# The Embryology of Aucuba Japonica

by

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In 1878 Eichler made the suggestion that Aucuba japonica might develop fruits apogamously, supporting his opinion on the fact, that he had found well developed embryos though male plants were entirely absent. Nothing having in the meantime been published for or against the the theory of Eichler, Winkler (1908) in his work over parthenogenesis in plants ranged Aucuba amongst the doubtful cases.

Winkler's article caused the second of us writers, when yet being assistant at the botanical laboratory in Utrecht, to take up a cytogical and embryological study of Aucuba. But, leaving Holland for India, the till then obtained results were not published, though the main points of the research were already settled. His meeting in the same laboratory in Buitenzorg with the first named of the authors caused them to work out together the following account.

The question of apogamy in Aucuba was soon settled. All facts found join to prove this not to be the case. Already the experience of the growers tend to show that.

In the platework "Flora" — by the hortulanus Witte of Leiden — we read that the japanese Aucuba, introduced into Europe for its decorate leaves, only then began to produce the beautiful red berries, when male individuals were brought over from Japan. And the "Revue horticole" for 1909 makes the statement that the female Aucuba japonica was introduced into Europe about 1783, but no fruits were found till 1860, when male plants came into european cultivation.

The following experiments show the absolute necessity of pollination. Out of 300 female flowers, isolated by means of paper bags, not a single fruit was formed. And again, 600 other female flowers, that, had been isolated in the same manner after artificial pollination, the great majority produced normal fruits.

Probably Eichler has come to his opinion about Aucuba through the fruiting of a lonely standing female plant, which occasionally had developed male flowers. This is suggested by the fact, that the second writer repeatedly has found male flowers on female stocks. In one case, too, a male inflorescence with 80 purely male flowers was met with on a female plant.

That the reversed might happen, has been found by Lombard—Dumas (1904). This author reports male individuals now and then producing female flowers.

To confirm these observations microscopically, material of Aucuba was fixed and cut. The development of pollen and embryosac offers nothing very unusual. The pollen was easily made to germinate in three hours.

The fact, that Aucuba shows no case of apogamy, is clearly demonstrated by the number of chromosomes in the nuclei of different tissues.

In the second division of the embryosac mother cell 18 chromosomes were numbered in one case and 17 in another. During the pollen formation the number 18 was found, too, in several instances. The nuclei of root tips gave the 2x number of chromosomes repeatedly as 36. In the endosperm the exact number was not made out with absolute exactness. In one mitosis, however, 48 chromosomes could clearly be distinguished of which number at least 30 were nicely arranged in pairs. The figure 54 was awaited, but rather often, as Tischler (1916) recently has pointed out, a lower number is found.

These figures make it highly probable that $x = 18$ and $2x = 36$.

The female flowers of Aucuba remain open for a rather long time. The embryosac is usually not ready untill about 4 weeks after the opening of the flowers. When the flowers open, the megaspores are either not yet or just formed. The divisions in the embryosac take place at long intervals.

Already Warming (1878) described the ovulum of Aucuba japonica as provided with a single, thick integument, surrounding a rather strongly developed nucellus. Figs 1—2 show these features better than any description. The next two figs have been drawn to point out another point of interest [1]). In fig. 3 is the single embryosac mother cell covered with a tapetum only of some few cellayers thickness. This tapetum increases rapidly in all dimensions and has, on fig. 4, already buried the embryosac mother cell at the bottom of the nucellus, where the gametophyte will remain during the following development. As a mighty cap on the embryosac the tapetum continues its growth till late in endospermformation. The ripe embryosac occupies only about $^1/_4$ of the nucellus and seems to get a certain amount of nutrition from there for the ripening of the embryo, the cells of the nucellus being largely filled up with starch grains about that period. In other, till now studied members of Cornaceae, belon-

[1]) Figs 3—12 200 ×.

ging to the genera Benthamia (Jönson 1880) and Davidia (Horne 1909), a rather massiv nucellus has been found. But they differ from Aucuba in that respect that in both genera a many celled sporogenous tissue is developed; in Aucuba we have always seen, as stated above, but a single archesporial cell (figs 3-5).

The embryo sac mother cell having been definitely buried at the base of the nucellus, the negaspores are formed quite normally (fig. 5—7) Almost invariably, of the four megaspores the upper three begin to desintegrate it deserves to be observed that they by no means are crushed by the growing young embryosac, as is so commonly seen.

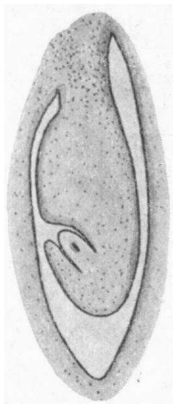

Fig. 1.

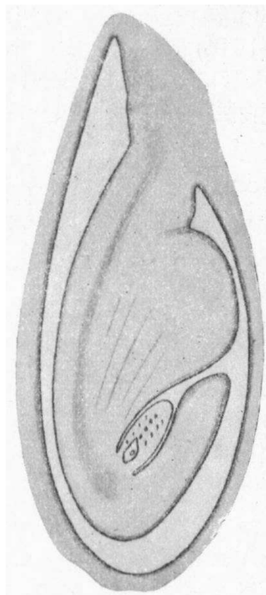

Fig. 2.

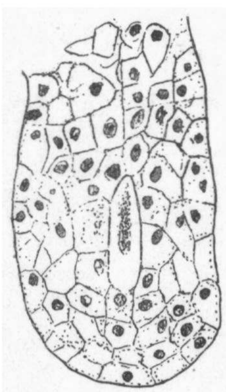

Fig. 3.

Fig. 4.

Fig. 5.

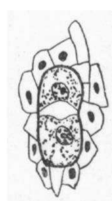

Fig. 6.

Figs 8 and 9 depict the gradual disappearance of their cell content.

In one case, however, it was found that both the megaspores nearest the chalaza and the next following one had begun to germinate. Fig. 10 shows the former one containing two nuclei in resting condition and the later one with the nucleus preparing to divide. The two crushed upper megaspores are to be seen as a dark staining mass on the top of the "row of two". Similar diviations from the usual course of events are regularly met with in Benthamia and Davidia, where either all, the middel one or the chalazal one of the megaspores formed

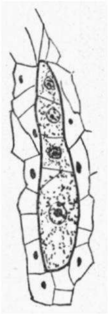

Fig. 7.

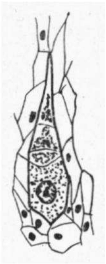

Fig. 8.

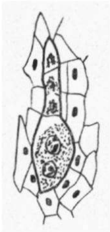

Fig. 9.

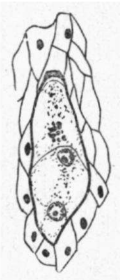

Fig. 10.

in the great sporogenous tissue begin to struggle for dominance. Even for the related family of Araliaceae Ducamp (1902) has figured ressembling stadia. Most often such "abnormalities" are met with only occasionally, especially, when scanty material is used; surely they are of more common occurence than generally supposed and should never be neglected. In another paper one of us (Palm 1915) has discussed at some length the different factors that might be supposed to bring about the growing out of the chalazal megaspore as well as of other cells of the tetrade.

It should be mentioned, too, that the sort of megaspore formation found in Aucuba, suffers from one exception in the family. So in Cornus florida, as reported by Morse (1907). In this plant no walls separate the four megaspore nuclei; they remain in the same mass of cytoplasm, where the upper three of them degenerate.

The development of the gametophyte of Aucuba, posterior to megaspore formation, has proved to be

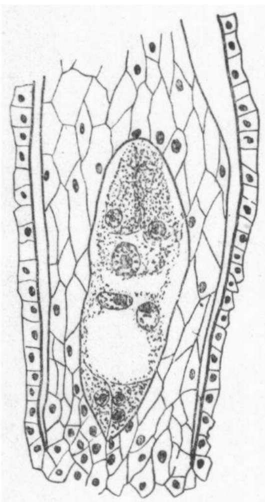

Fig. 11.

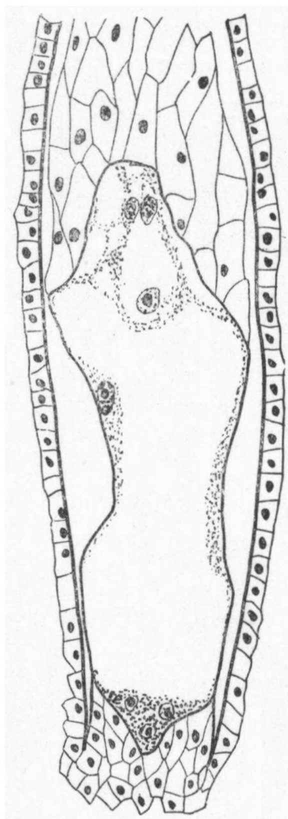

Fig. 12.

remarkably uniforme and as it does not in any respect deviate from the normal type amongst Angiosperms, no figures or description were deemed necessary. The ripe embryosac contains the two rather big synergids — with the characteristical reticulated appearance topwards — the well defined eggcell, the two polars and the three minute antipodals (fig. 11).

The embryo sac is not sooner formed, as it seems, than fertilization might occur. Always fertilization is proceeded by the fusion of the polars. Too, the formation of endosperm is somewhat previous to the begin of the growth of the embryo, so the resting oosphere might sometimes be easily overlooked in the rapidly growing mass of endosperm.

Fig. 12 figures an exception. We feel justified to believe that in this case no fertilization has occured. Nevertheless a considerable growth of the whole sac has taken place as a comparision between figs. 11 and 12 will show. The sac is in an indubitable state of degeneration, the scanty amount of strongly vacuolated protoplasm illustrating that fact sufficiently. The other parts of the ovulum are quite healthy. In spite of the non-occurence of fertilization, the development might, as we have found in some rare cases, be continued to embryoless fruit; of course, then, the embryosac sooner or later completely degenerates. Thus Aucuba japonica is added to the growing list of plants, capable of forming parthenocarpic fruits (Tischler 1912).

In spite of prolonged search we have not been able to find in the material at hand the early stages of endosperm formation. The youngest endosperm seen, contained already sixteen nuclei, each of wich was separated from its neighbours by delicate cell walls. The arrangement of the cells gives the impression that the content of the embryosac has undergone regular division by means of walls since the starting of endosperm formation; but unfortunately we cannot be positiv on that point. As nothing is known about endosperm in Cornaceae, a solution of that question would be rather interesting from many points of view. At the endosperm stage spoken of above, the cells seem to be, at least at the bottom of the embryosac, arranged in two more or less regular rows while upwards their position is more irregular. The lower endosperm cells have a denser plasma and nuclei richer in chromatin, thus suggesting "haustorical" activity. Later stages show the embryosac wholly filled up with a massiv cellular endosperm.

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