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Studies in *Sapindaceae*, I. Embryology of *Dodonaea viscosa*

By

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With 62 Figures

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1. Introduction

The present day knowledge about the embryology of *Sapindaceae* is meagre. SCHNARF 1931 has reviewed the earlier literature. MAURITZON 1936 recorded some embryological stages in *Cardiospermum halicacabum*, *Sapindus marginatus*, *S. mukorossi*, *S. surianeus*, *Dodonaea cuneata* and *Diplopeltis hugelii*. In all these, the type of the ovule and nucellus is same but for the minor variations. DAVID 1938 studied the embryology of *Cardiospermum*, *Sapindus* and some other members of the family. BANERJI & CHAUDHURY 1944 gave an account of some aspects of the life history of *Litchi chinensis*. The embryology of *Cardiospermum halicacabum* has been thoroughly investigated by KADRY 1946, 1950 and NAIR & JOSEPH 1960. JOSHI 1938 has recorded parthenocarpy in *Dodonaea viscosa*, PIJL 1957 has worked on the seeds and arilloids of *Nephelium*, *Euphoria* and *Aesculus*.

2. Materials and methods

Dodonaea viscosa grows locally. The material was fixed in formalin-acetic-alcohol. Usual paraffin procedure was followed. The young flowers

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were cut at 6—10 μ while the seeds, fruits and older flowers were cut at 10—15 μ. Preparations were stained with iron-haematoxylin and combinations such as safranin and fast green, and safranin and light green were used.

3. Observations

3: 1 Organogeny and organography

Flowers are small yellowish and mostly unisexual with three to five sepals. Corolla is absent. Seven to ten stamens in staminate flowers and two to three carpels in carpellate flowers. Glandular trichomes with multicellular stalks and multicellular heads are present on the ovary wall and on the petiole (Fig. 1). The gland precursor cell becomes papillate, protudes out (Fig. 2) and divides twice by vertical divisions (Fig. 3). The resulting three cells undergo transverse divisions (Fig. 4) to form the multicelled stalk. The terminal cell of the stalk by further divisions form the head of the stalk.

Each locule of the ovary contains two ovules, the upper ones are ascending anatropous and the lower ones are hanging anatropous. The

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Explanation of Figures

(arl-arillode; di-disc; eg-egg; end-endosperm; cr-carpel; cot-cotyledon; anp-antipodal cells; hy-hypostase; oi-outer integument; ii-inner integument; oe-outer epidermis; ie-inner epidermis; nu-nucellus; ob-obturator; pt'-pollen tube; se-sepal; sm-stamens; syd-synergids; su-suspensor).

Figs. 1—4. Development of the multicellular glands. — Figs. 5, 6. Development of floral organs. — Figs. 7—12. Sections of anther at different stages. — Fig. 13. Part of tapetum and middle layers. — Figs. 14—16. Meiotic divisions of the microspore mother cell. — Figs. 17, 18. Microspore tetrads. — Figs. 19—21. Pollen grains. — Fig. 26. Primary parietal cell and a sporogenous cell. — Fig. 27. Part of the ovule at the micropylar end to show nucellar cap and deeply stained inner layer of the inner integument. — Fig. 28. Part of an ovule after the fertilization showing the outer layer of the inner integument which has become palisade-like. — Figs. 29, 30. Megaspore mother cells. — Figs. 31, 32. Megaspore tetrads.

Figs. 33—35. Developmental stages of embryo sac. — Fig. 36. An ovule immediately after fertilization. — Fig. 37. Pollen tube entering through the micropylar end. — Figs. 38—39 (Reconstructed) Post-fertilization stages. — Fig. 40. Aggregation of endosperm nuclei at the chalazal end. It is an enlarged portion marked as X in the figura 41. — Fig. 41. L. S. of a seed. — Fig. 42. Cell wall formation in the endosperm. — Figs. 43—54. Various stages of the embryo.

Fig. 55. An outline of the heart-shaped embryo. — Fig. 56. An enlargement of the portion marked in the Figure 55, showing the root initials. — Fig. 57. Portion of the mature embryo enlarged showing its contents. — Fig. 58. Mature embryo with two coiled cotyledons. — Figs. 59—62. Stages in the development of the seed coat.

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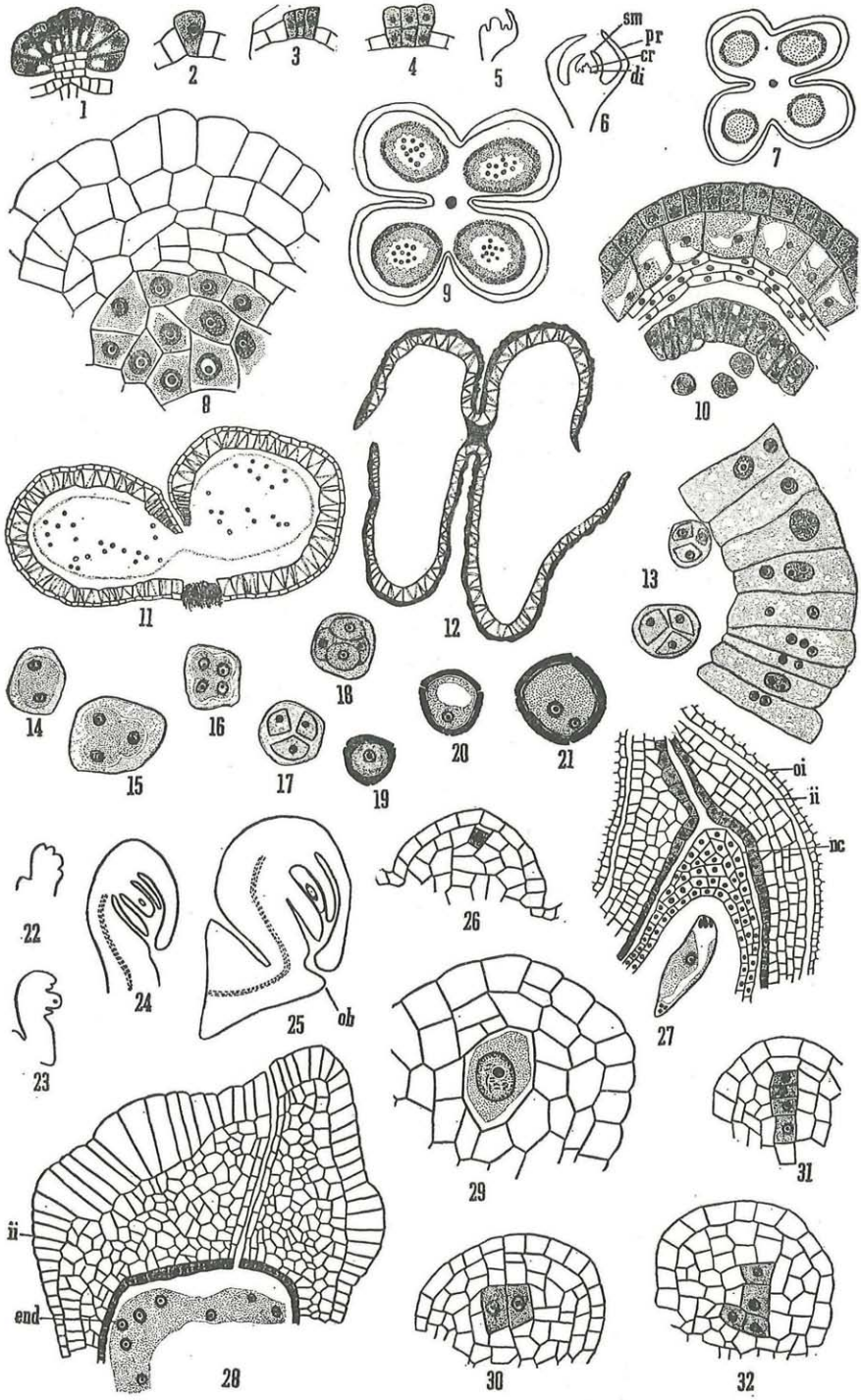

Figs. 1—32. For explanation see opposite page.

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ovules later on become ana-amphitropous. A distinct placental obturator is present, which grows to cover the micropylar part of the ovule (Fig. 25).

The floral primordium of the female flower arises in the axil of a bract. Soon the sepals arise and cover the apex. The staminodes develop as eight to ten humps of the meristematic tissue on the inner side of which arises the disc in the form of ring. The carpels arise as three groups of cells. They grow upwards and later on fuse by their margins. The terminal portion elongates gradually to form the style and a trifid stigma (Figs. 5, 6).

3: 2 Microsporangium and male gametophyte

The young anther of the staminate flower is fourlobed (Fig. 7, 8). The primary parietal layer cut off by the archesporium divides to form four layers of cells beneath the epidermis .The first layer beneath the epidermis is endothecium, the second, third and fourth form the middle layers, while the last one develops into the tapetum. The cells of endothecium elongate radially and become thickened and vacuolated at the time of the meiotic division (Fig. 9, 10). The characteristic fibrous thickenings develop only after the formation of the pollen grains in the microsporangium (Figs. 11, 12).

The cells of the tapetum are uninucleate at first but become two- to three-nucleate at the time of meiotic divisions in the microspore mother cells. Some of the tapetal nuclei are very large and contain many nucleoli. The tapetal cells are vacuolated and the tapetum is of a glandular type (Fig. 13). The middle layers and the tapetum get absorbed leaving no traces in the mature anther (Fig. 12).

The primary sporogenous cells function directly as the spore mother cells (Fig. 8). The mother cells undergo usual meiotic divisions in a simultaneous manner. Isobilateral as well as tetrahedral tetrads are formed, of which the latter are predominant. Quadripartition takes place by centripetal furrowing and later on the microspores acquire their own walls (Figs. 14—18).

In the mature pollen the exine is very thick and ornate while the intine is thin. The pollen grains are tricolporate (Figs. 19—21). The development of the male gametophyte is in a normal way. The pollen grains are shed at two-celled stage.

At maturity the partition wall between the two microsporangia breaks down (Fig. 11). The mature anther wall consists only of the fibrous endothecium and remnants of the epidermis.

3: 3 Megasporangium and female gametophyte

The ovules are bitegmic and crassinucellate. The ovular protuberance is erect at the earlier stages (Fig. 22) but soon curves down at the megaspore mother cell stage (Fig. 23) and at the binucleate embryo sac stage (Fig. 24) it is almost anatropous. Figure 25 shows the ovule at the eight-nucleate embryo sac stage.

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The inner integument develops when the hypodermal archesporium can be distinguished in the young nucellus (Fig. 26). The outer integument also develops soon after. The micropyle is formed by the inner integument. At the mature embryo sac stage the inner integument consists of five to six layers (Fig. 27) and the outer of eight to ten layers.

The inner most layer of the inner integument and the outer most layer of the outer integument stain deeply with safranin probably due to the presence of tannin. The nucellar cap is formed by the repeated divisions of the nucellar epidermis. It consists of five to seven layers of cells at the mature embryo sac stage (Fig. 27). After fertilization, the outer layer of the inner integument becomes palisade-like at the micropylar region (Fig. 28).

A single hypodermal archesporium cell cuts off a primary parietal cell (Fig. 26). This in turn divides once or twice and the megaspore mother cell comes to lie three or four layers deep (Fig. 29). Usually a single megaspore mother cell is observed but sometimes two are seen lying side by side (Fig. 30).

The megaspore mother cell increases in size and undergoes the usual meiotic divisions to give rise to a linear tetrad (Fig. 31). Sometimes an almost T-shaped tetrad of megaspores is observed (Fig. 32).

Usually the chalazal megaspore functions. The functioning megaspore nucleus divides in the usual way to give rise to a Polygonum-type of embryo sac (Figs. 33—35). The mature embryo sac has a narrow chalazal end and a broad micropylar end. The synergids are hooked. The three antipodal cells seen degenerate. The mature embryo sac contains many starch grains. Thick-walled cells constitute the hypostase (Fig. 36).

3: 4 Pollination and fertilization

Entry of the pollen tube into the ovule is through the micropyle (Fig. 37). Figure 38 shows the remains of a pollen tube and a number of endosperm nuclei. The zygote, the remnants of the pollen tube and a few endosperm nuclei are observed in Figure 39.

3: 5 Endosperm

The primary endosperm nucleus divides earlier than the zygote and there are formed nearly thirty free nuclei at the two-celled proembryo stage. Since the early divisions are not followed by wall formation, the endosperm is of Nuclear type. A large number of free nuclei are formed before wall formation takes place and there is an aggregation of endosperm nuclei in dense cytoplasm at the chalazal end of the embryo sac (Fig. 40, 41). Some of the nuclei are multinucleolate. The free nuclear chalazal end of the endosperm functions as a haustorium.

The cells of the endosperm are richly cytoplasmic and contain prominent nuclei (Fig. 42). During the enlargement and maturation of the

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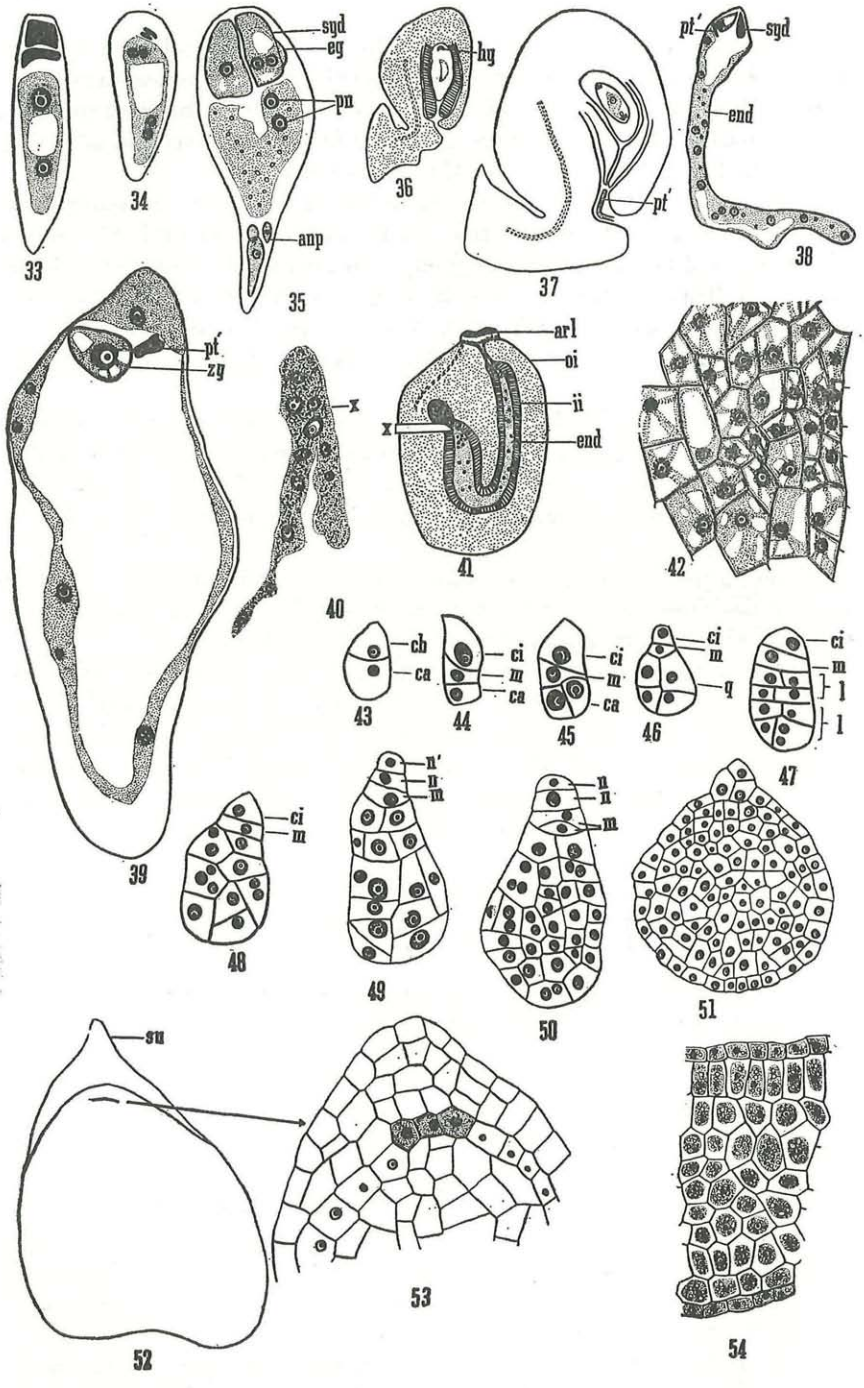

Figs. 33—54. For explanation see page 84.

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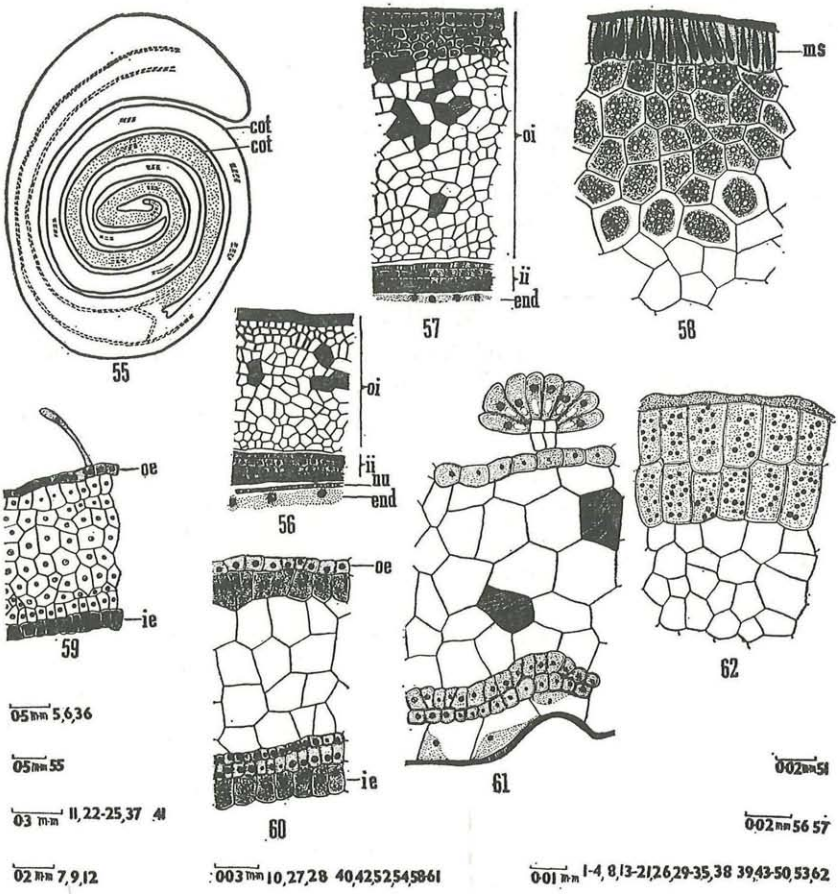

Figs. 55—62. For explanation see page 84.

embryo the endosperm is consumed and no trace of it is seen in the mature seed.

3: 6 Embryo

The zygote divides transversely to produce a terminal cell **ca** and a basal cell **cb** (Fib. 43). The basal cell **cb** undergoes a transverse division giving rise to cells **m** and **ci** (Fig. 44). Later on the cell **ca** divides by a longitudinal wall resulting in an inverted T-shaped proembryo composed of four cells (Fig. 45). Each of the daughter cells of **ca** now divides by a vertical wall at right angles to the first, so as to result in the quadrant stage (Fig. 46). The quadrant cells in turn become partitioned by transverse

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walls, to form the octant (Fig. 47). Of these the lower four **l** are destined to give rise to the stem tip and cotyledons and the upper four **l'** to the hypocotyl. All the eight cells of the octant divide periclinally (Fig. 48). The cell **ci** divides into **n** and **n'** (Fig. 49). The cell **m** is the hypophysis and gives rise to the root tissues and to the root cap. The cell **m** also divides into two daughter cells (Fig. 50). The root initials are laid down even at the mature globular stage (Fig. 51). In the heart-shaped embryo root initials are quite distinct (Figs. 52, 53). The cells of mature embryo contain a large amount of reserve food (Fig. 54).

3: 7 Seed

Due to the enlargement of the embryo sac, much of the nucellus is crushed and only three or four layers of it remain at the globular stage of the embryo. Gradually these are also consumed and no trace of the nucellus is left afterwards.

The mature embryo is typically dicotyledonous. The two cotyledons are unequal in length and are coiled (Fig. 55). The vascular tissue is well differentiated in the hypocotyle and extends into the cotyledons. Each seed contains only a single embryo.

At the globular stage of the embryo there are about five to six layers of cells in the inner integument and eleven to twelve layers in the outer integument (Fig. 56). The outer epidermis of the outer integument elongates radially. Five to six layers of cells just below this epidermis are thick-walled and darkly stained, while the remaining layers are thin-walled and parenchymatous (Fig. 57).

The elongated cells of the epidermis in the mature seed contain macrosclerides (Fig. 58). Below this layer, six to seven layers of cells contain aleurone grains. Some traces of the inner integument were seen in the micropylar region of the mature seed.

The ovary wall is eight-to ten-layered during the early stages (Fig. 59). The inner epidermis contains dense cytoplasm in comparison to the outer. Unicellular and multicellular glands are present on the outer epidermis. After fertilization the ovary wall increases in thickness and undergoes changes (Figs. 60, 61).

3: 8 Arillode

A small arillode composed of parenchymatous cells with a large amount of deep staining contents is present (Fig. 62).

4: Discussion

The pollen grains are tricolporate and usually have a thick exine and a thin intine. They are shed at the two-celled stage, also as reported by Nair & Joseph 1960 in *Cardiospermum halicacabum*. The ovules become ana-amphitropous at the postfertilization stage. The presence of inte-

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gumentary bundles in *Dodonaea viscosa* is not a new observation. This is already recorded by NAIR & JOSEPH 1960 in *Cardiospermum halicacabum*. The obturator in *Dodonaea viscosa* is placental in origin. BANERJI & CHAUDHURY 1944 while studying the embryology of *Litchi chinensis* have stated: "The outer integument is absent at the ventral side of the ovule where it is congenitally fused the funicle. At this region a hump-like obturator is present".

The occasional occurence of the two megaspore mother cells in one case of *Dodonaea* seems to be peculiar though only one of these develops further. According to NAIR & JOSEPH 1960, in *Cardiospermum halicacabum* sometimes many of the archesporial cells develop into megaspore mother cells.

The occurence of almost inverted T-shaped megaspore tetrad in *Dodonaea viscosa* has been recorded by the authors. Such tetrads are already on record in many other plants (See MAHESHWARI 1950).

The endosperm is of Nuclear type. MAURITZON 1936 stated that in some members of *Sapindaceae* no wall formation takes place in the endosperm even when the embryo is fully developed. However he observed a single layer of cellular endosperm in *Cardiospermum halicacabum, Sapindus marginatus* and *Diplopeltis*. KADRY 1946 reported that endosperm is free nuclear in *Cardiospermum halicacabum* even when the embryo is mature, while NAIR & JOSEPH 1960 have observed in the same plant one or two layers of cellular endosperm in the mature seeds. The present authors have observed 6—8 layers of cellular endosperm at the globular stage of the embryo in *Dodonaea viscosa,* but in mature seeds there is no trace of the endosperm. The occurence of endosperm haustorium at the chalazal end in this plant supports to this belief.

KADRY 1946 has described an Onagrad-type of embryo in *Cardiospermum halicacabum* while NAIR & JOSEPH 1960 in have reported the Asterad-type of embryo. The development of embryo in *Dodonaea viscosa* is however of Onagrad-type.

There is a lot of controversy regarding the origin and nature of the aril in *Sapindaceae*. PIJL 1957 has distinguished between aril and arillode. According to him a small arillode is present in *Dodonaea viscosa*. No true funicle is present in this plant.

5. Summary

Glandular trichomes are present on the ovary wall and on the petiole. The floral parts develop in the sequence sepals stamens and gynoecium. Each locule of the ovary has two anatropous ovules. Placental obturator is present. The development of the male gametophyte is normale. The pollen grains are shed at the two-celled stage. The development of the female conforms to Polygonum-type and the entry of pollen tube into the ovule is through micropyle. The development of the embryo is of Onagrad-type.

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The endosperm is Nuclear. Endosperm haustorium at the chalazal end is present. A small arillode is present which is actually a fleshy outgrowth of the integument.

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