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EARLY STAGES IN AVOCADO (PERSEA AMERICANA MILL.) FRUIT DEVELOPMENT: ANATOMICAL ASPECTS[1]

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Early stages of avocado (*Persea americana* Mill.) fruit development are described and illustrated. Three types of fruitlets were found: (1) normal fruitlets containing healthy embryo and endosperm; (2) pseudo fruitlets with a swollen ovary, similar to normal fruitlets (but within the ovule there was no development of endosperm or embryo), which dropped within 2–4 wk after pollination; (3) degenerate fruitlets in which the endosperm, the embryo, or both degenerated at different stages from 7 to 42 days after pollination. Degeneration appeared in varying degrees of severity.

Introduction

This work is part of a series of anatomical studies of flowers, fertilization, and fruit set in avocado (*Persea americana* Mill.). Within this framework normal and defective ovules at anthesis (TOMER, GOTTREICH, and GAZIT 1976), normal and abnormal ovule development (TOMER and GOTTREICH 1978), and part of the fertilization process (TOMER and GOTTREICH 1975) have been described. Some stages of normal fruit development were described by SCHROEDER (1952) and SEDGLEY (1977). The present report deals with normal and abnormal development of young fruitlets during the early postfertilization stages.

Material and methods

Seven hundred flowers of 'Fuerte' and 300 flowers of 'Tovah' were hand-pollinated in the experimental orchard of the Agricultural Research Organization, Bet Dagan, during the second half of April 1976. This was a suitable period for fruit set with temperatures above 14 C by night and less than 35 C by day. 'Fuerte' flowers were pollinated with pollen from 'Hass,' and 'Tovah' flowers with pollen of 'Fuerte.' Fruitlets were sampled at different dates after pollination.

'Fuerte' fruitlets of unknown age (free pollination) were sampled in early May. The fruitlets were divided at harvest into two groups. Those which detached readily with a slight touch were termed "weakly attached," and those which were attached firmly and had to be picked with force were termed "strongly attached." In the laboratory the fruitlets were further divided into three sizes, averaging 3, 4, and 7 mm long. 'Ettinger' fruitlets of unknown age were also sampled and divided into two sizes, averaging 3 and 4 mm long.

'Fuerte' fruitlets were sampled on May 8 and 19 in an orchard of Kibbutz Yaqum and were also divided into weakly attached and strongly attached.

All samples were immediately fixed in FAA solution and subsequently processed for paraffin embedding (SASS 1958). Longitudinal sections, 15 μm thick, were cut serially and stained with safranin-fast green.

Results and discussion

NORMAL FRUIT DEVELOPMENT (AFTER HAND-POLLINATION).—At 3 days after pollination, initiation of endosperm formation had proceeded from the division of the secondary nucleus to a two- to six-celled endosperm. At 5 days the endosperm had eight to 10 cells (fig. 1). At 7 days endosperm cells con-

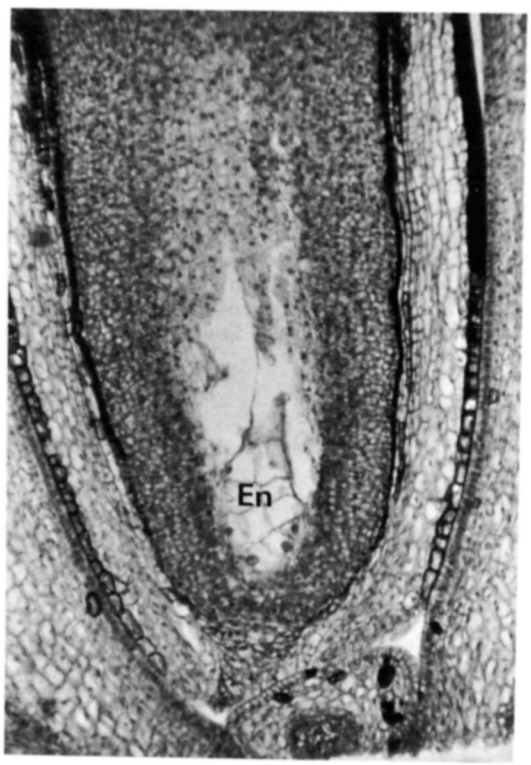

FIG. 1.—Early stage of endosperm (*En*) development, 5 days after pollination; × 300.

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tinued to divide; in some ovules the zygote had divided into two cells (fig. 2). At 9 days in most ovules the endosperm formed a large cellular body. A proembryo of two to six cells was present, distinguishable by its small and compact cells compared with the large and loose cells of the endosperm. At 11 days division of endosperm cells continued, and in most ovules an embryo of six to 10 cells was seen. At 14 days the young embryo was spherical in shape and consisted of 20 cells (fig. 3). At 21 days the globular embryo was 60–150 μm in diameter, and some were kidney shaped (figs. 4, 5). At 27 days the embryo had developed cotyledons, and the endosperm filled the whole space of the embyo sac. At 42 days the cotyledons occupied most of the space previously taken up by the endosperm, while the shrunken endosperm was pressed to the nucellus layer (fig. 6). In the embryo the plumule and the radicle were recognized as two meristematic zones with small, dense cells (fig. 7).

"PSEUDO" AND DEGENERATE FRUITLETS.—In addition to normal fruitlets, we found two other types. which we termed "pseudo" and "degenerate." The pseudo fruitlets had a swollen ovary with a green surface, similar to normal fruitlets, but within the ovule there was no development of an endosperm or embryo. These fruitlets dropped within 2–4 wk (table 1).

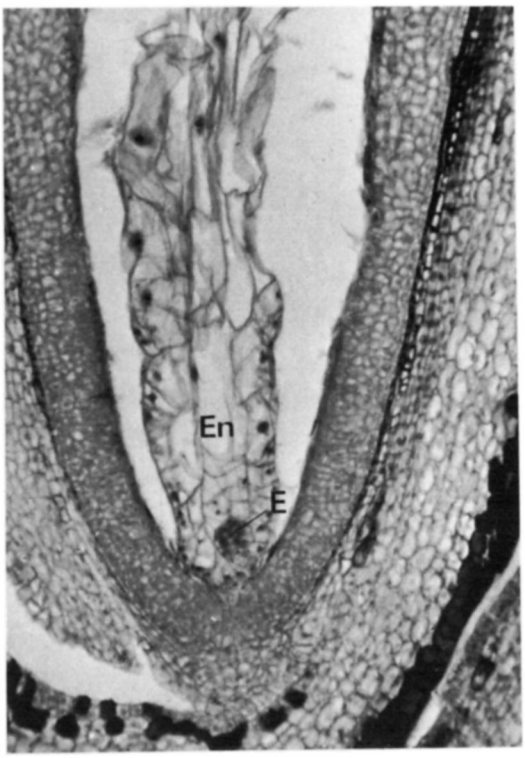

FIG. 3.—Young embryo (*E*) and endosperm (*En*), 14 days after pollination; × 300.

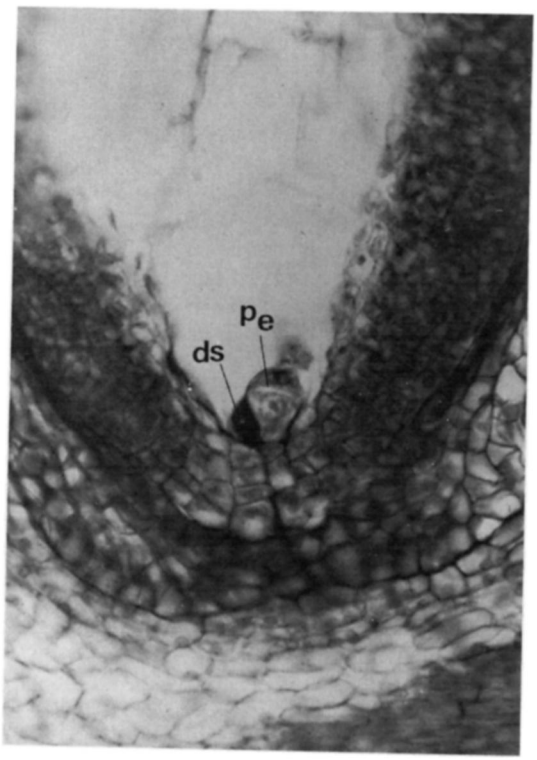

FIG. 2.—Proembryo (*pe*) containing two cells after first division of the zygote, 7 days after pollination; *ds* = degenerate synergid; × 500.

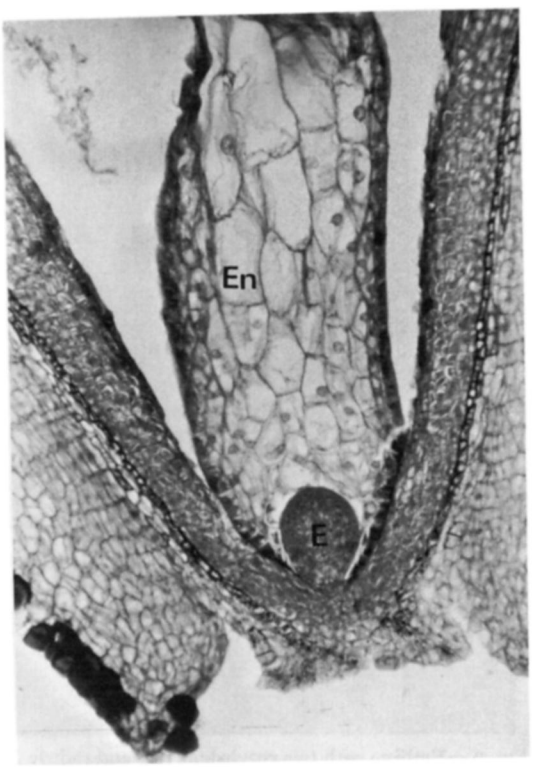

FIG. 4.—Spherical-shaped embryo (*E*) and endosperm (*En*), 21 days after pollination; × 300.

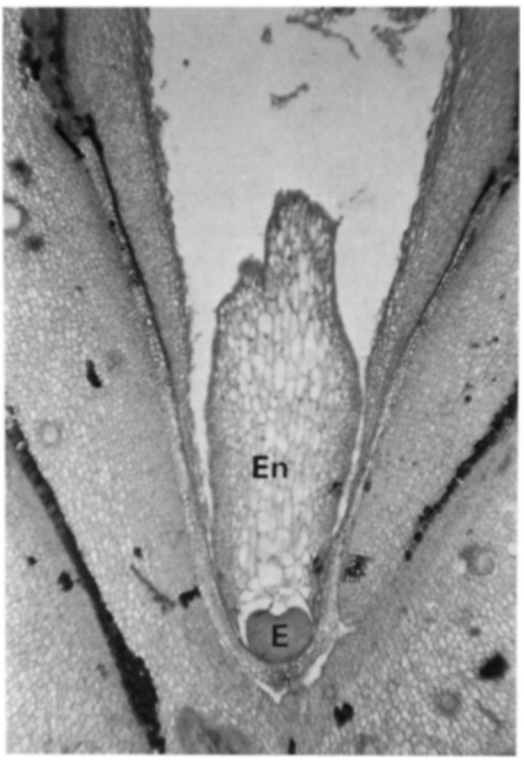

FIG. 5.—Heart-shaped embryo (*E*) and endosperm (*En*), 21 days after pollination; × 125.

TABLE 1

PERCENTAGE OF NORMAL, PSEUDO, AND DEGENERATE FRUITLETS AT DIFFERENT DAYS AFTER HAND POLLINATION IN 'TOVAH' AND 'FUERTE'

CULTIVAR AND DAYS AFTER POLLINATION	NO. OF FRUITLETS EXAMINED	FRUITLETS (%)		
		Normal	Pseudo	Degenerate
'Tovah':				
7.....	26	8	12	80
13.....	31	13	10	77
21.....	19	78	11	11
27.....	10	90	0	10
'Fuerte':				
7.....	20	10	30	60
14.....	21	29	52	19
21.....	13	69	0	31

In the degenerate fruitlets, degeneration of the embryo and/or endosperm expressed itself as cell deformation and shrinkage, so that the whole endosperm occupied only a minor part of the embryo sac cavity (figs. 8–10). Degeneration was observed in all developmental stages from 7 to 42 days (figs. 8–12) and varied in degree of severity, ranging from slight (where only a few of the cells of the embryo had degenerated) to severe (where the entire embryo turned into a dark mass with no recognizable cell structure). The bulk of the fruitlets that had a degenerate endosperm or embryo dropped after fruit set. About 2 mo after fruit set most of the fruits on

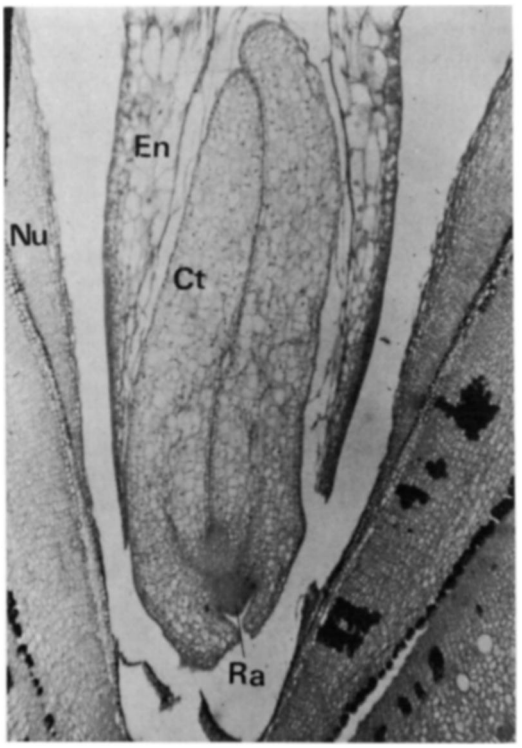

FIG. 6.—Embryo with two cotyledons (*Ct*) and radicle (*Ra*), 42 days after pollination; *En* = endosperm; *Nu* = nucellus; × 125.

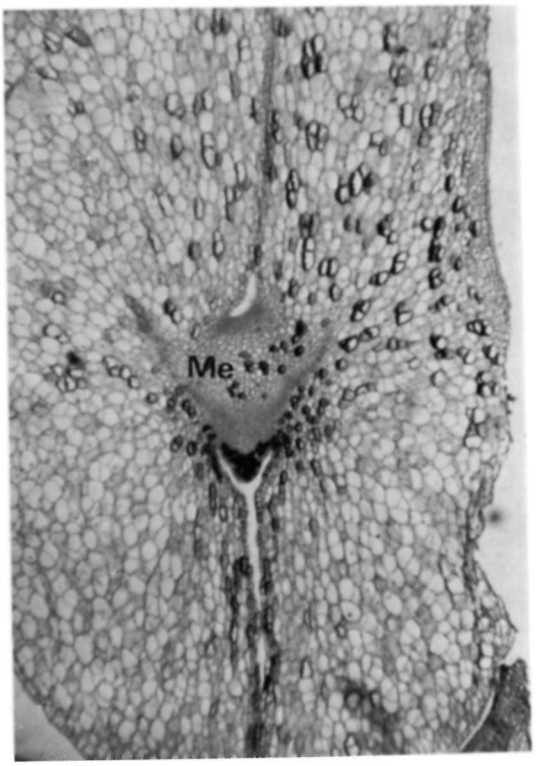

FIG. 7.—Meristematic (*Me*) zones in the embryo, 42 days after pollination; × 500.

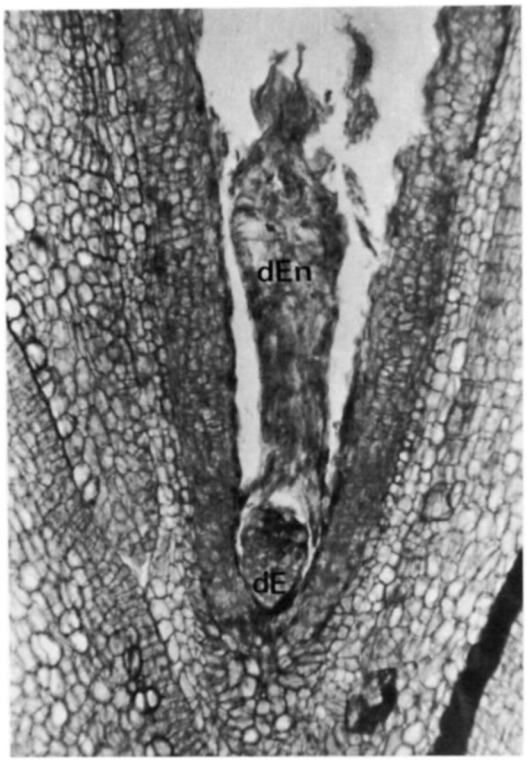

FIG. 8.—Degenerate embryo (*dE*) and endosperm (*dEn*), 21 days after pollination; × 125.

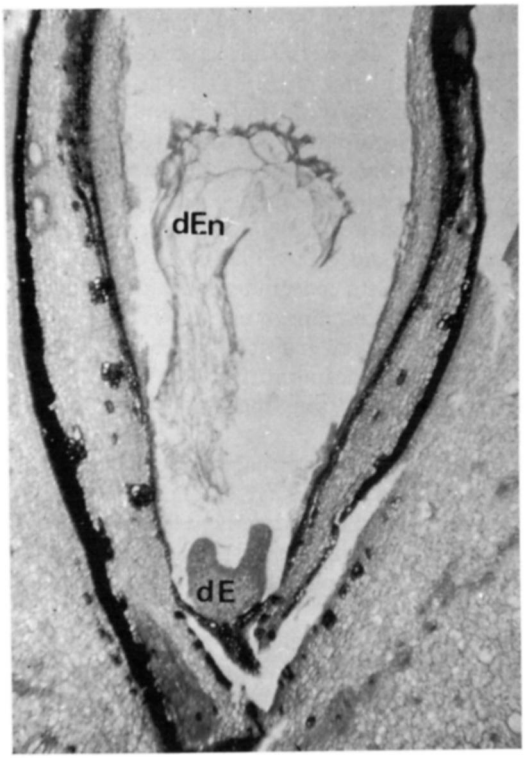

FIG. 10.—Degenerate embryo (*dE*) and endosperm (*dEn*), 42 days after pollination (note space between the endosperm and the nucellus); × 40.

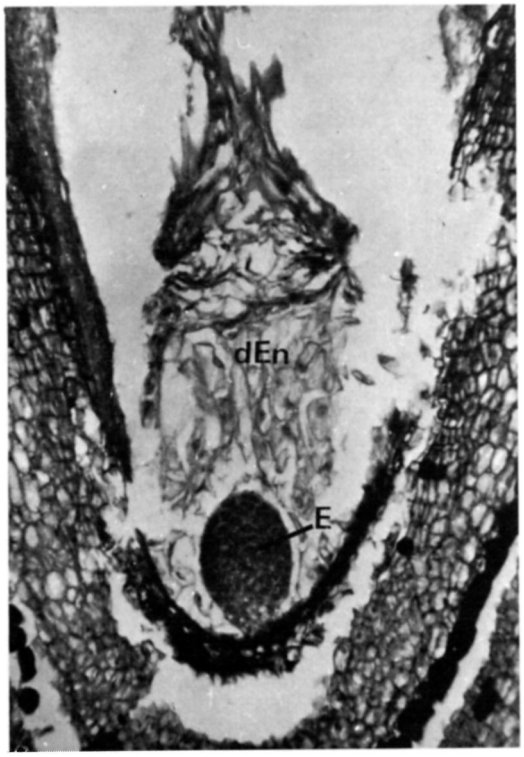

FIG. 9.—Normal embryo (*E*) and degenerate endosperm (*dEn*), 21 days after pollination; × 125.

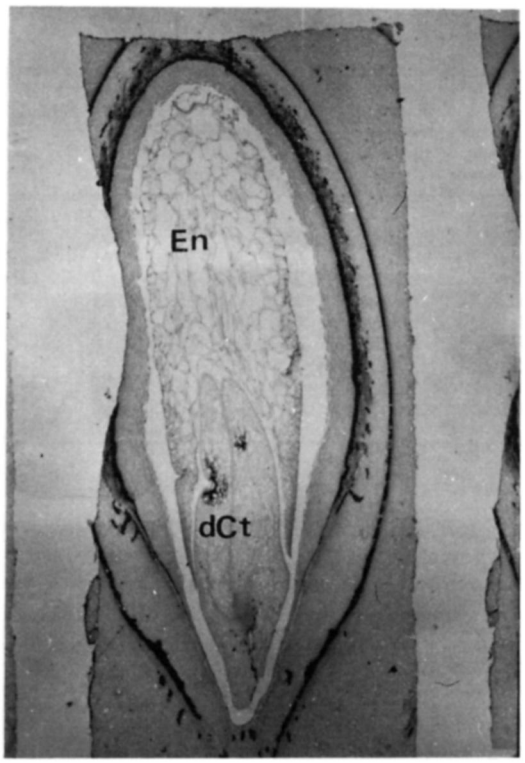

FIG. 11.—Beginning of cotyledon degeneration (*dCt*), 42 days after pollination; *En* = endosperm; × 40.

the trees possessed healthy seeds or were seedless. The seedless fruits were characterized by a specific type of chalazal degeneration which began at the chalazal end of the ovule (nucellus and integuments) and spread toward the micropylar region, culminating in extensive destruction of the nucellus and a large part of the integuments. Some of these seedless fruits did not drop and reached maturity (BLUMENFELD and GAZIT 1974).

In some fruitlets containing a healthy endosperm, we did not find an embryo or any traces of it. Likewise, we found a few fruitlets possessing an embryo but lacking an endosperm (fig. 13). Fruitlets of this type also dropped from the trees in the course of time.

The percentage of normal fruitlets increased noticeably with advancing age (table 1) or size (tables 2, 3), especially in the strongly attached group. It is noteworthy that apparently perfectly normal fruitlets were found among the weakly attached group (tables 2, 3).

Shortly after fruit set, a large percentage of the fruitlets lacked both endosperm and embryo. The incidence of these pseudo fruitlets decreased quickly with age (table 1) and size (tables 2, 3); they disappeared completely about 3–4 wk after fruit set. Our data do not indicate whether ineffective polli-

FIG. 12.—Degenerate radicle (*dRa*) of the embryo, 42 days after pollination; *Ct* = cotyledons; × 125.

TABLE 2

RELATIONSHIP OF SIZE TO PERCENTAGE OF NORMAL, PSEUDO, AND DEGENERATE FRUITLETS IN 'FUERTE' AND 'ETTINGER'

CULTIVAR AND AVG. SIZE (mm)	FRUITLET RESISTANCE TO SEPARATION	NO. OF FRUITLETS EXAMINED	FRUITLETS (%)		
			Normal	Pseudo	Degenerate
'Fuerte':					
3.....	Strong	23	17	35	48
4.....	Strong	63	37	41	22
7.....	Strong	23	70	0	30
3.....	Weak	20	5	75	20
4.....	Weak	63	2	74	24
7.....	Weak	21	33	0	67
'Ettinger':					
3.....	...	94	8	76	16
4.....	...	80	27	0	73

TABLE 3

PERCENTAGE OF NORMAL, PSEUDO, AND DEGENERATE FRUITLETS IN 'FUERTE' FROM KIBBUTZ YAKUM

FRUITLET RESISTANCE TO SEPARATION	SAMPLING DATE	NO. OF FRUITLETS EXAMINED	FRUITLETS (%)		
			Normal	Pseudo	Degenerate
Strong....	May 8	113	29	47	24
Strong....	May 19	60	42	0	58
Weak.....	May 8	113	15	38	47
Weak.....	May 19	87	17	0	83

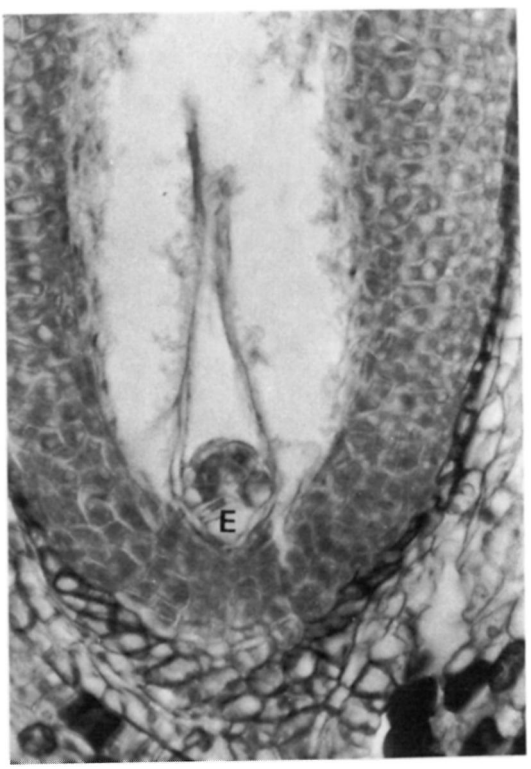

FIG. 13.—Normal embryo (*E*) without endosperm, 14 days after pollination; × 300.

nation or aborted fertilization preceded the transitory occurrence of these pseudo fruitlets. The absence of endosperm and embryo excludes the possibility that such fruitlets could develop into seedless avocado fruits.

Ovule degeneration was found in many fruitlets that had an endosperm and embryo. The percentage of degenerate fruitlets increased with the disappearance of the pseudo fruitlets (tables 1–3). Although most of the degenerate fruitlets eventually abscise, some of them may stay on 'Fuerte' and 'Ettinger' trees and develop into seedless fruits.

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