have been due to a limiting gas exchange rate at $H_1$ when fruits had only begun to ripen and $CO_2$ production rates were low. By $H_3$, the fruit tissue barrier was no longer the limiting factor to gas exchange and the $CO_2$ was perhaps indicative of a greater respiratory and ripening rate, as indicated by significant negative correlations of internal $CO_2$ with firmness.

Respiratory (5) and $C_2H_4$ production (4, 3) rates have been shown to be correlated with the $CO_2$ and $C_2H_4$ contents respectively of the internal atmospheres of apples. The data also show that a commonly utilized index of quality, i.e. red color, could not be used as an accurate predictor of other quality indices such as percent soluble solids and firmness as has been done with tomatoes and cherries (8, 9).


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# Placental Tissue and Ovule Development in 'Lodi' Apple[1, 2]

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*Abstract.* The 'Lodi' apple has heavy bearing characteristics. This study shows it to have profuse numbers of ovules compared with other commercial cultivars. The principal morphological difference between 'Lodi' and other cultivars is that 'Lodi' contains numerous smaller seeds attached to the placental tissue, not only at the proximal end, but extending all the way to the distal end.

The 'Lodi' apple, known for heavy bearing, has distinct morphological differences in placentae and ovullary attachment compared to 'Delicious', which does not set heavy crops of fruit. Variability of fruit-set continues to be of great concern to commercial apple growers. The 'Lodi' apple originated in Geneva, New York in 1924 from the cross 'Montgomery' X 'Yellow Transparent'.

Studies have shown definite morphological differences in placental and ovule attachment between 'Jonared' and 'Golden Delicious' compared with 'Starking' (7, 8). These differences appear at the ovule base where it attaches to placental tissue, with the ovullary vascular strands being constricted as they enter the proximal end of the ovarian locule. A comparison of 'Jonared' and 'Golden Delicious' showed the ovules to be supported by a well-differentiated vascular system entering a thick, well-formed placental tissue. Earlier studies of fruit setting in 'Delicious' revealed embryo-sac irregularity (3).

Crane (1) states "the asymmetrical growth of other fruits in which fertilization in some of the ovules does not take place or in which abortion of some ovules occurs may be ascribed to the lack of gradient being set up by them. Conversely, the larger the number of developing seeds in a fruit, the larger the number of sinks toward which nutrients flow and the greater the growth and development of the fruit".

MacArthur and Wetmore (5) found that ovules of 'Wagener' are longitudinally oriented in bi-partite locules, with one ovule on each side of the locule. There is no such regularity of ovule orientation in 'McIntosh'. Ovules in 'McIntosh' are generally horizontal in position, stretching across the bi-partite locule or occupying the central cavity at the axis.

In aborted ovules, placentae had not developed sufficiently to be good supportive tissue for functioning normal ovules (7, 8).

Murneek (6) reported "the polyembryonic apple fruit usually does not set unless fertilization has occurred in a considerable number of the 10 ovules. With self-pollination, the average number of seeds per fruit was 3-5 or less, while with good cross-pollination it was 5-8 and up to 10. When the crop is fairly heavy, fruits with less than 3 seeds usually abscise. There is a relationship not only between seed number and fruit size but also between leaf area and fruit volume. When fruit set is relatively large, then foliage becomes the limiting factor; when it is light, seed number seems to determine size of fruit".

Crane (1) concluded that marked correlations exist between seed number and ultimate fruit size, and also between seed distribution and fruit shape.

Tukey and Young (9) reported that the cartilaginous portion of the carpels develops rapidly for 2-4 weeks after full bloom,

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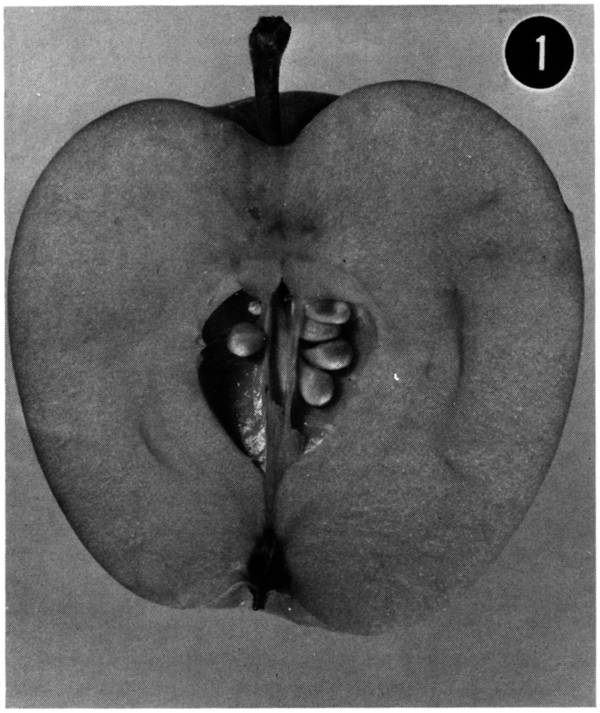


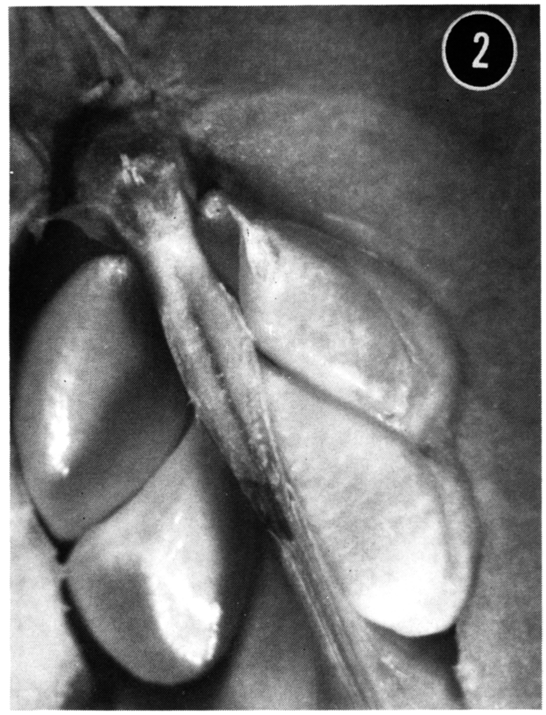




*Fig. 1, 2.* Longitudinal section through a mature fruit showing seed complement orientation in the carpel cavity.



reaching max size in transverse diameter earlier than other tissues making up the bulk of the fruit. The fleshy portion of the carpels continues growth approx 2 weeks longer and is the next tissue to reach max size.

Dorsey (2) found that suppression of the embryo sac, as evidenced by a reduced number of nuclei or their early disintegration, occurs in the weaker growing flowers before bloom. With greater tree or spur vigor, organization of the embryo sac develops further and persists longer. Consequently, fertilization is impossible in a large number but variable proportion of the ovules of apple flowers. He also discussed the extensive suppression of ovules in ripe fruits. Even when grown under the best cultural conditions, a large proportion of ovules may be lost as far as seed production is concerned.

Luckwill (4) found a hormone first appearing in the seed in large quantities 30 days after petal fall. Its appearance coincided with the formation of the endosperm and with cessation of the post-bloom drop. These events coincide with the phasic development described by Murneek (6).

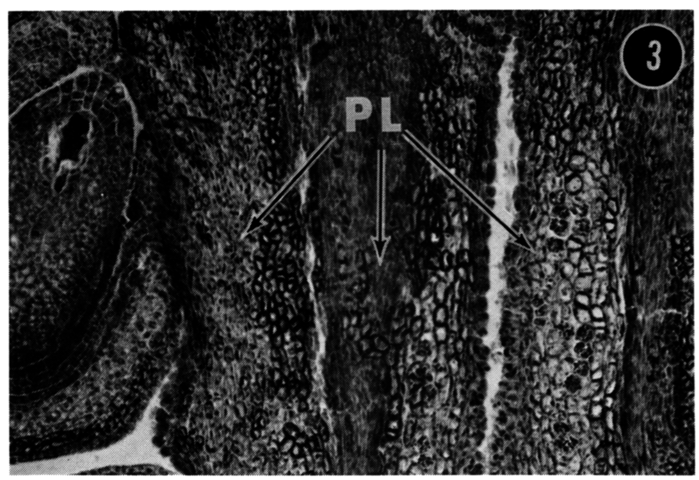
The 'Lodi' apple will have more seed development than other fruit cultivars. Under normal growing conditions, this cultivar usually sets too many fruit and requires heavy thinning for good size development. Conversely, Hartman and Howlett (3) suggested that delayed development and early degeneration of the embryo-sac nuclei at and subsequent to anthesis has a genetic basis in 'Delicious', thus requiring the most satisfactory conditions for pollination.

This study provides one basis for comparing 'Lodi' apples with other cultivars having a tendency for inadequate fruit set.

### Materials and Methods

Samples were collected 4 times, at anthesis which included (terminal) "King" blossoms, 10 and 31 days after full bloom, and at fruit maturity, with 40 samples (flowers or fruit) collected at each date.

The material was killed and fixed in formalin-acetic-alcohol, dehydrated through alcohol-xylol and infiltrated with paraffin (melting point 52.5°C). Sections were cut longitudinally at 12$\mu$ and stained with safranin and fast green.



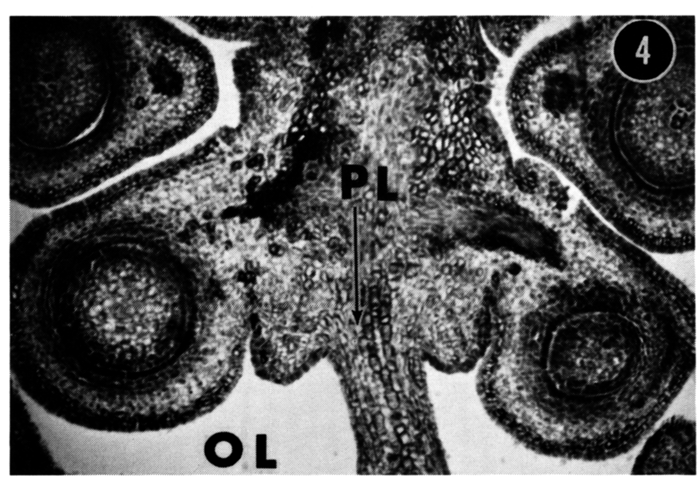




*Fig. 3, 4.* Longitudinal section showing placental tissue (PL) with ovule attachment and orientation in the ovarian locule (OL). Fig. 3, X 80; 4, X 100.

## Results and Discussion

A median-longitudinal section through the mature fruit shows location of seeds and the locular cavities (Fig. 1, 2). It was evident that there were 3-4 seeds in each carpel, and in some cases there was a total of 20 seeds in 5 locules. The seeds were attached to the placental tissue from the proximal to the distal end (apex) in the carpel cavity. In hand sectioned mature fruit, the seeds shattered from the carpel cavity so that it was not possible to obtain illustrations for this stage of development. Fruit growth had separated the carpel cavities, and the placental tissue (axial in orientation) was separated into individual strands (Fig. 2). This abundance of seed development in 'Lodi' may be compared with the fewer number of seeds found in 'Jonared' and 'Delicious'. Also, in the latter cultivars, the number of ovules and their point of origin on the placental tissues varied (7, 8).

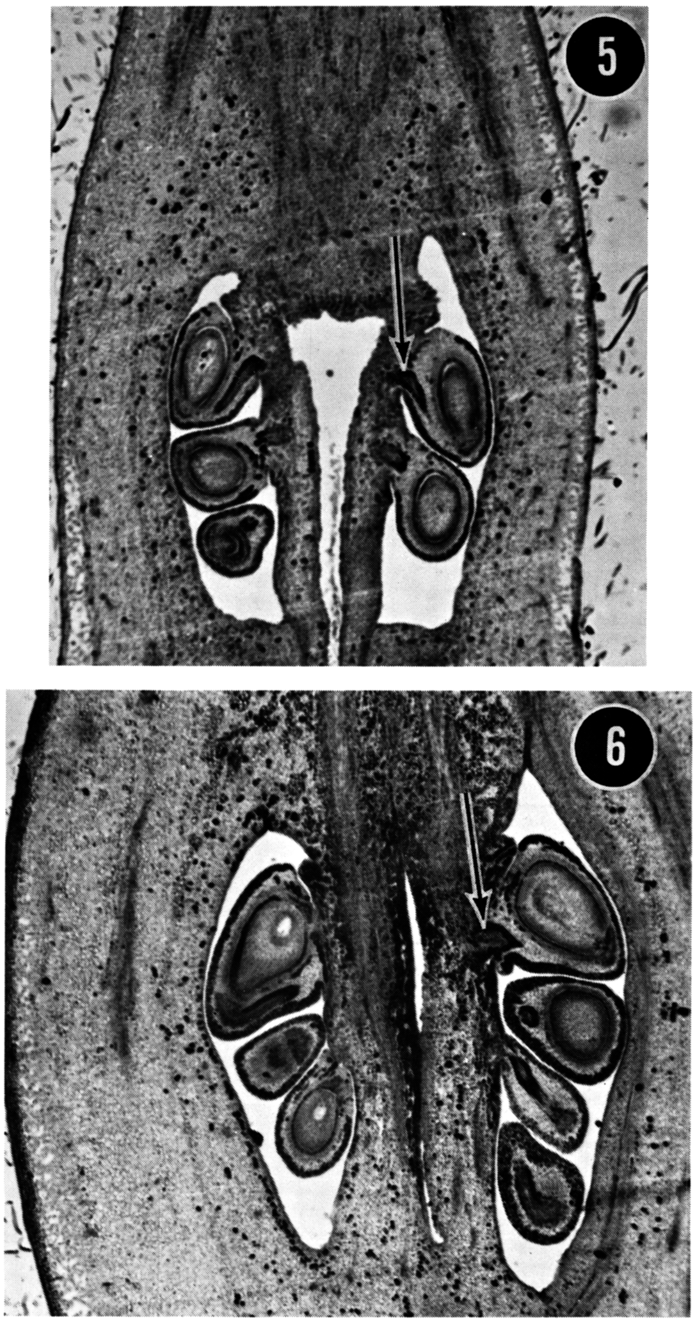


*Fig. 5, 6.* Longitudinal section showing ovule orientation of 'Lodi' at anthesis. Arrows indicate funicular bundle attachment to placentae. Both X 16.

Placental tissue supporting ovullary development at anthesis, as indicated by arrows, shows viable meristematic activity at the point of ovule attachment to the placentae (Fig. 3, 4). Due to plane of sectioning, the outline of other carpel cavities can not be seen. Transverse thickness of tissues separating the carpel cavities was well defined. Placental tissue (Fig. 3) produced a greater mass of parenchymatous cells at the point of ovullary attachment in 'Lodi' than in 'Jonared', 'Golden Delicious' or 'Starking' (7, 8).

The ovule attachment of 'Lodi' differed from that of 'Starking' (8) in that the ovules were attached to the placental wall at several points which occurred from the proximal to the distal end of the carpel cavity. The transverse diameter of this tissue was greater than that of 'Starking'. Typical placental tissues were meristematic with large vascular bundles supporting each ovule (Fig. 4). The regularity in pairing of the ovules was found throughout the locular cavity and was evident from the proximal to the distal ends of the placentae. Ovules of 'Starking' were located at the proximal end of the cavity. Vascular bundle branching occurred at one point and resulted in constriction of the supporting tissues in relation to these vascular bundles. This was particularly true with abortive ovules.

As many as 4 viable ovules appeared in each carpel cavity at full bloom (Fig. 5, 6). The ovules are oriented longitudinally in the fruit, and encompass the entire area of the placental tissue (proximal to distal end). As many as 20 seeds were found as a full compliment for 5 locules. Placentae at this stage of development had thick supporting tissues, including unbroken vascular strands continuing into the vascular bundle (Fig. 6).

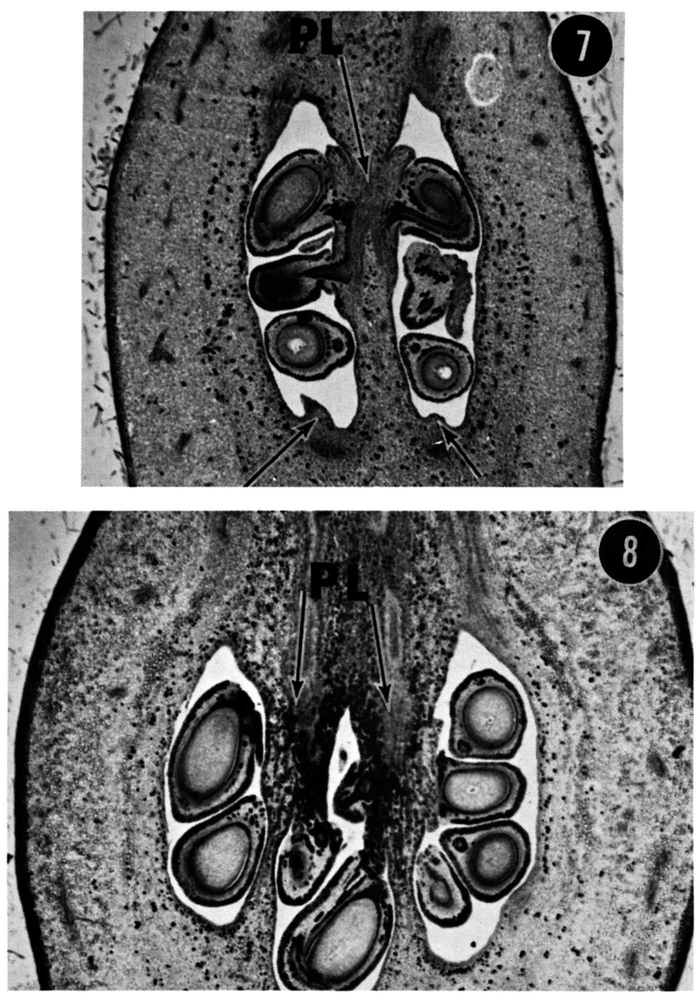



*Fig. 7, 8.* Longitudinal section showing ovule orientation and attachment to placentae (PL) 10 days after anthesis. Both X 16.

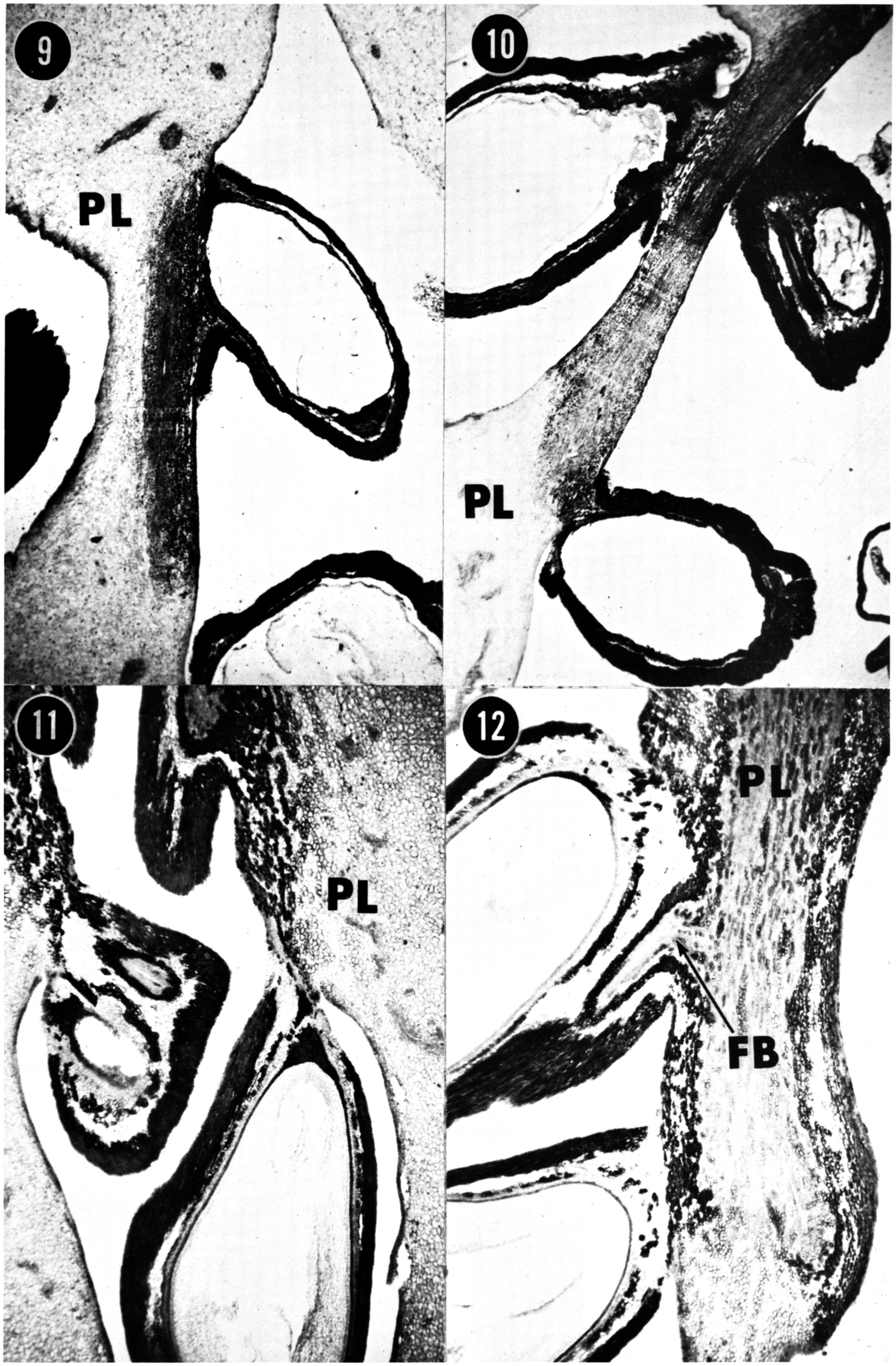



*Fig. 9 - 12.* Longitudinal section showing ovule and placental tissue (PL) development 31 days after anthesis showing funicular bundle (FB) attachment. All X 10.

The ovules were not oriented into position close to the locular walls. In some cases, the viable ovule extended to the opposite side of the wall, thus filling the locular cavity (Fig. 6). Tissues supporting ovullary development within the core line constituted 50-60 percent of the total area of the developing fruit at full bloom. Placentae developed into distinct strands that supported numerous ovules with large lacunae which separated each strand (Fig. 5, 6). Locular growth increased ovular size at the proximal end of the cavity (Fig. 6).

Ten days after full bloom, there was increased fruit size and some change in ovule orientation (Fig. 7, 8). Cortical cells expanded from the core line through the hypodermal-epidermal region. Median longitudinal sections showed functioning, well-developed vascular tissues supporting the placental tissue and ovullary development (Fig. 7, 8). Three locular cavities showed the ovular attachment occurring on opposite sides of the placental tissue and the diverse number of meristematic areas of tissue that have been initiated for ovule development (Fig. 8). MacArthur and Wetmore (5) found that in 'McIntosh', the ovules, generally 10 or more as in the 'Wagener', failed to orient themselves in a position close to the locular wall. The ovule itself in its young stage differentiates through an angle of $90^{\circ}$ to become anatropous, but the angle is, in general, a horizontal one, not vertical as in 'Wagener'. This variability between ovule development and between locules is shown in Fig. 7, 8.

It was impossible to obtain a median-longitudinal section through a large number of ovules as they were distributed over a large area of the fruit and existed in many different planes. The protuberances (arrows) at the distal end of the locular cavity are remnants of placental tissue that had been cut off in another plane (Fig. 7). This would be part of another locular cavity on the opposite side of the fruit. Existing lacunae had become filled with placental tissue and additional parenchyma formation occurred within these areas (Fig. 8).

Placental development of enlarging fruit in relation to ovule development (31 days after full bloom) shows the relationship between ovule development and carpel cavity (Fig. 9-12). Supporting placental tissue has areas that have senesced or are beginning to senesce adjacent to the funicular bundle attachment to the seed, although the major portion of the placental strand continues to be viable functioning tissue. Ovule origin on the placental strand appears to be on opposite sides, and developes at many points between the proximal and distal ends of the strand. The same proportion between carpel cavity space and seed development existed in mature fruit (Fig. 1, 2) as did the younger fruit 31 days after full bloom.

One growth difference shown by 'Lodi' is that, although the seed count was large, the locular cavity is often considerably larger than the number of seeds (Fig. 9-12). The ovarian locule in 'Lodi' is nearly engulfed by seed development as compared to mature 'Golden Delicious', 'Jonared' and 'Starking' (7, 8).

The main morphological difference between 'Lodi' and the other cultivars is that 'Lodi' contains numerous smaller seeds attached to the placental tissue, not only at the proximal end, but extending all the way to the distal end.

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