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VARIATION IN THE DEVELOPMENT OF ASCIDIFORM CARPELS, AN S.E.M.-INVESTIGATION

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SUMMARY

Attention is drawn to the differences in place and time of origin of the abaxial (upper) and adaxial (lower) parts of the margin of ascidiform carpel primordia. It is assumed that the adaxial parts will develop more fully when the primordia have more space and time to develop on an expanding floral apex. The favoured occurrence of the margin at the base of the primordia seems a prerequisite to incipient syncarpy.

INTRODUCTION

A technical improvement resulting in less shrinkage of the primordia enables a more accurate and more convincing presentation of my results. By this a better insight can be gained in the differences of the origin of the carpel primordia which exist between genera. These differences do not disturb the common oblique ascidiform developmental pattern (Van Heel, 1981, 1983).

Formerly I fixated the primordia (very young flower buds) in FAA or in CRAF fixatives as in use for the preparation of microtome sections. This material was passed through alcohol 50% and acetone, and then critical-point dried in Freon. This proved already better than passing the material through alcohol 96% and amylacetate. However, to improve the quality of scanning-images test series were set up using other fixatives, and other formulas of FAA and CRAF fixatives. In addition other chemical dehydration methods were tried out. As a test object I used vigorously growing ground-shoots of *Tilia platyphyllos*. These experiments showed that quick and good scanning images can be obtained by the method as described by P. Gerstenberger and P. Leins (1978). Small variations on that scheme are possible. I have used this method as follows. Firstly the primordia were fixated in a FAA-fixative containing little alcohol (15–20%), 10% glacial acetic acid, and 5% formaldehyde solution. Secondly the material was passed through 50% alcohol and dehydrated in dimethoxymethane. Finally the objects were critical-point dried in CO_2. The use of freon is not recommended.

It should be added that this method will be effective only if the plant under consideration is in a good condition at the time of collection of its flower buds. In my test series I did not include those methods that are derived from T.E.M.-techniques, because they are very unpractical for this kind of research which starts with the fixation of rather large plant parts in the field or in botanic gardens.

RESULTS

1. Ranunculus sceleratus (Ranunculaceae). — **Photos 1–5**

A series of photos at the same magnification shows how lateral hemispherical primordia become larger and longer. They change into a proximal tapering half and a slightly broader distal half. The latter starts flattening eccentrically on the upper side. Dermal anticlinal cell division walls can be observed in a circle around the flattening region. A circular low wall is formed: a margin bordering a slight depression (cf. Rohweder, 1967). Abaxial and adaxial regions (curves) of this margin arise at the same time. Immediately afterwards the primordium, on getting larger, bends upwards. Then the abaxial region of the primordium grows faster than the adaxial one, and the depression is carried upwards. The total result is that an originally hemispherical primordium has developed into an oblique ascidiform organ. The later development is described in my paper of 1981.

2. Clematis montana (Ranunculaceae). — **Photos 6–9**

A series of photographs at the same magnification shows that the approximately hemispherical carpel primordium is flattened above. As the primordium grows the flattened region is extended, its outline is circular. The flattening appears prior to the proximal tapering of the primordium. Thus, as compared with *Ranunculus sceleratus* the flat region is located on the primordium closer to the floral apex. The cells at the outline of the flat region grow upwards as a margin around a depression, the accompanying anticlinal cell division walls can be observed in the dermatogen. In the meantime, on growing bigger, the primordium is elevated, curving upwards. The origin of the circular carpellary margin is as fast in abaxial as in adaxial parts. On the adaxial side at the base of the primordium one cell layer remains under the ring-shaped carpel margin to form the carpellary base later on. Thus the adaxial part of the carpellary margin differentiates near the base of the carpellary protuberance. The total result is the development of an approximately hemispherical carpellary protuberance into an oblique ascidiform organ that tapers a little at the base. The further development is described in my paper of 1981.

3. Geum urbanum (Rosaceae). — **Photos 10–16**

Approximately hemispherical primordia originate on the floral apex laterally. At first they become more or less cone-shaped. Then, while growing upwards slightly, they are flattened on the upper side. On the adaxial side the flattening is less evident, there is a gradual transition between the primordium and the floral apex. On further enlarging the development of a carpellary margin starts along the flat region laterally and abaxially. A shallow depression is formed of which the adaxial slope is given by the transition region between the primordium and the floral apex. On growing further the primordium slightly tapers basally, and the abaxial part curves upwards, the middle part gets deeper. Only in a later stage (between the stages given in photos 13 and 14), an adaxial part of the carpel margin is formed at the transition region of carpel primordium and floral apex. This part does not grow fast, the lateral parts of the primordium advance. Later the base of the carpel develops more clearly below the adaxial part of the margin. The further development has been described in my paper of 1983.

Whereas there is an equal rate of development in the two preceding species, in *Geum* the abaxial part of the carpel margin is developing faster than the adaxial part, together with the upward curving of the primordium. Already with the onset the approximately hemispherical primordia in *Geum* look different, rather with layered cells, as if the abaxial carpel margin is started directly.

4. Calycanthus fertilis (Calycanthaceae) — **Photos 17–24**

The carpel primordia arise as small protuberances along the sides and toward the bottom of an urceolate floral apex. These protuberances do not form primordia that are hemispherical, they form slightly broader primordia that are flat on the adaxial surface. Laterally along this flat side the formation of the carpel margin begins. At first this formation is not taking place at the base of the primordium, so that the transition between the primordium and the floral apex is gradual. Also at the top (the 'abaxial' region) the formation of a margin is not well-marked, it is rather the bending tip of the primordium itself which borders the primordium. As a result the space of the primordium is surrounded by a carpellary margin, except on the side of the floral apex. On that side this formation does not start earlier than in a stage shown in photo 19. In photo 20 it is clearly present, the carpel margin there extends as an adaxial basal curve which marks the border between the carpel primordium and the floral apex. Later the carpellary base arises below. The development in *Calycanthus*, also described by Erbar (1983), is similar to that in *Geum*, but shows still more clearly the strongly advancing development of the abaxial (upper) carpellary margin part, and as compared with that the late formation of the adaxial (lower) part. The latter originates quite on the base of the carpel primordium at the transition toward the floral apex.

DISCUSSION

An approximately circular meristematic field gives rise to a more or less convex protuberance which – on growing larger – differentiates into an oblique ascidiform upper part and a basal support of a carpel primordium. Usually the adaxial region of the ascidiform part is small, so that the carpel primordium is chair-like. By differential growth it changes into a carpel of conduplicate appearance.

It is sometimes thought that similar organs are still more similar in development. However in this case the oblique ascidiform primordia show some variation in their origin according to the genera. This variation concerns the extent and rate of development of the carpellary protuberances, the position of the peripheral margin differentiating on them, and the rate of development of the abaxial versus the adaxial regions of the margin. The latter was described by Erbar (1983) in a comparison of the carpel development in *Drimys winteri, Magnolia, Liriodendron*, and *Illicium*. I described the differences in the later development of the adaxial regions of the margin in my paper of 1983.

In *Ranunculus sceleratus* and *Clematis montana* the circular margin arises at once on the carpellary protuberance at some distance from the floral apex. This may also occur in *Alisma*. A favoured position of the adaxial part of the margin is at the base of the carpellary primordium, or in the transition region of the primordium and the floral apex. This occurs for instance in *Drimys, Calycanthus, Geum, Rubus, Quassia*, and *Ailanthus*. Theoretically in this position non-development (loss?) of the adaxial margin in the median plane of the primordium clears the way for meristematic continuity between the margins of adjacent primordia, leading to incipient syncarpy (*Aquilegia*, fig. 41 in Van Heel, 1981; *Sorbaria*, photos 25–27*).

It was shown in my paper of 1983 that the carpellary primordium may not be fully formed toward the adaxial side at the time when the abaxial part of the margin already starts differentiating on it. The abaxial margin formation may advance. Sometimes it seems that the margin there already has a beginning stigmatic-stylar form (*Quassia*).

One may suppose that a more free location of carpel primordia on a widening and lengthening floral apex, or a position unhampered by succeeding primordia, may favour the development of the adaxial regions of the carpel primordia. I have described (1983) that the upper carpels of a flower in a number of cases can have median adaxial regions, whereas the lower ones have not. Single carpels form a special problem here too. A single carpel at the side of a salient residual floral apex is described by Endress & Sampson in *Trimenia* (1983). The carpel in this genus is markedly ascidiform. A peculiar case is that of some last formed carpel primordia that arise upon the flat bottom of the urceolate receptacle of *Calycanthus*. In contrast with carpels arising higher up along the wall of the receptacle, they have pronounced adaxial parts that originate early in relation with the abaxial parts (photos 23 & 24). When mature the carpels of *Calycanthus* are similar, whether lateral or basal (Schaeppi, 1953).

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* This material was still processed according to the CRAF-Alcohol 50%-Aceton-Freon schedule.

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EXPLANATION OF PLATES

All scales at the photographs on pages 448–452 represent 0.1 mm.

Plate 1. — 1–5. *Ranunculus sceleratus.*

Plate 2. — 6–9. *Clematis montana.*

Plate 3. — 10–16. *Geum urbanum.*

Plate 4. — 17–24. *Calycanthus fertilis.*

Plate 5. — 25–27. *Sorbaria arborea.*

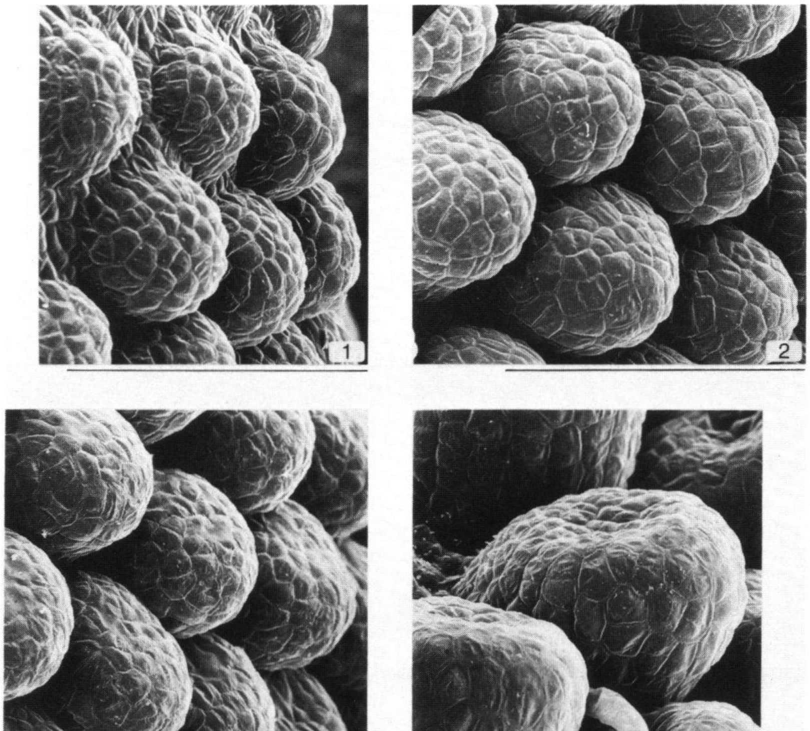


PLATE 1

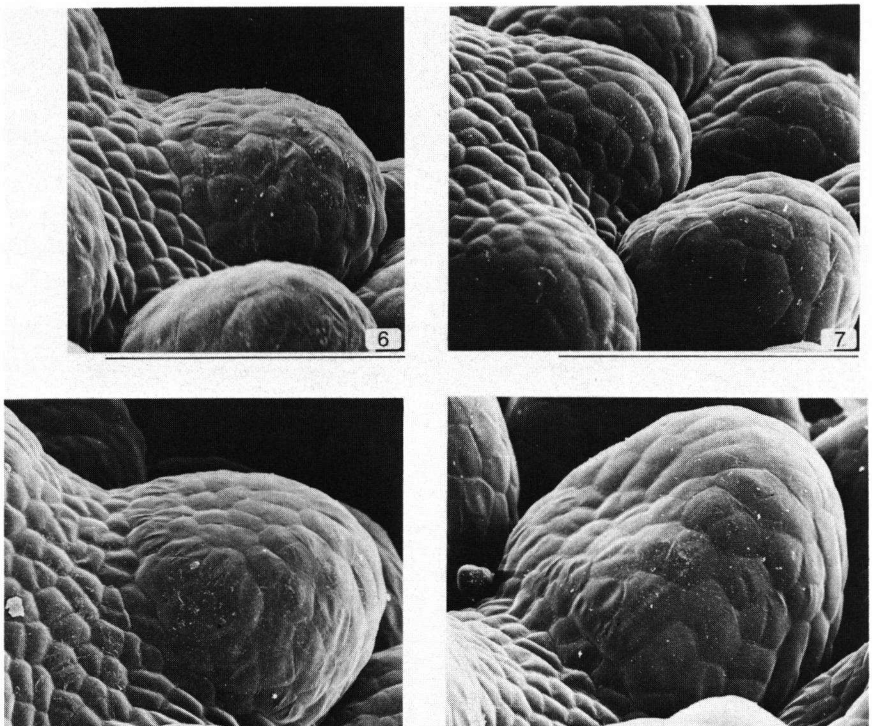
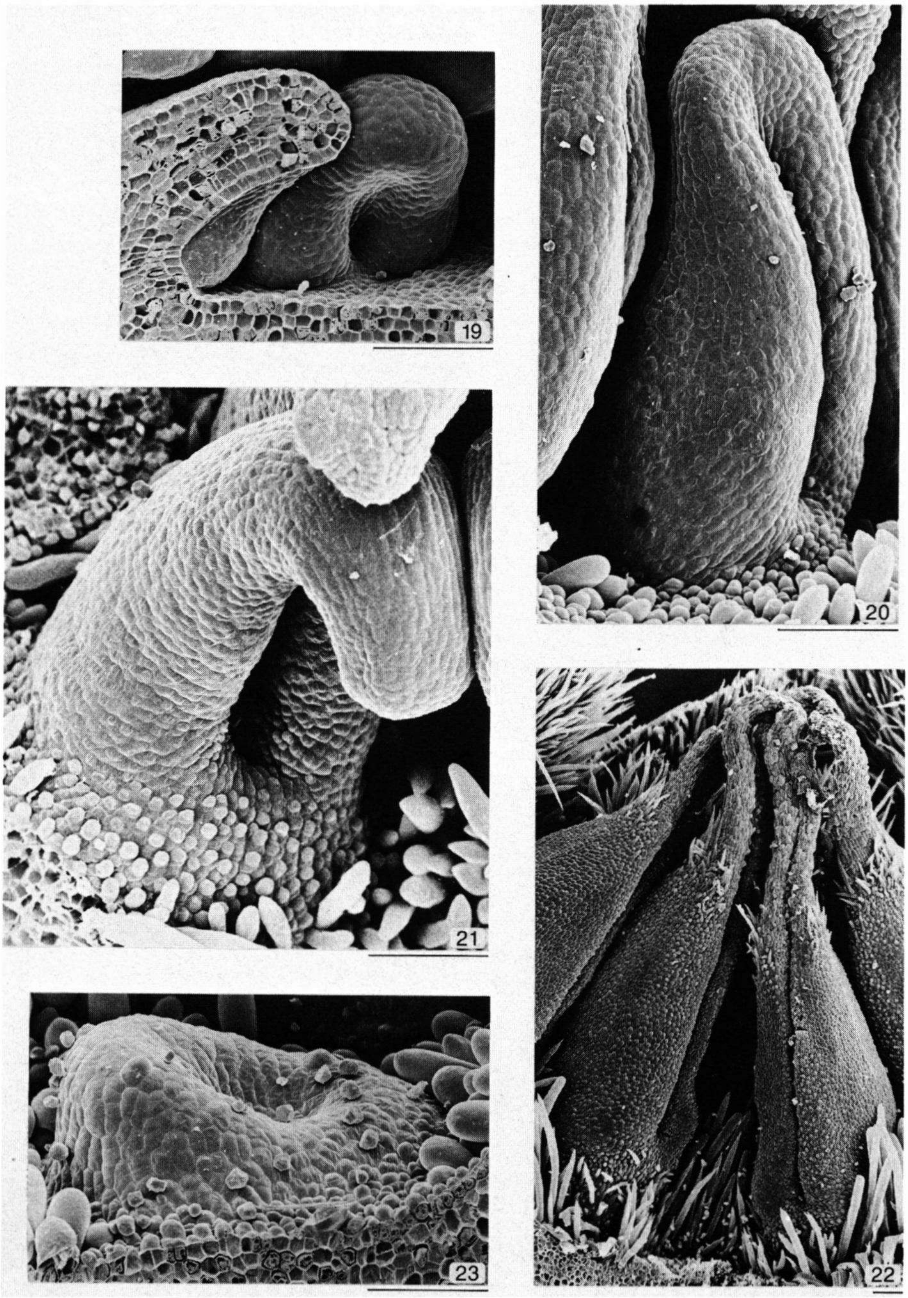


PLATE 2

PLATE 3



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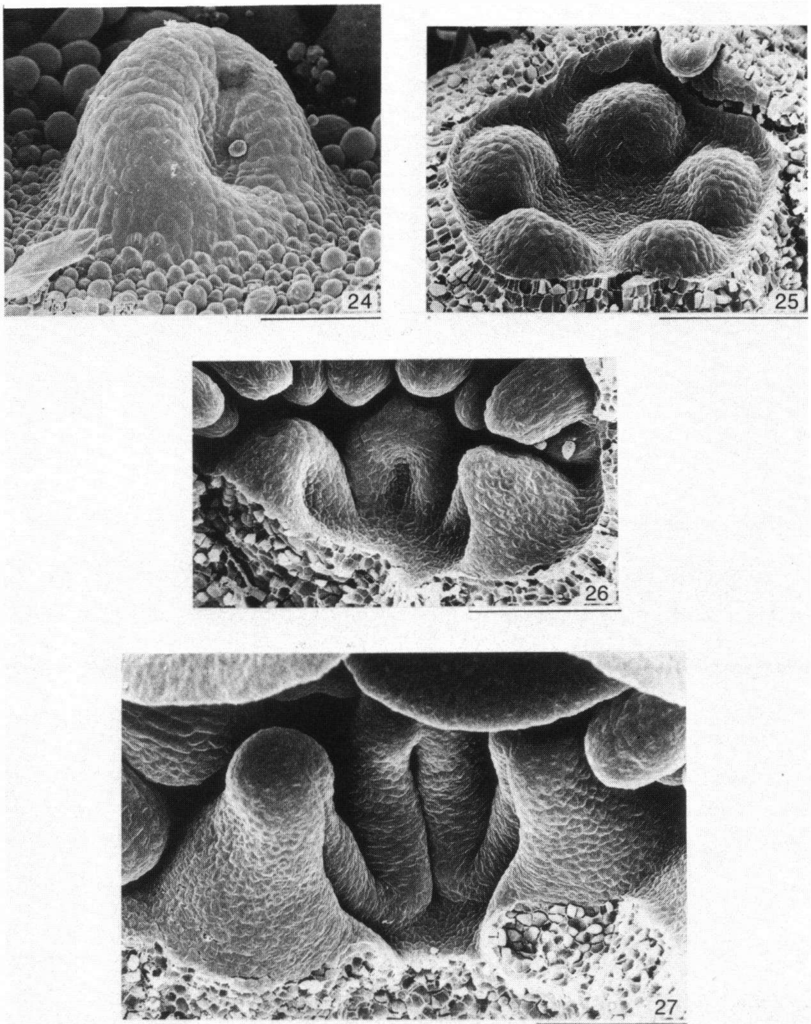

PLATE 5