

# Development of Intra-Ovarian Ovaries in *Carica papaya* L.<sup>1</sup>

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**Abstract.** The occurrence of intra-ovarian ovaries in certain strains of *Carica papaya* L. is not uncommon. Approximately 150 hermaphroditic and 25 female ovaries from a hybrid progeny contained internal ovaries in stages of development ranging from thread-like appendages to round or elongated pistils of various sizes and shapes. A few were large enough to fill the entire seed cavity of the primary fruit and possessed their own cavities with non-viable seeds.

Internal ovaries originate either from stimulated growth of rudimentary pistillate structures extending from the central axis of the receptacle or from placentae in positions normally occupied by ovules. The placenta may be in its normal parietal position or a single strand may become free, extended from the base of the primary ovary and support a mal-shaped secondary ovary as well as ovules. The occurrence of internal ovaries supports theories proposed by other investigators on the evolution of floral morphology in the papaya.

The formation of secondary ovaries within fruits and other teratological features have been observed in various plant species. Masters (3), in 1869, reported many kinds of abnormalities. He reported adventitious fruits occupying the positions of seeds in grapes, and the presence of flower buds within the ovary of *Sinapis arvensis*. He reported similar cases in *Nasturtium amphibium*, *Brassica rapa* and *Passiflora quadrangularis*. Formation of stamens from the ovary walls in *Baeckea diosmaefolia* and the formation of pollen within ovules of *Passiflora caerulea* and *P. palmata* were also described. Masters (3) also cited Berkeley's description of a carnation in which both ovules and carpels were found on the placentae.

Prain (5), in 1895, and Bergman (1), in 1921, described the presence of incompletely developed secondary ovaries within the seed cavity of *C. papaya*. Prain also described a tertiary ovary with its carpels alternating with those of the secondary ovary. Both authors discussed the probable modes of origin of these accessory ovaries. The occurrence of internal ovaries in the papaya apparently is not uncommon, especially in certain strains. Recently, a hybrid progeny was observed to produce a large number of fruits with internal ovaries or proliferating tissues in various stages of development. This afforded the opportunity to study the nature of the internal ovaries and their probable origins.

## Materials and Methods

The progeny we used was the third generation of a hybrid papaya strain which originated from a cross between a yellow variety (yellow leaves and fruits) from Southeast Asia and an inbred, low bearing strain developed in Hawaii. The latter strain has produced internal ovaries occasionally. Examination of approximately 150 fruits from hermaphroditic trees of the hybrid progeny showed only a few without internal ovaries.

Initial observations were made by halving ovaries ranging from bud to mature fruits longitudinally, noting the positions of the internal ovaries as well as color, size, shape, seed development, and number of stigmatic lobes.

Histological studies were conducted after ovaries of buds and flowers were fixed in FAA (Formalin-Aceto-Alcohol), dehydrated by a standard tertiary butyl alcohol series, infiltrated with paraffin, and embedded in tissuemat. Sections were stained with safranin-fast green (4).

## Observations and Discussion

Papaya fruits vary greatly in size and shape, the latter being closely related to the sex of the plant. Fruits from female trees are spherical while those from hermaphroditic trees range from cylindrical to oval and pyriform in shape. Regardless of shape or size, all fruits have internal cavities filled with ovules attached to parietal placentae.

Normally, fruits are halved longitudinally for serving. Frequently, rudimentary thread-like structures, 1-2 mm in diameter and 1-2 cm in length project from the receptacle into the cavity (Fig. 1). In this illustration the fruit on the left shows some swelling at the base (see arrow). This phenomenon is common in many papaya strains.

Observations were made on undeveloped pistil-like structures similar to those shown in Fig. 1. The pistillate nature of these structures may be seen in Figs. 2 and 3, the ovary of the latter being somewhat enlarged. Both ovaries show a single stigmatic lobe. These stigma-like tissues may be compared with an actual stigmatic lobe excised from a normal ovary (Fig. 4). Figure 5 shows 6 internal pistils of different sizes and shapes found at the base of the primary fruit cavity. In one case (Fig. 6), a pair of internal ovaries 4-5 mm in length and somewhat shrivelled, was found growing from the terminal region of a rudimentary pistil-like structure. The terminal region supporting the two ovaries resembled the stigmatic morphology shown in Figs. 2 and 3. The origin of the pair of ovaries was not determined as no further samples showing this interesting phenomenon were found.

Another abnormality was ovule development on what appeared to be the structure from the central axis (Fig. 7). However, morphologically, this closely resembled a placental strand.

Devi (2) presented evidence indicating that the ancestors of *Carica papaya* possessed axile placentation from which placental strands split apart and extended sideways to parietal positions. If such were the case, a slight reversion to ancestral form could result in the development of an extra placental strand from the basal region, free from other strands.

Many fruits of our hybrid produced large internal ovaries and carpel-like structures. Figures 8, 9, 10 and 11 show these ovaries in various sizes, shapes and stages of development. Figure 12 shows fruits each with two internal ovaries growing towards the center from opposite ends. These and many other fruits examined indicate 2 areas in which secondary ovaries may originate.

There are secondary ovaries which develop from the rudimentary pistils attached to the basal region of the primary ovary. Prain (5) described such an ovary arising from the axis of

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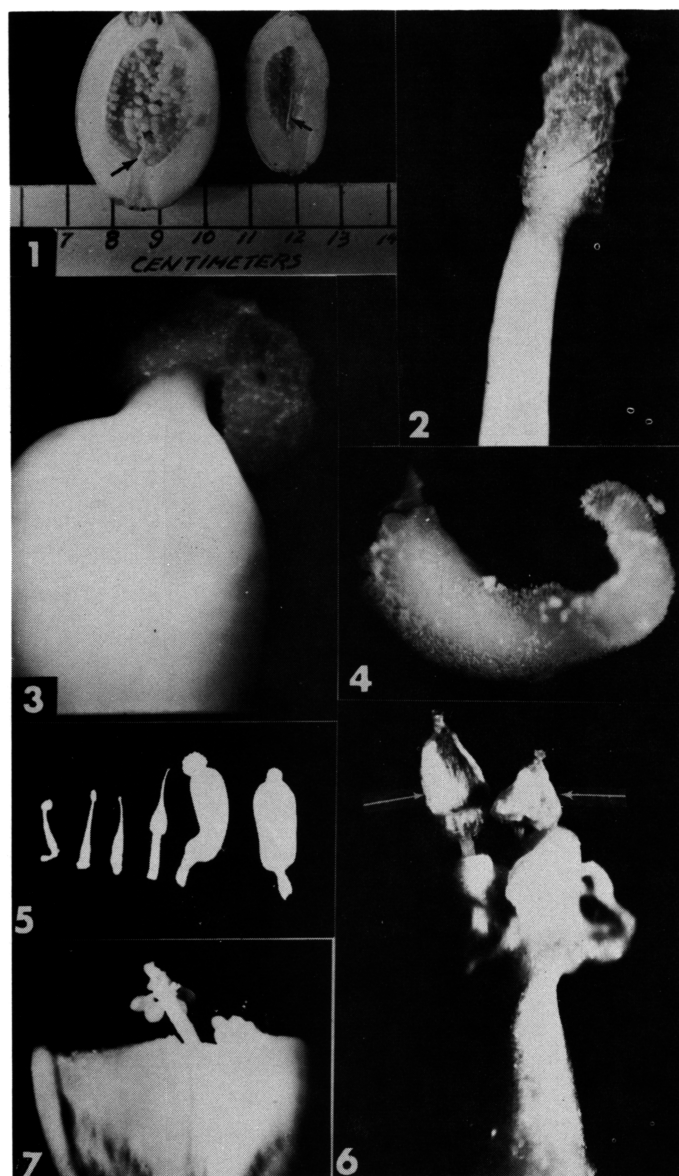


Fig. 1. Rudimentary pistil-like structures (see arrows) at the base of the fruit cavity. Primary ovary on the left is approximately 15 days and one on the right is 5 days after anthesis.

Fig. 2. Rudimentary pistil-like structure magnified (4.7X) shows the morphological similarity of its terminal region to stigmatic tissue shown in Fig. 4.

Fig. 3. Enlarged internal pistil with one stigmatic lobe in a female fruit (4.0X).

Fig. 4. An actual stigmatic lobe excised from a hermaphroditic flower for comparative purpose (12.0X).

Fig. 5. Excised internal pistils of various shapes and sizes from female fruits (actual size).

Fig. 6. Vestigial pistil-like structure from the central axis with a pair of distinct ovaries attached to the terminal stigmatic area. (4.5X).

Fig. 7. Ovule development on a structure extending from the central axis. (1.8X).

the flower within the normal ovary. These secondary ovaries are usually more completely developed and take the shape of the primary fruit. They are composed of one to several carpels. Membranous corolla-like tissue surrounds the base of some secondary ovaries. Structures which might be comparable to stamens or stamen traces were not found, nor did Bergman (1) report these features in his specimen. Epidermal cells of the internal ovaries were larger, and stomata were fewer, than those of the primary ovary. The ovary wall color was white to creamy-white but become orange-yellow, similar to the color of the ripe primary fruit. These features were reported by

Bergman.

Histological studies showed that these ovaries develop from the internal pistils, with the vascular bundles extending from the receptacle of the primary fruit and diverging into the secondary ovary in much the same way as the vascular system of the primary fruit (Fig. 13).

The well-developed secondary ovaries possess their own seed cavities (Fig. 11) with ovules which appear normal in size but have soft, poorly developed seedcoats and watery contents. None of the ovules was viable. This type of internal ovary was not found by Bergman (1).

The other point of origin is from placentae at positions normally occupied by ovules (Figs. 12, 14, 15, 16). The secondary ovaries which developed from the blossom-end of the cavity (Fig. 12) were attached to the placenta. In several cases, what appeared to be incompletely-developed secondary ovaries with seeds exposed on one side were found attached to structures which developed from the base of the primary fruit (Figs. 14, 15). A critical examination showed these ovaries to be attached to the free central placentae with normal ovules attached in expected positions. This gave the appearance of an exposure of the ovules from an incomplete ovary development, but actually, they are not the product of the secondary fruit as Bergman reported (1).

Approximately 25 fruits from female trees ranging from 3 weeks after anthesis to near maturity were examined for the presence of internal ovaries. This phenomenon was not so frequent in fruits from female trees as in fruits from hermaphroditic trees. Large, well-developed internal ovaries were not found in any of the fruits examined. In most cases the central rudimentary pistils attained the size shown in Figs. 3, 5 and 16. The largest pistil was approximately 2.0 cm in diameter (Fig. 16). The same illustration shows 2 small secondary ovaries about the size of normal seeds, replacing the ovules which normally would occupy those positions on the placentae. In all cases the shape of the secondary ovaries resembled that of the primary fruit. The large ovary in Fig. 16 showed one poorly developed stigmatic lobe.

The secondary ovaries formed on the placentae, particularly the small ones shown in Fig. 16, superficially resemble transformed ovules but whether they actually were could not be determined. Dissection showed these structures to be composed of undifferentiated mass of parenchymatous tissue. Transitional forms between ovules and ovaries were not found. That these ovaries might have originated from adventitious buds should not be discounted since such structures were reported by Masters (3).

The presence of rudimentary pistil-like structures and the development of secondary internal ovaries may be explained by Storey's (6) theory of the derivation of dicliny from ancestral hermaphrodites in *Carica papaya*. That author concluded from his studies that the female flower is the reduced form of an unknown ancestral type from which floral organs have been lost in phylogeny at several levels. He stated further that the occurrence of intra-ovarian pistils and of functional supernumerary carpels in the pistil attests to the former existence of carpels in a whorl above those presently found in the typical bisexual flower.

Storey presented morphological and anatomical evidence to show that the pistillate flower was derived through 2 series of losses in which one whorl of 5 stamens transmutated into functional carpels with the loss of the ancestral carpels. This was followed by the transformation of the second whorl of 5 stamens into carpeloid structures, replacing the first set of stamen carpels. These evolutionary changes would explain the presence of structures resembling rudimentary pistils capable of reconstituting themselves into secondary ovaries under undetermined biochemical stimuli. What cannot be explained at this time are the frequent occurrence of well-developed internal



Fig. 8, 9 and 10. Well-developed internal ovaries of various shapes and sizes, all attached to the base of the primary ovarian cavity. Fig. 10 shows a near mature fruit. (2.3X).  
 Fig. 11. Internal ovary split longitudinally, showing its cavity with non-viable seeds.  
 Fig. 12. Fruits showing two internal ovaries growing from opposite ends.  
 Fig. 13. Histological section showing the attachment of the internal ovary to the primary ovary and the vascular system leading into the internal ovary from the primary fruit (14.0X).  
 Fig. 14 and 15. Malformed internal ovaries adnate to free central placentae with seeds attached to one side but on the placentae. Fruit in Fig. 14 is reduced 1/2X.  
 Fig. 16. Internal ovaries in female fruit. Large one in the center (2 cm in diameter, actual size) is attached to the base of the primary fruit cavity while the two secondary ovaries (see arrows) are attached to the placentae.

ovaries in the bisexual flowers and the less frequent presence of well-developed internal ovaries in the pistillate flowers, at least in the hybrid progeny used.

### Conclusions

It is apparent from this study that various teratological forms of internal ovarian development occur in strains of *Carica papaya*. Internal ovaries in various stages of development can originate either from rudimentary pistillate structures extending from the central axis of the receptacle, or from placentae in positions normally occupied by ovules. The internal ovaries found attached to placentae may be either transformed ovules or adventitious buds.

The presence of rudimentary pistillate structures in the primary fruit of *Carica papaya* can be explained by Storey's (6) theory based on evolutionary changes that took place in the ancestral bisexual flower, and on derivation of the pistillate flower by a sequence of transformations of stamens into carpeloid structures with the loss of the ancestral gynoeceum.

Implications of the presence of a free central placenta with

ovules and occasionally, ovaries, are supported by Devi's concept of axile placentation in ancestral forms. The biochemical nature of stimulative secondary growth and the possibility of finding viable embryos in the haploid condition in well-developed internal ovaries warrant further studies.

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