MORPHOLOGICAL STUDIES IN SOLANACEAE—II

Morphology, Development and Structure of Seed of *Browallia demissa* Linn.

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The ovule of *Browallia demissa* Linn. is anatropous, unitegmic and tenuinucellate. The embryo, which is slightly curved, is of the Solanad type. The starchy cellular endosperm envelops the embryo. The testa is only two-layered. The outer epidermis consists of very large cells whose inner tangential and part of the radial walls are thickened and lignified. The endothelium is tangentially elongated. The seed with verrucate surface is deep chocolate and scabiform.

The development of ovule and embryo sac in *Browallia demissa* was reported in the first paper of this series (Mohan 1966). The ovule is anatropous, unitegmic and tenuinucellate. The developing female gametophyte consumes the nucellus and comes in direct contact with the endothelium. This paper describes the post-fertilization development of the ovule.

Souèges (1907, 1920*a*, *b*) studied the embryogeny of a number of solanaceous genera and pointed out that it follows a uniform pattern. Bhaduri (1936), on the other hand, observed a number of variations in *Nicotiana plumbaginifolia*, *Petunia nyctaginiflora*, *Physalis minima* and *Withania somnifera*. He stated that the interval between fertilization and division of the zygote varies in different genera of the Solanaceae.

In *Physalis minima*, Bhaduri traced four principal types of embryonal development. According to him, the suspensor consists of five to ten cells.

Choudhury (1958) studied the development of seed of *Lycopersicum esculentum* and also reviewed the work of Tognini (1900), Smith (1935) and Sanders (1948). Tognini investigated the embryo development in *Atropa, Datura*, *Physalis* and *Solanum*; Smith followed pollination and life-history of tomato; and Sanders described embryo development in four self- and cross-pollinated species of *Datura*.

A review of literature on endosperm shows much variation in its development. Nuclear type has been reported in *Salpiglossis* (Hofmeister 1858) and *Schizanthus pinnatus* (Samuelsson 1913), and Helobial in *Hyoscyamus niger* (Sevensson 1926). These reports need confirmation. Bhaduri (1936), Cooper (1946), Choudhury (1958), Dnyansagar and Cooper (1960) and Mohan Ram and Isha Kamini (1964) observed Cellular type of development in one or more of the following: *Lycopersicum esculentum, Nicotiana plumbaginifolia, Petunia nyctaginiflora, Physalis minima, Solanum phureja* and *Withania somnifera*.

Ferguson's (1927) observations in *Petunia* show that, before the pollen tube discharges sperms, the secondary nucleus divides to form two cells. Similar observations by Bhaduri (1936) in *Lycopersicum esculentum* and *Petunia nyctaginiflora* are doubtful. Magtang (1936) and Dnyansagar and Cooper (1960) noted a chalazal haustorium in *S. melongena* and *S. phureja*, respectively, which absorbs certain nutrients from the adjoining cells of the vascular strand. It is unfortunate that no details are given regarding these nutrients.

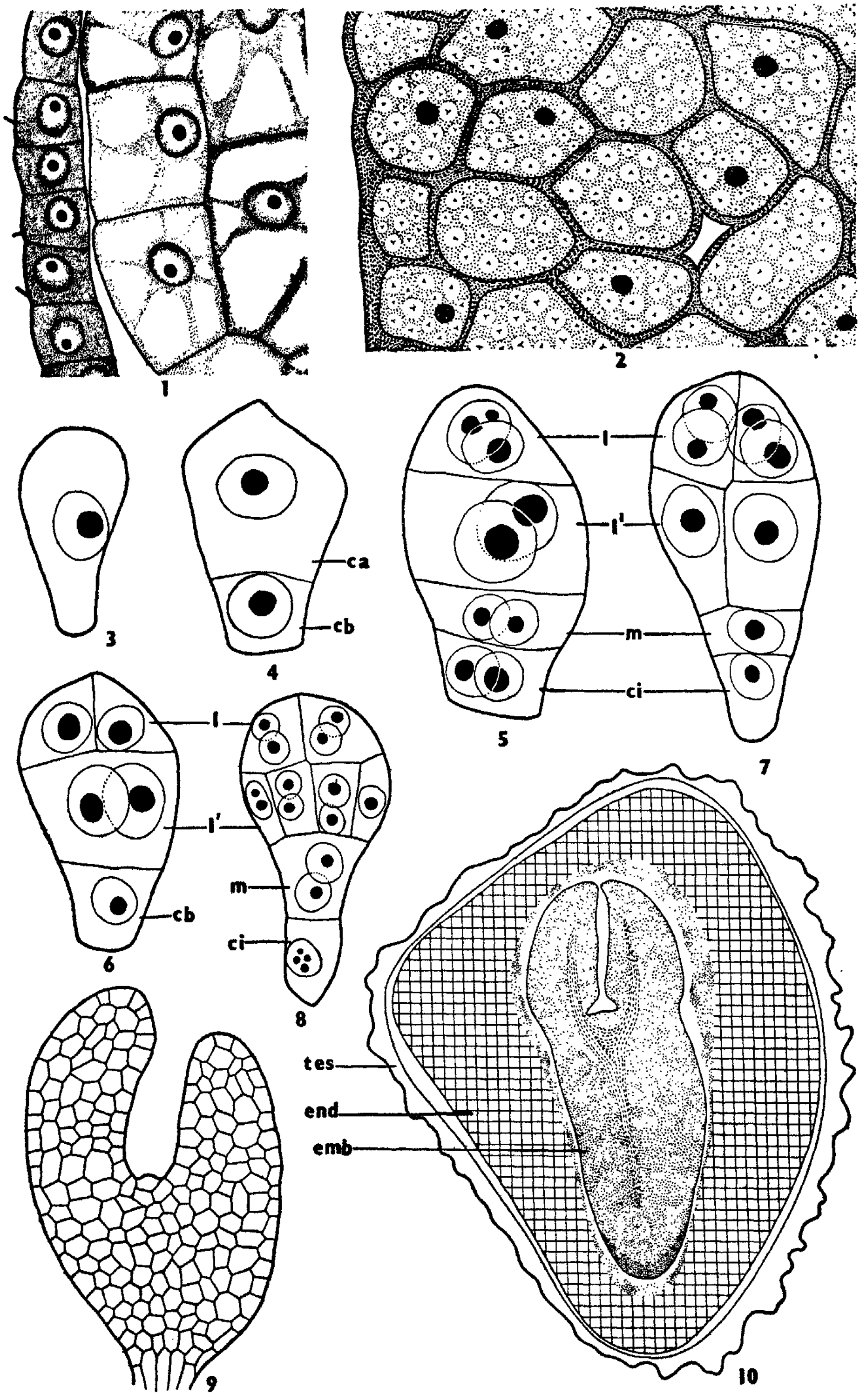
Endosperm:

During the present investigations the author could neither observe the earlier divisions of endosperm nor the haustorium. The earliest stage showed a four-celled endosperm. With further development of the seed, the endothelial cells become progressively compressed. There is no starch in the endosperm cells during earlier stages of seed formation. The cells are thin-walled (Fig. 1). Later on, however, their walls become thick due to the deposit of cellulose. Starch then develops slowly and fills up the cell cavities completely (Fig. 2). A good amount of endosperm is consumed by the developing embryo, still a massive endosperm persists in the mature seed. The inner layers of endosperm, which are near the embryo, are depleted of starch by the growing embryo while other layers are still densely filled with it. The size of starch grains varies from two to six. The nuclei show an appreciable increase in size. Later they are discernible only in some cells as deeply stained bodies.

Embryo:

The zygote (Fig. 3) divides transversely when the embryo sac contains at least eight or ten endosperm cells. The bicelled proembryo possesses a bigger terminal cell, *ca*, and a basal cell, *cb* (Fig. 4). Both the cells divide transversely thus forming a linear proembryonic tetrad, consisting of *l*, *l'*, *m* and *ci* respectively (Fig. 5). Rarely, it was found that the cell *ca* divides transversely while the cell *cb* does not divide at this stage, resulting in a three-tiered proembryo, whose uppermost cell, *l*, undergoes a vertical division followed by a wall (Fig. 6). Further divisions in this type of proembryo were not observed.

The next division in both *l* and *l'* is vertical and at right angles to each other, forming a quadrant. Due to one more longitudinal division in each daughter cell of *l* and *l'*, at right angles to the previous division, an octant is formed. The second division in *l'* is somewhat delayed on account of which a six-celled stage intervenes (Fig. 7). Periclinal walls soon arise in the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l' tier of the octant (Fig. 8) followed by those in *l* tier. The proembryo thus acquires a single layer of dermatogen on the outside and ultimately a several-celled globular proembryo is formed. Further divisions in the outer layer are always anticlinal while in the inner layers they take place in all possible directions.

The cotyledonary primordia arise laterally at the apical end of the globular proembryo, leaving a depression in the middle, thus forming a heart-shaped embryo (Fig. 9). The mature embryo shows two comparatively small cotyledons and a large hypocotyledonary axis which is formed by repeated divisions of the cells of the lower octant of the globular proembryo. The suspensor is two-celled and degenerates before the embryo reaches maturity. The mature embryo is slightly curved (Fig. 10). It lies in the middle of the seed with its vascular supply formed of procambial strands. The cotyledons do not show any differentiation of palisade tissue at this stage.

Testa:

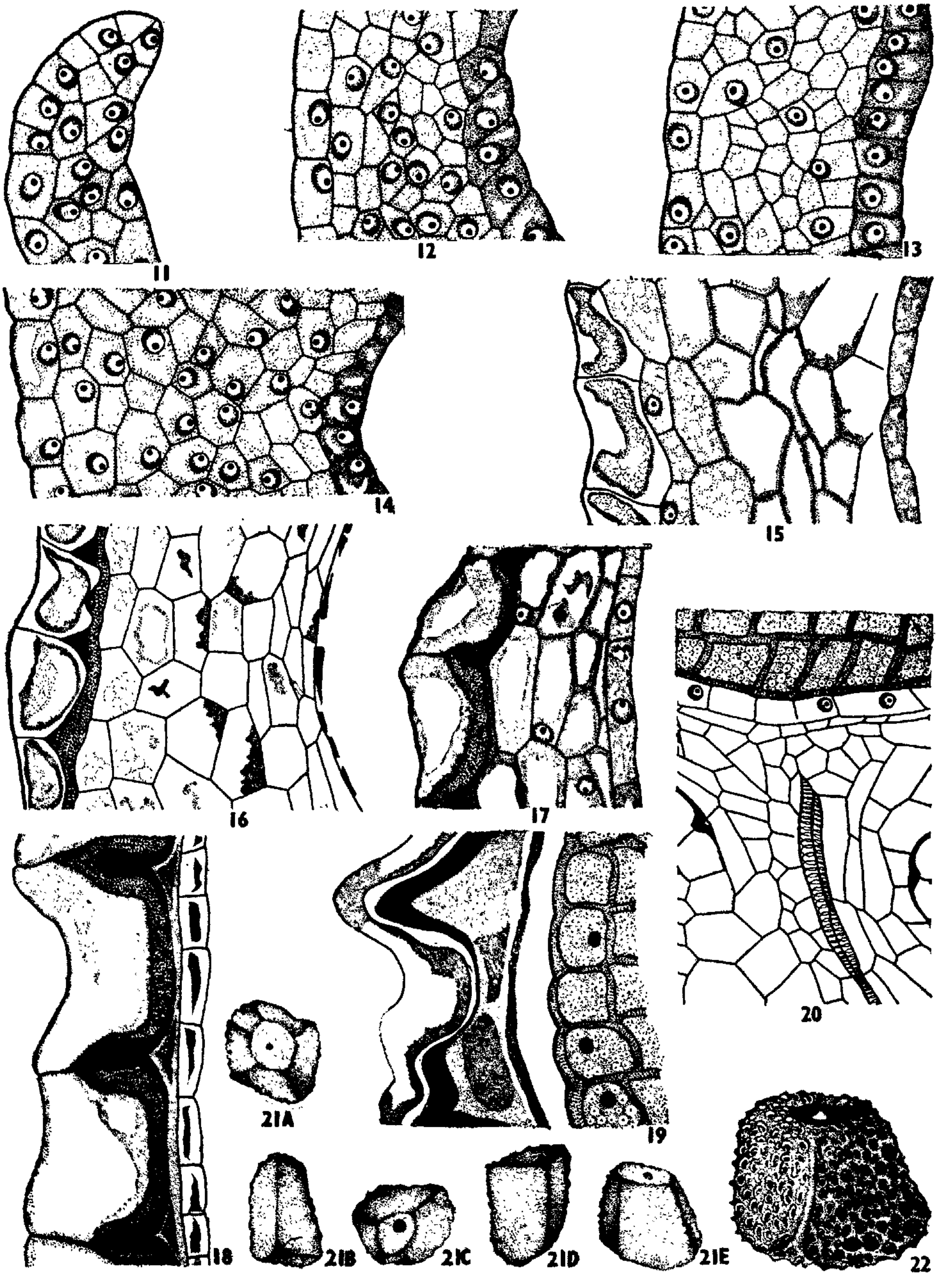
At the megaspore tetrad stage the integument consists of three or four layers (Fig. 11). At the two-nucleate stage of embryo sac the integument shows six or seven layers (Fig. 12). The inner epidermal layer elongates radially and the outer one tangentially. Vacuoles appear in the entire integumentary cells. At the four-nucleate stage the inner epidermis forms an endothelium (Fig. 13). By the time the zygote is formed an appreciable change is discernible in the integument which now possesses nine or ten layers of cells with prominent vacuoles (Fig. 14).

With the extension of endosperm, the middle layers of integument become somewhat compressed. This is quite clear in young seeds showing the quadrant stage of the proembryo. The cytoplasm of the outer epidermis starts degeneration and some hypodermal layers adjacent to the outer epidermis show an accumulation of starch grains. In the middle layers the cytoplasm can be seen only at the periphery, the centre of these cells being vacuolar (Fig. 15).

It is interesting to find that the endothelium persists up to maturity of the embryo. As the seed matures the cells of the endothelium show some well-marked changes. These cells, which are radially elongated to start with, begin to grow tangentially; their dense cytoplasm becomes vacuolar and the cells become extremely elongated.

At the globular stage of the proembryo the inner tangential wall of the outer epidermis becomes thickened but the thickening is of cellulose (Fig. 16).

FIGS. 1–10. Endosperm and embryo. 1, L.S. portion of endosperm showing thin-walled uninucleate cells at early stage of embryo. ×765. 2, same from mature seed; note the thick-walled cells with starch grains and degenerated nuclei. ×550. 3–7, developmental stages of embryo. ×1260. 8, early globular proembryo showing periclinal division in *l'* tier. ×765. 9, heart-shaped embryo. ×350. 10, L.S. mature seed (semi-diagrammatic). ×40.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At the heart-shaped stage the thickenings of the integumentary epidermis show the beginning of lignification (Fig. 17). In a nearly mature seed the greater part of the testa is found to be only two cell-layers thick, being formed of the outer and inner epidermal layers of the integument (Fig. 18). At some places, however, there is only one layer of cells left while at others a layer of small degenerating mesophyll cells is discernible jutting into the basal part of the junction of two outer epidermal cells of the testa (Fig. 19). In a mature seed the testa possesses degenerating cytoplasm as very joint markings. The vascular supply, which is promeristematic in ovular stage, forms well-developed xylem and phloem. It travels through the raphe to terminate at the chalaza (Fig. 20).

There is a heavy deposition of starch in the placenta prior to detachment of the seed. A few layers of cells surrounding the vascular supply in the chalazal region are conspicuous by the absence of any starch grains. This suggests that the nutrition supplied by the vascular strand to the developing seed is translocated in a soluble form; when an appreciable quantity of it is deposited in various layers of the seed it begins to be transformed into an insoluble form, the starch, which as already pointed out, first appears in the outer layers.

External morphology of seed:

The seeds are somewhat flattened, scabiform and more or less rectangular (Fig. 21 A–E). The funiculus is present in a wide depression of the seed whose micropylar end is slightly pointed. The surface (Fig. 22) is more or less verrucate (having wort-like outgrowths). It is deep chocolate and under the reflected light of sterioscopic microscope shows several shining dots on each wort. The size of the seed varies from 3·8 to 4·9 mm in length and 2·9 to 4·00 mm in breadth and the weight of a hundred seeds is 0·1 gm.

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FIGS. 11–22. Seedcoat and seed (Fig. 11 from distal part of the integument and Figs. 12–19 from its middle). 11, L.S. portion of integument at megaspore tetrad stage. ×510. 12, 13, L.S. part of integument at two-, four-nucleate embryo sac stage respectively. ×510. 14–17, same at zygote and quadrant, early globular and heart-shaped stages of embryo respectively; 14–16, ×287; 17, ×433. 18, L.S. testa at maturity formed of outer and inner epidermal layers only; note marked thickening of the inner tangential wall and part of the radial walls of the outer epidermis. ×366. 19, L.S. testa represented by epidermal cells and occasional mesophyll cells. ×433. 20, L.S. funicular region showing vascular supply at maturity. ×253. 21, 22, various shapes of seeds. Seed enlarged to show verrucate testa. Note hilum projection is surrounded by a depression.

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