembryanthemaceae* (just started) demonstrated that the vascular groundplan, to which all *Mesembryanthemaceae* should be reduced, is much more complex than would have been expected from the present study.
- b. There is no unanimity in the interpretation of the placental vascularisation in the *Caryophyllaceae* (see e.g. Bocquet, 1959; Moeliono, 1970; Rohweder, 1967, 1970; Thomson, 1942). Therefore a critical examination of the literature and even of the flowers of some *Caryophyllaceae* is necessary.

The vascular pattern in the flower of *Melandrium rubrum* (Weig.) Garcke and of *Myosoton aquaticum* (L.) Moench. have been studied in part. This study demonstrated that the vascularisation of the outer floral whorls of both species is the same (unpublished).

At the moment it is safe to say that the vascular patterns in the outer floral whorls of *Melandrium* and the ovary wall of *Aptenia* show a high degree of similarity, despite some differences.

4.4. The interpretation of the inferior ovary.

Traditionally, on the basis of the vascular pattern two types of inferior ovary are distinguished (Douglas, 1957; Eames, 1961). Comparison of the vascular pattern in an inferior ovary with that in a superior ovary led to the theory that an inferior ovary can be formed by adnation of the bases of the outer floral whorls to the carpels ('*appendicular-type*'), or that an inferior ovary can be formed by invagination of the receptacle ('*receptacular-cup-type*'). The latter has two systems of stelar bundles, each system demonstrates in a transverse section a circle of vascular bundles, the inner bundles are inverted. According to Puri (1951, 1952), however, an inferior ovary can originate by zonal growth, and the morphological nature of the ovary wall will vary with the region which is most active in zonal growth. He suggested that there is an intermediate condition between the '*appendicular-type*' and the '*receptacular-cup-type*', perhaps recognisable only in histogenetic and cytological studies. Leins (1972) observed in an ontogenetic study that an inferior

ovary is formed by intercalary growth in the tissue underneath the primordia of the gynoecium, the androecium, and the perianth. In his opinion there is only the 'receptacular-cup-type'.

According to Ihlenfeldt (1961) the ovary of the *Mesembryanthemaceae* in general must be considered as a 'receptacular-cup'. Traditionally, and in the opinion of the present author, it should be possible to detect this in the vascular pattern, as is e.g. the ontogenetic shifting of the placentation in *Dorotheanthus* (4.1.). In the present study, in *Aptenia* no inverted bundles are found. Moreover, as is mentioned above (4.3.), there is a high degree of similarity in the vascular pattern of the outer floral whorls of *Melandrium* (with a superior ovary) and of the ovary wall of *Aptenia* (with an inferior ovary). So on the basis of the vascular pattern in the flower one is tempted to think that the inferior ovary of *Aptenia* must be interpreted as an 'appendicular-type'. However, in *Aptenia* there are two vascular commissures on the level of the hypanthium rim. From the outer one the midveins and the lateral bundles of the sepals are given off, from the inner one many bundles are given off to the stamens and staminodes. In *Melandrium* such commissures cannot be observed, nor in other species of the *Caryophyllaceae* (Thomson, 1942). In *Oenothera* de Vos (1975) observed a commissure on the level of the hypanthium rim in which structures, interpreted as leaf-gaps, occur. On that ground he interpreted the outer regions of the ovary wall as stelar, so the inferior ovary of *Oenothera* must be considered as a 'receptacular-cup'. If in the commissures in *Aptenia* structures like leaf-gaps could be inferred, the inferior ovary could be interpreted as a 'receptacular-cup'. However, as this information is not yet available, it is not possible to be certain as to which type of inferior ovary is present in *Aptenia*. A detailed examination of the commissures is needed. Regarding *Dorotheanthus*, one is tempted to think that the inferior ovary must be considered as a 'receptacular-cup', because of the presence of inverted vascular bundles. However, these are the ventral carpellary bundles (D), inverted as the result of the shifting in the ovary wall. In an ovary of the 'receptacular-cup-type' the inverted bundles are stelar ones (Douglas, 1957; Eames, 1961). Moreover, the vascular pattern in *Dorotheanthus* can be interpreted as being derived from that in *Aptenia* (4.1.). Because it is not yet clear which type of inferior ovary is represented in *Aptenia*, the same applies to *Dorotheanthus*.

4.5. Conclusions.

In comparing the vascular patterns in the flowers of *Aptenia cordifolia* and *Dorotheanthus bellidiformis* it is concluded that the vascular pattern of the pseudo-parietal placentation in *Dorotheanthus* must be interpreted as derived from that of the axile placentation in *Aptenia* by a shifting in the ovary wall. So typologically *Dorotheanthus* must be considered as derived from *Aptenia*. As a result of the foregoing it can be stated that:

1. The vascular bundles in the flower show relative conservatism within the groundplan. For example, the ventral carpellary bundle D has not shifted from its position in the septal radius to a position alternating with the septa inspite of the fact this would give it a shorter distance to travel, both from the point of origin to the end of the bundle, and from this bundle to the whole placenta. However, the branches E from bundle D to the placenta are much more extensive in *Dorotheanthus* than they are in *Aptenia*.
2. General remarks concerning *Aptenia* apply also to *Dorotheanthus*. More research needs to be done into the vascular pattern in *Aptenia* and into the comparison between the vascular pattern in the outer floral whorls of *Melandrium* and the ovary wall of *Aptenia* before it is possible to be sure whether the 'appendicular-' or 'receptacular-cup-type' of ovary is present in *Aptenia* and in *Dorotheanthus* which is derived from *Aptenia*.

ACKNOWLEDGEMENTS

I wish to express my sincere thanks to Dr. B. M. Moeliono for the encouragement and discussions, and for his helpful guidance in the preparation of this paper. Thanks are also due to Mrs. A. Dijkstra who introduced me into the several techniques. Finally, I am grateful to Mrs. Y. M. Butler for correcting the English text.

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