

ON THE MORPHOLOGY OF THE OVULES IN SALACCA (PALMAE)

W. A. VAN HEEL

Rijksherbarium, Leiden, Netherlands

Female inflorescences in several stages of development of *Salacca edulis* Reinw. were collected from stands in the Kebun Raya at Bogor and near the village Depok, West Java. In addition to this, material of *S. wallichiana* Mart. collected in the Kebun Raya, Bogor, was used in this morphological study*).

Salacca belongs to the subfamily *Lepidocaryoideae* of *Palmae*, which is distinguished by its large fruit scales. As one of the results of the present study I could observe that the early development of these scales takes place in the epidermal cells of the young ovaries. The *Lepidocaryoideae* are furthermore distinguished by the position of their ovules. In Palms there is one axillary basal ovule in each locule. Usually the ovules are ascendent and anatropous, the micropylae facing the dorsal walls of the locules. In *Lepidocaryoideae*, however, the micropylae face the central column of the ovary. Uhl & Moore (1971), who recently published a morphological study on the Palm gynoecium, think that the ovules in this group have turned 180 degrees. These authors studied *Plectocomiopsis geminiflorus*, and their results are very similar to mine in *Salacca*. The vascular bundle in the funicle is reported to be twisted, which is regarded as evidence of the turning of the ovule.

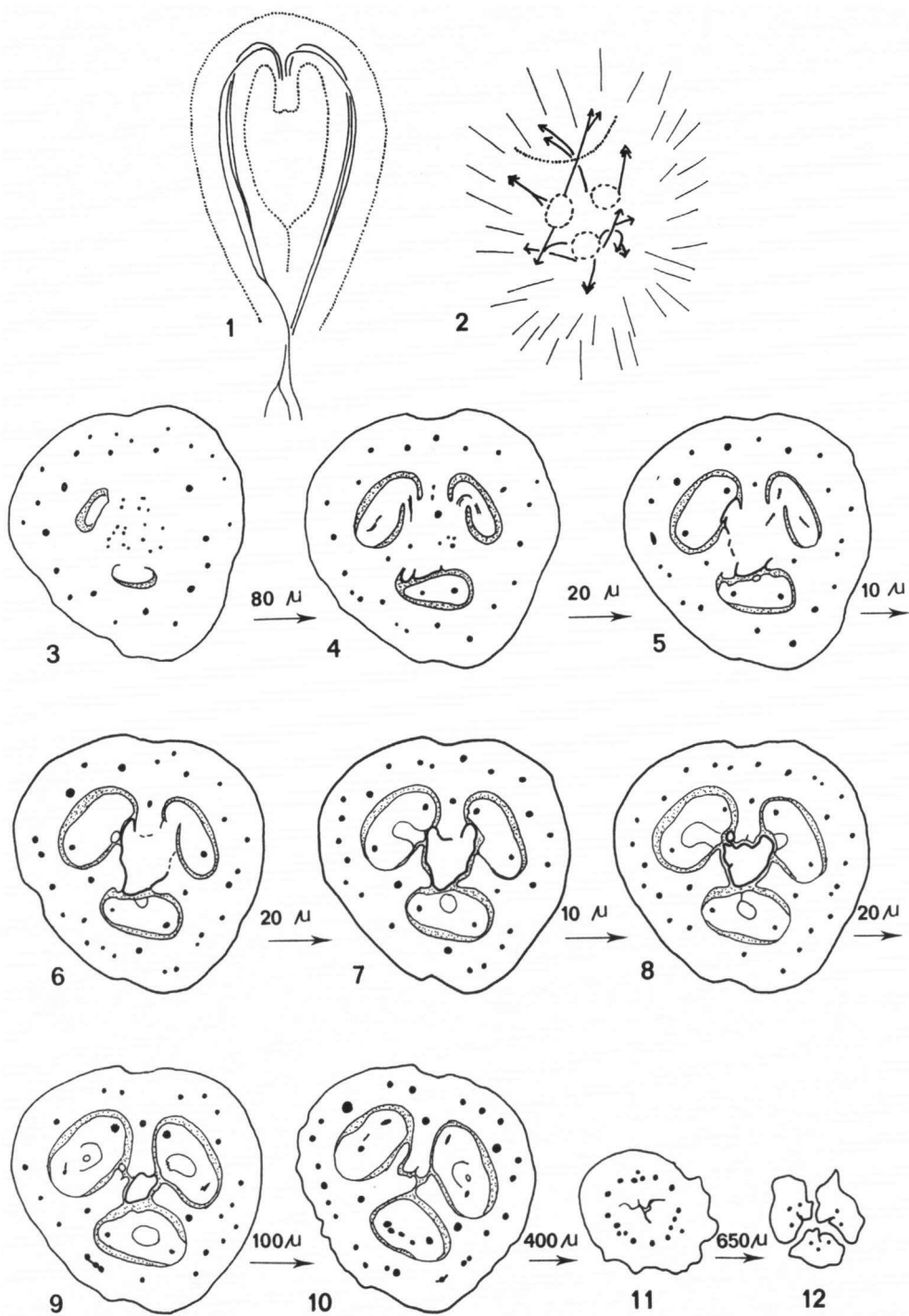
In *Salacca* the ovules possess a small nucellus which is soon absorbed by the young embryosac. There are two free integuments; both undergo extensive growth in the course of seed formation. However, whereas the inner integument is entirely absorbed by the embryosac, the outer integument pursues its growth in thickness and ultimately forms a sarcotesta in the ripe seed. Already Beccari (1918) reported that the seed of *Salacca* has a fleshy integument. The edible part of the *Salacca* fruit can be called an aril in a loose functional sense only, not in a precise morphological context.

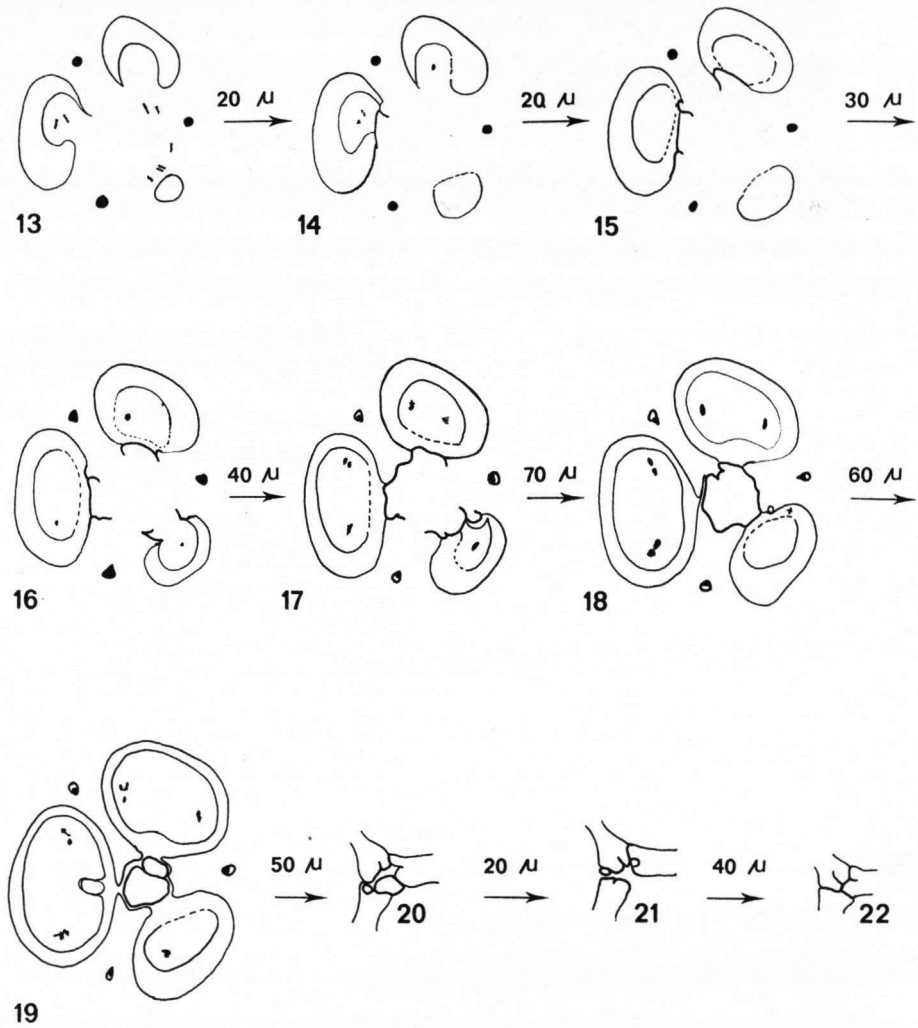
The young seeds, if subjected to clearing procedures, reveal two dorso-lateral vascular bundles in the outer integument, which dichotomise twice (fig. 1). The resultant branches run upwards close together, with opposing xylem poles. At the top of the seed they bend downwards into a large 'postament' (Dahlgren, 1940) which is prominent in the embryosac after absorption of the whole of the inner integument.

In the ripe fruit the sarcotestae reveal the same vascular bundle pattern as is present in the outer integuments of the young seeds. The hard kernels are formed by the white endosperm. A subulate black postament projects into the base of the kernel, and a turbinate undifferentiated embryo lies on top. The pistil wall develops into a thin lorica around the sarcotesta seeds, which breaks away easily.

At the base of the gynoecium a mass of vascular bundles separates into peripheral

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Salacca edulis — Fig. 1. Dorsal view of vascular bundles in young seed, cleared. 7 x. — Fig. 2. Transverse slice of base of young fruit, vascular supply towards the seeds as arrows, towards septa as double arrows, cleared. — Figs. 3—12. Series of transverse sections of pistil, from below upwards. 30 x. — Figs. 13—22 Ibidem.

bundles towards the gynoeceum wall and into three large central complexes of bundles. The three central complexes are located on a level below the locules, and alternate with them. This is different from reports by Uhl & Moore who stated that for all their cases the complexes — which they called carpellary steles — are located in line with the locules. Some of the peripheral bundles, namely the innermost ones, take their positions dorsal to the locules. Also some of them may form 'medium laterals', which is especially evident in the material of *S. wallichiana*. The three alternating complexes each separate into a septal vascular bundle outwards and into ovular traces upwards. The two vascular traces of the ovule may have a simple or a multiple base with which they link up with either one or two neighbouring members of the three basal vascular bundle complexes mentioned above. Of great interest, however, is the observation that the traces always cross, the left hand trace branching into the right hand vascular bundles of the outer integument and the right hand traces into the left hand bundles (fig. 2). Even if the traces together form one bundle in the short funicle — which they frequently do in Palms, according to Uhl & Moore — the clearing procedures reveal that xylem groups in these bundles remain separate as part of the continuing, crossed traces. The crossing, together with the twisting of the traces, as noted by Uhl & Moore, is good proof for the hypothesis of the turning of the ovules for 180 degrees. It is my guess that the ovules are initiated normally, so that the two traces normally link up with the pre-existing vascular system, but that at a very early stage of development the ovule primordia together with their procambial traces begin to turn. Perhaps this happens even before the start of integument formation. The turning should be proved by studying developmental stages younger than I could collect. Also comparative developmental studies could eliminate any questions on 'conservatism of vascular bundles', that could arise in this case. A third feature special for Lepidocaryoids is found in a large floral axis in the middle of the gynoeceum. In other Palms a small comparable protrusion may be present (see Uhl & Moore). In my material of *S. wallichiana* some vascular bundles in the centre can be designated as bundles continuing into the direction of this sterile axial extension.

The presence of the apical extension offers the opportunity to investigate whether the ovules are located on the carpel margins rather than on the axis. For this purpose series of cross-sections have been made of young stages, some of which are presented here (Figs. 3—22). The protruding axis can be easily discerned by the special, possibly stigmatoid, epidermis which consists of large cells with dense cytoplasm and large nuclei. After careful consideration of the slides, it appeared that there is no crossing zone (Querzone) — meaning a strip of ventral carpellary tissue produced by late marginal meristem extension of the carpel along the apex in upward direction. Therefore, in the conventional theory, the carpels would be epeltate, their margins, funicles and arils being fused directly to the floral axis, as Uhl & Moore stated. Bosch (1947) considered the carpels to be peltate on the ground of the presence of inverted median ventral vascular bundles. However, the descriptions of Bosch are oversimplified. Moreover, as Uhl & Moore wrote, in many Palms ventral bundles have no connection with the large ovular supply. In my material the ovules always appeared to be attached at a level on which the carpellary margins are not or only partially free from the central column. As a consequence it would be necessary to hypothesize that the carpel margins have grown up at the apex to that level, if the carpellary origin of the ovules is to be held up. From the present material it is impossible to prove or disprove this 'fusion'. The only statement which can be made is that the ovules are axillary to the gynoeceal appendages (Sattler, 1974).

Some minor points may be relevant in this respect. It is possible to conclude from my preparations that the so-called arils of Uhl & Moore can be lobes of the protruding axis

in close connection with the funicles. The free axis fits close to the funicles or it is situated immediately above them. However, in a few cases the arils were clearly lobes of the free appendage margins. The funicles — short as they are — are not normally inserted; rather they seem to be placed somewhat laterally, like in various other cases in Palms described by Uhl & Moore. This may be related with the turning of the ovule. It is my opinion that the term aril — as used by Uhl & Moore — should be avoided for this case. As stated by them the arils — covered by stigmatic tissue — are probably obturators, homologous with sterile ovule primordia (*cf.* their figures of *Latania!*). I fully agree with this view (see my future paper in *Phytomorphology* 26, 1977). The consequence is that ovule primordia differentiating as obturators may be attached to the axis. As a conclusion I think that in the case of *Salacca* the axillary position of the ovule — or ovule pairs, if one partner differentiates as an obturator — may vary slightly either to the bract (carpellary) or axis side. Morphogenetic study of younger stages would offer the solution for this problem.

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