THE EMBRYO SAC OF ERAGROSTIS CILIANENSIS (ALL.) LINK

A New Type Embryo Sac and a Summary of Grass Embryo Sac Investigations

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The embryo sacs of the grasses have been examined by about twenty-five investigators. Of the sixty grasses studied only twenty-three species have fairly complete data recorded concerning the development of the embryo sac, and forty-seven species have the type of embryo sac recorded. The number and position of the antipodals, which vary from three to sixty (Bambusa, in tables), have attracted more attention than any other phase of the embryo sac studies, for the antipodals have been studied in fifty-five species. Information about the group as a whole is scattered and incomplete, as will be seen in the accompanying tables, and there is variation in the records.

Eragrostis cilianensis (All.) Link, is the name preferred in Hitchcock (18) for the grass known to many as *Eragrostis major* Host. The spikelets were prepared by killing and fixing in hot crom-acetic or hot F. A. A. and kept in 50% Hydroflouric acid from five to ten days before embedding.

THE SPIKELETS AND OVULES

The spikelets of this grass have from ten to forty flowers with the basal flowers maturing first. Longitudinal sections of the whole spikelet show the flowers in various stages of maturity from the base to the tip. The young ovule develops at right angles to the carpel wall (Fig. 1) and gradually grows so that its longitudinal axis is finally parallel with that of the carpel (Fig. 10). The inner integument develops faster than the outer, which never completely covers the ovule and finally disappears (Figs. 12 and 13).

THE ARCHESPORIAL CELL AND MEGASPORES

There is one archesporial cell and no tapetal cell. Four megaspores are formed and are arranged in the T-form (Figs. 2, 3, 4, 5). The young ovules of Eragrostis are so small that 4-micron sections had to be cut to be certain of the T-form tertad. Schnarf (1926, ***Bambusa, Coleanthus***) and Horton and Beck (1932), ***Bromus marginatus***) show T-form tetrads; and Miller (1920, ***Zea***) reports no walls between the megaspores and says that all four function ("lily type"). Weatherwax reports a linear tetrad in Zea, as is the case in all other species reported.

The inner megaspore (Figs. 3, 4, 5) of Eragrostis always grows into the embryo sac and its nucleus does not divide until after the disintegration of the other three megaspores (Fig. 5). This is the case in all other grasses that have been studied except that Anderson (1927) reports that in *Poa* the outer megaspore develops occasionally and that there are sometimes two rows of megaspores from two archesporial cells.

THE EMBRYO SAC

The embryo sac develops as the normal type through the two- and four-nucleate stages (Figs. 6, 7). With the formation of the eight-nucleate stage the four chalazal nuclei are immediately separated from the rest of the embryo sac as four antipodal cells (Figs. 8, 9, 10); one or two of these divide immediately so that there are commonly five or six antipodal cells (Fig. 11) at fertilization time. The number of antipodals in grass tribes varies from three to sixty, as shown in the tables.

The four nuclei at the micropylar end of the sac function, as the egg, one synergid, and two endosperm nuclei (polar nuclei) (Figs. 10, 11). This organization of an embryo sac is a new type not only for the grasses but for all plants. The number of antipodals in *Eragrostis* is always four or more and they are immediately separated from the rest of the sac as antipodal cells. Consequently no chalazal nucleus takes part in the formation of the endosperm. Only one synergid is ever formed, and the egg and the one synergid are separated from the remaining two nuclei as cells (Figs. 10, 11). These remaining two nuclei fuse in the formation of the endosperm nucleus (Figs. 10, 11). The pollen tube enters through the micropyle and fertilization occurs as usually described.

The embryo sacs of forty-two grasses have been reported as normal-T sacs. Three cases have been found to have the Scilla-T (*Coleanthus*, Schnarf, 1926; *Melica nutans* and *M. altissima*, Fischer, 1880). Miller (1920) found that in *Zea* all four megaspores function in the formation of the eight-nucleate sac as in the so-called "lily type" embryo sac, and Weatherwax (1919) found the normal-T in *Zea*.

DEVELOPMENT OF SEED COATS

The embryo sac elongates and the chalazal end absorbs its way into the nucellus, while the antipodals remain *in situ* and so become lateral to the embryo sac (Figs. 11, 12). Most of the nucellus is absorbed by the developing endosperm until practically only the outer layer remains (Fig. 12), and even that is at last partly destroyed (Fig. 14). The inner integument completely surrounds the ovule and the outer integument disappears; so that the seed coat is made up of the inner integument and one layer of the cells of the body of the ovule except on the side of attachment to the carpel (Figs. 14, 16). With but one exception in all species examined in the grasses the outer integument disappears and the inner integument becomes the seed coat (Figs. 14, 24, 36, et al). Anderson states that in *Poa* the outer integument does not entirely disappear but the cells are much crushed.

THE ENDOSPERM

The endosperm is free-nuclear, and by the time the fertilized egg has divided there are from 25 to 35 nuclei lying in the periphery of the cytoplasm. Cell walls are formed first against the walls of the seed coat and develop toward the center until the endosperm tissue fills the whole body of the ovule. All grasses that have been studied have a free-nuclear endosperm of the same type.

THE EMBRYO

The fertilized egg elongates and divides into a short four-celled embryo. The cell at the micropylar end sometimes does not divide immediately, but eventually it produces a several-celled suspensor (Figs. 15, 16, 17) that later is almost completely absorbed (Fig. 19). The upper cells of the young embryo soon form a bulbous tip, and the epidermis becomes distinct (Figs. 14, 15). The development of the scutellum is the next evidence of growth (Fig. 16). It is formed by the continued growth of that part of the bulbous embryo, the tip becoming the top of the scutellum and the cells above the suspensor forming the base of the scutellum. The stem tip and the coleoptile develop from the lower half of the outer side of the bulbous portion (Figs. 16, 17) opposite the base of the young scutellum. The scutellum develops rapidly and the basal portion pushes the lower end of the embryo away f om the endosperm (Figs. 18, 19).

The parts of the grass embryo have been much discussed. The opposing views are well presented in the papers of Avery (3) and Boyd (5).

SUMMARY OF ERAGROSTIS EMBRYO SAC DEVELOPMENT

1. There is no tapetal cell.
2. There is a T-form tetrad of megaspores.
3. The inner megaspore develops into the embryo sac.
4. The two- and four-nucleate stages occur as in the Normal-T embryo sac.
5. All four nuclei at the antipodal end of the sac are separated from the rest of the sac as antipodal cells.
6. Two of the nuclei in the micropylar end of the sac fuse in the formation of the endosperm nucleus.
7. The remaining two nuclei in the micropylar end of the sac become the egg and a synergid.
8. The pollen tube enters the sac through the micropyle and fertilization and triple fusion occur.
9. The endosperm is free-nuclear.
10. The seed coats are formed from the outer cell layer of the ovule and the inner integument.
11. The embryo develops as the ordinary grass embryo type.

SUMMARY OF THE GRASS EMBRYO SAC INVESTIGATIONS

1. The antipodals, embryo sacs, *et altera* are summarized in the accompanying tables showing lists of grasses studied and findings in each.
2. Archesporial Cells. Two archesporial cells have been reported in the grass ovules by Fischer (1893), Koernicke (1896), Tannert (1905), Kuwada (1920), Coulon (1923), Schnarf (1926), Anderson (1927).
3. Polyembryony. This condition in the grasses has been seen in *Oryza* by Jones (1928), Kuwada (1910), Komuro (1922); in *Zea* by Brown (1860); in *Poa* by Nishimura (1922) and Anderson (1927); in *Triticum* by Eichinger (1910); in *Eleusine coracana* by Rangaswami (1930). More than one embryo is occasionally found in *Zea* by those testing corn in germinators.
4. Parthenogenesis. This phenomenon was first observed in grasses by Coulon (1927) in *Nardus Stricta.* He found that the pollen was sterile. Gaines and Aase (1926) in *Triticum* and in *Secale,* and Stenar (1935) in *Calamagrostis* have found parthenogenesis.
5. Caryopsis. The fruits of grasses are all the typical caryopsis, and the inner integument forms the seed coat, except that in *Poa* the outer integument is also a part of the seed coat. Stopf (1904) in *Melocanna bambusiodes* of the Bambuseae found that the ovules were "naked, endospermless and viviparous." The embryos drop out of the fleshy fruit, and the fleshy part of the fruit is pericarp. Lyon (1928) has found wheat seeds without embryos. Harlen and Pope (1925) found fruits in barley without embryos and others without endosperm.

SUMMARY OF GRASS EMBRYO SAC INVESTIGATIONS SINCE 1849

ANTIPODALS

	Tapetal Cell	Mega-spores	Embryo Sac	Number of Antipodals	Number of Nuclei	Lateral, or Chalazal	Fertilization	Endo-sperm	Author
1. BAMBUSEAE									
Bambusa bambos...........	None	Linear-T or T-form?	N. T.	60				Nu. E.	Schnarf, 1926
2. FESTUCEAE									
Briza media			N. T.	Many	Multinucleate				Fischer, 1880
Briza maxima				Many	Multinucleate	Lateral			Westermaier, 1890
Bromus villosus	None	Linear-T	N. T.	3–10		Lateral	Observed		Beck and Horton, 1932
Bromus marginatus	None	T-form	N. T.	3–10		Lateral	Observed		Beck and Horton, 1932
Bromus rubens	None	Linear-T	N. T.	3–10		Lateral	Observed		Beck and Horton, 1932
Dactylis glomerata			N. T.	5–8	2–3 nucleate				Shadowsky, 1926
Diplachne serotina			N. T.	8–14	Uninucleate	Lateral			Shadowsky, 1926
Eragrostis cilianensis	None	T-form	Fusion of micropylar nuclei	4–6	Uninucleate	Lateral	Observed	Nu. E.	Stover, 1936
Melica nutans	One		Scilla-T	3					Fischer, 1880
Melica altissima	One		Scilla-T	3					Fischer, 1880
Molinia coerulea			N. T.	11–43	Binucleate	Chalazal			Shadowsky, 1926
Poa annua			N. T.	12	2–4 nucleate	Lateral		Nu. E.	Golinski, 1893
Poa Pratensis		Linear-T	N. T.	3–6	Multinucleate	Lateral		Nu. E.	Nishimura, 1922, Anderson, 1927
Poa compressa		Linear-T	N. T.	3–5		Lateral		Nu. E.	Anderson, 1927

SUMMARY OF GRASS EMBRYO SAC INVESTIGATIONS SINCE 1849—[*Continued*]

	Tapetal Cell	Mega-spores	Embryo Sac	Number of Antipodals	Number of Nuclei	Lateral, or Chalazal	Fertilization	Endo-sperm	Author
3. HORDEAE Agropyrum repens	None	Linear-T	N. T.	10–16			Observed; polar nuclei did not fuse	Nu. E.	Mowery, 1929
Elymus arenarius			N. T.	6–12					Hofmeister, 1861, Fischer, 1880
Hordeum sativa distichum				Many		Lateral			Westermaier, 1890
Hordeum tetrastichum				Many					Golinski, 1893
Hordeum murinum				15		Lateral			Lotscher, 1905
Hordeum vulgare			N. T. (H)	6–20			Observed (H.)		Hofmeister, 1861, Lotscher, 1905
Lolium italicum				3	Multinucleate	Lateral			Westermaier, 1890
Lolium tremulentum				3	Multinucleate	Lateral			Westermaier, 1890
Nardus stricta	None	Linear-T	N. T.	Many			Parthenogenic		Coulon, 1923
Secale cereale			N. T. (H)	20		Lateral(H.)	Parthenogenic (Gaines & Aasel, 1926)		Hofmeister, 1858–61, Fischer, 1880, Golinski, 1893, Westermaier, 1890, Lotscher, 1905
Triticum compactum splendens	None	Linear-T	N. T.	36	Multinucleate	Lateral	Observed	Nu. E.	Koernicke, 1896
Triticum repens				10	2–3 nucleate				Lotscher, 1905
Triticum vulgare				Many	Multinucleate		Observed	Nu. E.	Hofmeister, 1861 (1)
	One	Linear-T	N. T.	36+		Lateral	Observed	Nu. E.	Jensen, 1918 (2)
			N. T.	4 (P)			Observed (P.)		Percival 1921 (3)
				8–12	Multinucleate				Golinski, 1893 (4)
Aegilops ovata			N. T.						Schnarf, 1926

SUMMARY OF GRASS EMBRYO SAC INVESTIGATIONS SINCE 1849—[*Continued*]

	Tapetal Cell	Mega-spores	Embryo Sac	Number of Antipodals	Number of Nuclei	Lateral, or Chalazal	Fertilization	Endo-sperm	Author
4. AVENEAE Avena fatua	None	Linear-T	N. T.	25–30	Multinucleate	Lateral		Nu. E.	Cannon, 1910
Avena sativa		Linear-T	N. T.	11–30	Multinucleate	Chalazal	Observed	Nu. E.	Tannert, 1905, Golinski, 1893
Avena pubescens				3	Uninucleate	Lateral			Lotscher, 1905
Avena flavescens			N. T.	5–16	Multinucleate	Lateral			Shadowsky, 1926
Koeleria cristata			N. T.	4	Multinucleate			Nu. E.	Fischer, 1880
5. AGROSTIDAE Agrostis incana				6	Binucleate	Lateral			Shadowsky, 1926
Alepecurus pratensis		Linear-T	N. T.	3	4–nucleate			Nu. E.	Fischer, 1880
Coleanthus subtilis	None	T-form	N. T.	3	Multinucleate			Nu. E.	Schnarf, 1926
Cornupopiae nocturnum (Agrostis perennans)	One		Scilla-T	3	Binucleate	Lateral		Nu. E.	Guignard, 1882
6. ZOYSIEAE Tragus racemosus (Nazia)			N. T.	3–5	Uninucleate	Lateral			Shadowsky, 1926
7. CHLORIDEAE Chloris gayana			N. T.	6	Multinucleate	Chalazal			Shadowsky, 1926
Cynodon dactylon			N. T.	6–10	Multinucleate	Lateral			Shadowsky, 1926
Eleusine indica			N. T.	3					Cummins, 1929
Sesleria coerulea (Bulbilis)		Linear-T	N. T.	3	Multinucleate	Chalazal			Fischer, 1880
8. PHALARIDEAE Ehrharta panicea			N. T.	3–6	Binucleate	Lateral			Fischer, 1880
9. ORYSEAE Oryza sativa			N. T.	3–Many	Multinucleate	Chalazal		Nu. E.	Kuwada, 1910
	None						Observed		Terada, 1928
10. ZIZANIEAE Luzula pilosa (Luziola)		Linear-T	N. T.	3					Fischer, 1880

SUMMARY OF GRASS EMBRYO SAC INVESTIGATIONS SINCE 1849—[*Continued*]

	Tapetal Cell	Mega-spores	Embryo Sac	Number of Antipodals	Number of Nuclei	Lateral, or Chalazal	Fertilization	Endo-sperm	Author
11. MELINIDEAE									
12. PANICEAE									
Paspalum dilatatum			N. T.	5–14	2–3 nucleate	Chalazal			Shadowsky, 1926
Oplismenus undulatifolium			N. T.	10–18	Binucleate	Chalazal			Shadowsky, 1926
13. ANDROPOGONEAE									
Andropogon caucasicum			N. T.	4–6	Uninucleate	Lateral			Shadowsky, 1926
Andropogon ischaemum			N. T.	5–16	Uninucleate	Chalazal			Shadowsky, 1926
Eulalia japonica (Miscanthus sinensis)			N. T.	15–24	2-3 nucleate	Chalazal			Shadowsky, 1926
Gynerium argenteum			N. T.	8–13	Uninucleate	Chalazal			Shadowsky, 1926
Sorghum bicolor				Many		Chalazal			Hofmeister, 1842
Sorghum helpense				4					Fischer, 1880 (1)
			N. T.	Many	Multinucleate				Hofmeister, 1861 (2)
							Observed		Stephens, 1934 (3)
Saccharum officinarum	None	Linear-T	N. T.	5	Multinucleate		Observed	Nu. E.	Artswager, 1929
14. TRIPSACEAE									
Coix lacryma			N. T.	3	Multinucleate	Chalazal			Hofmeister, 1861
Zea mays			N. T.	25		Chalazal			Hofmeister, 1849 (1)
			N. T.						Westermaier, 1890 (2)
			N. T.						Golinski, 1893 (3)
			N. T.						Guignard, 1901 (4)
			N. T.						Lotscher, 1905 (5)
	None	Lily-T	Lily-T				Observed	Nu. E.	Miller, 1920 (6)
	One	Linear-T	N. T.				Observed	Nu. E.	Weatherwax, 1919 (7)

BIBLIOGRAPHY

(1) **Anderson, Alice M.** Development of the female gametophyte and caryopsis of *Poa pratensis* and *P. compressa.* Jour. Agri. Res. 34 (11): 1001–1018; 9 pl., 3 fig. 1927.

(2) **Artschwager, E.** Development of flower and seed of sugar cane. Jour. Agri. Res. 37: 1–30. 1929.

(3) **Avery, Geo. S.** Comparative anatomy and morphology of embryos and seedlings of maise, oats, and wheat. Bot. Gaz. 89: 1–39; 68 fig. 1930.

(4) **Beck, P.** and **Horton, J. S.** Microsporogenesis and embryogeny in certain species of Bromus. Bot. Gaz. 93: 42–54; 29 fig. 1932.

(5) **Boyd, Lucy.** Evolution in the monocotyledonous seedling. A new interpretation of the morphology of the grass embryo. Trans. a. Proceed. Bot. Soc. Edinbourgh, 30: 286–393; 5 fig. 1931.

(6) **Braun, A.** Uber Polyembryonie and Keimung von Caehbogyne. Ein Nachtrag Zu der Abhandlung über Parthenogenesis der Pflanzen. Abh. Akad. Berlin, phys. Kl. 6 Taf. 197–263. 1860.

(7) **Cannon, W. A.** A morphological study of the flower and embryo of the wild oat (*Avena fatna* L.). Proc. Calif. Acad. Sci. 3: ser. Bot. 1, 329–356. 1900.

(8) **Coulon, J. De.** Nardus stricta. Etude Physiologique, atomique et embrylogique. Mem. Soc. Vandoise sc. nat. 1: 245–332. 1923.

(9) **Cummins, Margaret P.** Development of the integument and germination of the seed of *Elusine indica.* Torrey Bot. Club. Bul. 56: 155–162; 6 fig. 1929.

(10) **Eichinger, K.** Polyembryonie bei Pflanzen. Ein Fall von Polyembryonie beim weize . Naturw. Wachenschr. 25: 769–773. 1910.

(11) **Fischer, A.** Zur Kenntniss der embryo-sac entwicklung einiger Angiospermen. Jenaische Zeitschrift Bd. 14: 90–132. 1880.

(12) **Golinski, J. T. J.** Ein Beitrag zur Entwicklunsgeschichte des Andreciums and des Gynaeciums der Gräser. Bot. Cent. 55: 1–17, 65–72, 129–1 5. 1893.

(13) **Gordon, M.** The development of the endosperm in cereals. Royal. Soc. Victoria, Proc. 34: 105–116. 1922.

(14) **Guerin, P.** Recherches sur le development du tegument seminal et du pericarpe des Graminees. Ann. Sci. Nat. Bot. 1: 1–59; 70 fig. 1899.

(15) **Guignard, L.** Recherches sur le sac embryonnaire des phanerogames angiosperms. Ann. Sci. Nat. Bot. 13: 136–199. Taf 3–7. 1882.

(16) **Guignard, L.** La double fecondation dan le mais. Jour. de Bot. 15: 37–50. 1901.

(17) **Harlan, H. V.** and **Pope, M. W.** Some cases of single fertilization in barley. Amer. Jour. Bot. 12: 50–53; 1 pl. 1925.

(18) **Hitchcock, A. S.** Manual of Grasses of the United States. Misc. Publ. No. 200, U. S. D. A. 1935.

(19) **Hofmeister, W.** Die Entste cung des embryo der Phanerogamen. Leipsig. 1849.

(20) **Hofmeister, W.** Neuerer Beobachtungen über Embryobildung der Phanerogamen. Jb. Wiss. Bot. 1: 82–190. Taf. 7–19. 1858.

(21) **Hofmeister, W.** Neue Beitrage zur Kenntnis der Embryobildung der Phanerogamen. II. Monokotyledonen. Abh. Kön. Söchs. Ges. Wiss. 7: 629–760. Taf. 1–25. 1861.

(22) **Jensen, J. H.** Studies on the morphology of wheat. Wash. Agri. Exp. Sta. Bul. 150: 1–21; 5 pl. 1918.

(23) **Jones, J. W.** Polyembryony in rice. Jour. Amer. Soc. Agron. 20: 774. 1928.

(24) **Kennedy, P. B.** The structure of the caryopsis of grasses with reference to their morphology and classification. U. S. De t. Agr. Div. Agros. Bul. 19: 44 p.; 8 pl. 1899; rev. 1900.

(25) **Koernicke, M.** Untersuchungen über die Entstehung und Entwicklung der Sexualorgane von Triticum. Verh. naturh. ver. preussichen Rheinlande. 53: 149–186. 1896.

(26) **Kudelka, F.** Uber die Entwicklung und den Ban der Fruchtund Samenschlaz unserer cerealien. Landw. Jobrb. 4: 461–478; pl. 56. 1875.

(27) **Kumoro, H.** A polyembryonal plant of Oryza sativa (Japanisch). Bot. Mag. Toyko. 36: 23–24. 1922.

(28) **Kuwada, Y.** A cytological study of Oryza sativa L. Bot. Mag. Toyko, **24**: 268–280. 1910.
(29) **Lermer and Holzner.** Beiträge zur Kenntniss der Gerste. Munich, **196** p.; 61 pl. 1888.
(30) **Lötscher, K.** Uber den Bau und die Funktion der Antipodals in der Angiospermum-Semenlage. Flora 94: 213–262. Taf. 1–2. 1905.
(31) **Lyon, Mildred E.** The occurrence and behavior of embryoless wheat seeds. Jour. Agri. Res. 36: 631–635; 4. fig. 1928.
(32) **Miller, E. C.** Development of the Pistillate spiklet and fertilization in *Zea mays*. Jour. Agri. Res. 18: 255–266. 1919–1920.
(33) **Mowery, M.** Development of the pollen grain and the embryo sac of *Agropyrum repens*. Bul. Torrey Bot. Club, **56**: 319–324; pl. 14–15. 1929.
(34) **Nishimura, M.** Comparative morphology and development of *Poa pratensis*, *Phleum pratense*, and *Setaria itilica*. Jap. Jour. Bot. 1: 1–85; 4 pl. 1922.
(35) **Nörner, C.** Beiträge zur Embryoentwicklung der Gramineen. Flora, **64**: 241–251, 257–266, 273–284. 1881.
(36) **Pammel, L. H.** The histology of the caryopsis and endosperm of some grasses. Trans. Acad. Sci. St. Louis, 8: 99–220; pl. 17–19. 1898.
(37) **Percival, J.** The wheat plant. London, Duckworth. 463 p. 1921.
(38) **Rangaswami, Ayyangar, G. N.** and **N. Krishnaswami.** Polyembryony in *Eleusine coracana* Gaertn. (Ragi). Madras. Agric. Jour. 18 (12): 593–595; 1 pl. 1930.
(39) **Schnarf, K.** Kline Beiträge zur Entwicklungsgeschichte der Angiospermen. VI. Uber die Samentwicklung einiger Gramineen. Ast. Bot. Ztschr. 75: 105–113. 1926.
(40) **Schnarf, K.** Embryologie der Angiospermen. mit 627 textfiguren. Im Handbuck d. Pflanzenanatomie, 10^2: Berlin. 1929.
(41) **Shadowski, A. E.** Der Antipodals apparat bei Gramineen. Flora 20 (4): 344–470; 16 fig. 1926.
(42) **Sibuya, T.** Histological studies on the seed coats of rice (Japanese). Proc. Crop. Sci. Soc. Japan. 2: 15–16. 1928.
(43) **Stenar, H.** Parthenogenesis in der Gattung Calamagrostis. Arkiv. för Botonik. Band 25A, 1–8. A Tafel., 2 fig. 1935.
(44) **Stopf, O.** On the fruit of *Melocanna bambusiodes* Trin. An endospermless, viviparous genus of Bambuseae. Trans. Lin. Soc. 6: p. 401, pl. 45–47. 1904.
(45) **Soueges, R.** Embryogenie des Graminees Development de l'embryon chez le Poa annua L. Compt. Rend. Acad. Sci. Paris, **178**: 860–862. 1924.
(46) **Stephens, J. C.** and **Quinby, J. C.** Anthesis, pollination and fertilization in Sorghum. Jour. Agric. Res. 49 (2): 123–136. 1934.
(47) **Tannert, P.** Entwicklung und Bau der Blute and Brucht von Avena sative L. Dist. 47 p. Zurich. 1905.
(48) **Terada, S.** Embryological studies in *Oryza sativa* L. Jour. Coll. Agric. Hokkaido. Imp. Univ. 19 (4): 245–260; 4 pl. 1928.
(49) **True, R. H.** On the development of the caryopsis. Bot. Gaz. 18: 212–226; pl. 24–26. 1893.
(50) **Weatherwax, P.** Gametogenesis and fecondation in *Zea mays* as the basis of Zenia and heredity in the endosperm. Bull. Torr. Bot. Club, **46**: 73–90; fig. 6-7. 1919.
(51) **Weatherwax, P.** Persistence of the antipodal tissue in the development of the seed of maize. Bull. Tor. Bot. Club, **53**: 381–384. 1926.
(52) **Wesestermaier, M.** Zur Embryologie der Phanerogamen insbesondere über die sogenannten Antipoden. Nova acta Leop. Carol Akad. Naturf. **46**: 1–39, 3 pl. 1890.

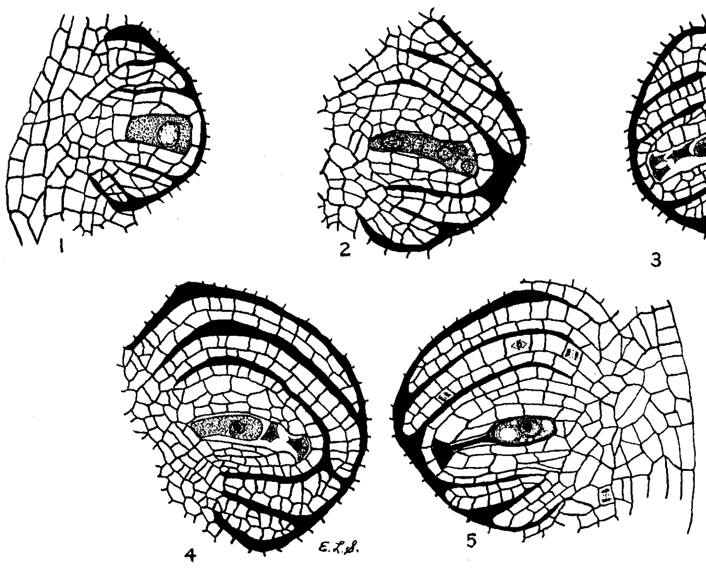
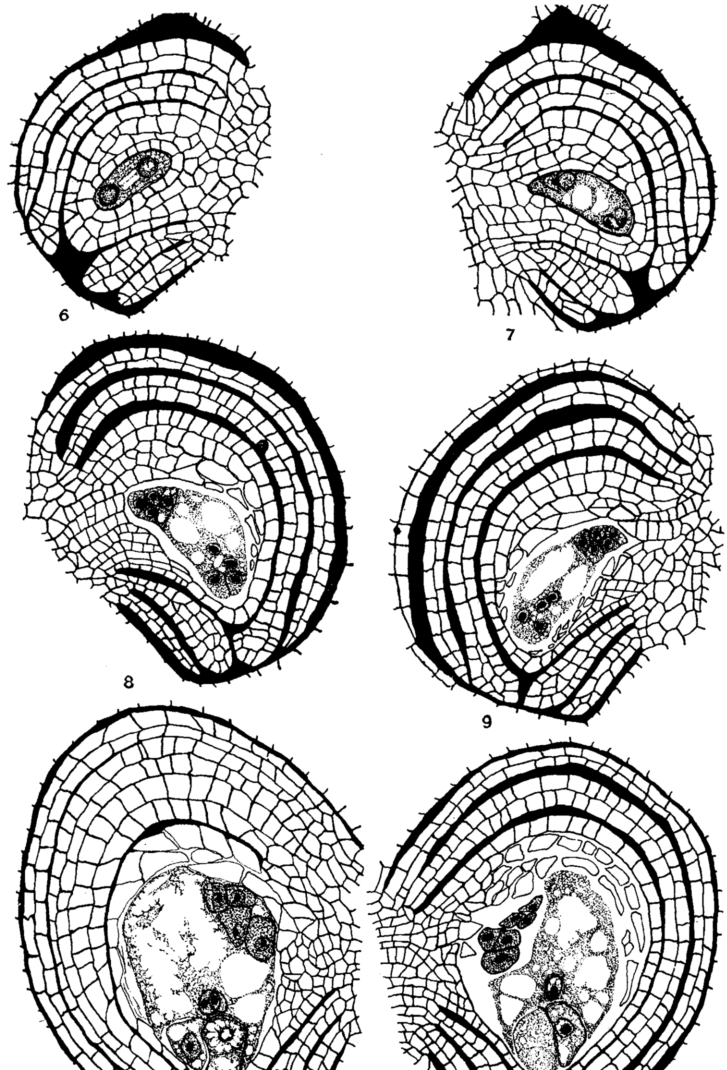


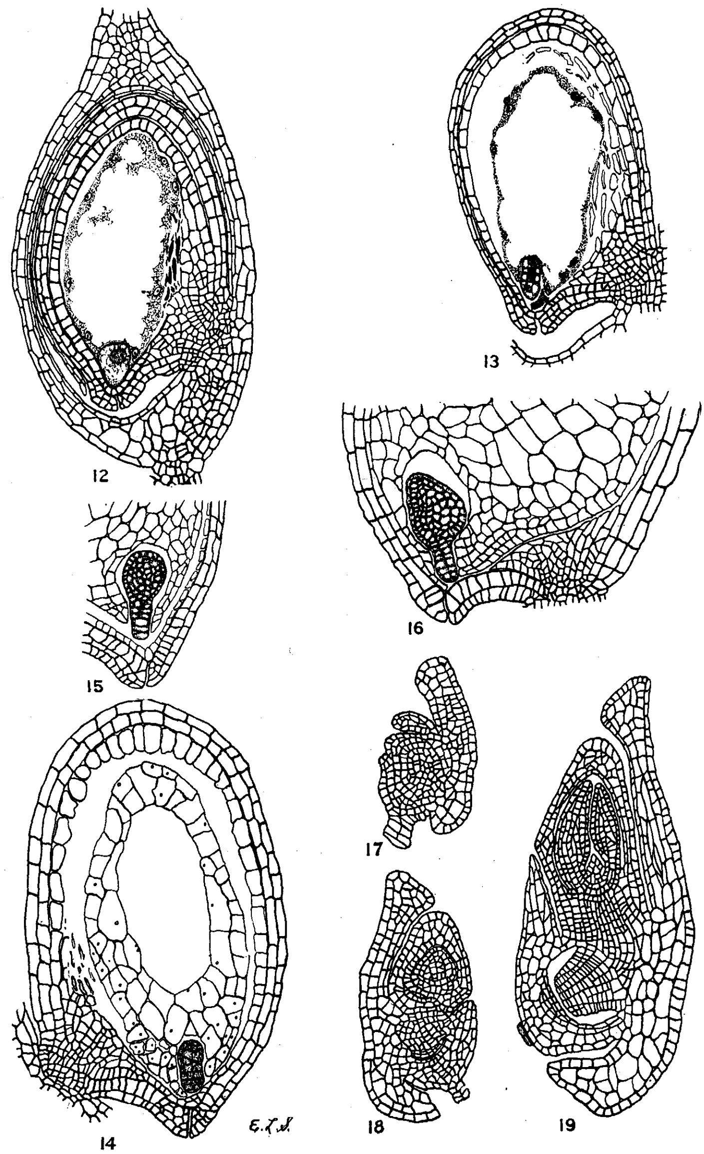
Fig. 1. Section of young ovule showing archesporial cell.
Figs. 2, 3, 4. Sections of young ovules showing T-form tetrad.
Fig. 5. Section of ovule showing persistence of the inner megaspore and the disintegration of the other megaspores.



Figs. 6 and 7. The two and four nucleate embryo sacs.

Figs. 8 and 9. The eight nucleate sac showing the separation of all four antipodals from the rest of the sac.

Figs. 10 and 11. The maturing embryo sac; one synergid, the egg, and the fusion of two micropylar nuclei forming the endosperm nucleus; the antipodals remaining *in situ* as the sac enlarges.



Figs. 12, 13, 14. Sections of ovule showing the fertilized egg and young embryo; the developing endosperm; antipodals in disintegrating stages; the disappearance of the outer integument.

Figs. 15–19. Development of the embryo.