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COMPARATIVE DEVELOPMENTAL STUDIES OF THE FLORET AND EMBRYO SAC IN FIVE SPECIES OF ORYZOPSIS (GRAMINEAE)

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ABSTRACT

Development of the floret and embryo sac of Oryzopsis virescens and O. hymenoides was studied. Evidence from this study and from other studies on grass floret and embryo sac development has brought the following interpretations. Histogenesis of the lemma, palea, posterior lodicule and the gynoecial wall is similar, and indicates their foliar nature. They are determinate organs, have a shallow site of initiation, and exhibit marginal growth. The anterior lodicules differ from them in having a deeper initiation site. The interpretation of the anterior and posterior lodicules as reduced perianth structures of one whorl rather than as structures 'de novo' is preferred. The callus is formed by the downward projection of the base of the lemma. Developmentally, the stamens are stem-like. The gynoecium consists of a unit ascidiform gynoecial wall surrounding a terminal ovule. There are two styles, each of which develops from the lateral portions of the gynoecial wall. The floret apex is not used up in the formation of the gynoecial wall. The residual floret apex develops into the ovule. The grass gynoecium may be considered acarpellate. The ovule is hemianatropous, bitegmic and pseudocrassinucellate. The micropyle is delimited by the inner integument. Embryo sac development is of the monosporic, 8-nucleate type. The antipodals are proliferated.

The development of the floret and embryo sac of three other species of Oryzopsis was also studied. They are, namely, O. micrantha, O. kingii, and O. asperifolia. Developmental features of all five species of Oryzopsis were compared with developmental features of

Oryzopsis miliacea, and of four species of Stipa, a closely related genus. These are, namely, S. lemmoni, S. hendersoni, S. tortilis and S. richardsoni. Cytotaxonomic studies by Johnson (1945. Bot. Gaz. 107: 1-31) in the genus Oryzopsis indicate that O. virescens (n = 12) and O. miliacea (n = 12) are members of the Old World section Piptatherum; O. micrantha (n = 11), O. kingii (n = 11), and O. asperifolia (n = 23), belong to the New World section Oryzopsis; O. hymenoides (n = 24) belongs to the New World section Eriocoma. Intergradation of the genera Oryzopsis and Stipa occurs in North America in the sections Oryzopsis and Eriocoma. Oryzopsis micrantha resembles O. miliacea in certain morphological features, while O. kingii is a 'borderline' Oryzopsis-Stipa species. Oryzopsis hymenoides is known to hybridise with eleven species of Stipa.

Thirty-one characters were abstracted from the developmental data and were analyzed statistically. The results indicate that O. virescens is set apart from the five other species of Oryzopsis and the four species of Stipa. The affinity of O. hymenoides on the basis of development is with Stipa. This further supports data from morphology, distribution and hybridization studies and suggests that Oryzopsis hymenoides belongs to the genus Stipa. There does not appear to be a discontinuous variation in development between O. miliacea, O. micrantha, O. asperifolia, O. kingii, S. richardsoni, O. hymenoides (Stipa), O. hendersoni, S. lemmoni and S. tortilis. It would seem that more comprehensive studies of the genus Oryzopsis will either lead to its mergence with Stipa or at least to a redefinition of the sections of Oryzopsis.

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GENERAL INTRODUCTION

This thesis consists essentially of two parts. Part I is an ontogenetic study of the floret and embryo sac of Oryzopsis virescens and O. hymenoides, as such data would lead to a better understanding of the floret of Oryzopsis in particular, and of the Gramineae in general. Part II is an attempt to elucidate the relationships of O. virescens, O. hymenoides, O. micrantha, O. kingii and O. asperifolia on the basis of data from developmental studies of the floret and embryo sac. It is hoped that developmental data can be used effectively as an adjunct to other characteristics in working out taxonomic problems.

An evaluation of ontogenetic studies

It is generally accepted by most taxonomists that taxa are properly established on the basis of multiple correlations of characters (Cronquist, 1968). Davis and Heywood (1965), stressed that all stages of development of the plant should be examined for possible characters. Yet ontogenetic features have not received much attention from taxonomists. Embryological studies have been employed, successfully, to solve certain taxonomic problems (Maheshwari, 1950, 1961). Recent work by Mehlenbacher (1970), and Maze and co-workers (1971), has shown that comparative studies on floret development in Oryzopsis and Stipa are useful in understanding the relationships of these two genera.

A few reasons could be offered for this lack of popularity of applied ontogenetic studies. Results from ontogenetic investigations have a history of not bearing out the popular existing dogma of the time. This

is especially true in the interpretation of the flower. This branch of research was set on a controversial course with the pronouncements of Schleiden in 1839 and Payer in 1857 (both cited by Moeliono, 1970), that ovules were not borne on carpels but were axis-borne. This was of course contrary to the prevalent carpel theory of that time. The fact that Schleiden was later shown to be wrong in his interpretation of fertilization did not help to foster faith in the ontogenetic method. Nonetheless, ontogenetic research has continued to be one of the chief lines along which attempts are made to solve the problem of organisation of angiosperm reproductive structures. Even with today's improved techniques, no agreement has been reached regarding the interpretation of the stamens and the carpels. The interpretation of the stamen on the basis of histogenetic analysis has resulted in diametrically opposed conclusions. Satina and Blakeslee (1943), Barnard (1957a, b), and Sharman (1960b) concluded that the stamens they studied were cauline, while Kaussman (1941), McCoy (1940), Boke (1947, 1949), and Kaplan (1968) hold that their investigations point to a foliar interpretation for stamens. Likewise, in the Cyperaceae the ovules are phyllosporous according to Schultze-Motel (1959), and cauline according to Barnard (1957b). In Datura stramonium, Satina and Blakeslee, (1943) concluded that the ovules are axis-borne, but Verzar-Petri and Baranyai Szentpetery (1960) stated that the ovules are carpellary.

It would appear, therefore, that the ontogenetic method cannot be used with any measure of reliability in studies on descriptive floral morphology, and much less so in comparative studies. It is the writer's contention that such a view-point is erroneous. The place of ontogeny in floral enquiry has been staunchly defended by Thompson (1937). One of the

causes for all these contradictions is that most workers have not analysed their results strictly on the basis of the histogenetic data they have obtained. An example is seen in Schultze-Motel's paper (1959). In his diagrams (Abb. 7, 10d, 12, 17, 18, 20) the ovules are formed directly from apical cells and are therefore terminal, but he interprets them to be phyllosporous. He adheres to the concept of the 'Entwicklungsfeld des Karpells' of Goebel (or 'scheitelbedeckendes Feld' of Eckardt, 1957), as shown by the following excerpts "Die Primordien der Karpelle treten als 'scheitelbedeckendes Feld' (Eckardt, 1957, S. 76) auf. Die Samenanlage (o in Abb. 7) entwickelt sich aus diesem Feld, is also phyllospor". The description of his results is dictated by the use of certain interpretive terms. As long as terms are used in such a way, the discussion about phyllosporous- versus axis- borne ovules becomes a travesty (Fagerlind, 1958). Another example is illustrated by the studies of Roth (1959), and Pankow (1959), on the Primula placenta. Using the same method (micro-technique), they obtained almost identical results, which were interpreted by them in diametrically opposed directions. Pankow, on the basis of his histogenetic results, interpreted the placenta as a continuation of of the floral apex. Roth, however, by a series of 'reasoned' deductions concluded that the placenta is of carpellary tissue.

The value of developmental studies has been stated cogently by Maze and co-workers (1971, 1972). However, one must guard against an over-emphasis of the results obtained by developmental studies. In this connection, it is well to bear in mind the opinions of von Guttenberg (1960), and Rohweder (1963), on the significance and limitations of histogenetic methods.

A brief botanical history of Oryzopsis

The genus Oryzopsis was established in 1803 by Michaux, based on a single New World species, Oryzopsis asperifolia. The genus has a very complicated taxonomic history, an excellent account of which was given by Johnson (1945a). Only a brief resumé of the taxonomic relationships in the genus is given here.

As presently understood, the genus Oryzopsis consists of approximately 16 species, occurring in the cool and temperate regions of both the eastern and western hemispheres. The species are placed in three main morphological groups, each a taxonomic section (Hackel, 1889; Johnson, 1945a). The taxonomic arrangement is given below:

Section Piptatherum

O. miliacea (L.) Benth. and Hook.

O. virescens (Trin.) Beck.

O. paradoxa (L.) Nutt.

O. coerulescens (Desf.) Hack.

O. holciformis (Biel.) Hack.

O. racemosa (J.E.Smith) Ricker

Section Oryzopsis

O. micrantha (Trin. and Rupr.) Thurb.

O. pungens (Torr.) Hitchc.

O. canadensis (Poir.) Torr.

O. exigua Thurb.

O. kingii (Boland.) Beal

O. asperifolia Michx.

O. swallenii Hitchcock and Spellenberg

Section Eriocoma

O. hymenoides (Roem. and Schult.) Ricker

O. contracta (B.L.Johnson) Shechter

The Old World section, Piptatherum, consists of 5 diploid species (2n = 24) which range in distribution from southern Europe and Northern Africa to Asiatic Russia. The sixth member, O. racemosa, is a polyploid (2n = 46) occurring in North America.

Species of the New World section Oryzopsis are rather distinct at the diploid level (2n = 22) from those of Piptatherum. The two polyploids in the section are O. asperifolia (2n = 46) and O. swallenii (2n = 34).

Eriocoma is a New World section of two polyploids, O. hymenoides (2n = 48) and O. contracta (2n = 48). The latter species is purported to represent a stabilized hybrid line derived from an O. hymenoides x O. micrantha cross (Shechter and Johnson, 1968).

The genus Oryzopsis is extremely difficult to circumscribe. Considerable uncertainty still exists in delimiting Oryzopsis from Stipa, a closely allied genus which tends to merge with Oryzopsis through the section Oryzopsis. Characters of the lemma, awn, and callus, are traditionally relied on to distinguish Oryzopsis from Stipa. In Oryzopsis the lemma is relatively broad, short, and indurate, the callus blunt and the awn deciduous. In Stipa the lemma is long and slender, less indurate, the callus is sharp-pointed and the awn is persistent. Also, in most species of Oryzopsis the inflorescence is an open panicle, while in Stipa the panicle is contracted. Taken independently, these characters are highly unreliably. Even when considered together they do not effectively

distinguish between the two genera, for certain species resemble Oryzopsis in some features, and Stipa in others. It has been the tendency for systematists to assign uncertaind cases to Oryzopsis. A recent example is O. swallenii (Hitchcock and Spellenberg, 1968).

Studies in floret development and embryology in the two genera have been undertaken by Maze et al. in recent years (1970, 1971, 1972) and are continuing. Their data have proved to be useful in assessing relationships of three species of Stipa. Mehlenbacher (1970), after a thorough study of O. hendersoni Vasey found that this species is closer to Stipa than to Oryzopsis, and subsequently transferred it to Stipa (Spellenberg and Mehlenbacher, 1971).

The development of the floret and the embryo sac (up to fertilization) of 5 species of Oryzopsis was studied by the author. The 5 species are, namely, O. virescens, O. hymenoides, O. micrantha, O. kingii and O. asperifolia. They were chosen for the following reasons: O. virescens has the vegetative and floral features traditionally associated with Oryzopsis (flat broad leaves, open panicle, short deciduous awn, plump lemma and blunt callus), and is considered to be most representative of the genus. Oryzopsis hymenoides is of interest because of its resemblance to species of the section Piptatherum in several features, and because in nature it forms hybrids with several species of Stipa, as Johnson demonstrated in a series of papers (1943, 1945b, 1960, 1962, 1963). It is easily distinguished from the Old World species by its pubescent lemma and sharp pointed callus. Oryzopsis micrantha, O. kingii and O. asperifolia are members of the section Oryzopsis — a section

marked by specialization in characters which merge with the genus Stipa. Oryzopsis micrantha possesses an admixture of Piptatherum and Oryzopsis characters. Its affinity to the section Piptatherum is recognized by Elias (1942), who placed it in that section. Oryzopsis kingii can best be described as a borderline Stipa-Oryzopsis species. It possesses features which are associated regularly with Stipa (narrow involute leaves, closed panicle, twisted awn, narrow lemma and sharp callus). Its assignment to either genus islargely arbitrary. Oryzopsis asperifolia, the type species of the genus, seems to occupy a position, morphologically speaking, between the two extreme ends of the section Oryzopsis, as expressed by O. micrantha and O. kingii (see Johnson, 1945a).

Morphological and cytological studies so far have not resulted in a satisfactory delineation of the genus Oryzopsis, or a taxonomic arrangement that reflects the intricate relationships between species of Oryzopsis, and between Oryzopsis and Stipa. More comprehensive studies of the genus Oryzopsis are needed, and towards that end the author has chosen developmental studies. A thorough study of floret development and embryology of two species, O. virescens and O. hymenoides, is attempted — O. virescens because it approaches the traditional 'Oryzopzoid' description; O. hymenoides because of its affinities with section Piptatherum and its hybridization with species of Stipa. It is hoped that such a study will lead to a better understanding of the Oryzopsis floret. A logical extension of the above investigation is to seek characters of a developmental nature for purposes of comparison. This is done for the 5 species mentioned.

PART I

Developmental studies of the floret and embryos sac of Oryzopsis virescens and O. hymenoides.

INTRODUCTION

In recent years knowledge of the grass floret has increased through contributions from histogenetic studies. Published descriptions of such studies are found in the papers by Cannon (1900), Bonnett (1953, 1961), Barnard (1955, 1957a), Sharman (1960a, 1960b), Klaus (1966), Mehlenbacher (1970), and Maze et al. (1970, 1971, 1972). However, there is still no unanimous interpretation of the grass floret, which remains a controversial topic in plant morphology. The controversy centres mainly on the nature of the lodicules, the stamens and the gynoecium, that is, whether they are of a phyllome or caulome nature.

Because of the imprecision of morphological terminology, it is imperative that the author clarifies her use of terminology, especially the terms phyllome and caulome. Used in a descriptive sense, morphological terms such as leaf, bud, etc., are merely words for structural entities. In a comparative sense the same words signify mutually exclusive categories. While it is not wrong to use the word 'leaf' in the sense of a category, the word conjures in most minds the picture of a foliage leaf. An alternative term of a more generalized character — phyllome — is preferred. Likewise, the structure described as a 'bud' is a member of the category caulome. Defined in general terms, a

phyllome is an abstract entity to which belong lateral appendages of determinate growth. These lateral appendages are dorsiventral, exhibit marginal growth and have a shallow site of initiation. The category caulome encompasses structures of an axial nature. These are of indeterminate growth, usually radial in shape, do not undergo marginal growth, and have a deeper site of initiation. It is rather fortunate that the vegetative structures of the grasses that have been studied developmentally lend themselves easily to categorization.

The preceding paragraph will undoubtedly unleash a torrent of criticism at the author, identified by 'Croizatian' and 'Sattlerian' tags. Sattler (1966) made a very eloquent and valid plea for a more precise approach to comparative morphology. But his semi-quantitative homology concept does not lend itself readily to application, as he himself admitted. For lack of additional methods, the author has to use the 'traditional tools of the trade' — the established vocabulary of comparative morphology is still the most useful for communication of ideas (at least at the present time).

In this part of the thesis, the author reports her studies on the floral histogenesis in two species of Oryzopsis, O. virescens and O. hymenoides. Her present observations on floral histogenesis will be applied to the interpretation of the Oryzopsis floret in particular, and to a critical discussion of the Gramineae floret in general.

MATERIALS AND METHODS

The floret of O. virescens is short and plump, the awn is short and deciduous, and the callus is blunt (Figs. 1, 2, 3). Oryzopsis hymenoides is a wide-ranging grass in arid areas of western North America. In the shape of its floret and the deciduous nature of its awn, it approaches O. virescens (Figs. 4, 5, 6), but its sharp callus and its pilose lemma are characters found in Stipa, a genus closely allied with Oryzopsis, (see Johnson, 1945a for the intricate relationships within Oryzopsis and between it and Stipa).

Materials used in this study were collected from plants growing in the Botany Garden at the University of British Columbia. Plants of O. virescens were grown from seed obtained through the International Seed Exchange; plants of O. hymenoides were transplants of populations collected in Canal Flats, British Columbia.

Florets, entire young inflorescences, or portions of young inflorescences were fixed in a Formalin-Acetic Acid-Alcohol mixture, using 50% ethyl alcohol (Johansen, 1940). They were dehydrated in a 2,methoxyethanol - absolute alcohol - n-propanol - n-butanol series (Feder and O'Brien, 1968), and embedded in Paraplast. Florets longer than 1 mm. were oriented before sectioning. This was done very simply by using a pair of fine forceps and a small spatula. These instruments were heated and used to melt the wax around the floret. With the aid of a stereo-microscope the floret was then moved around and positioned for sectioning either in a frontal or sagittal longitudinal plane. Sections were cut at 6 - 7 u and stained in a combination of safranin, tannic acid, orange G and iron alum (Sharman, 1943). Drawings were

traced from a projection head on a Zeiss Ultraphot II microscope. All drawings are of sagittal sections unless otherwise stated, with the front (= anterior) side of the floret to the reader's left. Information from sections of florets in early stages of development was supplemented by scanning electron micrographs.

The terms anterior (= front) vs. posterior (= back), and abaxial vs. adaxial are used to describe the orientation of the various parts of the floret. These are used with reference to two axes: the rachilla axis and the floret axis.(Fig. 7). In those spikelets with more than one floret, the lemma is situated away from the rachilla, while the palea is next to the rachilla. That side of the floret with the lemma is said to be the anterior side; the palea side is correspondingly the posterior side. Adaxial and abaxial denote two opposing surfaces of the same lateral structure, with reference to the axis on which it is borne (in this case the floret axis). For example, the lemma has an adaxial surface (adjacent to the floret axis), and an abaxial surface (away from the floret axis).

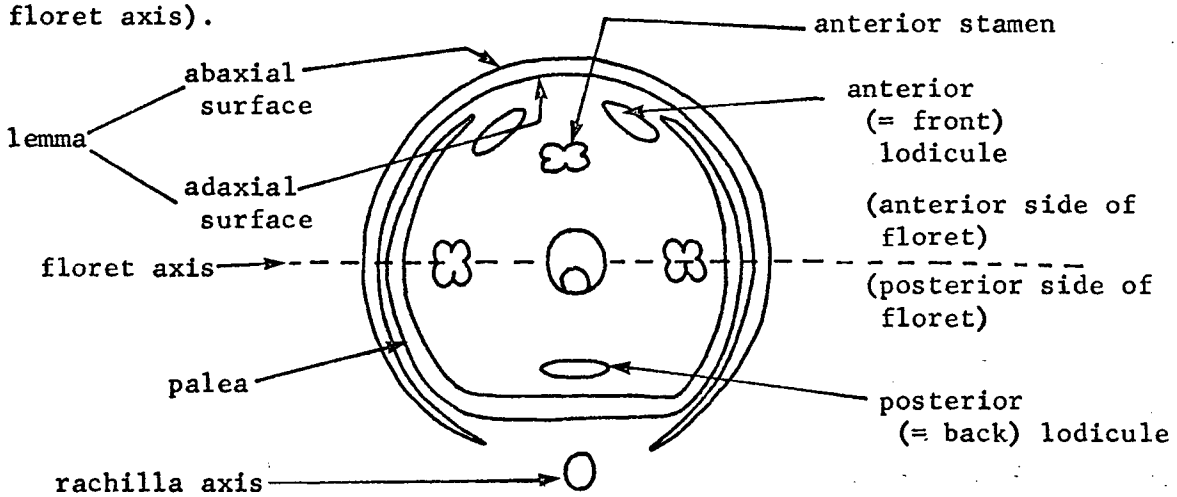

FIG. 7. Cross-section of grass floret (diagramatic).

OBSERVATIONS

Oryzopsis virescens (Trin.) Beck.

General floret organogenesis

The first structure to be initiated on the floret apex is the awn-lemma (Figs. 8, 15). This occurs after the initiation and early growth of the first and second glumes. The palea and the stamens appear next (Figs. 9, 18). There are three stamens, one anterior and two lateral, and unless otherwise stated, the stamen featured in the drawings is the anterior one. The lodicules, two anterior and one posterior, follow closely (Figs. 10, 19). The callus and the gynoecial wall then initiate, at approximately the same time (Figs. 11, 20). The last floral structure to develop is the ovule (Fig. 13). The shape of the floret at the megaspore stage in embryo sac development is shown in Figure 14.

Floret apical meristem

The floret apical meristem has a tunica-corpus organization. The tunica is one-layered. The outermost corpus cells often seem to form a distinct layer beneath the tunica (Fig. 15). The floret apex is dome-shaped and remains so throughout organ formation, though it undergoes some displacement in the course of floret development (cf. Figs. 15, 18, 19, 20). Early in floret development, the floret apex is more or less aligned with the floret axis (Fig. 15). During early growth of the anterior stamen and anterior lodicule the floret apex becomes posteriorly directed (Figs. 10, 19), and continues to be so oriented during early growth of the gynoecial wall (Figs. 12, 34). After the completion of

initiation of the gynoecial wall, the floret apex continues growth as the ovule, but it gradually becomes re-oriented to a vertical and then to an anteriorly-directed position (Figs. 78, 79, 80).

Awn-lemma

Following the terminology and reasoning of Maze et al. (1971), the awn and the lemma are considered together in early development, and are referred to collectively as the awn-lemma. Awn-lemma initiation is indicated by a periclinal division in the protoderm on the anterior side of the floret apical meristem, just below the apex (Fig. 15). The initiating division is followed by further periclinal divisions in the protoderm and ground meristem, involving three to four cells in the vertical direction. The awn-lemma is formed from cells of the protoderm and the first layer of the ground meristem. From the anterior side, initiating divisions spread around the lateral flanks of the floret apex. The lateral spread of divisions results in the formation of a crescentic protusion which is higher on the anterior side and slopes down posteriorly (Figs. 16, 16a). Upward growth of the primordium is mainly the result of sub-apical activity (Fig. 17).

Increased apical activity at the point of origin of the awn-lemma primordium results in a free extension (Figs. 18, 290). This anterior extension is the young awn. For ease of discussion, growth of the anterior portion of the awn-lemma primordium will be considered first, and the lateral portions later.

In the young awn increase in height by apical activity is soon followed by intercalary growth. Cellular differentiation, using cell

vacuolation as an indication, occurs very early in awn development. The cells at the distal end become vacuolated when the awn-lemma primordium is ca. 150 u in height. Growth in girth of the awn is the result of cell vacuolation and periclinal divisions in the ground meristem (Fig. 19). At this stage it is not possible to distinguish the awn base from the lemma below it. The cells in the proximal one-third of the awn-lemma primordium are smaller than those in the distal two-thirds of the primordium, and are also vacuolate to a lesser degree. Certain interesting growth phenomena are observed at the time the gynoecial wall initiates. In the adaxial ground meristem of the awn-lemma, at a point more or less level with the initiating gynoecial division, oblique divisions are seen (Fig. 20). The adaxial ground meristem cells in this region become actively mitotic and form a group of small, densely cytoplasmic cells with no particular arrangement (Figs. 21, 22). At the same time the corresponding abaxial ground meristem cells undergo periclinal and anticlinal divisions. Figure 22 shows the awn-lemma junction when the gynoecial wall appears on the posterior side of the floral apex. Further divisions in the ground meristem on the adaxial side are mostly periclinal, forming regular cell files. The lemma apex becomes slightly expanded (Fig. 23). Adaxial protodermal cells of the lemma apex also start to divide periclinally, while the abaxial protoderm remains one-layered. Continued meristematic activity, together with re-oriented planes of growth, greatly increases the thickness of the lemma apex (Fig. 24). Cell enlargement and vacuolation of the cell files push each side of the apex outwards so that the fully expanded lemma apex has a double convex shape, with the apex of each convexity directed

upwards. This is seen in Figure 25, at a stage when the integuments of the ovule are formed. The abaxial protoderm has adjusted to the increase in bulk of the abaxial ground meristem by an increased number of anticlinal divisions. On the adaxial side there is a multiple protoderm of about two to four cells deep, spread over the upper one-third of the convexity. Accomodation of the adaxial protodermal cells to the increased volume of the ground meristem is through cell division and enlargement.

The portion of the lemma that eventually encloses the palea and the rest of the floret develops from the lateral portions of the lemma (Fig. 292). Growth of the lateral portions is of course co-ordinated with that of the rest of the lemma. The lateral portions of the lemma grow around to the posterior side of the floret but do not meet. Initially they are taller on the anterior side and barely cover the base of the floret (Fig. 291). Concurrent with the growth of the anterior portion of the lemma, the lateral portions grow upwards, elongate tremendously and overtop the rest of the floret. Just prior to the formation of the integument in ovule development, the upper portions of the free margins of the lemma have increased in height more than that part of the lemma to which the awn is attached (Fig. 24). This results in the free edges of the lemma forming two lobes (or 'ears') in front of the awn.

Cell enlargement in the lemma finally obscures the patterns of cell divisions that resulted in the characteristic shape of the lemma apex. Cells at the awn-lemma junction remain small, and eventually become heavily lignified, with abundant simple pits in the cell walls. They do not form a cambium-like layer as that reported for Stipa lemmoni by Maze et al. (1972).

Callus

The callus is initiated through cell enlargement and cell division in the ground meristem at the base of the lemma, on the anterior side of the floret (Fig. 26). This occurs at about the time of initiation of the gynoecial wall. At this stage the base of the floret where it is attached to the rachilla is almost horizontal.

Initial growth stages of the callus involve periclinal divisions, vacuolation and expansion, in a direction parallel with the adjacent protoderm of the cells of the ground meristem (Fig. 27). The protoderm cells neither divide periclinally nor enlarge perceptibly. They divide anticlinally to keep pace with the increase in volume of the groumd meristem (Figs. 27, 28). By the time the gynoecial wall is fully initiated the callus has developed into a rounded hump with a downward-directed apex (Figs. 27, 28).

Concomitant with the growth of the callus, the formerly horizontal floret-rachilla junction starts to tilt in an anti-clockwise direction. The rachilla also increases in width (Figs. 27, 28, 29, 30). Re-orientation of the floret-rachilla junction can be attributed in part to the following growth phenomena. On the anterior and posterior sides of the rachilla, periclinal divisions in the ground meristem produce files of cells perpendicular to the protoderm (Figs. 27, 28). Anticlinal divisions in the ground meristem on the posterior side of the rachilla form files of cells parallel with the adjacent protoderm (Fig. 29). Cell enlargement in the ground meristem on the posterior side of the rachilla in the axil of the second glume (Fig. 30) and possibly cell enlargement in the tissues below the second glume (unfigured) lead to growth upward

of the posterior sides of the rachilla and the lemma base.

The continued enlargement, parallel with the protoderm, of the ground meristem cells in the callus, together with the elongation of the protodermal cells, pushes the callus further down (Fig. 30). This downward growth is concomitant with further tilting upwards of the lemma base and the rachilla on the posterior side, as discussed above (Figs. 29, 30). When fully mature, the rounded tip of the callus is on, or close to, the vertical axis of the floret (Fig. 14).

Palea

The palea arises after early growth of the awn-lemma primordium through the periclinal divisions of several protodermal cells on the posterior side of the floret apex (Figs. 18, 31). The initiating divisions spread around the flanks of the apex to the anterior side, but do not encircle the apex. Following initiation, the cells underlying the protodermal initials divide periclinally, but the major contribution to the palea is made by derivatives of the protoderm (Figs. 32, 33). Growth of the palea is through apical and subapical activity. Oblique-anticlinal divisions of the apical initials give rise to the palea protoderm, while meristmatic activity of the subapical cells gives rise to the internal tissues of the palea (Figs. 34, 35). Marginal growth is due to marginal and submarginal initials. Growth of the palea in early stages is mainly due to cell division . After the gynoecial wall is completely initiated around the apex, the palea grows mainly through cell elongation. At maturity the palea has a short biseriate apical portion and a broad base (Figs. 36a,b,c). The cells which

enlarge the most are those on the adaxial surface.

Posterior lodicule

The posterior lodicule (Figs. 291, 292) appears shortly after the palea. Its initiation is indicated by periclinal divisions in the protoderm on the posterior side of the floret apical meristem , just above the palea (Figs. 20, 33). In other words, it initiates directly from the floret apical meristem. Protodermal derivatives contribute solely to the tissues of the posterior lodicule. Early growth is the result of apical and subapical activity (Figs. 34, 35), and results in an organ which is considerably thinner than the palea (Fig. 37). At maturity the posterior lodicule is a thin flap of homogenous, non-vascularised tissue, about three to four cells thick (Figs. 38, 39).

Anterior lodicule

The inception and development of the anterior lodicules is different from that of the posterior lodicules. Initiation of the anterior lodicules is through periclinal divisions in the first layer of the ground meristem, in between the bases of the developing stamens. The site of initiation occurs over 2 - 3 cells in longitudinal section (Figs. 19, 40). It has a deeper site of initiation than the posterior lodicule. Following the initiating divisions, the protoderm cells divide periclinally (Figs. 34, 42). In cross section, two separate sites of initiation of the anterior lodicules are seen (Fig. 45). Through repeated periclinal divisions in the ground meristem short files of cells are formed (Fig. 41). The anterior lodicules at this stage appear as bulges (Fig. 42).

Growth in height of the anterior lodicules is intercalary (Figs. 43, 44). Apical growth is not distinct. Each anterior lodicule is attached to the floret axis by a very broad base (Fig. 48). The cells of the mature anterior lodicule form a homogenous tissue, supplied by two vascular strands (Fig. 49).

Marginal growth is initiated when periclinal divisions in the protoderm spread from the site of lodicule initiation in a posterior direction (Fig. 46). A distinct posterior margin is soon formed (Fig. 47). When this is discernible an anterior margin starts to grow (Fig. 47). Growth is maximum in the anterior portion of the lodicule so that this portion of the lodicule is thickest (Figs. 48, 49, 50).

Stamens

Stamen initiation starts with periclinal divisions in the first layer of the ground meristem (Figs. 18, 51). At initiation and during subsequent stages of development the protodermal cells divide anticlinally only. Early growth results from divisions in the ground meristem (Figs. 19, 40). The young stamen primordium very early assumes a globose form (Fig. 291).

Anther formation involves almost all the cells of the stamen primordium. Only a few cells at the basal portion of the primordium undergo extensive elongation to form the filament. A young anther primordium in cross section soon becomes slightly 4-lobed (Fig. 52). Several hypodermal cells become differentiated in each lobe and are recognised by their larger size and conspicuous nuclei (Fig. 53). These form

the archesporial cells. Stages in anther development are shown in Figures 54, 55, and 292. The fully developed anther has four wall layers. The innermost wall layer, or tapetum, is of the secretory type.

Gynoecium

The gynoecium is the last structure to develop from the floret apical meristem. The gynoecial wall is first indicated by one or two periclinal divisions in the protoderm on the anterior side of the floret primordium, between the adaxial furface of the anterior stamen and the apex of the primordium (Fig. 57). That is, it initiates as a lateral appendage. This is followed by similar divisions in the ground meristem underlying the protodermal initials. A fold develops laterally on the apex (Figs. 58, 293). Such mitotic activities, starting on the anterior side of the floret apex, extend around both flanks of the apex (Figs. 59, 60, 61), and eventually appear on the posterior side (Figs. 62, 63). The gynoecial wall is thus transformed from a crescent-shaped primordium to a ring-shaped one. The posterior rim of the gynoecial wall becomes the site of active mitotic divisions (Figs. 64, 65, 66). The gynoecial wall then grows upward as a tube (Figs. 67, 68, 69, 70).

The total floral apex is not used up in the formation of the gynoecial wall. Following the initiation of the ring-shaped primordium, the apex of the floret primordium increases in size (Figs. 64, 65). It develops directly into the ovule.

The two lateral sides of the gynoecial wall develop into style branches (Figs. 68, 71, 72). The style branches are solid and initiate stigmatic hairs through cell elongation in the protoderm cells (Fig. 73),

at a time when the megaspore mother cell is formed in embryo sac development. These enlarged club-shaped cells undergo anticlinal and oblique divisions to form stigmatic hairs (Fig. 74). The stigmatic hairs are mostly localized on the inner surfaces of each style.

Each style has two areas of specialized tissue, the stigmatoid and the vascular. In Figure 74, the unfilled space in the style, towards the outer surface of the style, represents the vascular region, and the stigmatoid region, which is not represented, is situated towards the inner surface of the style, near the stigmatic hairs. Illustrations of the stigmatoid region are given in the account on O. hymenoides.

The loculus of the ovary does not appear to be closed prior to or during fertilization (Fig. 76). Tissue proliferated on the inner surfaces of the ovary wall bring the edges of the ovary wall closer together, but a cleft is left at the top of the ovary (Figs. 75, 75a, 76). The closing tissue consists of a group of small cells, and is the 'stylar core' described by Arber (1934).

The vasculature of the gynoecium was studied from serial sections of florets. Figure 77 shows a series of transverse sections of a floret at the megaspore stage. Subsequent to the detachment of a trace to each of the three stamens, the provascular tissue of the floral axis is in the form of a cylinder (Fig. 77a). At a higher level, an anterior gynoecial trace is detached from this provascular cylinder (Fig. 77b), and a little higher than this, two lateral traces become detached. The remainder of the central provascular axis continues directly to the ovule (Figs. 77c,d). There are, as shown in Figure 77d, four vascular

bundles in the ovary: two lateral, one anterior and one posterior. Each of the lateral vascular bundles enters a style (Figs. 77e,f,g). The posterior vascular bundle is the largest, and supplies the ovule. Both the anterior and posterior vascular bundles terminate in the ovary wall (Figs. 82a, 83a).

Early ovule and embryo sac development

Ovule

The whole floret apex is not consumed in the formation of the gynoecial wall. The residual apex forms a small convex dome, consisting of dense meristematic cells (Fig. 78). It develops directly into the ovule. With the formation of the ring-shaped gynoecial wall there is a slight shift in position of the floret apex so that instead of its being directed towards the palea it becomes anteriorly directed (Fig. 79). Concomitant with the growth of the posterior side of the gynoecial wall, the apex increases rapidly in size, and continues to tilt anteriorly (Fig. 80). By the time the integuments are initiated, the ovule appears to be borne laterally on the posterior side of the gynoecial wall (Fig. 81). As the ovule continues to grow, it tilts towards the lemma (Fig.82a), becoming orthotropous at the megaspore mother cell stage (Fig. 83a), then bending downward (Figs. 85a, 88a, 90a), finally becoming hemianatropous at the 8-nucleate stage in embryo sac development (Fig. 91a).

Integuments

Both the inner and outer integuments are of protodermal origin. They

are initiated as ring meristems. The inner integument initiates first and is indicated by protodermal periclinal divisions on both the upper and lower sides of the nucellus (Fig. 81). Initiating divisions of the outer integument are first seen on the upper side (Fig. 82), by which time the megaspore mother cell is distinct.

The inner integument forms the micropyle. In early stages of its development the inner integument is two cells thick. By the megaspore stage the micropyle is formed. Cells at this end of the inner integument start to divide. The result is an inner integument with a thickened micropylar portion while the rest of it remains two cells thick (Figs.90, 91). This thicker portion delimits the micropyle. Throughout development the inner integument stains more intensely than the outer integument. This feature, plus the smaller cells, implies that the inner integument adjusts to the increase in size of the ovule more by cell division than by cell expansion.

The outer integument is two cells thick throughout except on its upper side at the chalazal region. In this region there are two bumps (Fig. 88), the result of a few internal cell layers. The bump nearest the micropyle is discerned very early, at the time when the megaspore mother cell is differentiated (Fig. 83). The one further away from the micropyle appears at the tetrad stage, through periclinal divisions in the outermost cell layer (Fig. 86).

The cells of the outer integument are larger and more vacuolate than those of the inner integument. Accomodation of the outer integument to increasing ovule size is mainly through cell enlargement. As

the ovule grows, the bumps increase in size. The first bump (that is, the one nearer the micropyle) assumes an inverted cone shape (Fig. 90). The second bump (that is, the one further away from the micropyle) becomes a flange of tissue adpressed against the first bump. Both the bumps remain close to the point of ovule attachment. At the 8-nucleate stage, the two bumps are so closely adpressed that they appear as one structure (Fig. 91). This structure projects up into the cleft between the stylebranches (Fig. 91a), and may, as has been postulated, (see True, 1893; Weier and Dale, 1960), direct pollen tubes towards the micropyle. The outer integument begins to disintegrate soon after fertilization. It is almost obliterated by the time a 4-cell embryo is developed.

Nucellus

Growth of the nucellus and re-orientation of the ovule occur simultaneously. During early megasporogenesis the ovule is pushed from an uptilt to an orthotropous position through divisions of the nucellar cells adjacent to the megaspore mother cell (Fig. 82). Subsequent divisions of the nucellar cells around the megaspore, and later around the embryo sac, are oriented at an angle to the axis of the embryo sac (Fig. 83). This growth contributes to increase in thickness of the ovule. By the 8-nucleate stage, mitotic activities of these cells cease and the cells elongate parallel to the longitudinal axis of the embryo sac, thereby increasing the length of the ovule (Fig. 91). Some of the cells next to the embryo sac are crushed by the transverse expansion of the latter.

The nucellar protoderm starts to divide periclinally at the late megaspore mother cell stage (Fig. 83). By the 4-nucleate stage most of the protodermal cells have divided at least once. Their contribution to the bulk of the ovule is most obvious at this stage (Fig. 90). From then on, as the ovule further increases in size the protodermal contribution becomes less obvious (Fig. 91).

Most of the growth of the nucellus is actually due to activity in the chalazal region. Early growth is in length (Fig. 84). Later growth is the outcome of cell divisions in variously oriented planes, contributing to increase in bulk of the ovule as well as shifting the ovule to a hemianatropous position (Figs. 85, 88, 91). Further differentiation of the nucellar cells mostly involves cell expansion.

Embryo sac

The embryo sac is of the Polygonum type (sensu Maheshwari, 1950). The archesporial cell is differentiated as the megaspore mother cell before the floret is extruded from the inflorescence sheath. Figure 84 shows a stage in megasporogenesis. The tetrad that is formed is usually linear (Fig. 85), but is occasionally T-shaped (Fig. 87). The functional megaspore is the chalazal one. The first megaspore to degenerate is either the one above the chalazal megaspore, or the next one above. The chalazal megaspore is the functional megaspore.

The embryo sac undergoes changes in shape as it develops. At the 2-nucleate stage it is oblong (Fig. 89), and becomes broadly fusiform at the 4-nucleate stage (Fig. 90). At the beginning of the 8-nucleate stage the micropylar end has broadened out so that the embryo sac appears

broadly ovate at this end, while at the chalazal end it abruptly narrows to a slot (Fig. 91). Just before fertilization the slot widens (Fig. 94). The embryo sac at this stage is ovate (Fig. 94). From this stage on, it increases in length (Figs. 97, 98).

At the early 8-nucleate stage (Fig. 91), it is not possible to distinguish the egg from the synergids. As the synergids differentiate a large vacuole develops in each of them at the lower (= chalazal) end, and the nucleus is at the upper (= micropylar) end (Fig. 92). No filiform apparatus is seen in the synergids. When the egg and the synergids have differentiated the antipodals have divided once (Fig. 92). The antipodals lie in the slot at the chalazal end of the embryo sac. Their cytoplasm is dense, granular, and non-vacuolate. The polar nuclei at this stage are situated above the egg and synergids and are very close to them.

Just prior to fertilization certain visible changes occur. The cytoplasm of the synergids becomes dense and granular. One synergid decreases in size (Fig. 94), and then degenerates. The antipodals have proliferated even more and have moved to a lateral position. The outlines of the antipodals are difficult to distinguish. No mitotic figures were seen. Each antipodals appears to have one nucleus only. The polar nuclei move away from their position next to the egg and synergids to a higher position in the central cell.

Fertilization

Fertilization occurs after one synergid has degenerated. The pollen

tube travels through the micropyle and nucellus and seems to enter the embryo sac between the base of the persistent synergid and the embryo sac wall (Figs. 96, 97). The tip of the pollen tube appears to have a deposit of a darkly staining material. Actual discharge of the male gametes was not seen. It could not be ascertained whether the pollen tube contents are discharged into the synergid before entering the egg, or are discharged directly into the egg. A quantity of chromatin-like materials is seen on top of the egg. This may be pollen tube contents plus remnants of the degenerated synergid. The polar nuclei do not fuse before fertilization.

Post-fertilization

This was studied up to the 4-cell embryo stage. The endosperm is free-nuclear and initially develops faster than the embryo (Fig. 98). The hitherto persistent synergid begins to degenerate.

Oryzopsis hymenoides (Roem. and Schult.) Ricker

A comparison of Oryzopsis hymenoides with O. virescens will be emphasized in this account.

Floret organogenesis

Organ inception follows this sequence: awn-lemma (Fig. 99), palea and stamens (Fig. 100), lodicules and callus (Fig. 101), gynoecial wall (Fig. 102), and finally, the ovule (Fig. 104). Oryzopsis hymenoides

differs from O. virescens in the precocious development of the callus and the early differentiation of the awn-lemma junction. By the time the gynoecial wall reaches the posterior side of the floret apex the awn-lemma junction and the callus are well-marked (Fig. 103). Further development of the floret is seen in Figures 104 and 105.

Floret apical meristem

As in O. virescens there seems to be no inner tunica in O. hymenoides (Figs. 99, 100). The floret apical meristem also becomes displaced and re-oriented in the course of floret development.

Awn-lemma

Initiation of the awn-lemma primordium is as in O. virescens (Fig. 99). Subapical activity is involved in the growth of the young primordium (Fig. 100), but cessation of this activity occurs earlier than in O. virescens. A shorter awn in O. hymenoides is perhaps an expression of the earlier cessation of subapical activity. Intercalary growth and cellular differentiation have produced a broader awn by the time of lodicule initiation (Fig. 106; cf. Fig. 19). Differentiation of the awn-lemma junction is seen when the gynoecial wall initiates (Fig. 107). This process is comparable with that seen in O. virescens. Cells in the region of the presumptive junction are small, have dense cytoplasm, and undergo oblique divisions (Fig. 108). Re-orientation of divisional planes and continued divisions result in an expanded lemma apex which is similar to that in O. virescens except for two features: in O. hymenoides

fewer periclinal divisions occur in the ground meristem; the adaxial protoderm remains one-layered (Figs. 109, 110, 111). Hairs on the mature lemma are protodermal outgrowths. As in O. virescens the upper portion of the free margins of the lemma is longer than the portion of the lemma attached to the awn and forms two 'ears' in front of the awn (Fig. 105). At maturity, where the awn base is attached to the lemma apex, the cells remain small (Fig. 112). This zone presents a line of weakness and accounts for the easily deciduous nature of the awn.

Callus

The callus of O. hymenoides differs from that of O. virescens in its earlier development and its shape at maturity. But they are similar in their initial stages of development and in their cellular composition. Initiation occurs at the time that the lodicules appear, and is through expansion, vacuolation and division of ground meristem cells (Fig. 113). At the base of the lemma on the anterior side, ground meristem cells near the protoderm become vacuolate and enlarge, in planes parallel with and perpendicular to the adjacent protoderm (Fig. 113), forming a slight bulge outwards. Continued cell enlargement of the ground meristem cells, accompanied by periclinal and oblique divisions, increases the size of of the bulge (Fig. 114). The protoderm adjusts to this increase in size by dividing anticlinally. The callus shown in Figure 114 is at the stage when the gynoecial wall initiates on the anterior side of the floret apex. It is comparable with the callus of O. virescens seen in Figure 27, which is during the growth of the anterior portion of the

gynoecial wall. During the early growth of the anterior portion of the gynoecial wall in O. hymenoides, increase in size of the callus is mainly through cell expansion, in a direction perpendicular to the adjacent protoderm (Fig. 115). Further growth of the callus sees a shift in the direction of expansion of the ground meristem cells. When the gynoecial wall appears on the posterior side of the floret apex, expansion of the cells of the callus is predominantly in a direction parallel with the protoderm (Fig. 116). Thus the callus is distended downward instead of outward, as in the earlier stages. At the same time, some of the protodermal cells begin to form hairs. Continued development of the callus involves extensive elongation of the ground meristem cells, not only downward but at an angle to the adjacent protoderm, so that the callus grows downward and obliquely outward (Figs. 117, 118, 119). The protodermal cells at the tip of the callus remain small, but those higher up on the callus extend longitudinally to keep pace with the expansion of the ground meristem cells. When fully formed, the callus has a sharp pointed tip, directed away from the vertical axis of the floret (Figs. 105, 119). The anti-clockwise tilting of the floret-rachilla junction seen in O. virescens is absent in O. hymenoides.

For ease of comparison, a table is given of the figures that illustrate comparable stages in awn-lemma and callus development in the two species, using gynoecium development as the standard of reference (Table I).

TABLE I. Reference table for comparison of stages in awn-lemma and callus development in O. virescens and O. hymenoides, using the stage of gynoecium development as a marker. The numbers refer to figures at the pertinent stages.

Stage of gynoecium development	O. virescens		O. hymenoides	
	awn-lemma	callus	awn-lemma	callus
Initiation of lodicules	19	19	106	113
Initiation of anterior gynoecial wall	20	26	107	114
Growth of anterior gynoecial wall	21	27	108	115
Gynoecial wall appears on posterior side of floret apex	22	28	109	116
Ring-shaped gynoecial wall	23	none	110	117
Prior to integument initiation	24	29	none	none
Initiation of inner integument on upper side	none	none	111	118
Complete inner integument	25	30	none	none
Ovule in orthotropous position	none	none	112	119

Palea

Development of the palea in O. hymenoides is similar to that in O. virescens (Figs. 120, 121, 122). At maturity the palea differs in the presence of elongate protodermal cells at the distal end (Figs. 123, 123a).

Lodicules

No visible difference can be seen in the initiation of the posterior lodicule as compared with that in O. virescens (Figs. 120, 121). However, the fully developed posterior lodicule in O. hymenoides is relatively thicker and has a blunt distal end (Fig. 124; cf. Fig. 38). This is undoubtedly due to more cell division as development proceeds. The anterior lodicules initiate and develop as in O. virescens (Fig. 125). At maturity they are uniformly thick structures with an acute abaxial tip (Figs. 126, 127, 128), unlike those in O. virescens which have an exceptionally thickened anterior portion (cf. Fig. 50).

Stamens

Development of the stamens is as in O. virescens, except for the presence of 'bearded anthers' in O. hymenoides. The anther 'beard' consists of multicellular, uniseriate hairs formed from protodermal cells at the distal end of the anther . An early stage of development of these hairs is seen Figure 129.

Gynoecium

This structure initiates and develops in a similar manner as described for O. virescens (Fig. 130). Figures 131 and 132 show that that portion of the floret apex which remains after the initiation of the ring-shaped gynoecial wall continues to grow as the ovule. At anthesis the inner margins of the ovary wall meet but do not fuse, so that the opening between the margins is not completely closed, but remains as the stylar canal (Figs. 113, 294, 295). Around the stylar canal is a region of smaller cells — this is the 'stylar core'.

There are two styles, each formed from a lateral portion of the gynoecial wall. The styles are closer here than they are in O. virescens (Fig. 134; cf. Fig. 76). The vascular supply of each style is an extension of a lateral vascular bundle of the ovary (Fig. 294). The stigmatoid tissue in each style runs parallel with the vascular bundle in the style. According to Bonnett (1961), the stigmatoid tissue in Avena sativa initiates in the ovary wall above the first cell layer of the inner surface of the ovary wall and proceeds acropetally into the styles. Initiation of stigmatoid tissue was not studied by the author. Figure 295 shows the position of the stigmatoid tissue in the ovary wall.

Early ovule and embryo sac development

Ovule

The ovule of O. hymenoides is similar to that of O. virescens except for some slight differences in size. The ovule in O. hymenoides at the inner integument stage is narrower (Fig. 135). At the 8-nucleate stage

it is also not as wide at the chalazal end (Fig. 143b).

Integuments

Inception and development of the integuments does not differ much from that in O. virescens (Figs. 135 to 138). Some differences between them are noted. The chalazal portion of the outer integument in O. hymenoides differs from that in O. virescens. In O. hymenoides the outer integument has only one bump in the chalazal region, whereas in O. virescens two bumps are present. Whereas in O. virescens the two bumps are adpressed to appear as one prominent bump which projects into the cleft between the style branches and persists until after fertilization, the single bump in O. hymenoides is poorly developed (Fig. 141), and it starts to flatten out prior to fertilization (Fig. 142). At the time of fertilization the outer integument has already started to degenerate (Fig. 143b).

Nucellus

Growth patterns in the nucellus are similar in both species, except that there are more periclinal divisions in the nucellar protoderm in O. virescens (cf. Figs. 142, 90).

Embryo sac

As in O. virescens there is one archesporial cell in O. hymenoides. Megasporogenesis is the same in both species (Figs. 139, 140).

The two species differ notably in the shape of the early embryo sac and in the differentiation of the synergids. In O. hymenoides the embryo sac is almost rectangular at the 4-nucleate stage and in the early 8-nucleate stage. The chalazal slot that is so characteristic of

the embryo sac in O. virescens is absent in O. hymenoides. At maturity, but before fertilization, the shape of both the embryo sacs becomes ovate (Fig. 143b).

Differentiation of the egg visibly resembles that in O. virescens (Fig. 142a). The mature unfertilized egg is highly vacuolate and also lacks starch grains (Fig. 143a). The differentiated synergids, instead of possessing a large vacuole at the lower (= chalazal) end, as is seen in O. virescens, have a number of scattered smaller vacuoles. A filiform apparatus develops in each of the synergids. Even before fertilization the two synergids are different from each other — one degenerates and stains deeply, while the other becomes highly vacuolate and stains lightly.

The polar nuclei and antipodals appear similar to those of O. virescens.

Fertilization

This process appears to be different from that observed in O. virescens in two respects: the presence of two synergids as opposed to one in O. virescens, and the discharge of the pollen tube contents into the degenerate synergid. From serial sections of the floret shown in Figures 144a,b,c, chromatin-like bodies are seen in the egg. Also, remnants of the pollen tube can be found in the degenerate synergid (Fig. 145a). The sections examined seem to indicate that the pollen tube contents reach the egg via the degenerate synergid (Figs. 144a,b,c). The polar nuclei are not fused prior to fertilization.

Post-fertilization

Observations were made up to the 2-cell embryo stage (Fig. 146). The hitherto persistent synergid begins to degenerate. Endosperm formation is initially free-nuclear.

DISCUSSION

General remarks about the interpretation of histogenetic data

Histogenetic studies usually follow one or both of these approaches: 1. the vegetative shoot axis and/or the reproductive axis of one or more species are/is studied and the histogenetic data obtained are compared and used to deduce the phyllome or caulome nature of an organ; 2. a broad comparative histogenetic survey is made of an organ-category in as many species as possible (such as the study by Sprotte, 1940).

The first method is by far the more popular and is the one used in this study (see Rohweder, 1963, for a critique of the method). It has to be borne in mind that interpretative histogenesis has no vocabulary of its own but is expressed in the language of comparative morphology. Moreover, concepts of organs such as 'leaf', 'stem', 'lemma', and 'stamen' originate from comparative morphology. An illustration of these two statements is given in these words used to describe the development of the lemma, viz., the lemma is leaf-like. To the author, this simply indicates that the nature of the lemma can best be understood by comparing it to a leaf. Both organs fit the criteria of a phyllome. At no

time is it implied that the lemma had been, at some stage in the past, a leaf which became modified into a lemma. To visualize the lemma as having been derived from a foliage leaf is to replace a purely morphological concept by a historical concept for the validity of which histogenetic data provide no evidence.

Any morphological interpretation of an organ on the basis of its histogenesis has to be approached with caution. This is especially crucial when isolated developmental observations are made on highly specialized structures, particularly the stamens and carpels. There is always the possibility of wrong inferences, as the developmental variation within these organs is not well known and has not been observed sufficiently. The interpretation of the leaf and the stem as being of a phyllome and caulome nature respectively can be made with more confidence, especially in the grasses. Leaf and bud development in the Gramineae has been studied in numerous species (Sharman, 1945; Pankow and Guttenberg, 1959). In this family the leaves have a shallow site of initiation (in the tunica), and show marginal growth. In comparison, the lateral shoot axes are established in the deeper layers of the main axis (in the corpus), do not show marginal growth but approach a radial symmetry. Also, a shell zone is present. Generally, leaves have a shallow site of initiation, but there have been occasional reports in other angiosperms in which the leaf initiates in the deeper layers of the apex. In Iris germanica (Rudiger, 1939), periclinal divisions which initiate leaf formation occur first in the two outermost corpus before they occur in the second tunica layer. In Euphorbia lathyris (Soma,

1959), leaf initiation involves the two tunica layers as well as the outermost corpus layer. However, in both cases, no account was given of axillary bud initiation. Later growth stages of the leaf were not described. Rohweder (op. cit.) concludes from this and Schnabel's work (Schnabel, 1941, cited by Rohweder) that in 'diesem Falle verhalten sich die Blattprimordien in sehr jungen Stadien also ganz wie ein Achsen-VP, um so mehr, als sie anfänglich annähernd radiär-symmetrische Gebilde darstellen'. The writer feels that caution is as much in place in the negation of the phyllome nature of a structure as in its affirmation.

Floral morphology

Awn-lemma

In initiation and development the lemmas in O. virescens and O. hymenoides resemble leaves. That the lemma is leaf-like is a description that agrees with all the grass lemmas that have been described so far (Cannon, 1900; Philipson, 1934, 1935; Bonnett, 1953, 1961; Holt, 1954; Barnard, 1955, 1957a; Sharman, 1960a, 1960b; Klaus, 1966; Mehlenbacher, 1970; Maze et al. 1971, 1972), and is probably applicable to all grass lemmas. As currently interpretated, the lemma represents a bract borne on the spikelet axis, specialized for flower protection, and in the axil of which arises the rest of the grass floret.

There have been numerous attempts in the past to equate the component structures of the awn-lemma with those of the grass leaf. About a hundred years ago, Van Tieghem propounded the view that when the lemma has a subterminal awn, the awn is equivalent to the grass blade, and the parts

of the lemma above and below the insertion of the awn are the equivalents of the ligule and sheath respectively. In those lemmas where the awn is terminal, the awn is considered as the blade, the whole of the lemma the sheath, and its lateral lobes, if any, as stipules which by fusion are supposed to give rise to the ligule. Philipson (1934), challenged this interpretation and suggested that in lemmas with abaxial awns, the awn does not represent the whole blade but only a part of the blade which has become separated from the main portion of the blade, and this main portion is represented by the median and terminal portion of the lemma. Recently an interesting parallel was drawn by Maze et al. (1971), between the growth pattern of the awn-lemma of Stipa tortilis and Oryzopsis miliacea and that of the leaf of Oryza sativa (Kaufman, 1959). Certain growth phenomena in the awn-lemma of S. tortilis which were used for comparison with Oryza by Maze et al. are also seen in O. virescens (viz., multiple periclinal divisions in the adaxial protoderm and ground meristem of the expanded lemma apex). The author concurs with Maze et al. that the developmental similarity between the Oryza leaf and the awn-lemma of species of Stipa and Oryzopsis is a reflection of the fact that plants are developmentally very simple, and that this similarity does not imply the derivation of one structure from the other. Furthermore, the awn-lemma of the Stipeae is like a grass leaf in that it has a sheathing base (lemma), and an appendage (awn). It is highly questionable if anything can be gained from trying to speculate what are the parts taken in the lemma by the various regions of the grass leaf.

Whether any significance can be attached to the presence of a

multiple protoderm in the lemma apex of O. virescens and the absence of such in O. hymenoides cannot be answered in this study. It does, however, result in a fatter apex in O. virescens.

Callus

The term callus is usually used for the hardened lower end of the lemma (Hitchcock, 1951; Pohl, 1968). Developmentally the callus is formed by the downward projection of the base of the lemma. This observation agrees with the earlier observation of Weatherwax (1942), on O. hymenoides. Maze et al. (1971) were non-committal as to the origin of the callus.

In some grasses, such as Heteropogon, Chrysopogon, the base of the spikelet at the point of its articulation with the rachilla forms a sharp projection which simulates the callus formed by the lower end of the lemma in Oryzopsis. The sharp structure at the base of the spikelet is also termed a callus.

The development of 'spikelet calluses' has not been studied. It is possible that the development of 'spikelet calluses' and 'lemma calluses' might be different. A sharp callus, whether it is a structure on the spikelet or the lemma, is an adaptation for dispersal by animals, by adhering to their skin or fur (Stebbins, 1956). In the Gramineae, the development of a similar mechanism for seed dispersal may involve different original structures. Another example is seen in the modification into bristles for wind dispersal of awns in Aegilops umbellulata and much divided glumes in Sitanion (Stebbins, 1972).

Palea

Like the lemma, the palea initiates and develops in the manner of a phyllome. Most workers interpret the palea as a bracteole borne on the floral axis, which, together with opposing lemma, encloses the grass flower. The lemma, palea, and the grass flower collectively form the grass floret. Schuster (1910), postulated the homology of the palea with two fused sepals, which, together with a hypothetical third sepal, formed the outer perianth series of the grass flower. The example cited by Schuster to support his hypothesis is the extant South American genus Streptochaeta, in which the palea is bifid almost to the base. On the basis of histogenetic data, the palea seems to fit best the current interpretation as a bracteole. Its phenetic similarity with a prophyll has been discussed by Arber (1925, 1934), and Philipson (1934).

Lodicules

Much controversy has centred on, and still does, the interpretation of the nature of the lodicules. These structures have been variously interpreted as bracts (Hackel, 1881), or modified perianth members (Rowlee, 1898; Schuster, 1910; Arber, 1934; Gould, 1968). Recent histogenetic studies have brought the following interpretations. Barnard (1955, 1957a) describes lodicules as 'appendages with a foliar-like origin developed on the axis of the flower primordium'. Bonnett (1953, 1961) reports that the anterior lodicules in Zea and Avena

initiate in the corpus, below the uniseriate tunica, and hence are to be considered as modified stems. Mehlenbacher (1970) found that in Oryzopsis hendersoni the anterior lodicules are partially stem-like and partially leaf-like. Maze et al. (1971) contend that anterior lodicules are 'de novo' structures and are not comparable with any other plant structures. Moreover, Maze et al. decry the interpretation of the anterior lodicules as homologues of perianth members, or any other modified structures, on the grounds that such an interpretation would require the assumption that lodicules evolved from perianth or any other structures, and in the process of evolution lost all their characteristic features.

In view of the varying opinions on the nature of the lodicules, the author would like to discuss the interpretation of the lodicules in some detail.

Hackel (1881), considered the anterior lodicules to be lateral halves of a leaf alternating with the palea, the middle part of which rarely develops fully. The posterior lodicule when present was supposed to continue the distichous arrangement of the palea and the anterior lodicules. This interpretation has to depend on a distichous arrangement of the lodicules, and cannot be upheld. The trimerous disposition of the lodicules in grasses, especially in the bamboos, has been demonstrated. Barnard (1955, 1957a) regards the grass flower as a branch system and categorizes the lodicules as foliar structures which are borne laterally on the main axis of the branch system. His interpretation of the lodicules as foliar structures is rather non-committal.

That the lodicules are stem-like is the conclusion Bonnett (1953, 1961) arrived at after some elegant studies on maize and oat. This interpretation is based primarily on the deeper site of initiation of the lodicules. Bonnett's text-figures in this connection are not convincing. For example, in his paper on maize in 1953, Figure 15D shows a leaf-like lodicule primordium with periclinal divisions in the protoderm; and in his paper on oat in 1961, Figures 13B and 17E show leaf and lodicule initiation respectively, both with initiating periclinal divisions in the cell layer beneath the protoderm.

Maze et al. (1971, 1972) contend that the majority of developmental features seen in the anterior lodicules (= dorsal lodicules in the papers by Maze et al.) are unique and point to a 'de novo' origin for these structures. The unique features cited by Maze et al. are: (1) the anterior lodicules do not initiate directly from the floret apical meristem, but, instead, from the base of the developing stamens; (2) they initiate in an area of some cell differentiation; (3) initiation is spread over a considerable area as seen in longitudinal section; (4) early growth in the lodicules is the result of mitotic activities over a considerable portion of the organ ; (5) the pattern of marginal growth in the anterior lodicules has not been described in any other organ.

The author disagrees with the extreme interpretation of Maze et al. and will review in detail each of their above arguments. (1) That the anterior lodicules do not arise directly from the floret apical meristem is a consequence of the time of their initiation -- they arise later than

the stamens. In other words, their inception is centrifugal. While a centripetal (= acropetal) sequence of organ inception occurs in many of the floral apices studied so far, a centrifugal sequence has been reported in several plant taxa (see, for example, Corner, 1946). Cheung and Sattler (1967) report that in Lythrum salicaria centrifugal inception occurs in the formation of not only one but three kinds of appendages, sepals, petals and stamens. Sattler (1967) cites a few genera in which the petal primordium is initiated on a common stamen-petal complex, so that a petal primordium does not always have to initiate directly on the floral apex. (2) This feature is a direct corollary of (1) and should not be considered. (3) This argument is based on a very limited number of observations (Stipa tortilis and Oryzopsis miliacea, Maze et al. 1971; Stipa lemmoni, Maze et al., 1972), and is not upheld by other histogenetic studies, including the author's (cf. Figs. 40, 41, for Oryzopsis virescens and Fig. 120 for O. hymenoides). In Bambusa arundinacea (Barnard, 1957a, Figs. 3, 5), and Avena sativa (Bonnett, 1961, Figs. 17 E,F), initiation of the lodicules involves only two to three cells in the vertical direction. (4) While this is a valid point with respect to anterior lodicule growth in those species of Stipa and Oryzopsis that have been investigated by Maze et al. and the author, there are no data on other grasses for comparison. Moreover, the limited observations available, as mentioned above, are on closely related taxa, so that any generalization of the uniqueness of this feature is open to suspicion. (5) The same criticisms leveled at (4) also apply to (5).

In the author's opinion, some of the 'unique' features that Maze et al. describe are not so unique after all, and others are based on too limited a sample. Furthermore, the interpretation of Maze et al. is that the posterior lodicule is different from the anterior lodicule. These workers offer three possible interpretations of the posterior lodicule on the basis of their histogenetic studies, viz., (1) as a 'de novo' structure; (2) as a foliar structure which is in the process of being lost; (3) as a foliar structure which is in the process of conversion to an organ similar to the anterior lodicules. Again, available data on posterior lodicule growth are too scanty to permit any generalization of this nature. Moreover, in the bamboos, such as Bambusa nutans (Arber, 1925), Arundinaria falcata (Rowlee, 1898), the anterior lodicules and and the posterior lodicule are alike in structure, and it is not unlikely that the posterior lodicule is histogenetically similar to the anterior lodicules. It seems more logical to the author to consider all lodicules as one whorl of floral appendages of one class.

There are perianth-like features in the anterior lodicules. These are: (1) the initiation of the anterior lodicules involves periclinal divisions in the protoderm; (2) the anterior lodicules are determinate organs; (3) development of the anterior lodicules involves marginal growth.

Histogenetic data do not preclude the interpretation of lodicules as modified perianth structures, and the author prefers this view. On the other hand, there are no histogenetic data at present that unequivocally support or negate this view. The amount of information on grass-floret

development is very scanty.

The difference in form between the anterior and posterior lodicules is perhaps related to their function. At anthesis, the anterior lodicules become turgid and force the lemma outwards. The posterior lodicule is relegated to an insignificant role. It is interesting that protogyny occurs in certain grass species, such as Anthoxanthum odoratum L. and Alopecurus pratensis L., in which there are no lodicules.

Arber (1926, 1927, 1928, 1934) described structures intermediate between lodicules and stamens in cultivated plants of Cephalostachyum virgatum and in wild plants of Schizostachyum latifolium. She labeled them as stamen-lodicules and commented that although the existence of lodicular stamens may not in itself prove the perianth nature of the lodicules, it lends probability to this view, as it is not unusual to find perianth members associated with stamens. Of course these unusual structures could also be dismissed as tetralogical organs of no importance.

Although both Arber and Schuster interpreted the lodicules as members of an inner perianth series, they differed in their interpretation of the outer perianth series. Arber's view is that the outer perianth series has been lost in the evolution of the grass flower. The reason she postulated a biseriate lodicular series was to bring the grass flower closer to the typical monocotyledonous floral diagram. She acknowledged that her floral diagram of the grasses 'merely formed a hypothetical framework upon which to arrange her ideas'. Schuster's views are extremely interesting and deserve more than the scant attention that is paid to

them.

Schuster suggested that the palea was homologous to two outer perianth members and that the third outer perianth member probably disappeared during the evolution of grasses from their ancestral forms. The lodicules formed the inner perianth. In the evolution of the grass flower the lodicules became reduced in structure as a result of the enveloping of the flower by the lemma. The formation of the lodicules as thickened structures was a later adaptation, brought about by the fusion of the originally two separate paleas. As a result, the flower became completely enclosed. Because of an altered situation, the lodicules had adapted to another function, and this was to open the opposing lemma and palea by swelling.

However interesting these two hypotheses are, it has to be kept in mind that they are speculative reconstructions of ancestral forms and have no factual existence.

Stamens

In the two species of Oryzopsis studied, the histogenesis of the stamens differs from that of a foliar structure. The stamens have a deeper site of initiation, and in early stages of growth assume a globose form. Also, in stamen initiation the protoderm undergoes anticlinal divisions only. Similar developmental features have been reported in stamen histogenesis in other grasses by Bonnett (1953, 1961), Holt (1954), Barnard (1955, 1957a), Mehlenbacher (1970), and Maze et al. (1971, 1972). Maze et al. also report the presence of a shell zone in

stamen formation in Stipa tortilis and Oryzopsis miliacea. These workers consider the stamens to be stem-like in grasses. Stem-like stamens have also been reported by Satina and Blakeslee in Datura (1943), by Barnard in Carex, Scirpus and Cyperus (1957b), in Juncus and Luzula (1958), and in Stypandra and Bulbine in the Liliaceae (1960).

Various other workers, among whom may be mentioned McCoy (1940), Boke (1949), Tepfer (1953), Tucker (1959), Cheung and Sattler (1967), and Singh and Sattler (1972), consider stamens to be leaf-like. The stamens in question were found to initiate in the same layers as perianth members and carpels.

Stamens in Downingia bacigalupii (Kaplan, 1968), and Hordeum distichon (Klaus, 1966), initiate beneath the superficial layers of the floral meristem, but have been interpreted as morphologically of a phyllome nature.

The exact significance of these contradictory findings is not clear. One could as easily argue for leaf-like stamens as for stem-like stamens. It is interesting to note that Merxmüller and Leins (1967) have shown that in Sisymbrium strictissimum members of the same set of appendages (in this case stamens), may be initiated in different cell layers. Histogenetic data for stamen development in the grasses studied so far support a cauline interpretation for grass stamens.

Gynoecium

The unilocular ovary of the grass flower has often been interpretated as either unicarpellate or tricarpellate. Among those who have upheld

the tricarpellate condition may be mentioned Schuster (1910), Arber (1934), Hitchcock (1951), and Gould (1968). Among adherents of the opposite view are Hackel (1889), Bews (1929), and Pilger (1954).

Proponents of the tricarpellate condition consider the vasculature of the gynoecium and the presence of three styles in some grass flowers as evidence of three fused carpels. In most grass gynoecia four vascular bundles are present, one posterior, one anterior and two lateral. The anterior and the lateral bundles each represents the midrib of one carpel supposedly. The posterior bundle supplies the ovule and is interpreted as the fused lateral bundles of the lateral carpels. Such a tricarpellate gynoecium would fit in 'nicely' with the basic trimerous plan of the monocotyledonous flower.

Developmental studies have not upheld this interpretation. The gynoecial wall in those grasses studied by Bonnett (1953, 1961), Holt (1954), Sharman (1960b), Klaus (1966), Mehlenbacher (1970) and Maze et al. (1971, 1972) initiates as a single leaf-like structure. The author's observations in Oryzopsis virescens and O. hymenoides agree with the interpretation of these workers.

Barnard (1957a) has suggested that the grass gynoecium consists of four carpels, one anterior, two lateral, and one posterior. It is ~~Barnard's~~ Barnard's opinion that different parts of the gynoecial wall initiate at different levels and at different times, and that the different parts of the gynoecial wall represent different carpels. The morphologically lowest is the anterior carpel, the second is the posterior carpel, and the two

lateral carpels are the most distal. Barnard's claim is not substantiated by evidence and has been rejected by later workers.

With the exception of Barnard, all students of grass-floret histogenesis interpret the gynoecial wall as a single, continuous, leaf-like structure. But the relation between the gynoecial wall and the ovule is a hotly debated issue. The question is: Are grass ovules terminal (stachyosporous), or are they borne on the gynoecial wall (phyllosporous)?

In Oryzopsis virescens and O. hymenoides the formation of the gynoecial wall does not use up the whole floret apex. The residual floret apex is gradually transformed into an ovule. These observations correspond with the observations of Holt (1954), Bonnett (1953, 1961), Sharman (1960b), Pankow (1962), Mehlenbacher (1970), and Maze et al. (1971, 1972), all of whom interpret the grass ovule to be terminal on the floret axis. A corollary of this interpretation is that the concept of 'carpel' no longer applies to the grass gynoecium, since a carpel is defined as a phyllome that bears ovule(s). The point at issue is the criterion by which an organ may be judged to be terminal. This question is discussed in some detail in connection with the author's review of Klaus' work, as it concerns Klaus' interpretation of the grass gynoecium.

According to Klaus, in Hordeum distichon L. the gynoecial wall arises as a peltate carpel and the ovule is borne on the 'cross-zone' ('querzone') of the carpel (see Troll, 1939, for terminology). The floral apex is nearly used up in the formation of the carpel, that is, the carpel is nearly terminal. The grass gynoecium is phyllosporous.

In view of the controversial reports of phyllospory versus stachyospory not only in the Gramineae but also in other Angiosperms (see, for example, Barnard, 1957b; Schultze-Motel, 1959; Eckardt, 1957; and Pankow, 1962), the author will discuss Klaus' work in some detail and attempt to resolve the contorversy.

Two points are involved: Where the gynoecial wall arises and whether a floral apex remains after gynoecial wall initiation. Klaus' statement that the floret apex is nearly used up in the formation of the gynoecial wall is very vague. The fate of the residual apex is not mentioned. His illustrations contradict his interpretation (see Klaus, 1966, Abb. 37, 38, 39). In the formation of a terminal, or nearly terminal, gynoecial wall, the corpus of the floret apex shows increased mitotic activity, and many cell divisions are seen in the apical surface initials (Brooks, 1940; Tucker and Gifford, 1966a, 1966b). Both features are not manifested in Hordeum distichon. A floret apex remains after gynoecial wall formation, and it is gradually transformed into an ovule. If one follows Buder's criterion (1928) that for an organ to be considered terminal, it must develop from apical initial cells, then the grass ovule is terminal.

The presence of a cross-zone ('querzone') in the grass gynoecial wall is highly questionable. According to continental European literature, the development of the Angiosperm carpel (sensu lato) is similar to the development of a peltate leaf, and where the marginal meristems of the carpel meet, they form a transverse meristem, the cross zone. Whether the 'querzone' is something new, or an extension of the marginal meristems, it is not identifiable in the two grasses

studied by the author. An analysis of the development of the gynoecial wall will explain why. The gynoecial wall is actually initiated by an encircling row of initials on the floral apex. These initiating divisions start on the anterior side and progress to the posterior side. Growth of the gynoecial wall outwards as a lateral appendage occurs very early and is greatest at the point where the initiating divisions first appear, that is, on the anterior side. This growth, which is mainly through apical activity, occurs simultaneously with the spread of the encircling initiating divisions around the flanks of the floral apex. When the initiating divisions reach the posterior side of the floral apex, the shape of the gynoecial wall may be likened to a cylinder that has been cut diagonally in half. From then on, the posterior rim shows active apical activity and the gynoecial wall grows upwards as a tube. In this sequence of events, is there anything which can be said to fuse?

The grass gynoecium is interpreted by the author as a unit structure which develops from a single gynoecial primordium and which encloses a terminal ovule. It is in fact acarpellate (Sattler, personal communication).

Embryo sac development

The ovule is hemianatropous, bitegmic and pseudocrassinucellar. The embryo sac is of the monosporic, 8-nucleate type. The antipodals proliferate soon after the mature 8-nucleate embryo sac is formed. These observations in Oryzopsis virescens and O. hymenoides are similar to those described by Brown (1949), in Stipa leutotricha, and Mehlenbacher

and Maze et al. in species of Stipa and Oryzopsis. This seems to be the usual type of embryo sac development in the Gramineae (Davis, 1966). The only grasses that do not follow this pattern of embryo sac development are those of the Bouteloua curtipendula (Michx.) Torr. complex, described by Mohamed and Gould (1966). In these grasses, embryo sac development is of the Adoxa type, and the antipodals do not proliferate.

The number of bumps in the outer integument is interesting. The presence of one bump in the outer integument in the chalazal region has been reported in Stipa hendersoni (formerly known as Oryzopsis hendersoni Vasey) by Mehlenbacher in 1970, in S. tortilis (Maze et al., 1970), S. lemmonii (Maze et al., 1972) and S. elmeri (Maze and Bohm, 1973). In O. hymenoides, one bump is present. In O. virescens there are two bumps, and in the only other species of Oryzopsis studied, O. miliacea, there are also two bumps.

Fertilization in the two species appears to be different. In O. virescens no filiform apparatus is seen. The synergids degenerate before fertilization, but in those florets examined, one synergid persists in a degenerate form until fertilization. The site of pollen tube enbry seems to be between the persistent synergid and the embryo sac wall. In O. hymenoides, in which each synergid has a distinct filiform apparatus, the behavior of the synergids prior to fertilization is different. One synergid decreases in size, becomes densely-staining and degenerates, while the other becomes highly vacuolate and shows no visible signs of degenerating. Both synergids persist until the 2-cell proembryo stage. The pollen tube enters the embryo sac

via the degenerate synergid. The entry and discharge of the pollen tube into one of the synergids has been demonstrated for Vallisneria (Wylie, 1941), Zea (Diboll, 1968), Gossypium (Jensen and Fisher, 1968) and species of Stipa. Of these examples, all but Vallisneria have synergids in each of which a filiform apparatus is present. On the other hand, in Cardiospermum halicacabum (Kadry, 1946), each synergid has a distinct filiform apparatus but the pollen tube enters the embryo sac between the synergids and the sac wall.

CONCLUSION

In Oryzopsis virescens and O. hymenoides histogenesis of the lemma, palea, posterior lodicule and the gynoecial wall is similar, and indicates their foliar nature. The anterior lodicules differ from them in having a deeper initiation site. The interpretation of the anterior and posterior lodicules as reduced perianth structures rather than as structures 'de novo' is preferred. Developmentally the stamens are stem-like. The gynoecium consists of a unit gynoecial wall surrounding a terminal ovule. There are two styles, each of which develops from the lateral portions of the gynoecial wall. The grass gynoecium may be considered acarpellate.

Embryo sac development is of the monosporic, 8-nucleate type.

PART II

Comparative developmental studies of the floret and embryo sac in *Oryzopsis virescens*, *O. hymenoides*, *O. micrantha*, *O. kingii*, and *O. asperifolia*.

INTRODUCTION

The problems of circumscribing the genus *Oryzopsis* have been discussed in the general introduction. The systematic disposition of the five species studied is briefly reviewed here.

Oryzopsis virescens (n = 12; Avdulov, 1928, as cited by Darlington and Wylie, 1955; Johnson, 1945a), is an Eurasian species and belongs to the Old World section *Piptatherum*. Its floret characters, which are described in PART I, (Figs. 1, 2, 3), fit in well with those features which are generally employed to set *Oryzopsis* apart from *Stipa*.

Oryzopsis hymenoides (n = 24, Johnson, 1945a) is in the North American section *Eriocoma*. It was originally known as *Stipa hymenoides* Roem. and Schult. (see Syst. 2: 339, 1817, for description). The generic transfer to *Oryzopsis* was proposed by Ricker, and was formally presented by Piper in 1906 (see volume II, page 109, U.S. Natl. Herb. Contrib., 1906). This species is widespread in arid areas throughout western North America. It resembles *O. virescens* in its open panicle and its indurate lemma, but it is distinctively set apart from *O. virescens* by its sharp callus and densely villous lemma (Figs. 4, 5, 6). A sharp callus and a villous lemma are features that are used to distinguish *Stipa* from most species of *Oryzopsis*. Moreover, *O. hymenoides*

crosses spontaneously with various species of Stipa. To date, such hybrids involing eleven different species of Stipa have been reported (Johnson, 1972, and the references therein). No other species of Oryzopsis is known to hybridize with Stipa. One other supposed case of intergeneric hybridization, Oryzopsis hendersoni x Stipa lemmoni, reported by Spellenberg and Mehlenbacher (1971), is in fact, not such. Oryzopsis hendersoni Vasey is more closely allied to Stipa than to Oryzopsis, (Mehlenbacher, 1970). In the joint publication of 1971, Mehlenbacher made a formal transfer of the species to Stipa. According to Shechter and Johnson (1968), O. contracta (B.L.Johnson) Shechter may have evolved through hybridization between O. hymenoides and O. micrantha. No other interspecific crosses have been reported in Oryzopsis.

Oryzopsis micrantha, O. kingii and O. asperifolia are North American species and are placed in the New World section Oryzopsis. The first two species are diploids (n = 11; Johnson, 1945a), while the third one is a polyploid (n = 23; Johnson, 1945a). Bowden (1960) reported a chromosome count of 2n = 48 for O. asperifolia. Oryzopsis micrantha is known to occur in British Columbia, Alberta, Montana, North Dakota, south to Nebraska, Oklahoma, New Mexico, Arizona and Nevada. Oryzopsis kingii has a very restricted distribution. It is endemic to the meadows at high altitudes in the central Sierra Nevada mountains in California. Oryzopsis asperifolia occurs from Newfoundland to British Columbia, Maine to the Dakotas, including the Great Lakes region, and in the Rocky Mountains from Montana to New Mexico (Hitchcock, 1969).

The floret of O. micrantha has an obovate glabrous lemma which is fairly indurate, an indistinct callus and a weak, untwisted and deciduous awn (Figs. 147, 148, 149). With respect to these features O. micrantha approaches the section Piptatherum. However, the major affinity of this species, as discussed by Johnson (1945a), is to the section Oryzopsis. Oryzopsis kingii may be described as a 'borderline species' between Oryzopsis and Stipa. As indicated by the Synonymy in Hitchcock (1951), O. kingii was originally described by Bolander in 1872 as a Stipa, and was later transferred to Oryzopsis by Beal in 1896. It is so closely allied to Stipa on most characters that its assignment to either Oryzopsis or Stipa is largely arbitrary. Its narrow non-indurate lemma, with a sharp callus and a strong, twisted geniculate awn (Figs. 150, 151), and its narrow panicle and slender involute leaves are strongly suggestive of Stipa. Oryzopsis micrantha and Oryzopsis kingii represent the morphological extremes of the section Oryzopsis. At one end, O. micrantha presents some Piptatherum features, chiefly through its resemblance to O. miliacea. At the other end, O. kingii grades into Stipa. Not surprisingly, this definition of the section Oryzopsis has caused some uncertainty about the sectional and generic identity of certain species.

Oryzopsis asperifolia has the largest floret as compared to the other four species. The floret has a fusiform lemma which is convolute, a swollen, blunt, pubescent callus and a straight deciduous awn (Figs. 152, 153, 154). It is reputed to be an allotetraploid, and its combination of Piptatherum characters (weak and flexuous awn, many-nerved glumes, broad flat leaves, fairly indurate lemma) and Oryzopsis

features (glumes equal in length to lemma, first glume shorter than second glume) is used as an indication of its hybrid origin (Johnson, 1945a).

Developmental data have not been incorporated into the systematic studies of the genus Oryzopsis. Recent work by Mehlenbacher (1970) on Stipa hendersoni (Vasey) Mehlenbacher, and by Maze et al. (1971, 1972) on O. miliacea, S. tortilis, and S. lemmoni has showen that developmental data can add another facet of evidence towards a better understanding of Stipa and Oryzopsis. It is hoped that data from the present study, together with such developmental data on other species of Stipa and Oryzopsis as are available, can be used effectively as an adjunct to other characteristics in delimiting and working out the taxonomy of Oryzopsis. There are certain advantages to using developmental data. Studies of floral histogenesis lead to a better understanding of the morphological features of the mature floret, for the mature form is the result of developmental processes. The analysis of growth patterns, in the early stages of development of a structure, provide more features for comparison. In mature structures early growth patterns, which are due to the frequency and plane of cell division, are usually obliterated by the cell enlargement phase of growth.

MATERIALS AND METHODS

The preparation of materials for study is as described in PART I for O. virescens and O. hymenoides. Materials of O. micrantha and O. asperifolia were collected from transplants growing in the experimental

plots at the University of British Columbia. Plants of O. micrantha and O. asperifolia were originally from Marble Canyon Provincial Park and Williams Lake respectively; both locations are in British Columbia. Florets of O. kingii were collected from the high meadows in Yosemite National Park, California. Some live plants are maintained in the afore-mentioned experimental plots. Voucher specimens of all five species are deposited in the Vascular Plant Herbarium of the Botany department, University of British Columbia. Orientation of the sections follows that used in PART I.

OBSERVATIONS

Oryzopsis micrantha (Trin. and Rupr.) Thurb.

Floret organogenesis

The awn-lemma primordium is the first structure to appear on the floret apical meristem (Figs. 155, ,56). This is followed by the palea and the stamens, which initiate at the same time. Initiation of the lodicules occurs next (Fig. 157). The callus and the gynoecium are the last structures to appear (Figs. 158, 159). The sequence of initiation of the floral parts parallels that in O. virescens.

Floret Apical Meristem

The floret apex has a one-layered tunica (Fig. 155). As in O. virescens and O. hymenoides, the floret apex in O. micrantha undergoes a displacement and re-orientation in the course of floret development. Early in floret development, the floret apex is oriented more or less parallel with the floret axis (Figs. 155, 156). With the initiation

of the anterior stamen, the floret apex is deflected away from the axis to the posterior side of the floret (Fig. 157). The floret apex continues to be posteriorly directed during early growth of the anterior portion of the gynoecial wall (Figs. 158, 159). After initiating division of the gynoecial wall have encircled the floret apex (Figs. 160, 181), the floret apex continues growth as the ovule (Figs. 161, 182), but it becomes re-oriented to a vertical, and then to an anteriorly-directed position.

Awn-lemma

Initiation and early development of the awn-lemma primordium is similar to that in O. virescens (Figs. 155, 156). Differentiation of the awn-lemma junction is first indicated by a constriction which is the result of greater cell expansion in the awn base than in the lemma apex (Figs. 158, 159). Periclinal divisions occur in the ground meristem on both the abaxial and adaxial sides of the lemma apex, forming an expanded lemma apex (Figs. 163, 164, 165). The proportion of the lemma to the rest of the floret (excluding the awn) changes drastically as the floret develops. Prior to, and up till, the initiation of the anterior portion of the gynoecial wall, the lemma is relatively small and leaves the distal half of the floret exposed (Figs. 158, 159). By the time the ring-shaped gynoecial wall is formed, the lemma has extended to just above the top of the stamens (Fig. 160). Further growth of the floret sees extensive elongation of the lemma, as it overtops, (Fig. 161), and encloses, the rest of the floret (Fig. 162). These observations are similar to those

described for O. virescens and O. hymenoides. The upper portions of the free margins of the lemma increase in height more than the expanded lemma apex, and form two 'ears' in front of the awn (Figs. 161, 166). They are, however, smaller than the free 'ears' in O. virescens.

The mature lemma apex resembles that of O. virescens in its double-convex shape and the presence of periclinal divisions in the abaxial and adaxial ground meristem, but the resemblance is somewhat superficial. In O. micrantha (Fig. 167), the abaxial convexity is the result of ground meristem cell expansion rather than considerable periclinal divisions. In the adaxial ground meristem, periclinal divisions are not as extensive as in O. virescens. Unlike O. virescens, the adaxial protoderm has only a few isolated periclinal divisions (Figs. 165, 166, 167). At the point of attachment of the awn to the lemma, the cells are much smaller than the cells in the awn base and the lemma apex (Fig. 167).

Callus

Initiation of the callus is through periclinal divisions and cell enlargement in the ground meristem at the base of the lemma on the anterior side (Fig. 168). As in O. virescens, ground meristem tissue forms the bulk of the callus (Fig. 173). Early growth of the callus involves the expansion and vacuolation of the ground meristem cells, in a direction perpendicular to the adjacent protoderm, forming a rounded protuberance (Figs. 169, 170). This is accompanied by cell expansion in the adjacent protoderm (Fig. 170). At the time of initiation of the inner integument, the ground meristem cells in the

middle section of the callus on the anterior side begin to expand obliquely, that is, inward and at an angle to the adjacent protoderm (Fig. 171). The protodermal and ground meristem cells at the distal end of the callus, near the axil of the lemma, expand in a longitudinal direction, pushing the callus downward (Fig. 172). At the same time, the protodermal and ground meristem cells in the basal portion of the callus continue to expand obliquely, toward the axis of the floret (Figs. 172, 173). Consequently, the callus grows downward and inward, forming a rounded tip (Figs. 172, 173). As in O. virescens the floret-rachilla tilts in an anti-clockwise direction (compare Figs. 168, 169 and 171). The tilting is not as extreme as in O. virescens so that the rounded tip of the callus in O. micrantha is laterally directed and does not lie on the vertical axis of the floret (Fig. 162).

Two growth feactures seen in O. micrantha but not in O. virescens involve the protoderm of the callus and the rachilla. Some of the protodermal cells of the callus on the anterior side undergo random periclinal, oblique and anticlinal divisions at a time when the floret undergoes extensive elongation growth (Figs. 171, 172, 173). The protoderm of the rachilla on the posterior side elongates anticlinally to produce a slight projection (Fig. 173).

Palea

Development of the palea in O. micrantha is similar to that in O. virescens, except that in O. micrantha the palea does not have a biseriate distal portion (Figs. 174, 175).

Lodicules

Initiation and growth of the lodicules is similar to that in O. virescens. Stages in lodicule development are shown in Figures 176, 177, 178 and 179.

Stamens

The development of the stamens in O. micrantha and in O. virescens is remarkably similar. A description of stamen development in O. micrantha would be repetitious.

Gynoecium

Early stages in the development of the gynoecium are shown in Figures 180, 181. The ovule is terminal, and the gynoecial wall grows upward as a tube (Figs. 181, 182). The lateral sides of the gynoecial wall give rise to a style branch each (Fig. 183). The style branches are closer together in O. micrantha than they are in O. virescens, (Fig. 185; cf. Fig. 76). Proliferation of tissues ('stylar core') on the inner margins of the ovary wall brings the margins together (Figs. 184, 184a). The inner margins come in contact but do not fuse, so that the opening between the inner margins is not completely closed but remains as the stylar canal (Fig. 184).

Ovule and embryo sac development

Integuments

The inner integument is first seen on the upper side (Fig. 183). At this stage, the archesporial cell is not distinguishable. When the

inner integument appears on the lower side, the single-celled archesporium is distinguished by its larger size and its denser cytoplasm (Fig. 186). The outer integument is also first visible on the upper side (Fig. 187). In the chalazal region of the outer integument, a single prominent bump is formed (Figs. 189, 191). The outer integument starts to degenerate prior to fertilization.

Nucellus and embryo sac development

Growth patterns in the nucellus leading to increase in size of the ovule and its orientation to a hemianatropous position are similar to those observed in the previous species (Figs. 188, 191, 192). Oryzopsis micrantha is like O. hymenoides in that there are few periclinal divisions in the nucellar protoderm.

In megasporogenesis, a linear tetrad is more commonly found than a T-shaped one. In the linear tetrad the first megaspore to abort is the micropylar. In the T-shaped tetrad, both the micropylar megaspores degenerate at the same time and are the first ones to do so. Intermediate stages in megagametogenesis are seen in Figures 190 and 191.

The synergids have a filiform apparatus each (Fig. 193). They remain densely cytoplasmic throughout their growth (Figs. 193, 194). Starch granules are seen in the egg before fertilization (Fig. 193a). Crystals are present in the nucleoli of the polar nuclei (Fig. 193). The polar nuclei fuse before fertilization.

Fertilization

It was very difficult to trace the path of the pollen tube into the embryo sac. Both the synergids appear to degenerate at

fertilization. One decreases in size more than the other. Chromatin-like bodies are seen in the larger degenerate synergid (Figs. 195, 195a). This seems to indicate that the pollen tube contents enter the egg via one synergid.

Post-fertilization

Initially the endosperm is also nuclear.

Oryzopsis kingii (Boland.) Beal

Floret organogenesis

The floret apical meristem, with a one-layered tunica, first initiates the awn-lemma (Fig. 197). This is followed by the appearance of the palea and the stamens (Fig. 198). The lodicules are the next structures to develop, and during their early gorwth (Fig. 199), but before the gynoecium initiates, the callus and the awn-lemma junction become evident (Figs. 205, 212). The gynoecium is the last structure to initiate (Fig. 200). Changes in the shape of the floret during growth are shown in Figures 201 to 204. As in the other three species described previously, In O. kingii the floret apical meristem undergoes a displacement and re-orientation in the course of floret development (cf. Figs. 200, 201, 203, 204). Concurrently, there is a change in the porportion of the lemma to the rest of the floret (excluding the awn).

Awn-lemma

The awn-lemma primordium in its initiation and early growth is similar to that in the previous species. Differentiation of the awn-lemma junction starts early and is indicated by periclinal divisions and cell expansion in the adaxial ground meristem of the lemma apex (Figs. 205, 206, 207, 208). On the abaxial side the protoderm is one-layered, while some cells in the ground meristem may divide periclinally once (Fig. 209). The mature lemma apex is quite different from that of O. virescens, O. hymenoides and O. micrantha. Instead of a biconvex shape as present in the other three species, the lemma apex of O. kingii has a convex adaxial surface and a straight abaxial surface (Fig. 211). The adaxial convexity results from a combination of the expansion of the protodermal cells in an anticlinal direction, and periclinal divisions in the ground meristem (Fig. 211). Periclinal divisions are also seen in the protoderm (Figs. 210, 211). The upper free margins of the lemma do not extend above the expanded lemma apex to form 'ears'. The point of attachment of the awn to the lemma is not marked by a constriction. The awn base is approximately as wide as the rest of the awn. The absence of a group of smaller cells at the junction of the awn and lemma (Fig. 211) probably accounts for the presistence of the awn.

Callus

Initiation and early development of the callus is similar to that of O. virescens, O. hymenoides and O. micrantha. In all four species

periclinal divisions in the ground meristem at the base of the lemma indicate the beginning of the callus (Figs. 212, 213). Also, the ground meristem forms the bulk of the tissue of the callus. In the early stages of growth the young callus does not have the hemispherical shape that is so characteristic of the callus of O. virescens and O. micrantha. Instead, at the time of initiation of the posterior portion of the gynoecial wall, the callus has a downward-directed, broadly acute apex, similar in shape to that of O. hymenoides (Fig. 215).

The calluses in O. hymenoides show some interesting differences in their development. In O. hymenoides elongation of ground meristem cells downward and obliquely outward is responsible for the pointed shape of the callus (Fig. 119). The protodermal cells at the tip of the callus remain small (Fig. 119). In O. kingii ground meristem cells in the distal and central portions of the callus on the anterior side expand longitudinally downward, parallel with the adjacent protoderm (Fig. 216). The sharpe point of the callus is mainly the result of oblique expansion of the protodermal cells at the tip, in a direction outward and away from the floret axis (Fig. 216).

Two other developmental features are of interest. Where the callus is attached to the rachilla there are regular cell files (Fig. 217), described as tabloid cells by Maze et al. (1971) for Stipa tortilis. On the posterior side of the rachilla adjoining the base of the floret there is a projection (Figs. 204, 218). This projection differs from a similar one in O. micrantha in that it is formed primarily by the

anticlinal elongation of ground meristem cells.

Palea

The palea in O. kingii develops in the same manner as in the other three species (Figs. 219, 220, 221). At maturity, it has a narrow base and a rather long biseriate distal portion (Fig. 222).

Stamens

The anther 'beards' are of protodermal origin. Elongation of the protodermal cells begins when the anterior portion of the gynoecial wall is initiated.

Lodicules

Initiation and growth of the lodicules is as in the other three species. In O. kingii the lodicules are smaller. Development of the posterior lodicule is shown in Figures 220, 221, and 222. Stages in the growth of the anterior lodicules are seen in Figures 223 and 224.

Gynoecium

This structure is similar to the gynoecia of the other three species. However, the initiating divisions appear on the posterior side of the floret apex at a lower level, leaving a more distinct residual apex (Fig. 226). When the posterior side of the gynoecial wall begins to grow upward, the residual apex develops directly into the ovule (Fig. 227). As in the other species, the lateral sides of

the gynoecial wall develop as the styles (Figs. 228, 229). The styles are situated a short distance apart from each other (Fig. 231), as in O. virescens. At anthesis, the ovarian cavity is 'closed' by the proliferation of tissues on the inner margins of the ovary wall (Figs. 230, 230a).

Ovule and embryo sac development

Integuments

Both the inner and outer integuments are first seen on the upper side (Figs. 232, 233, 234). The archesporial cell is distinguished early in integument development (Fig. 232). This was also noticed in O. hymenoides. There is only one bump in the chalazal region of the outer integument.

Nucellus

Growth of the nucellus is as in the other three species. There are not as many periclinal divisions in the nucellar protoderm as there are in O. virescens.

Embryo sac

A hypodermal cell functions as the megaspore mother cell (Fig. 234). The megaspores are commonly arranged in a linear tetrad (Fig. 235). The chalazal megaspore is the functional one (Fig. 236). Stages in megagametogenesis are seen in Figures 237, 238, 239 and 240. Figure 238 shows a frequently encountered situation in which the abortion of the three non-functional megaspores is delayed until the 2-nucleate embryo sac stage.

The embryo sac before the differentiation of the egg and the synergids is spindle-shaped (Fig. 240). The micropylar and chalazal ends broaden out later in growth (Fig. 241). Visible signs of differentiation in each of the synergids are the development of small, scattered vacuoles and a filiform apparatus (Fig. 241). The egg becomes highly vacuolate (Figs. 240a, 241a). The polar nuclei fuse before fertilization.

Fertilization

The pollen tube seems to discharge its contents into one of the synergids. Inall the florets examined the two synergids degenerate prior to fertilization. In some florets one of the synergids disintegrates completely. Remnants of the pollen tube contents are seen in the persistent degenerate synergid (Figs. 242, 242a, 242b). In other florets, both the degenerate synergids persist, though one of them becomes appreciably smaller. Figure 243 shows the first zygotic division of the fertilized egg. Chromatin-like bodies are seen in the larger, degenerate synergid.

Post-fertilization

The outer integument is still prominent at the 2-cell embryo stage (Figs. 244, 244b). The endosperm is nuclear initially. The antipodals form a considerable mass at this stage. The synergids are still visible after the first zygotic division (Figs. 244a, 244b).

Oryzopsis asperifolia Michx.

Floret organogenesis

This species lacks a posterior lodicule. The initiation of the floret appendages follows this sequence: lemma, palea and stamens, anterior lodicules, gynoecium and callus. This is illistrated in Figures 245, 246, 247 and 248. The slow rate of development of the lemma, with respect to the rest of the floret, is unique here. At the time initiating divisions of the gynoecium form on the posterior side of the floret apex (Fig. 248), the lemma leaves the stamens and the gynoecium exposed. Up till the time of the 4-nucleate stage in embryo sac development, the lemma does not overtop the stamens and styles, but leaves half their length exposed (Figs. 249, 250, 251). Only at the 8-nucleate embryo sac stage does thelemma extend above the rest of the floret.

Awn-lemma

The awn-lemma primordium is the first structure to develop from the floret apical meristem (Fig. 245). The floret apex is striking in its large size. Like the other four species, the floret apex has a one-layered tunica and undergoes displacement and re-orientation in the course of floret development. Figures 247 and 252 show the awn-lemma primordium of a floret at the time of gynoecium initiation. The cells in the distal portion are larger and more vacuolate than the cells in the lower portion of the primordium. This distal portion is the future awn, and it elongates rapidly (Fig. 248). When the posterior portion

of the gynoecial wall is initiated, the awn-lemma junction is barely perceptible, and the lemma is more or less equally wide in sagittal section (Fig. 253). Ground meristem cells on both the adaxial and abaxial sides of the lemma apex start to divide periclinally. Just before the inception of the integuments in ovule development, the lemma apex becomes expanded, (Fig. 254), a result of the previously mentioned periclinal divisions plus some cell enlargement. There are fewer periclinal divisions in the abaxial ground meristem than there are in the adaxial ground meristem. At the same time, some adaxial protodermal cells have divided periclinally once.

At this stage the awn base is marked out from the lemma apex by a constriction, as a result of fewer cell divisions. The expanded portion of the lemma is spread over almost half the total length of the lemma (Figs. 249, 250, 254, 255). The convex adaxial side of the lemma apex is mainly the result of cell division in the ground meristem, forming a tissue of considerable size (Fig. 256). Just before the megaspore mother cell undergoes meiosis, the patterns of cell division on this side of the lemma apex are obliterated, as a result of cell expansion in a horizontal plane (Fig. 256). At the same time, on the abaxial side of the lemma apex, the ground meristem cells expand, parallel with the adjacent protoderm, and the growth patterns due to periclinal divisions are still obvious. The abaxial ground meristem cells at the lemma apex form a narrow strip of tissue in sagittal section as compared with the adaxial ground meristem (Fig. 256). Later, greater cell expansion in the abaxial ground meristem produces

a tissue as wide as the adaxial ground meristem (Fig. 257).

Callus

Like the awn-lemma, the callus is initiated at a later stage in floret development in comparison with the other four species of Oryzopsis that have been described. This structure is not obvious until the gynoecial wall has appeared on the posterior side of the floral apex (Figs. 258, 259). Initiation and growth of the callus is mainly through cell division in the ground meristem (Figs. 258, 259, 260, 261, 263). Early in its development the callus on the anterior side forms a rounded protuberance (Fig. 260). Some protoderm cells on the same side divide periclinally once (Figs. 259, 260, 261, 263). Continued cell divisions in the ground meristem increase the size of the rounded callus (Fig. 261). In a mature floret, the callus forms an open ring around the base of the floret, with the edges meeting on the median posterior side (Fig. 154). In off-set sections parallel with the sagittal plane, the posterior callus can be seen as a slight bulge, the result of periclinal divisions in the protoderm and the ground meristem (Figs. 262, 265). Figures 261 and 262 are of a floret at the stage when integument formation has been completed in ovule development. The initially rounded hump of the callus begins to be directed slightly downward at the megaspore mother cell stage in ovule development (Fig. 263). Some of the protodermal cells in the upper part of the callus elongate to form hairs. The protodermal cells at the base of the callus divide once or twice to form a small patch of

multiple protoderm (Fig. 263). Further distension downward produces an obtusely-angled callus tip (Fig. 264). The massive callus is mainly the result of the large number of cells rather than cell expansion. The basal patch of multiple protoderm on the anterior side is no longer recognisable at maturity. On the posterior side, the callus is also distended downward slightly, and a multiple protoderm is seen clearly in the rounded tip (Fig. 265).

For ease of comparison, a table is presented (TABLE II) of comparable stages in awn-lemma and callus development in the five species of Oryzopsis studied, using the stage of gynoecium development as the reference.

TABLE II. Reference table for comparison of stages in awn-lemma and callus development in O. virescens, O. hymenoides, O. micrantha, O. kingii, and O. asperifolia, using the stage of gynoecium development as a marker. The numbers refer to figures at the pertinent stages.

Stage of gynoecium development	O. virescens		O. hymenoides		O. micrantha		O. kingii		O. asperifolia	
	awn-lemma	callus	awn-lemma	callus	awn-lemma	callus	awn-lemma	callus	awn-lemma	callus
Initiation of lodicules	19	19	106	113	none	none	none	none	252	258
Initiation of anterior gynoecial wall	20	26	107	114	158	168	206	213	252	258
Growth of anterior gynoecial wall	21	27	108	115	163	none	207	214	none	none
Gynoecial wall appears on posterior side of floret apex	22	28	109	116	164	169	208	215	253	259
Ring-shaped gynoecial wall	23	none	110	117	165	170	209	none	none	none
Prior to integument initiation	24	29	none	none	none	none	none	none	254	260
Initiation of inner integument on upper side	none	none	111	118	166	171	210	216	none	none
Complete inner integument	25	30	none	none	167	172	211	217	255	261 & 262
Ovule in orthotropous position	none	none	112	119	none	none	none	218	256	263

Palea

Growth of the palea is similar to that in the other four species except that in O. asperifolia cell division ceases at a comparatively later stage (Figs. 266, 267, 268, 269).

Stamens

The stamens develop in the same manner as in the other species. They are hirsute-tipped at maturity. Periclinal divisions of the antherprotoderm occur at the time the anterior portion of the gynoecial wall initiates (Fig. 266). The hairs are elongate protodermal hairs.

Lodicules

Only the anterior lodicules are present in this species. Their initiation and growth is the same as in the other four species (Figs. 270, 271). At maturity they are distinctly two-nerved (Fig. 272).

Gynoecium

Development of the gynoecium is illustrated in Figures 266, 273, 274, 275, 276 and 277. The process is very much like that described in the other four species of Oryzopsis. There are two styles (Fig. 279). At anthesis, the ovarian locule is 'closed' by the adpression of the inner margins of the ovary wall (Figs. 278, 278a).

Ovule and embryo sac development

Integuments

Both the inner and outer integuments initiate on the upper side first (Figs. 280, 281). The outer integument has two bumps in the chalazal region (Figs. 282, 283).

Nucellus and embryo sac development

Stages in nucellus and embryo sac development are shown in Figures 284, 285 and 286. Like the other species of Oryzopsis development of the embryo sac is also of the monosporic 8-nucleate type.

Fertilization and post-fertilization

At fertilization only one synergid was seen. The pollen tube seems to enter the embryo sac via the persistent synergid, from which dense, chromatin-like bodies appear to be extruded (Fig. 287).

At the 2-cell proembryo stage, remnants of pollen tubes could still be seen. Where the pollen tube had entered the synergid, a densely-staining material was deposited (Figs. 288a, b).

DISCUSSION

Floret development

The sequence of organ initiation in the floret of the five species of Oryzopsis studied differs only in the time of initiation of the callus. In O. virescens, O. micrantha and O. asperifolia the sequence of organogeny in the floret is: (1) lemma; (2) palea and stamens almost

simultaneously; (3) lodicules; and (4) gynoecium and callus almost at the same time. In O. hymenoides and O. kingii the callus is precocious and appears before the gynoecium initiates. In those species of Stipa that have been studied developmentally, the callus also appears before the gynoecium initiates. Growth of the callus in O. virescens, O. hymenoides, O. micrantha and O. kingii is primarily due to cell enlargement. In O. asperifolia the conspicuous collar-like callus is mainly the result of cell division.

With the exception of the callus, the young stages of the developing florets prior to gynoecium development are remarkably similar in the five species of Oryzopsis studied. Comparable stages in species of Stipa and Oryzopsis studied by Maze et al. (1971, 1972), also bear a striking resemblance to those species of Oryzopsis studied by the author. Developmental differences that are diagnostic for the species begin to appear when the gynoecial wall is initiated on the posterior side of the floret apex. The probable basis for the similarity of the early stages in floret development is this: The mature form of an organism is the result of developmental processes. Genes produce effects on the visible morphological characters of the mature organism only through their influence on development. Similarly, mutations directly alter developmental processes, and only indirectly characters. Mutations which act relatively late in ontogeny are less likely to disorganise the whole process of development, with consequential deleterious effects, than those which alter the earlier stages (Stebbins, 1950). The mutations established, therefore, will be

those that affect development at the latest stage for the modification of the mature structure. That part of the ontogeny which is not affected by the mutations will exhibit similarity.

As a rule, embryological characters are constant within a genus, (Cave, 1953). Oryzopsis is no exception.

Inter-relationships of O. virescens, O. hymenoides, O. micrantha, O. kingii, O. asperifolia, O. miliacea, S. lemmoni, S. hendersoni, S. tortilis, and S. richardsoni.

Table III presents characters derived from developmental features in 6 species of Oryzopsis and 4 species of Stipa. Since the taxonomic problem presented by Oryzopsis involves not only the nature of the inter-relationships between its species but also its intricate relationship with Stipa, a comparison of Oryzopsis and Stipa species rather than a comparison of Oryzopsis species alone is more meaningful. Data on O. virescens, O. hymenoides, O. micrantha, O. kingii and O. asperifolia are from the author's own studies; data on O. miliacea, S. lemmoni, S. hendersoni and S. tortilis are from a publication of Maze et al. (1972). In this paper by Maze et al. the data on S. hendersoni were taken from Mehlenbacher (1970) and modified by them. Data on S. richardsoni are also from Maze, but unpublished. Some of the characters analyzed are similar to those analyzed by Maze et al. (1972), but the author has deleted some of the characters in the afore-mentioned publication, and has added some new ones. For each measurable character, only one measurement was taken. The author is

fully aware that there is no provision for a range of variation for each measurement. However, the time-consuming nature of developmental studies mitigates against multiple measurements.

For each character, data for all ten species were taken and the mean was calculated. A two-state coding of characters was used: those greater than the mean were treated as plus (+); those less than the mean minus (-). The percentage similarity among species was calculated using the simple matching coefficient of Sokal and Sneath (1963),

$$S_{sm} = \frac{m}{n} \times 100,$$

where S_{sm} = percentage of similarity,

m = the number of character matches (positive and negative),

n = the number of characters.

The coefficients of similarity obtained are presented in the form of a similarity matrix in Table IV. The coefficients of similarity of O. miliacea and S. tortilis, and of O. micrantha and S. tortilis are the lowest. This is interesting because these two species of Oryzopsis are considered to be clear-cut Oryzopsis species, and S. tortilis is a 'typically Stipoid' species. The other similarity coefficients seem to fall into a pattern of continuous variation.

TABLE III. Comparison of developmental features of Oryzopsis virescens, O. hymenoides, O. micrantha, O. kingii, O. asperifolia, O. miliacea, Stipa lemmonii, S. hendersonii, S. tortilis and S. richardsonii.

Character	O. vir.	O. hym.	O. mic.	O. kin.	O. asp.	O. mil.	S. lem.	S. hen.	S. tor.	S. ric.
1. Thickness in number of cells, of the ground meristem of the lemma apex.	19	18	12	8	14	6	19	20	21	13
2. Angle of growth, in degrees, relative to the longitudinal axis of the awn, in the ground meristem on the adaxial side of the lemma apex.	88	125	128	88	91	65	74	85	117	83
3. Angle of growth, in degrees, relative to the longitudinal axis of the awn, in the ground meristem on the abaxial side of the lemma apex.	10	56	22	80	75	68	90	27	66	73
4. Sclerenchyma mother cells in awn ground meristem.	-	-	-	-	-	-	+	-	+	+
5. Number of protoderm layers on the adaxial side of the lemma apex	4	1	2	2	2	1	5	6	7	1
6. Angle of growth, in degrees, relative to the longitudinal axis of the awn, in the multiple protoderm on the adaxial side of the lemma apex.	71	NA	82	77	88	NA	36	63	95	NA
7. Number of protoderm layers on the abaxial side of the lemma apex.	1	1	1	1	1	1	1	1	2	1
8. Number of protoderm layers on the adaxial side of the awn base.	1	1	1	1	1	1	1	1	5	1
9. Number of protoderm layers on the abaxial side of the awn base.	1	1	1	1	1	1	1	1	2	1
10. Ratio awn width at base/width of awn-lemma junction in saggital plane.	1.1	2.2	1.21	0.93	1.1	1.27	0.82	1.23	1.00	0.97
11. Ratio lemma width at apex/width of awn-lemma junction in saggital plane.	1.8	2.0	2.0	1.2	1.1	1.45	1.39	1.73	1.0	1.08
12. Ratio, longest cell (anticlinal plane) in protoderm on adaxial side of lemma apex/longest cell (anticlinal plane) in protoderm on adaxial side of lemma below apex.	0.73	1.2	1.5	3.3	1.2	1.33	3.5	3.5	0.63	1.0
13. Total number of protoderm cells in multiple protoderm at lemma apex.	24	NA	4	3	6	NA	16	31	47	NA
14. Height (in mm.) of apical portion of the free margin of the lemma above the awn-lemma junction when the magaspore mother cell is horizontal.	0.46	0.27	-0.04	0.016	0.017	0.30	0.50	0.08	0.001	0.02
15. Ridge in lemma apex in frontal plane.	-	-	-	-	-	-	-	-	+	-
16. Angle, in degrees, formed by the callus tip.	100	57	138	68	127	92	48	66	21	42
17. Ratio area of largest protoderm cell/area of largest ground meristem cell in callus.	0.43	0.19	0.48	0.17	0.65	2.46	0.73	1.25	0.39	0.54
18. Thickness in number of cells in the ground meristem of the callus along a line perpendicular to the longitudinal axis of the callus.	6	7	4	4	12	4	9	8	7	6
19. Tabloid cells at the attachment of the floret to the spikelet.	-	-	-	-	-	-	+	+	+	+
20. Protoderm peg on the posterior side of the spikelet axis.	-	-	+	+	-	+	-	-	-	-
21. Protoderm peg on the posterior side of the floret base.	-	-	-	-	-	+	-	-	-	-
22. Periclinal divisions in callus protoderm.	-	-	+	-	+	+	-	+	-	-
23. Ratio palea lenght/length of anterior gynoecial wall when the posterior wall of the gynoecium is initiated.	1.8	2.5	2.5	1.4	1.0	2.5	1.7	1.5	0.5	1.1
24. Thickness in number of cells at the palea base.	15	12	8	5	7	4	12	5	4	4
25. Height, in μ, above the attachment of the abaxial gynoecial wall, of the site of initiation of the posterior gynoecial wall.	0	3	3	-10	0	100	-100	-2	-1	-1
26. Angle, in degrees, of divergence of the ovule from the longitudinal axis of the floret when the integuments are initiated.	42	41	37	40	37	85	30	40	30	42
27. Number of bumps in the outer integument.	2	1	1	1	2	2	1	1	1	1
28. Ratio length of the ovule attachement to the placenta/length of the ovule ca. fertilization.	0.59	0.85	0.76	0.83	0.93	0.40	0.84	0.61	0.63	0.67
29. Filiform apparatus.	-	+	+	+	+	+	+	-	+	+
30. Ratio length/width embryo sac ca. fertilization.	2.7	1.9	2.2	2.6	1.7	3.0	2.4	2.7	3.6	2.3
31. Egg starch.	-	-	+	-	+	+	-	-	-	-

TABLE IV. Similarity matrix (%) of *Oryzopsis virescens*, *O. hymenoides*, *O. micrantha*, *O. kingii*, *O. miliacea*, *Stipa lemmoni*, *S. hendersoni*, *S. tortilis*, and *S. richardsoni*.

	O. virescens	*O. hymenoides*	*O. micrantha*	*O. kingii*	*O. asperifolia*	*O. miliacea*	*S. lemmoni*	*S. hendersoni*	*S. tortilis*
O. hymenoides	68.96								
O. micrantha	53.33	75.00							
O. kingii	45.16	55.17	60.00						
O. asperifolia	51.61	58.62	66.66	68.75					
O. miliacea	55.17	44.82	60.71	51.72	65.51				
S. lemmoni	58.06	68.96	50.00	67.74	54.83	34.48			
S. hendersoni	58.06	58.62	46.66	54.83	48.38	37.93	61.29		
S. tortilis	41.93	51.72	26.66	51.61	45.16	24.13	64.51	51.61	
S. richardsoni	58.62	55.17	46.42	82.75	68.96	55.17	65.51	55.17	62.06

Inter-relationships of the 10 species were analyzed using a 2-dimensional ordination. The ordination technique used is that used by Bray and Curtis (1957). This technique, which is outlined below, attempts to extract from a matrix of similarity coefficients a spatial pattern in which the distance between two species is directly related to their degree of similarity. In other words, a high degree of similarity will be represented by a low spatial separation.

In this technique, the inverse of the similarity coefficient between two species is equated with linear distance. The inversions are accomplished by subtracting each coefficient of similarity from a maximum similarity value of 100. The two species which have the lowest coefficient of similarity (= the highest inverse coefficient) are chosen as the end points of the X-axis. These two species are O. miliacea and S. tortilis, which are separated by a linear distance of 75.9 units. The position of any species on the X-axis is calculated by Beal's equation (cited by Gauch and Whittaker, 1972):

$$X = \frac{L^2 + D_1^2 - D_2^2}{2L} ,$$

where X = the position of the species on the X-axis,

L = distance between end points of the X-axis,

D_1 = distance of species from the first end point (= inverse coefficient of species and O. miliacea),

D_2 = distance of species from the second end point (= inverse coefficient of species and *S. tortilis*).

To construct the Y-axis, two new end points are selected which are in close proximity on the X-axis, but which are nevertheless separated by a high degree of dissimilarity. It is important that the end points are constructed of species which are most dissimilar, otherwise the axes will not cover the total range of variability expressed by the inverse coefficients. The results of this ordination technique are presented in Figure 289.

With regard to its correct generic disposition, *O. hymenoides* has been somewhat of an enigma. Johnson (1972) comments that its affinities are puzzling, because morphologically, (according to Johnson, 1945a), it resembles *O. virescens* in some respects (viz., an indurate lemma and an open panicle), while its distribution and hybridization with *Stipa* suggest some relationship with *Stipa*. Developmentally the affinities of *O. hymenoides* are with *Stipa* (Fig. 289).

Morphologically, *O. hymenoides* has been deemed to be an *Oryzopsis* on the basis of its diffuse panicle, deciduous awn, and indurate lemma. However, these three characters are not unknown in species of *Stipa*. An open panicle is present in *S. richardsoni* L., *S. porteri* Rydb. (= *Ptilagrostis porteri* (Rydb) Weber), *S. lepida* Hitchc., *S. cernua* Stebbins and Love; *S. neomexicana* (Thurb.) Scribn., *S. webberi* (Thurb.)

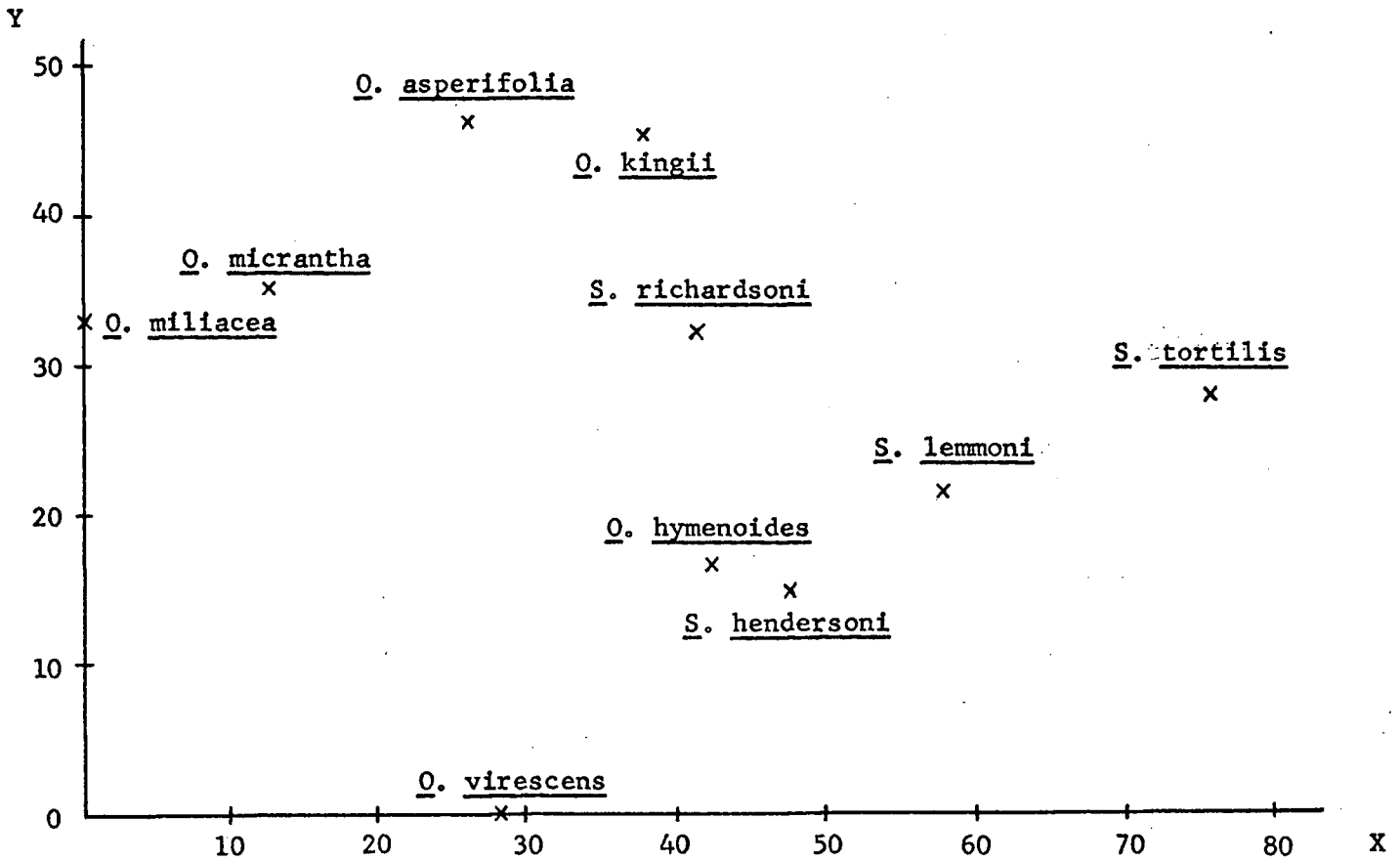

FIG. 289. Ordination results to show inter-relationships of Oryzopsis virescens, O. hymenoides, O. micrantha, O. kingii, O. asperifolia, O. miliacea, Stipa lemmoni, S. hendersoni, S. tortilis, and S. richardsoni.

Johnson, and S. ichu Hara have deciduous awns (see Maze et al., 1966); S. viridula Trin., S. lemmoni (Vasey) Scribn., and S. hendersoni (Vasey) Mehlenbacher have indurate lemmas. On the other hand, O. hymenoides possesses features that are strongly suggestive of a Stipa, viz., a sharp callus, pilose lemma, and involute leaves.

Besides the 'stipoid' morphological features present in O. hymenoides its crossibility with species of Stipa provide further positive evidence of its affinity with Stipa. Hybridization between O. hymenoides and eleven different species of Stipa have been documented by Weber (1957), Johnson and Rogler (1943), and by Johnson (1945b, 1960, 1962, 1963). A fertile amphiploid from a cross between O. hymenoides and S. viridula was recovered in nature by Nielson and Rogler (1952). Johnson suggests that the chromosome number of n = 24 in O. hymenoides could indicate its origin by amphiploidy between the 12-chromosome line of Stipa and the 12-chromosome line of Oryzopsis. Even so, its chromosome number and its postulated amphiploid origin do not preclude it from being a Stipa. A count of n = 24 in S. splendens Trin. was reported by Love and Myers in 1947 (cited by Darlington and Wylie, 1955). Evidence from developmental, morphological and hybridization studies suggest that the affinity of O. hymenoides is with Stipa.

Oryzopsis miliacea and O. virescens belong to section Piptatherum, which consists of a coherent group of species marked by specialization in characters that distinguish them from Stipa (reduction of callus, induration, dorsiventral flattening and increase in size of the lemma,

increase in length and nervation of the glumes). Morphological studies by Johnson indicate that in this section, O. virescens forms a closely-knit group with O. paradoxa, O. coerulescens and O. holciformis, while O. miliacea is set apart from them. The results in this study show that O. miliacea is closer to O. micrantha than it is to O. virescens. There are no developmental data on other Eurasian species of Oryzopsis for comparison, but it is not unreasonable to predict a high degree of similarity between O. virescens, O. paradoxa, O. coerulescens and O. holciformis on the basis of their development. The relationship between O. miliacea and O. micrantha will be discussed after a consideration of the section Oryzopsis, to which O. micrantha belongs.

The North American species of O. micrantha, O. pungens, O. exigua, O. canadensis and O. kingii constitute diploidsof the section Oryzopsis — they form a group marked by specialization in characters (differentiation of the callus; development of a twisted, persistent awn; indurate lemma) which merge with the genus Stipa. At one end, O. micrantha is detached from the other species of the same section by its resemblance to O. miliacea; at the other end O. kingii intergrades completely with Stipa. The three species in between reportedly form a gradated series towards Stipa. The sectional disposition of O. micrantha was questioned by Elias (1942), who placed it in Piptatherum.

On the basis of morphological and developmental data, O. miliacea should be removed from Piptatherum, and perhaps placed in section Oryzopsis. However, evidence from other sources must be considered

before such a re-arrangement is attempted. According to Johnson (1945a, 1972), the Eurasian species of Oryzopsis are diploids with a count of n = 12, and the North American diploids have a count of n = 11. However, in Oryzopsis and Stipa, it is difficult to relate the geographic distribution with chromosome number. In genera in which polyploidy is rampant, such as Oryzopsis and Stipa, chromosome number loses its value as a guide to generic and sectional delimitation (Rollins, 1953). Furthermore, a count of n = 12 in O. pungens has been reported by Bowden (1960).

Besides the five n = 11 diploids in section Oryzopsis, there are two other species, O. asperifolia (n = 23) and O. swallenii (n = 17; Hitchcock and Spellenberg, 1968). The latter species is, like O. kingii, a borderline species between Oryzopsis and Stipa (Hitchcock and Spellenberg, 1968). Until Mehlenbacher (1970) did a thorough study of S. hendersoni, (n = 17; Spellenberg, 1968), this species too was placed in the scetion Oryzopsis as Oryzopsis hendersoni (Vasey).

The relationships between O. micrantha, O. kingii and O. asperifolia, and between them and the other seven species, compared developmentally, are expressed in Figure 289. As they stand, O. virescens seems to be isolated from the other nine species, and there does not seem to be a discontinuity between the following nine species: O. miliacea, O. micrantha, O. asperifolia, O. kingii, S. richardsoni, O. hymenoides (Stipa), O. hendersoni, S. lemmoni and S. tortilis. In this connection, it is interesting to note that Hoover (1966),

considered O. miliacea (L.) Bentham and Hooker to be Stipa miliacea (L.) Hoover; and to quote Hoover, "the separation of a group of species as the 'genus' Oryzopsis does violence to the relationships of the plants".

CONCLUSION

Data from morphology, distribution, and hybridization studies suggest that Oryzopsis hymenoides belongs to the genus Stipa. Developmentally it also shows a high degree of similarity to Stipa. This further supports the contention that O. hymenoides be transferred to Stipa. Morphologically, O. miliacea is set apart from O. virescens and other members of the section Piptatherum. Developmental studies have upheld morphological data. It is suggested that O. miliacea be removed from Piptatherum. With the removal of O. miliacea, O. virescens, O. paradoxa, O. coerulescens and O. holciformis would form a more well-defined section. Further studies on other members in the Oryzopsis are needed before the inter-relationships between O. micrantha, O. asperifolia and O. kingii can be understood. It would seem that more comprehensive studies of the genus Oryzopsis will either lead to its mergence with Stipa or at least to a redefinition of the sections of Oryzopsis.

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APPENDIX

For ease of reference, the figures which are from the same floret are grouped together:

O. virescens (Trin.) Beck.

8, 15;

9, 18, 31, 51;

10, 19, 32, 40;

11, 20, 26, 33, 57;

12, 21, 27, 34, 41, 58;

13, 24, 29, 56, 67, 68, 80;

22, 28, 35, 42, 62, 63, 207;

25, 36a,b,c, 38, 44;

30, 37, 43, 81;

39, 48, 55;

46, 52;

47, 54;

60, 61;

64, 65, 66, 79;

69, 70, 71, 72;

73, 82.

O. hymenoides (Roem. & Schult.) Ricker

101, 106, 113, 120;

APPENDIX (continued)

102, 107, 114, 121;

103, 109, 116, 122, 125, 131;

104, 110, 117, 132;

108, 115, 130;

111, 118, 123, 123a, 124, 126, 129;

127, 128.

O. micrantha (Trin. & Rupr.) Thurb.

158, 159, 168;

160, 164, 169, 177, 181;

161, 165, 170, 175, 178, 182;

163, 174;

166, 171, 183;

167, 172;

176, 180.

O. kingii (Boland.) Beal.

199, 205, 212, 219;

200, 206, 213, 220;

201, 215, 221, 223;

202, 209, 227, 228;

203, 210, 216, 222, 224, 229;

207, 214;

FIGS. 1 - 6. Floral parts. Figs. 1, 2, 3, Oryzopsis virescens; fig. 1, spikelet; fig. 2, floret side view; fig. 3, floret posterior view. Figs. 4, 5, 6, O. hymenoides; fig. 4, spikelet; fig. 5, floret side view; fig. 6, floret posterior view. Line represents 1mm.; a, awn; c, callus; e, ears at apex of lemma; l, lemma; p, palea.

APPENDIX (continued)

208, 226;

204, 218;

211, 217.

O. asperifolia Michx.

247, 252, 258, 266;

248, 253, 259, 267, 270;

249, 254, 260, 268, 271;

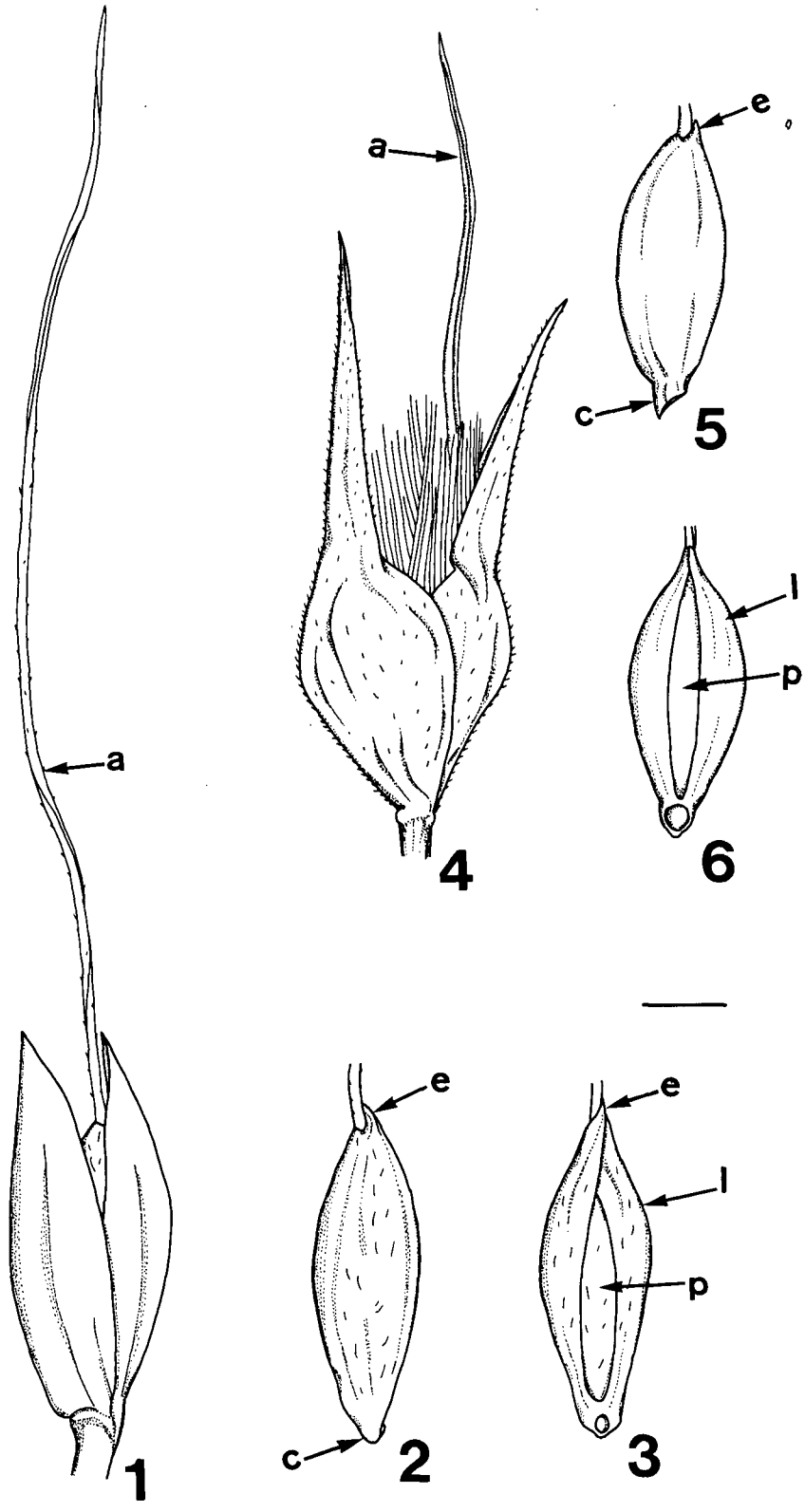
251, 257;

255, 261, 262;

256, 263, 269;

264, 265;

273, 274.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a
4
e
c
5
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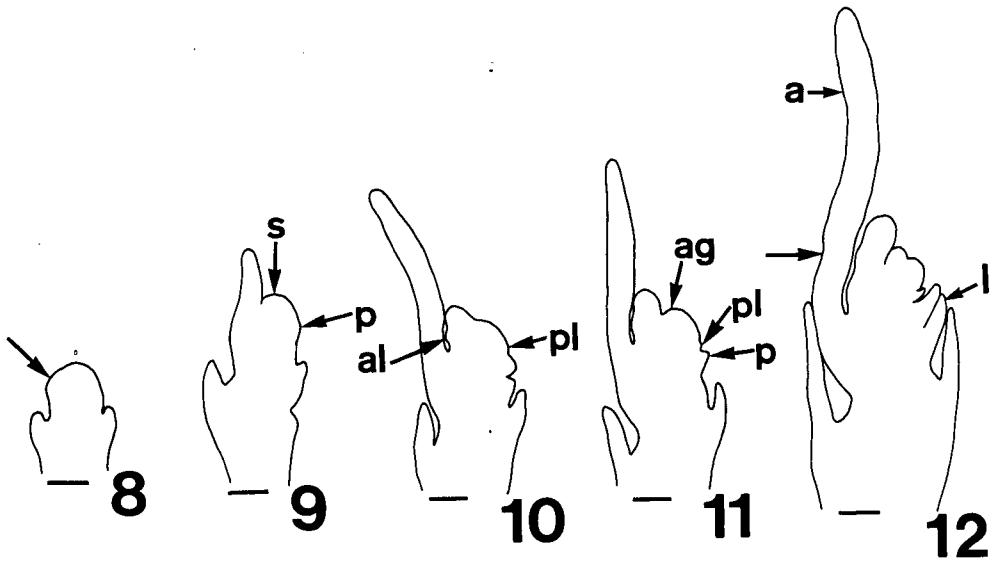
p
6
e
c
2
e
l
p
3

FIGS. 8 - 14. Stages in floret development in O. virescens. Fig. 8, awn-lemma initiation (unlabeled arrow). Fig. 9, palea and stamen initiation. Fig. 10, lodicule initiation. Fig. 11, gynoecium initiation. Fig. 12, spikelet during growth of anterior portion of gynoecial wall (unlabeled arrow shows awn-lemma junct on). Fig. 13, floret prior to integument initiation. Fig. 13 a, b, c, cross-sections of floret at levels shown in fig. 13. Fig. 14, floret at megaspore mother cell stage. Lines represent 0.05 mm.; a, awn; ag, anterior gynoecial wall; al, anterior lodicule; c, callus; l, lemma; p, palea; pl, posterior lodicule; s, stamen.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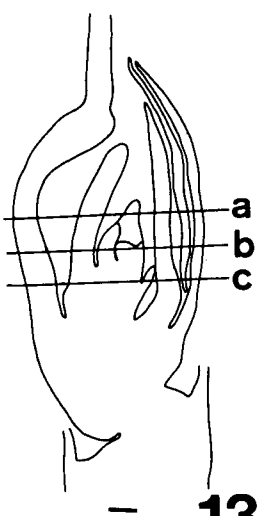
12


a
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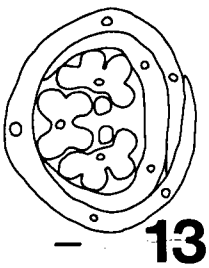
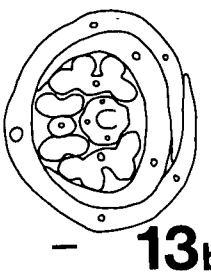

13a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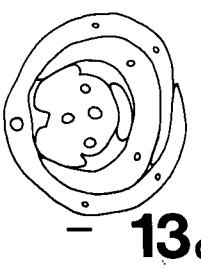
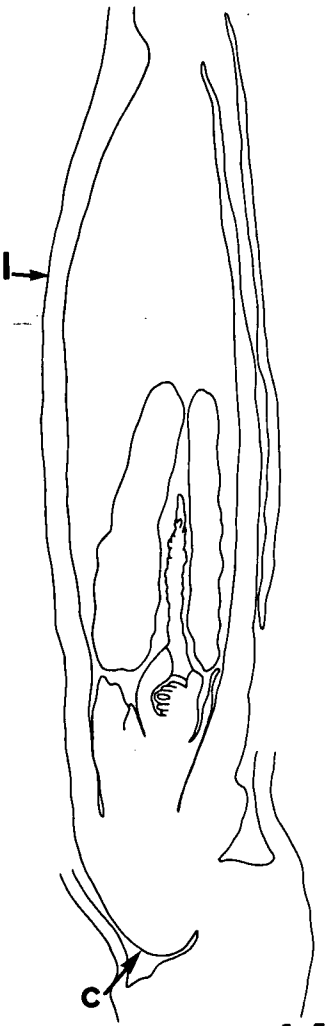
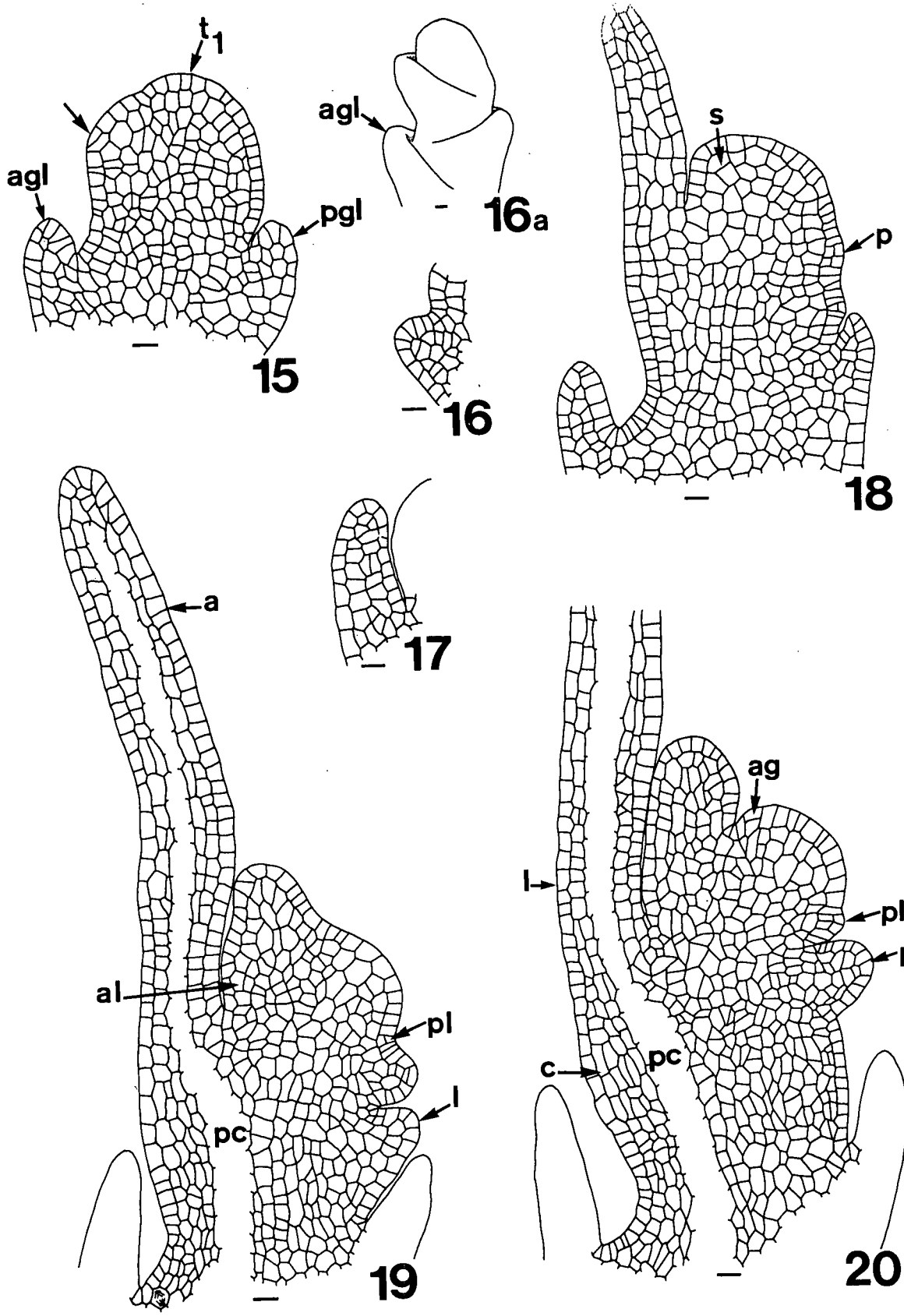

13c


l
c
14

FIGS. 15 - 20. Stages in floret development in O. virescens. Fig. 15, awn-lemma initiation (unlabeled arrow). Fig. 16, early awn-lemma growth. Fig. 16a, young spikelet at approximately the same stage as fig. 16. Fig. 17, awn-lemma at later stage. Fig. 18, palea and stamen initiation. Fig. 19, lodicule initiation. Fig. 20, initiation of gynoecium. Lines represent 0.01 mm.; a, awn; ag, anterior gynoecial wall; agl, anterior glume; al, anterior lodicule; c, callus; l, lemma; p, palea; pc, procambium; pgl, posterior glume; pl, posterior lodicule; s, stamen; t_1, outer tunica layer.


t1
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pgl
15
agl
16a
16
s
p
18
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17
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pl
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pc
19
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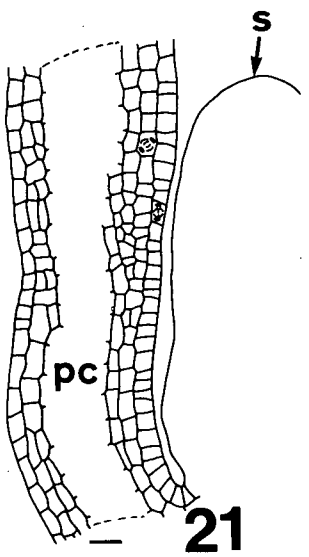
l
pl
p
c
pc
20

FIGS. 21 - 25. Stages in awn-lemma development in O. virescens. Lines represent 0.01 mm.; unlabeled arrows indicate junction between awn and lemma; e, ears at apex of lemma; pc, procambium; s, stamen; vt, vascular tissue.



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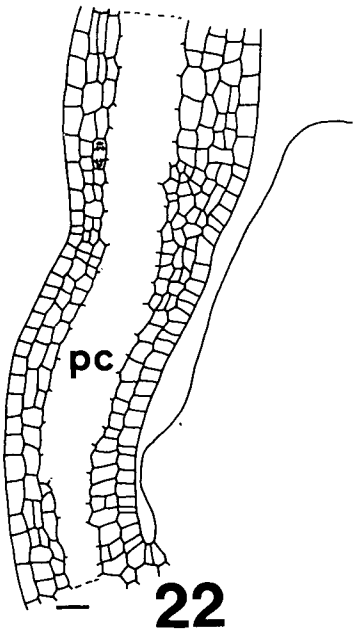

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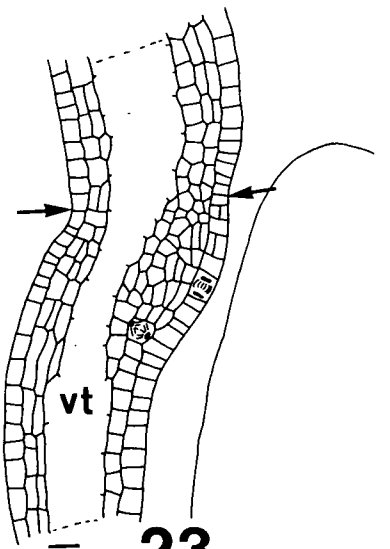

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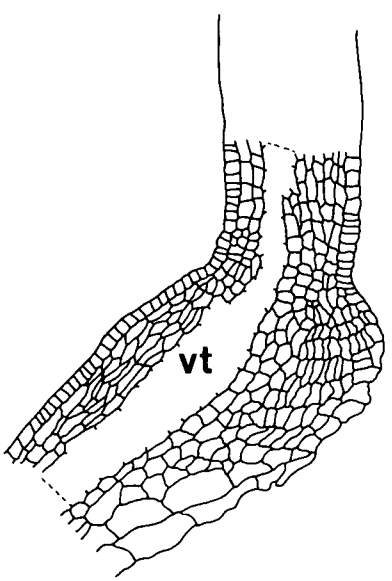

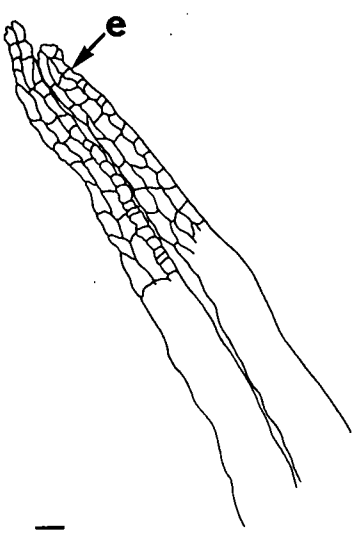

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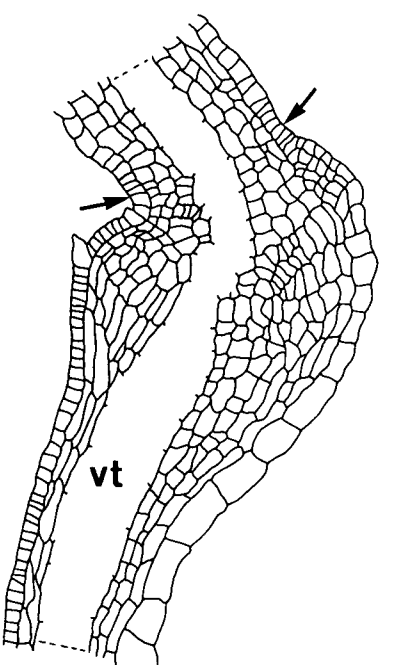

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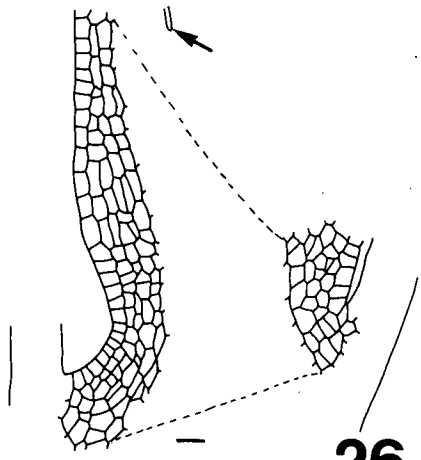
FIGS. 26 - 30. Stages in callus development in O. virescens. Lines represent 0.01 mm.; unlabeled arrows indicate axils of lemma; pc, procambium.



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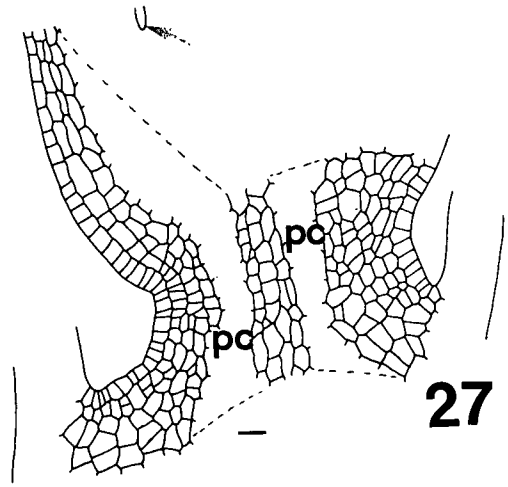

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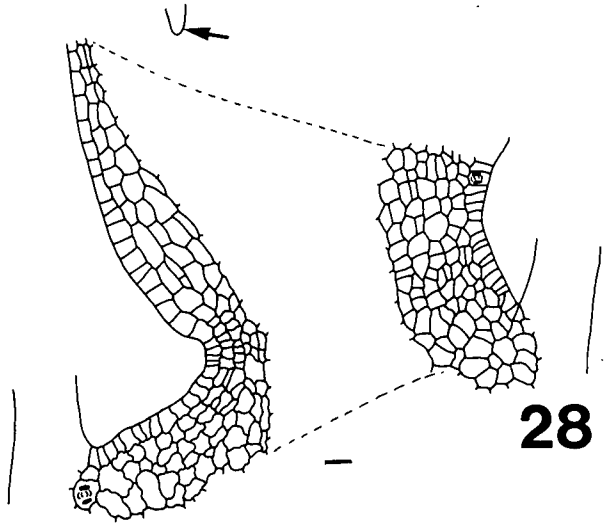

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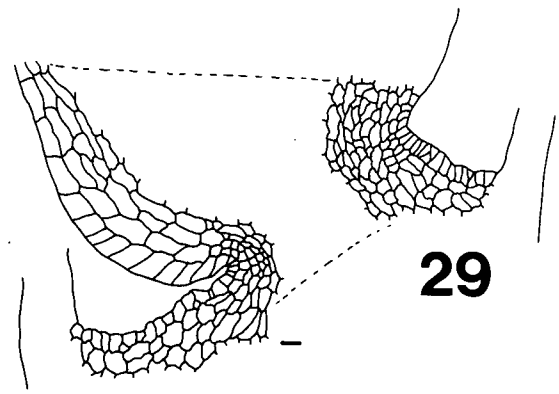

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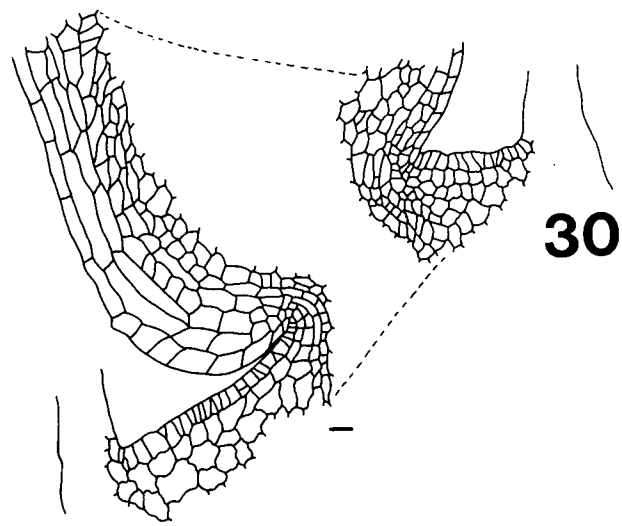
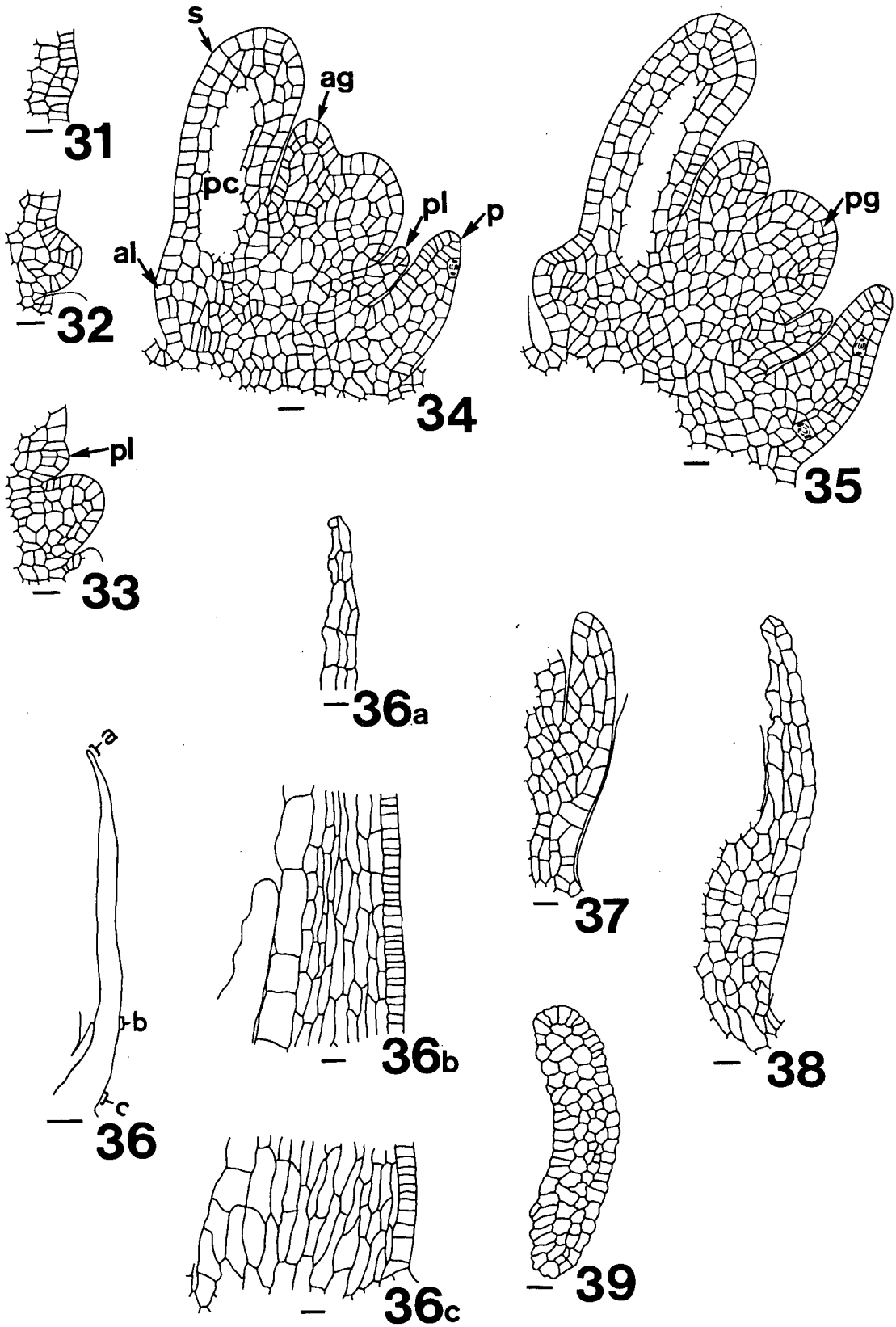


30

FIGS. 31 - 39. Stages in floret development in O. virescens. Figs. 31, 32, palea initiation and early growth. Fig. 33, posterior lodicule initiation and developing palea. Fig. 34, young flower and palea. Fig. 35, young flower and palea at initiation of posterior gynoecial wall. Fig. 36, palea and posterior lodicule. Fig. 36 a, b, c, portions of palea at levels indicated in fig. 36. Figs. 37, 38, developing posterior lodicule. Fig. 39, cross-section of posterior lodicule. Line in fig. 36 represents 0.05 mm., all other lines represent 0.01 mm.; ag, anterior gynoecial wall; al, anterior lodicule; p, palea; pc, procambium; pg, posterior gynoecial wall; pl, posterior lodicule; s, stamen.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36b
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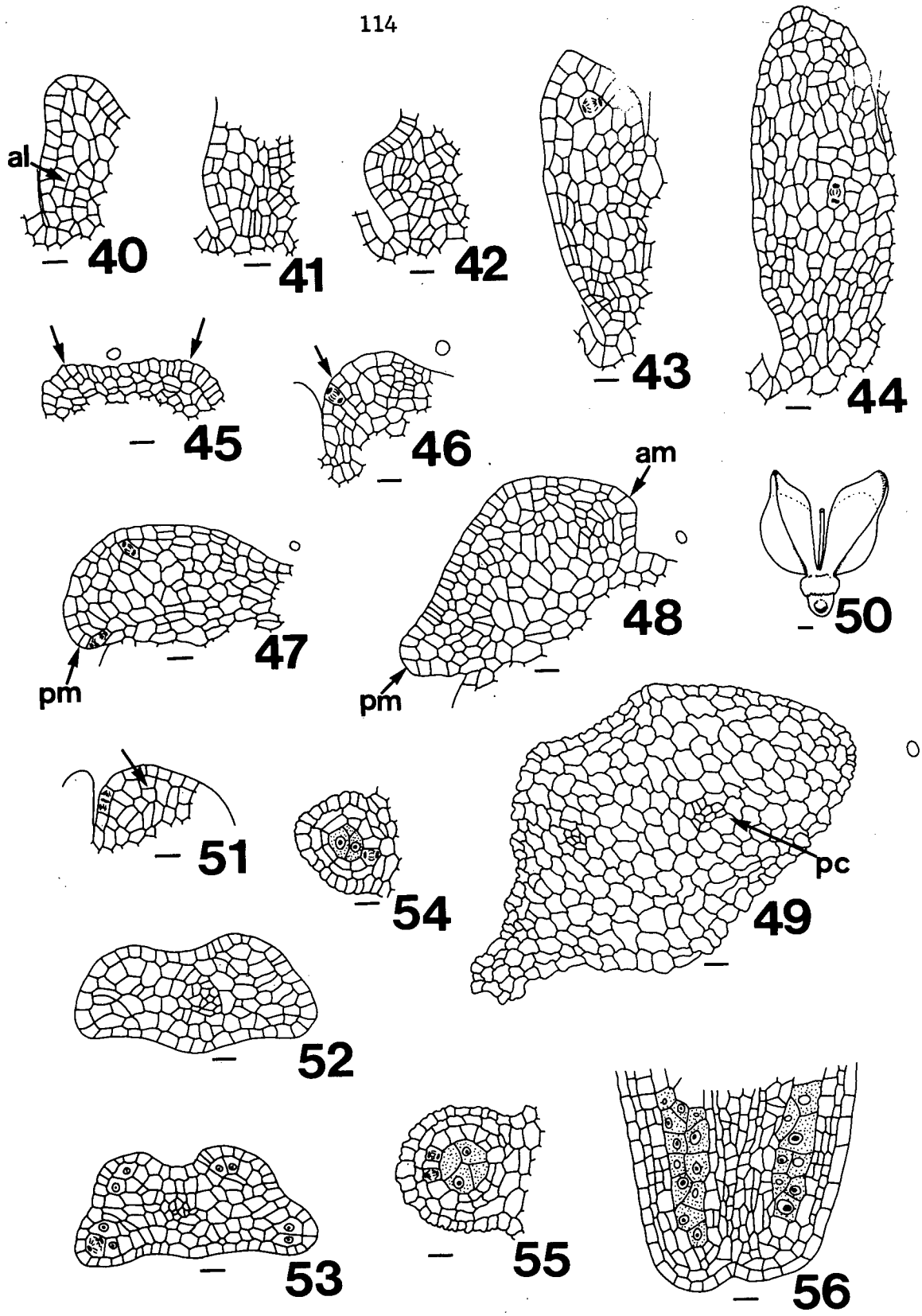
36c

FIGS. 40 -56. Stages in stamen and anterior lodicule development in O. virescens. Figs. 40 - 44, anterior lodicule. Figs. 45 - 49, cross-sections of anterior lodicule; fig. 45, initiation of anterior lodicules (unlabeled arrows); fig. 46, spread of initiation in posterior direction (unlabeled arrow); fig. 47, anterior lodicule with distinct posterior margin; fig. 48, posterior and anterior margins distinct; fig. 49, mature anterior lodicule. Fig. 50, whole structure of anterior lodicules, adaxial view. Fig. 51, stamen initiation (unlabeled arrow). Figs. 52 - 55, cross-sections of stamens, stippling indicates sporogenous cells. Fig. 56, lateral stamen, tangential section. Line in fig. 50 represents 0.1 mm., all other lines represent 0.01 mm.; circle in figs. 46 - 49 represents anterior axis of floret; al, anterior lodicule; am, anterior margin; pc, procambium; pm, posterior margin.


al
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pm
am
48
pm
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pc
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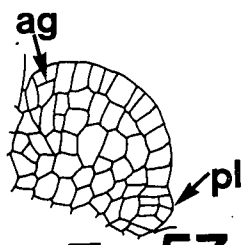
56

FIGS. 57 - 72. Stages in gynoecium development in O. virescens. Fig. 57, initiation of anterior gynoecial wall. Fig. 58, early growth of anterior gynoecial wall. Fig. 59, frontal section of young gynoecium Figs. 60, 61, cross-sections of young gynoecium, 14 μ apart; fig. 61 is at a higher level than fig. 60. Figs 62, 63, adjacent sections 14 μ apart. Figs. 64, 65, 66, adjacent serial sections 14 μ apart, showing a distinct posterior gynoecial wall ('querzone'), and the beginning of style branches. Figs. 69, 70, 71, 72, serial cross-sections of young gynoecium, 14 μ apart, and of increasing height from left to right. Lines represent 0.01 mm.; ag, anterior gynoecial wall; fm, floret apical meristem; lg, lateral gynoecial wall; pg, posterior gynoecial wall; pl, posterior lodicule; sb, style branch.



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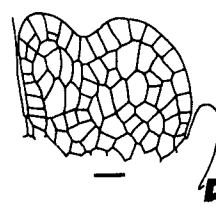

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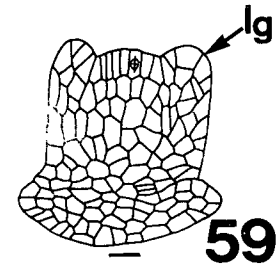

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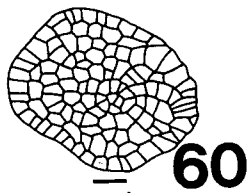

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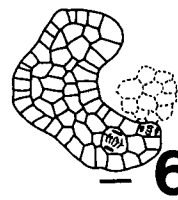

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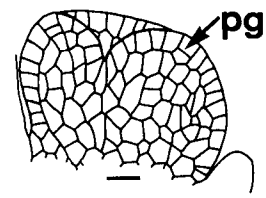

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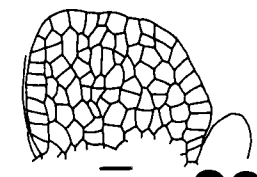

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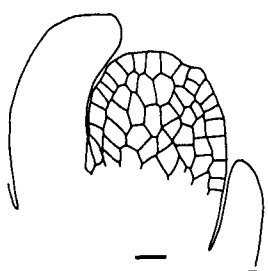

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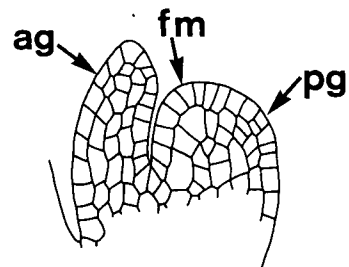

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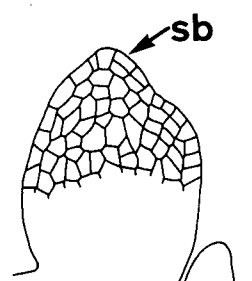

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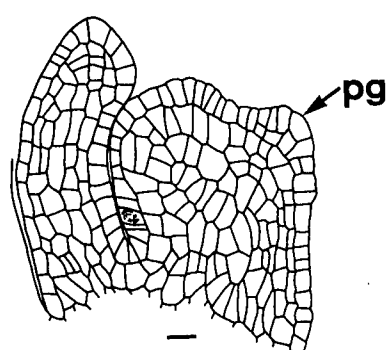

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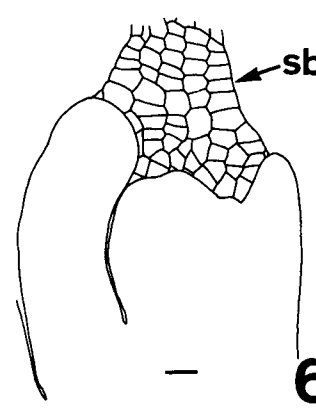

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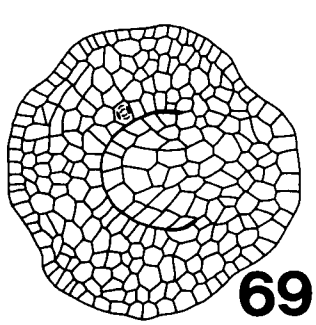

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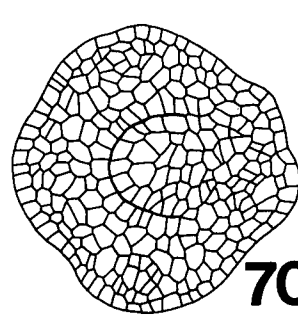

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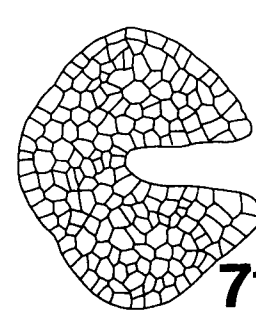

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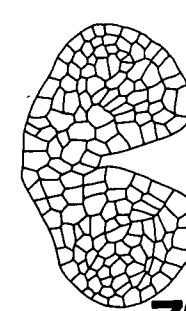

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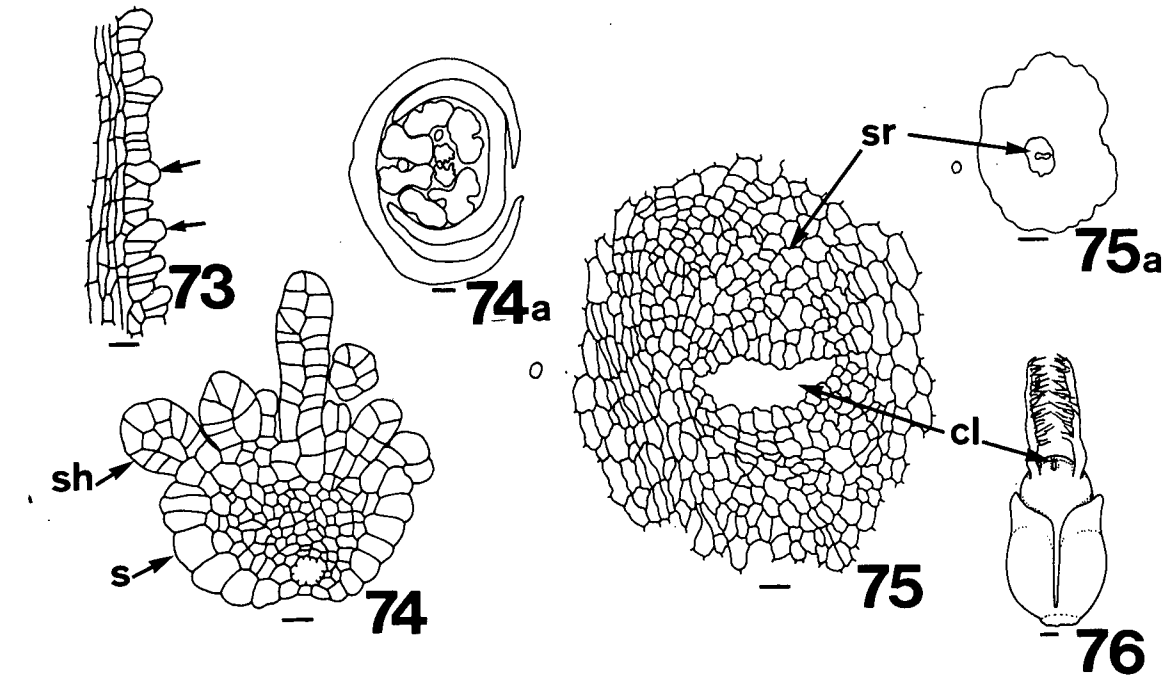
FIGS. 73 - 77. Stages in gynoecium development in O. virescens. Fig. 73, style branch with developing stigmatic hairs (unlabeled arrows). Figs. 74, 74a show the same cross-section; fig. 74a, floret. Figs. 75, 75a are from the same cross-section; fig. 75, 'stylar core'; fig. 75a, ovary; circle in both figs. represents the anterior axis of the floret. Fig. 76, ovary and anterior lodicules, abaxial view. Fig. 77, a series of transverse sections from the base upwards of a young floret at the megaspore stage; the sections are 14 μ apart. Lines in figs. 74a, 75a, 76 represent 0.1 mm., all other lines represent 0.01 mm.; agt, anterior gynoecial trace; alt, anterior lodicule trace; cl, cleft; lgt, lateral gynoecial trace; pgt, posterior gynoecial trace; s, style; sh, stigmatic hair; sr, stylar core region; st, stamen; stt, stamen trace. Stippling shows procambium.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74a
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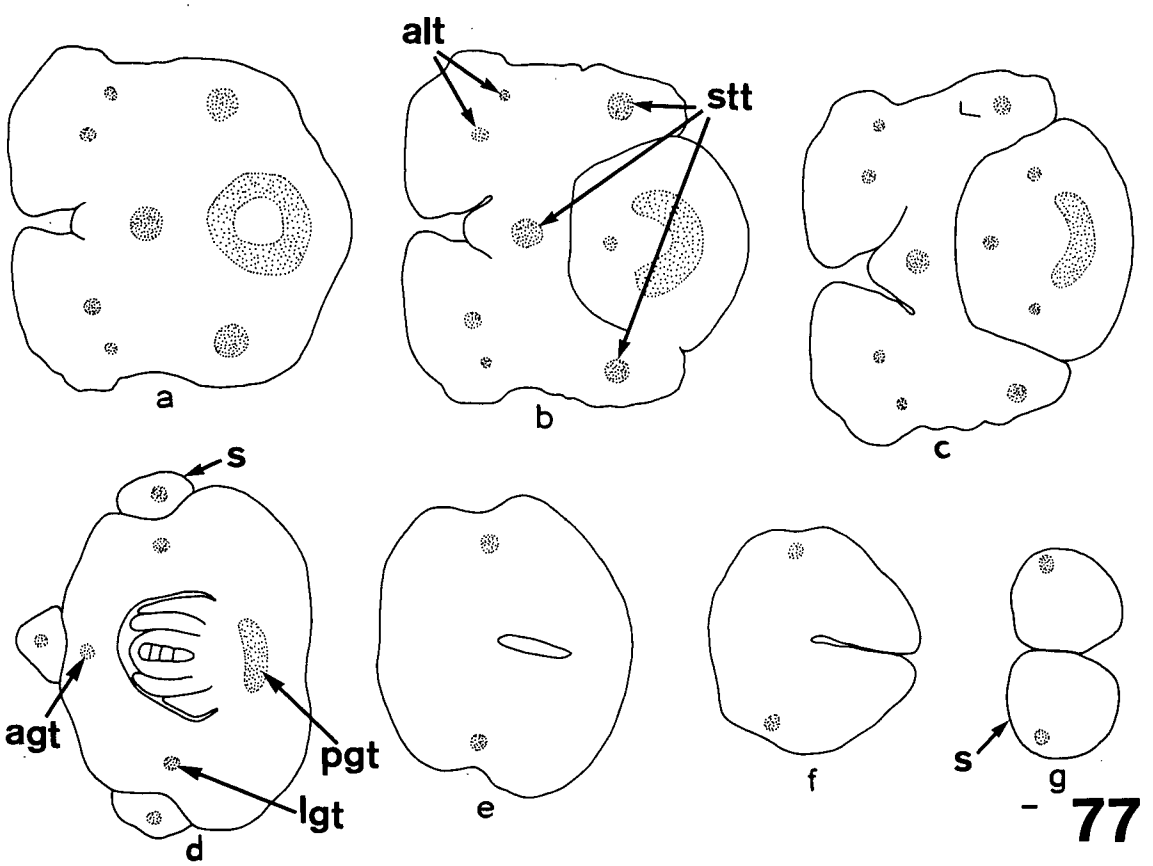
76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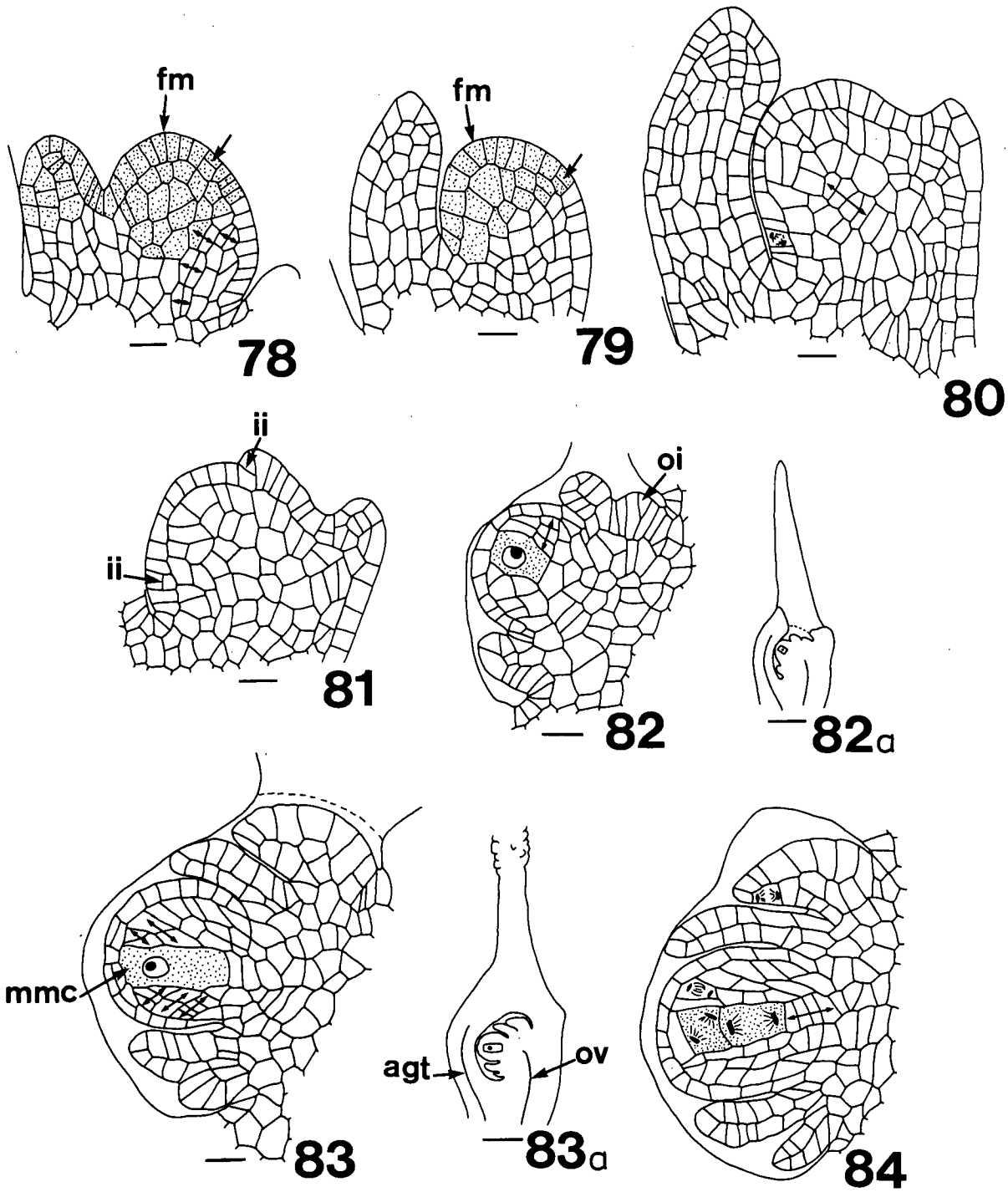
g
77

FIGS. 78 - 84. Early stages in ovule and embryo sac development in O. virescens. Figs. 78, 79, development of posterior portion of gynoecial wall (unlabeled arrows); stippling indicates densely cytoplasmic cells. Fig. 80, young gynoecium. Fig. 81, initiation of inner integument. Figs. 82, 82a, same section, initiation of outer integument. Figs. 83, 83a, same section, megaspore mother cell stage. Fig. 84, meiosis II. Lines in figs. 82a, 83a represent 0.05 mm.; all other lines represent 0.01 mm.; double-headed arrows indicate growth patterns; agt, anterior gynoecial trace; fm, floret apical meristem; ii, inner integument; mmc, megaspore mother cell; oi, outer integument; ov, ovule trace (= posterior gynoecial trace).


fm
78
fm
79
80
ii
ii
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oi
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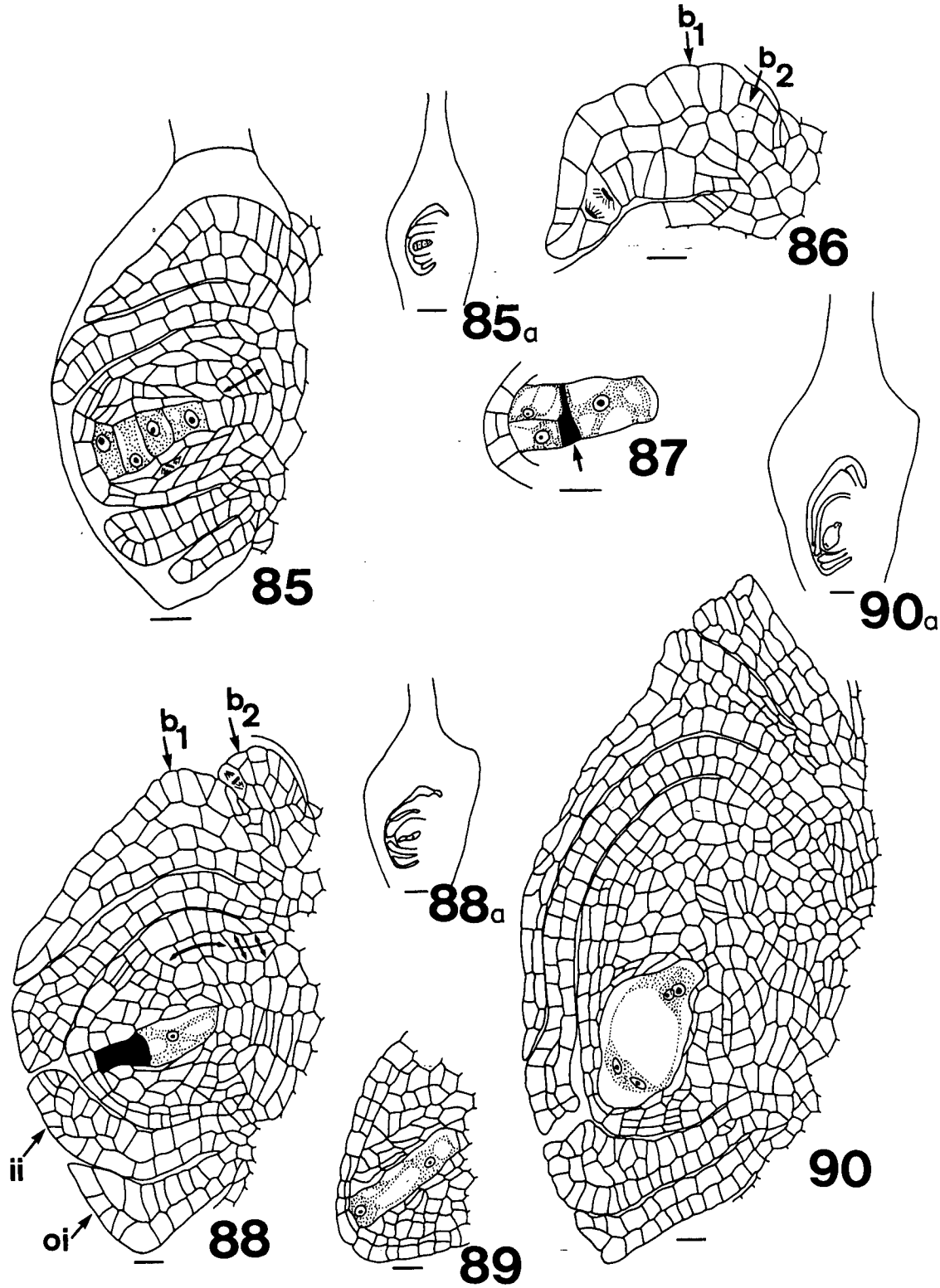
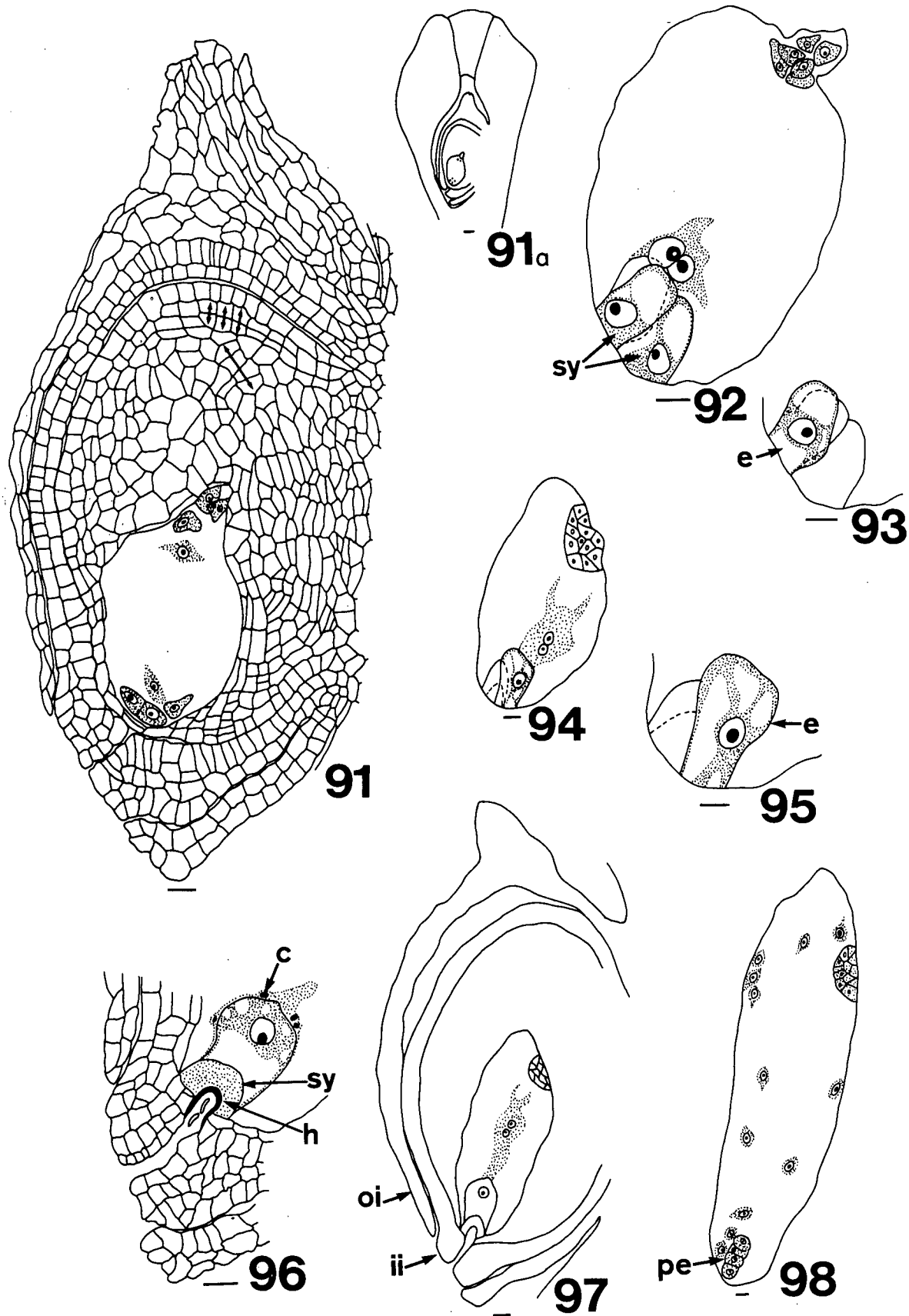
82a
mmc
83
agt
ov
83a
84

FIGS. 85 - 90. Stages in ovule and embryo sac development in O. virescens. Figs. 85, 85a, megaspore stage, from the same section; fig. 85, ovule; fig. 85a, gynoecium. Fig. 86, development of second bump in outer integument at megaspore stage. Fig. 87, T-shaped tetrad, with one degenerated megaspore (indicated by arrow and solid black). Figs. 88, 88a, same section at functional megaspore stage; fig. 88, ovule; fig. 88a, whole gynoecium. Fig. 89, 2-nucleate stage. Figs. 90, 90a, same section at 4-nucleate stage; fig. 90, ovule; 90a, whole gynoecium. Lines in figs. 85a, 88a, 90a represent 0.05 mm., all other lines represent 0.01 mm.; double-headed arrows indicate growth patterns; b_1, first bump; b_2, second bump; ii, inner integument; oi, outer integument.


b1
b2
86
85a
87
85
90a
b1
b2
88a
ii
oi
88
89
90

FIGS. 91 - 98. Stages in embryo sac development in O. virescens. Figs. 91, 91a, same section at 8-nucleate stage; fig. 91, ovule; fig. 91a, whole gynoecium. Figs 92, 93, same section at differentiated 8-nucleate stage; fig. 92, embryo sac; fig. 93, egg and synergids. Figs. 94, 95, same embryo sac prior to fertilization; fig. 94, embryo sac; fig. 95, egg and synergids. Figs. 96, 97, same section at fertilization; fig. 96, egg apparatus and surrounding nucellus and integuments; fig. 97, ovule. Fig. 98, embryo sac with proembryo and nuclear endosperm. Line in fig. 91a represents 0.05 mm., all other lines represent 0.01 mm.; double-headed arrows in fig. 91 indicate growth patterns; c, chromatin-like bodies; e, egg; h, homogenous dense staining material; ii, inner integument; oi, outer integument; pe, proembryo.


91
91a
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e
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c
sy
h
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oi
ii
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pe
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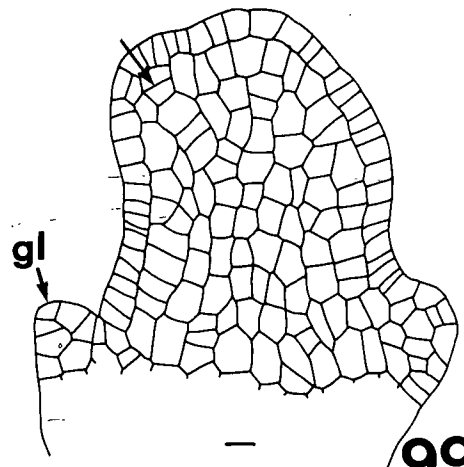
FIGS. 99 - 105. Stages in floret development in O. hymenoides. Fig. 99, lemma initiation (unlabeled arrow). Fig. 100, palea initiation (unlabeled arrow). Figs 101 - 105, outline diagrams of entire florets; fig. 101, at lodicule initiation (unlabeled arrow indicates site of posterior lodicule initiation); fig. 102, at initiation of anterior portion of gynoecial wall (unlabeled arrow); fig. 103, at initiation of posterior portion of gynoecial wall (unlabeled arrow); fig. 104, prior to integument initiation; fig. 105, megaspore mother cell stage. Lines in figs. 99, 100 represent 0.01 mm., all other lines represent 0.05 mm.; a, awn; alj, awn-lemma junction; c, callus; gl, glume; l, lemma; p, palea.



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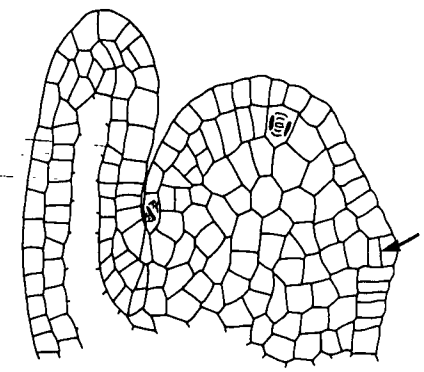

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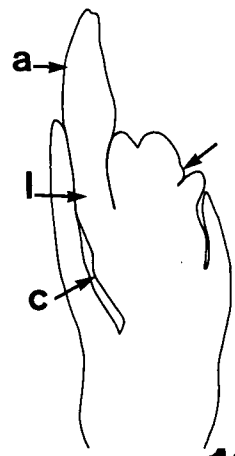

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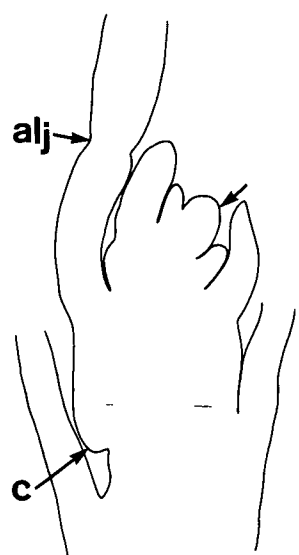

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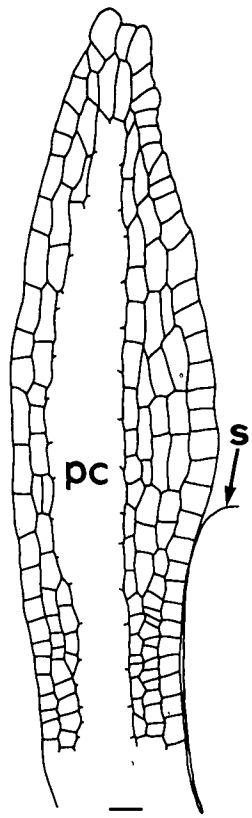
FIGS. 106 - 112. Stages in awn-lemma development in O. hymenoides. Lines represent 0.01 mm.; arrows indicate junction between awn and lemma; pc, procambium; s, stamen.



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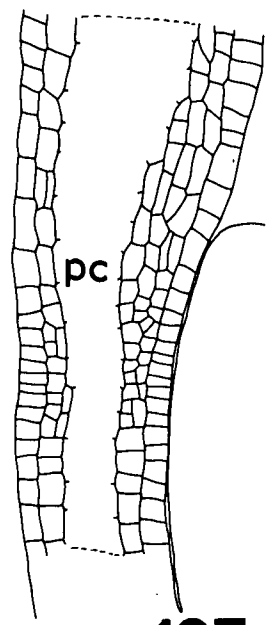

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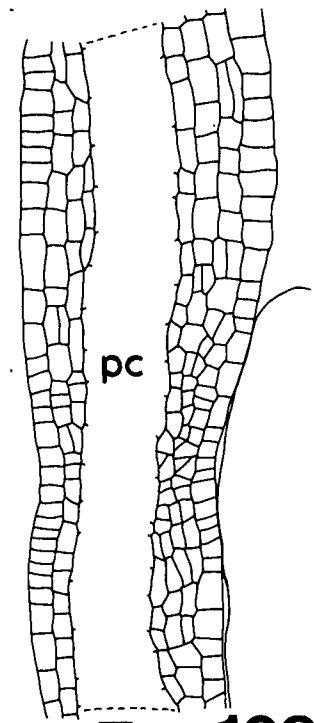

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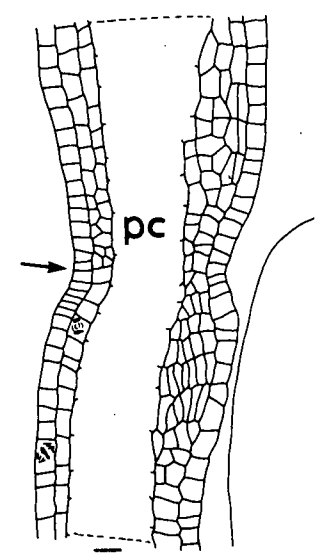

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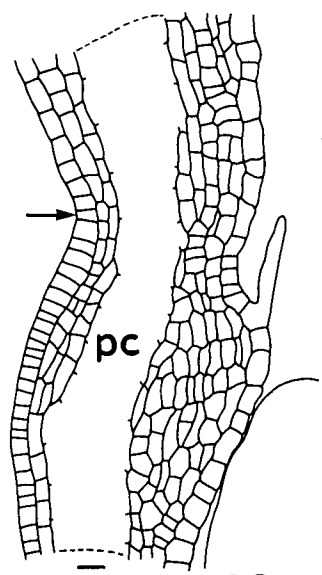

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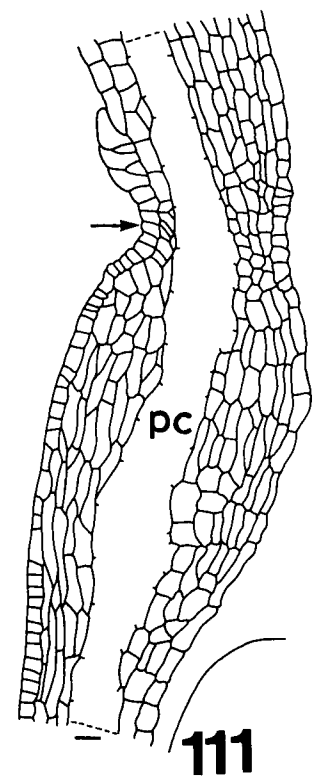

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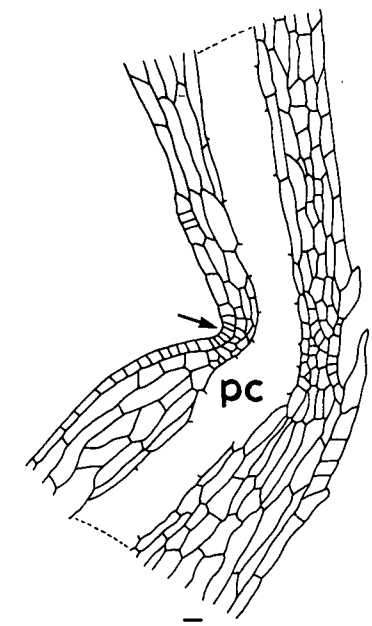

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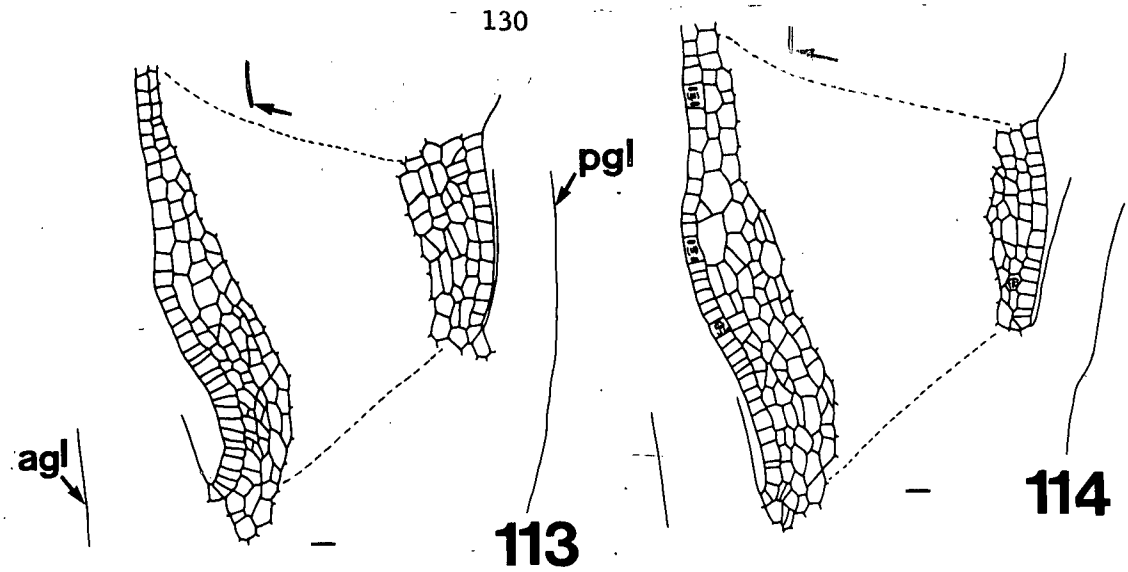
FIGS. 113 - 119. Stages in callus development in O. hymenoides. Lines represent 0.01 mm.; unlabeled arrows indicate axils of lemma; agl, anterior glume; pgl, posterior glume.



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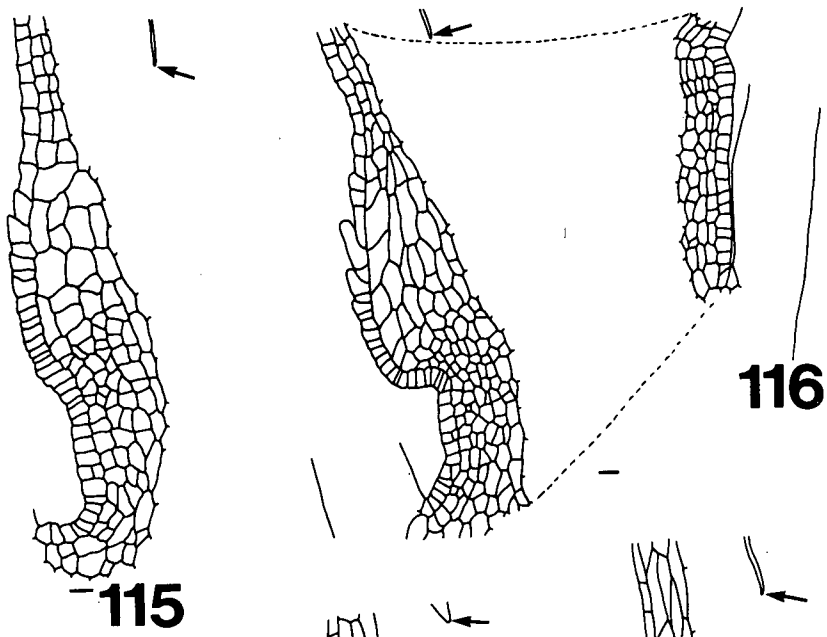

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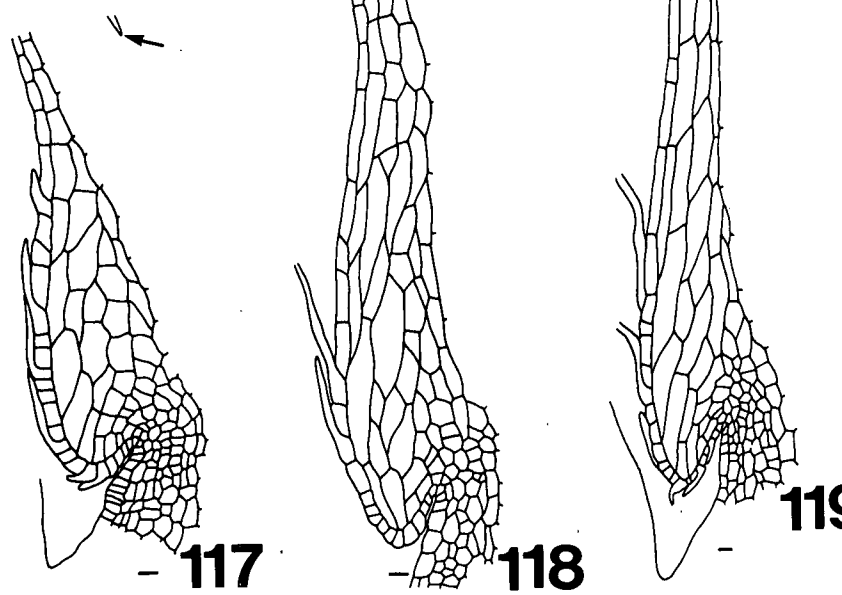
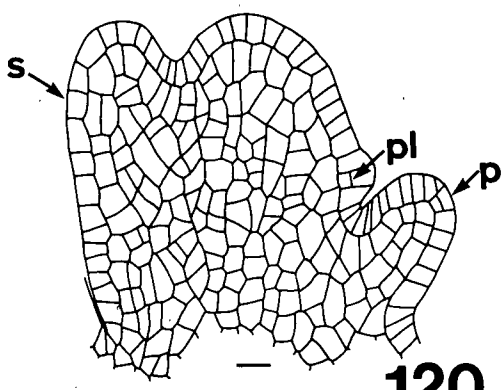


117 118 119

FIGS. 120 - 128. Stages in floret development in O. hymenoides. Figs. 120, 121, flower and palea. Fig. 122, posterior lodicule and palea. Fig. 123, posterior lodicule and palea. Fig. 123a, tip of palea shown in fig. 123. Fig 124, posterior lodicule. Figs. 125, 126, development of anterior lodicule. Fig. 127, whole structure of anterior lodicules, adaxial view. Fig. 128, same lodicules as fig. 127, but abaxial veiw and with ovary attached. Line in fig. 123a represents 0.05 mm., lines in figs. 127 and 128 represent 1.0 mm., all other lines represent 0.01 mm.; ag, anterior portion of gynoecial wall; p, palea; pc, procambium; pl, posterior lodicule; s, stamen.



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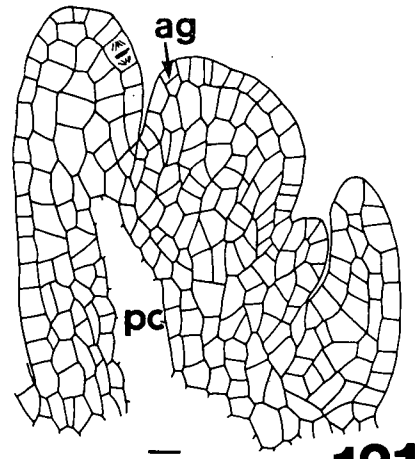

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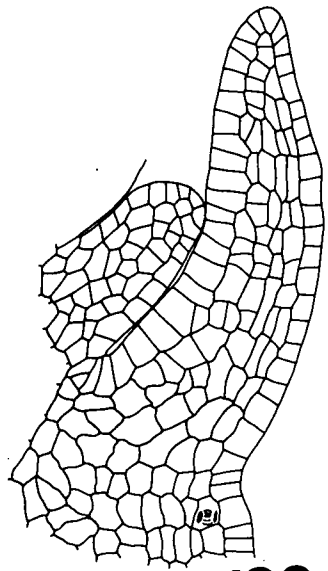

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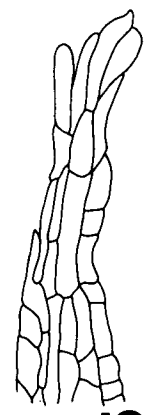
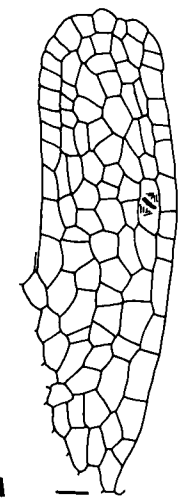


123a



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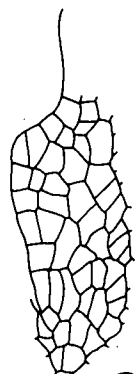

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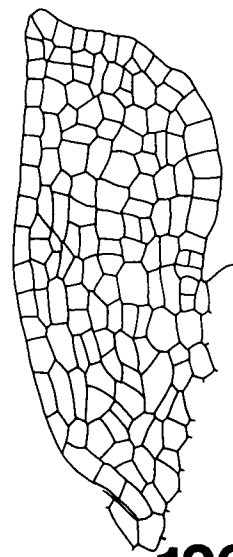

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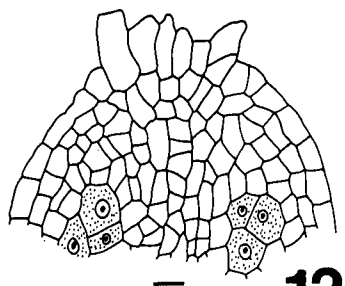
FIGS. 129 - 134. Stages in floret development in O. hymenoides. Fig. 129, portion of stamen, anther 'beard' initiation. Fig. 130, growth of anterior portion of gynoecial wall. Fig. 131, gynoecial wall appears on posterior side (unlabeled arrow). Fig. 132, young gynoecium. Fig. 133, cross-section of top of ovary to show stylar core tissue, heavy line (arrow) indicates 'closure' of locule. Fig. 133a, cross-section of gynoecium; figs. 133 and 133a are of the same section, circle in both indicates anterior axis of floret. Fig. 134, whole structure of ovary. Line in fig. 133a represents 0.1 mm., in fig. 134, 0.05 mm., all other lines represent 0.01 mm.; ag, anterior portion of gynoecial wall; fm, floret apical meristem; pg, posterior portion of gynoecial wall.



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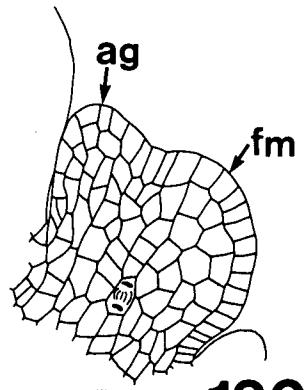

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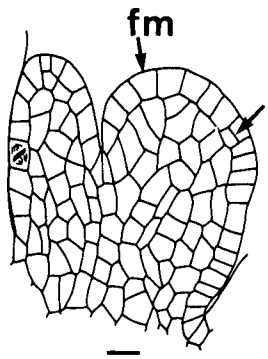

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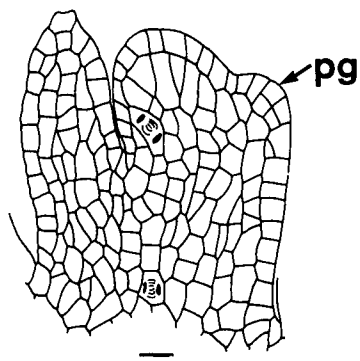

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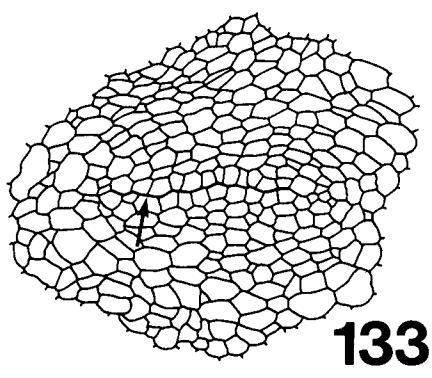

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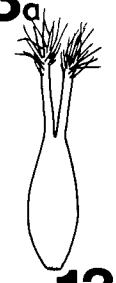
133a



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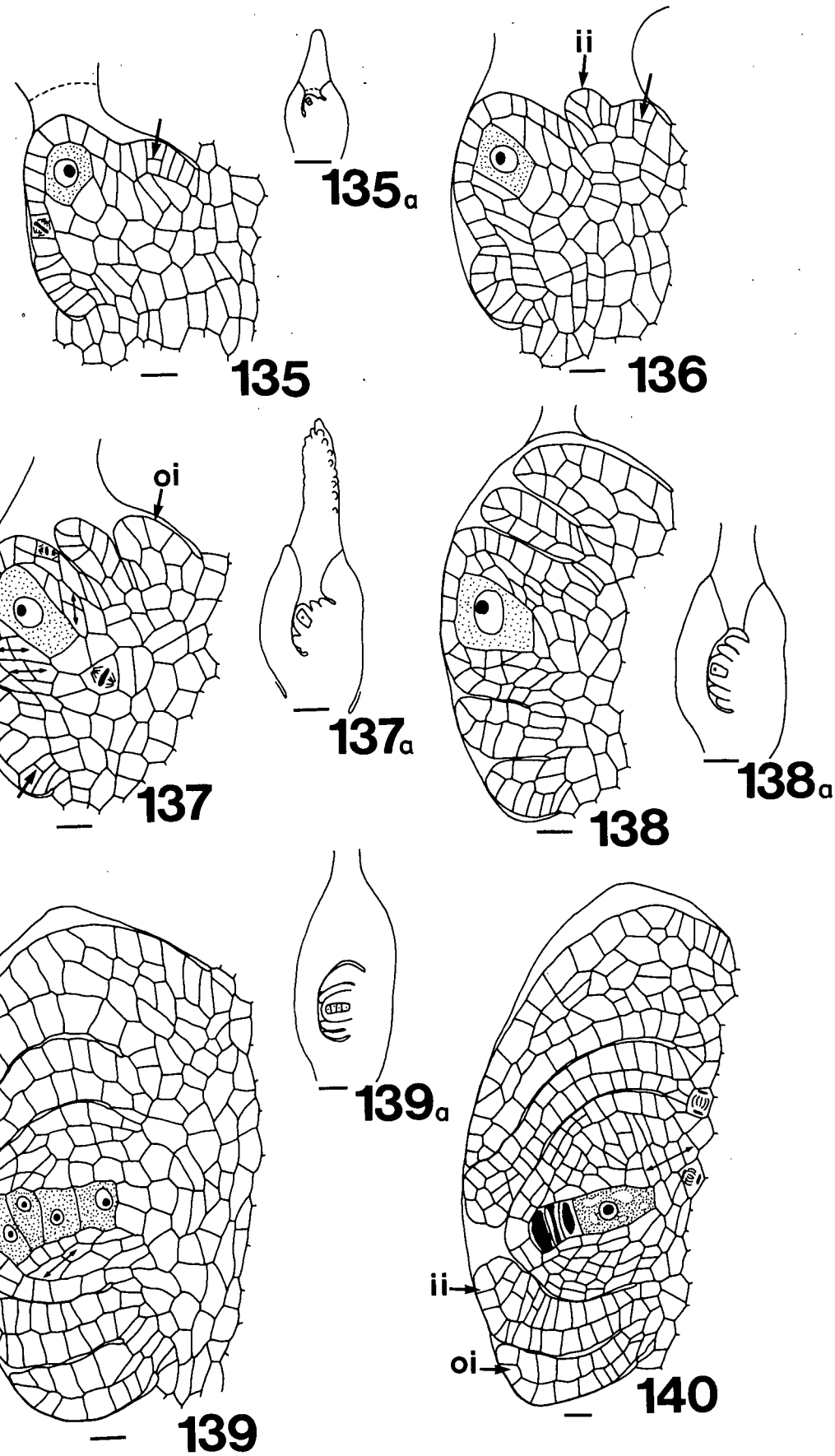
FIGS. 135 - 140. Ovule and early embryo sac development in O. hymenoide hymenoides. Figs. 135, 135a, same section at inner integument initiatio initiation on upper side (unlabeled arrow in fig. 135); fig. 135, ovule; fig. 135a, gynoecium. Fig. 136, ovule at initiation of outer integument on upper side (unlabeled arrow). Figs. 137, 137a, same section at initiation of outer integument on lower side (unlabeled arrow); fig. 137, ovule; fig. 137a, gynoecium. Figs. 138, 138a, same section at megaspore mother cell stage; fig. 138, ovule; fig. 138a, gynoecium. Figs 139, 139a, same section at megaspore stage; fig. 139, ovule; fig. 139a, gynoecium. Fig. 140, functional megaspore. Lines in figs. 135a, 137a, 138a, 139a represent 0.05 mm., all other lines represent 0.01 mm.; double-headed arrows indicate growth patterns; solid black in fig. 140 represents aborted megaspores; ii, inner integument; oi, inner integument.


135a
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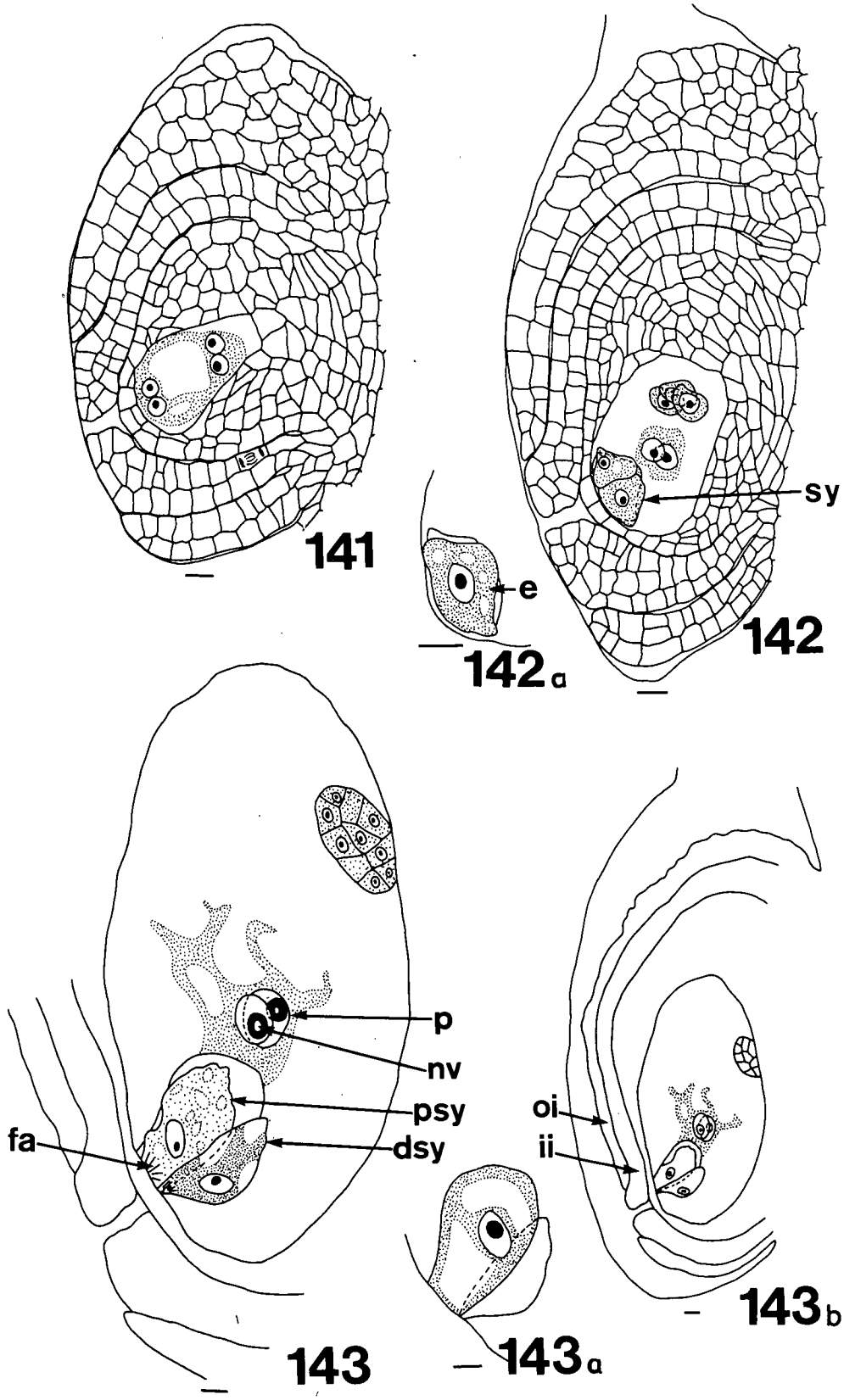
FIGS. 141 - 143. Stages in embryo sac development in O. hymenoides. Fig. 141, 4-nucleate stage. Figs. 142, 142a, from same same embryo sac at 8-nucleate stage; fig. 142, ovule; fig. 142a, egg. Figs. 143, 143a, 143b, from same embryo sac prior to fertilization; fig. 143, embryo sac; fig. 143a, egg and one synergid; fig. 143b, ovule. Lines represent 0.01 mm.; dsy, degenerating synergid; e, egg; fa, filiform apparatus; ii, inner integument; nv, nucleolar vacuole; oi, outer integument; p, polar nucleus; psy, persistent synergid; sy, synergid.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143a
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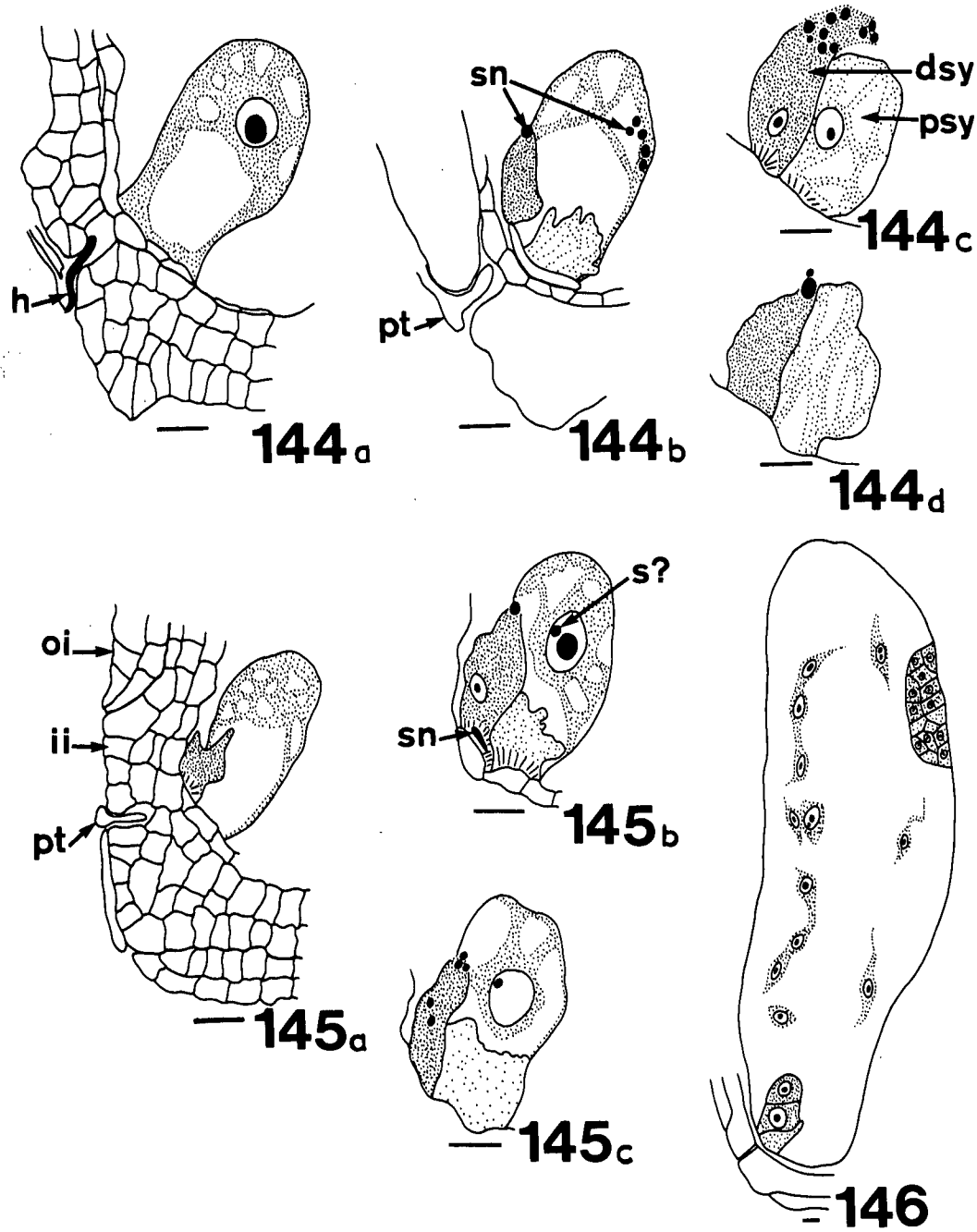
FIGS. 144 - 146. Fertilization and early post-fertilization stages in O. hymenoides. Fig. 144, adjacent serial section, 7 μ apart, of egg apparatus at fertilization; fig. 144a, egg and surrounding nucellus and inner integument; fig. 144b, egg and two synergids; figs. 144c, 144d, two synergids. Fig. 145, adjacent serial sections, 7 μ apart, of egg apparatus at fertilization; fig. 145a, egg, degenerat degenerate synergid and surrounding nucellus and integuments; figs. 145b, 145c, egg and synergids. Fig. 146, 2-cell proembryo stage. Lines represent 0.01 mm.; dsy, degenerate synergid; h, homogenous dense staining material; ii, inner integument; oi, outer integument; psy, persistent synergid; pt, pollen tube; sn, chromatin-like bodies; s?, sperm nuclei?.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144d
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145b
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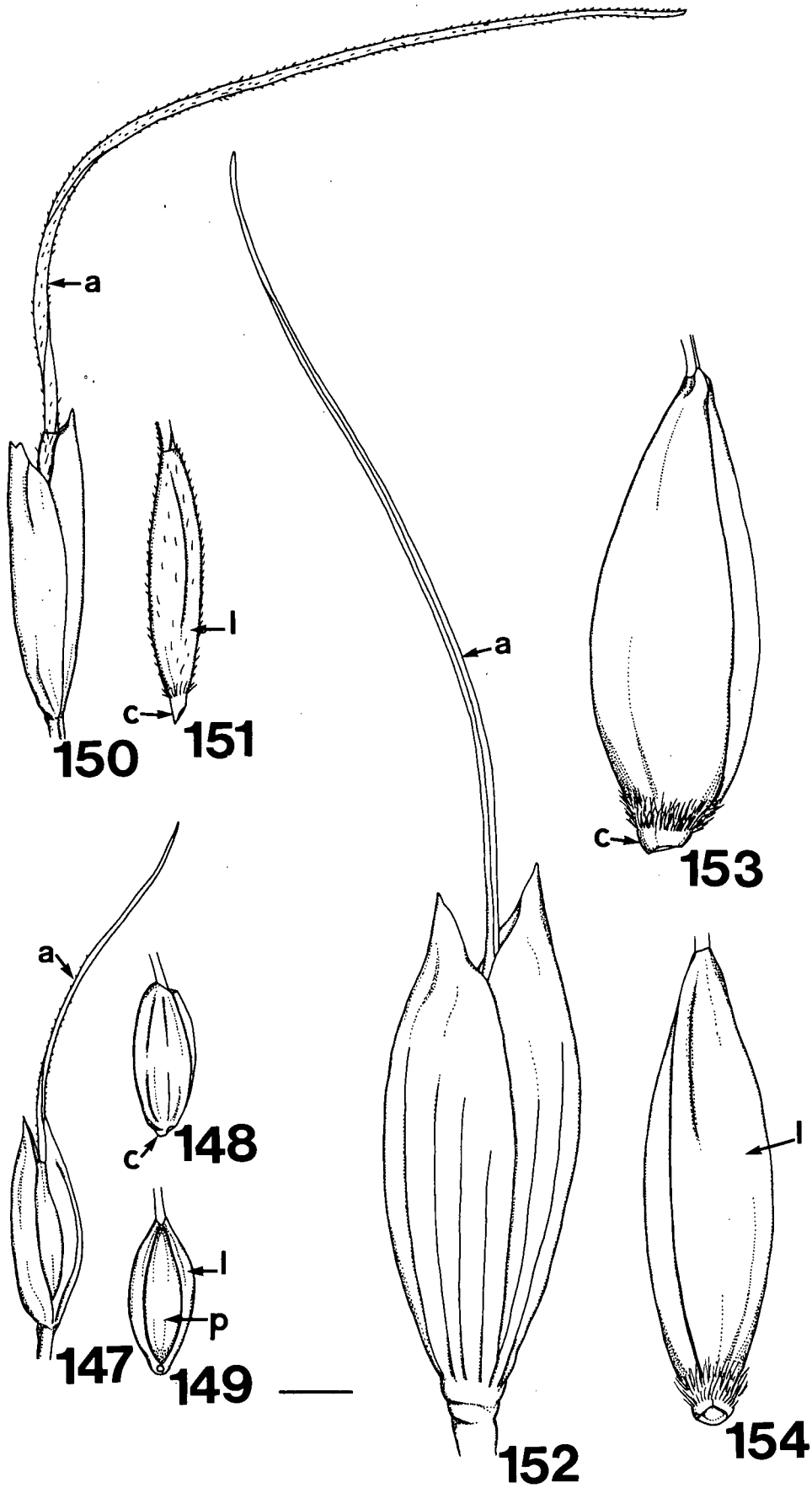
146

FIGS. 147 - 154. Floral parts. Figs 147, 148, 149, Oryzopsis micrantha; fig. 147, spikelet; fig. 148, floret side view; fig. 149, floret posterior view. Figs. 150, 151, O. kingii; fig. 150, spikelet; fig. 151, floret side view. Figs. 152, 153, 154, O. asperifolia; fig. 152, spikelet; fig. 153, lemma side view; fig. 154, lemma posterior view. Line represent 1.0 mm., all drawings at the same magnification; a, awn; c, callus; l, lemma; p, palea.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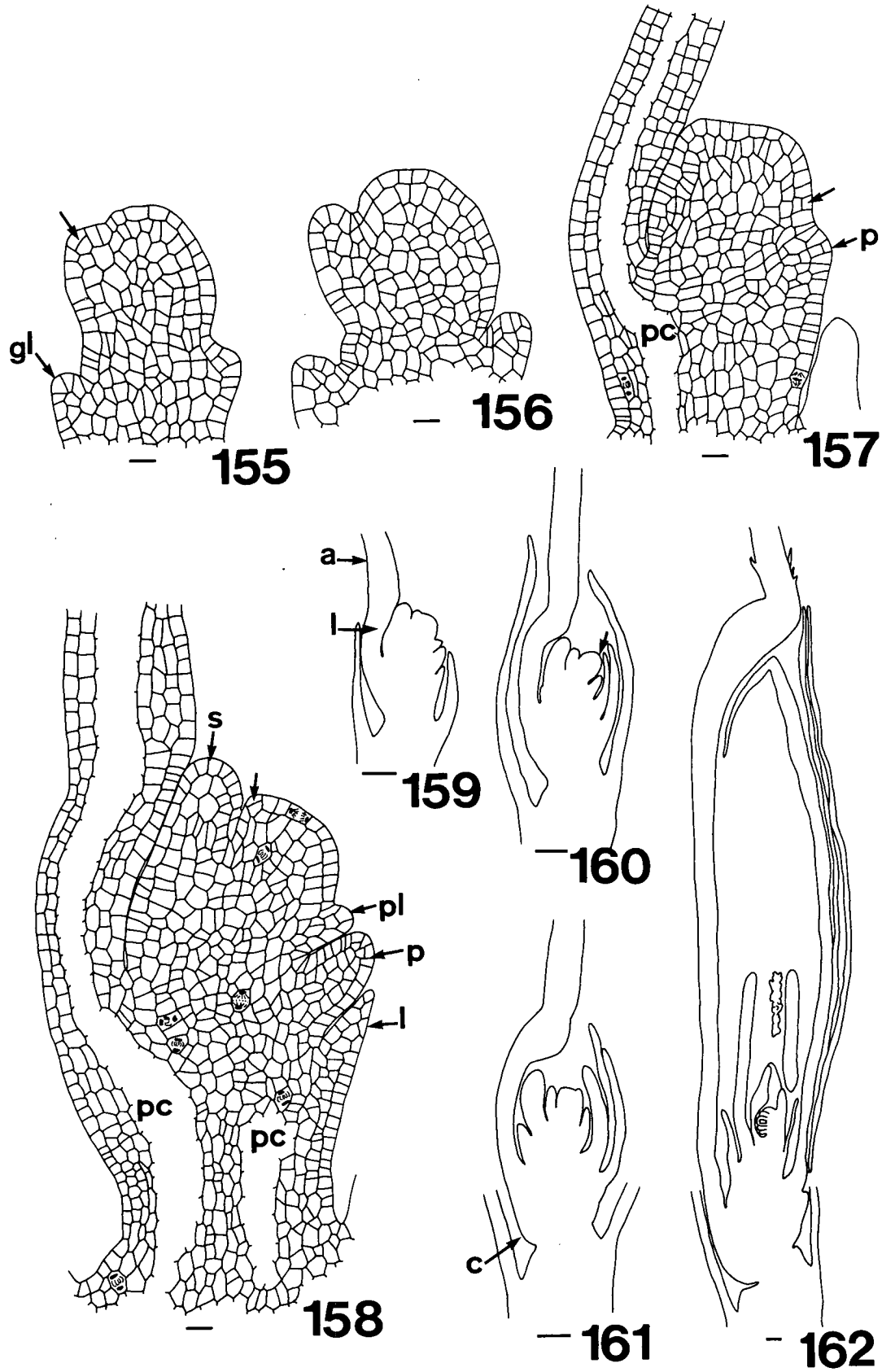
FIGS. 155 - 162. Stages in floret development in O. micrantha. Fig. 155, awn-lemma initiation (unlabeled arrow). Fig. 156, early awn-lemma growth. Fig. 157, initiation of posterior lodicule (unlabeled arrow). Fig. 158, initiation of anterior portion of gynoecial wall. Fig. 159, spikelet same section as fig. 158. Fig. 160, spikelet at initiation of posterior gynoecial wall (unlabeled arrow). Fig. 161, floret prior to integument initiation. Fig. 162, floret at megaspore mother cell stage. Lines in figs. 159, 160, 161, 162,represent 0.05 mm., all other lines represent 0.01 mm.; a, awn; al, anterior lodicule; c, callus; g, glume; l, lemma; pc, procambium; p, palea; pl, posterior lodicule; s, stamen.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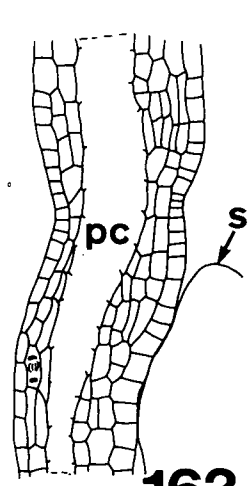
FIGS. 163 - 167. Stages in awn-lemma development in O. micrantha. Lines represent 0.01 mm.; e, ears; pc, procambium; s, stamen; vt, vascular tissue.



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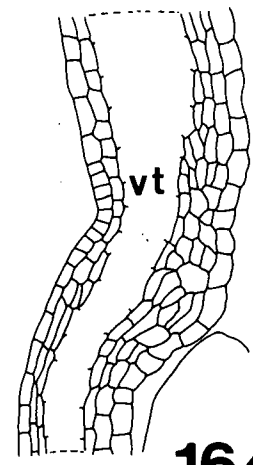

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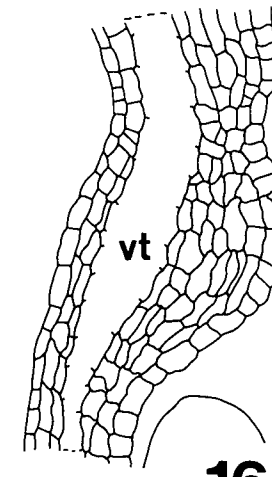

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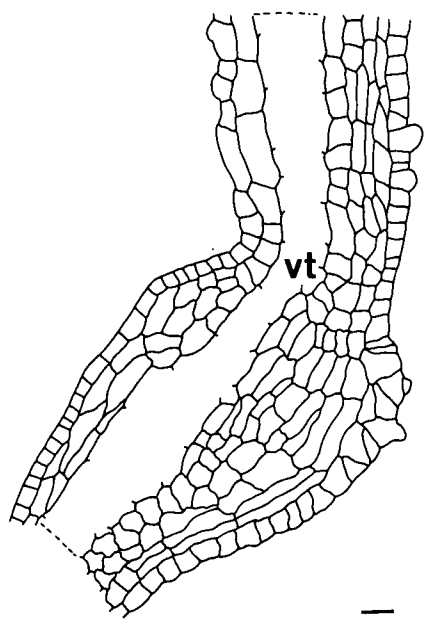

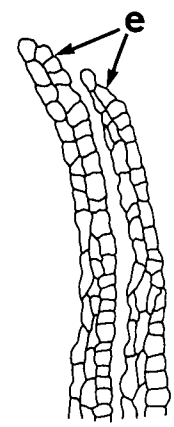

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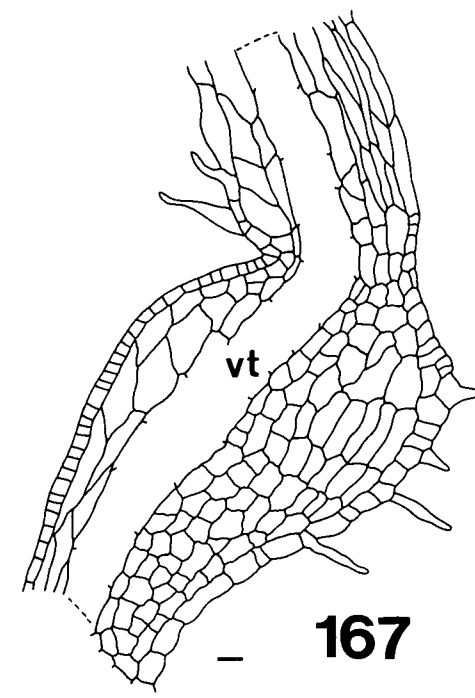

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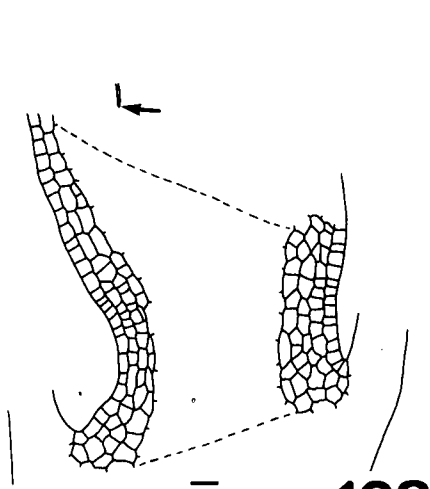
FIGS. 168 - 173. Stages in callus development in O. micrantha. Unlabeled arrows indicate axils of lemma; lines represent 0.01 mm.; vt, vascular tissue.



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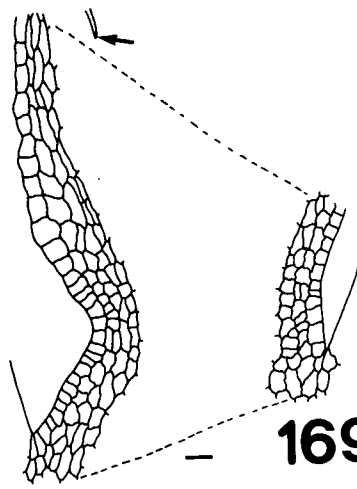

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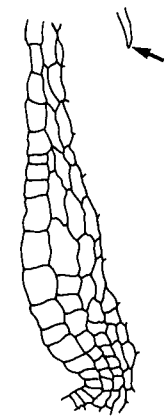

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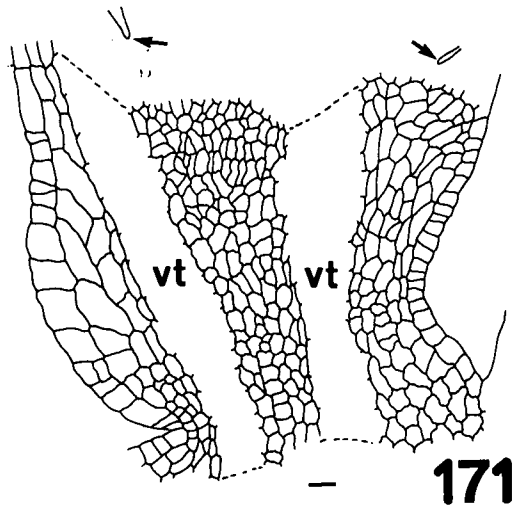

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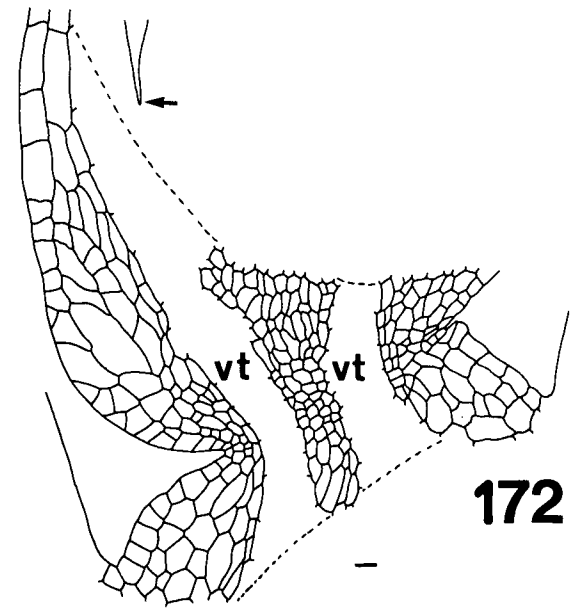

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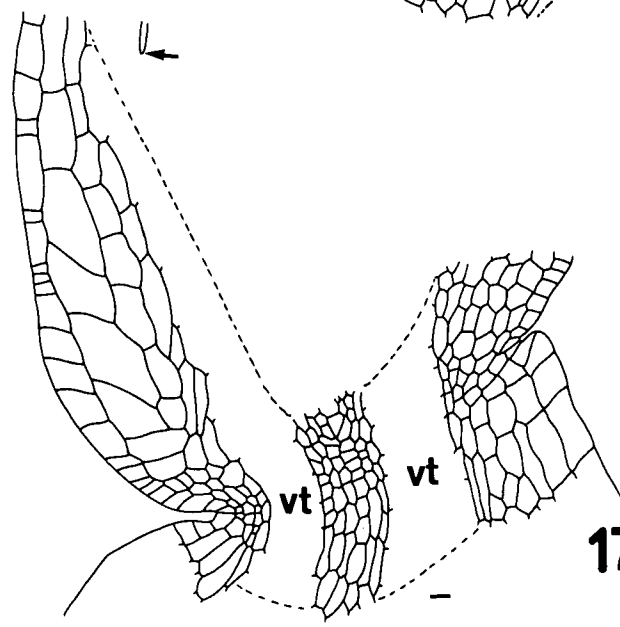
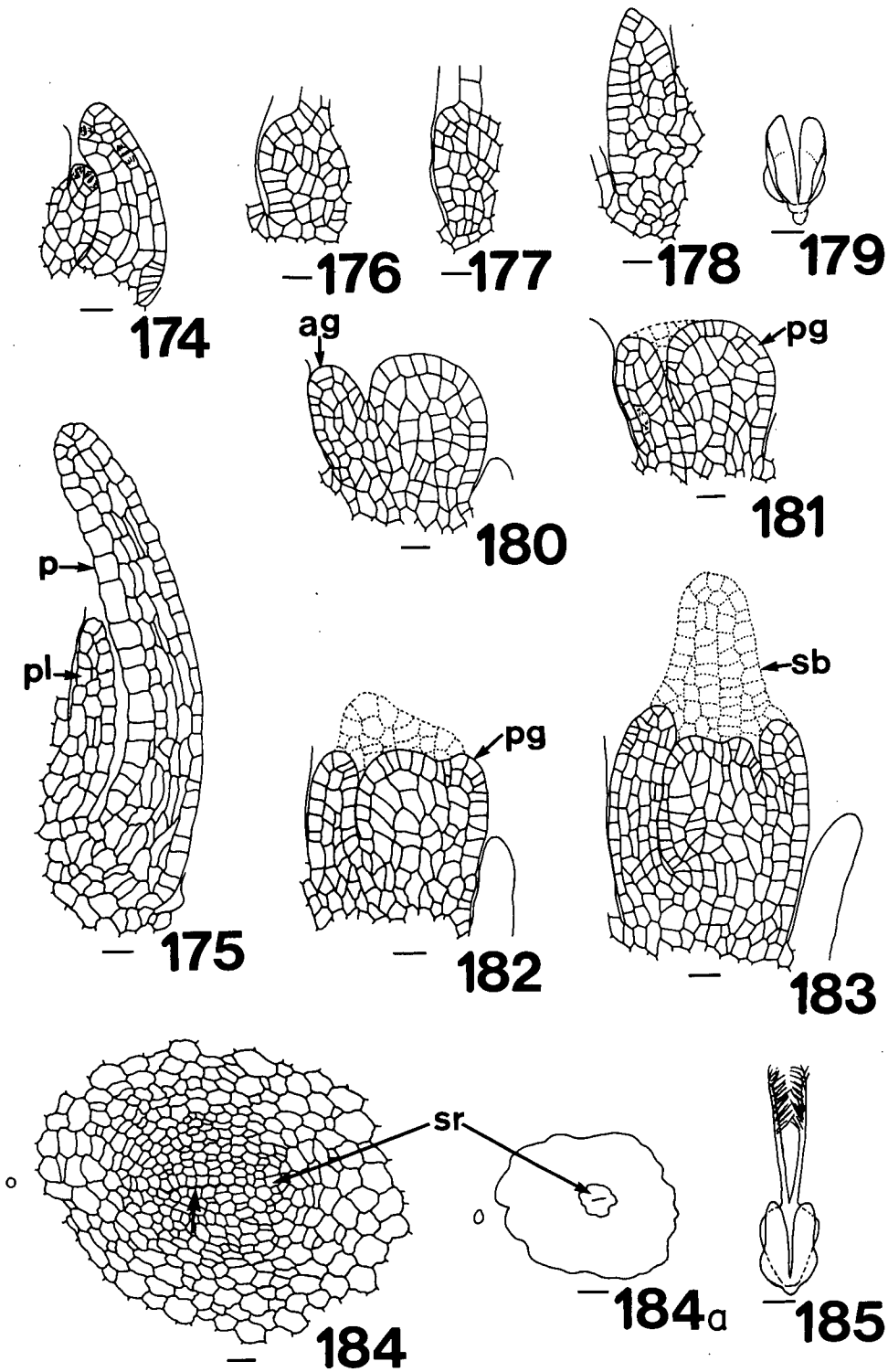


173

FIGS. 174 - 185. Stages in floret development in O. micrantha. Figs. 174, 175, palea and posterior lodicule. Figs. 176 - 178, anterior lodicule. Fig. 179, anterior lodicules, whole structures, adaxial view. Figs. 180, 181, development of gynoecial wall. Figs. 182, 183, later stages in gynoecial wall development. Figs. 184, 184a, same section of top of ovary; fig. 184, 'stylar core' region, heavy black line (arrow) indicates adpressed inner margins; fig. 184a, ovary; circle in both diagrams indicates anterior axis of floret. Fig. 185, ovary and anterior lodicules, abaxial view. Line in fig. 184 represents 0.1 mm., lines in figs. 179 and 185 represent 0.5 mm., all other lines represent 0.01 mm.; ag, anterior gynoecial wall; fm, floret apical meristem; p, palea; pg, posterior gynoecial wall; pl, posterior lodicule; sb, style branch; sr, 'stylar core' region.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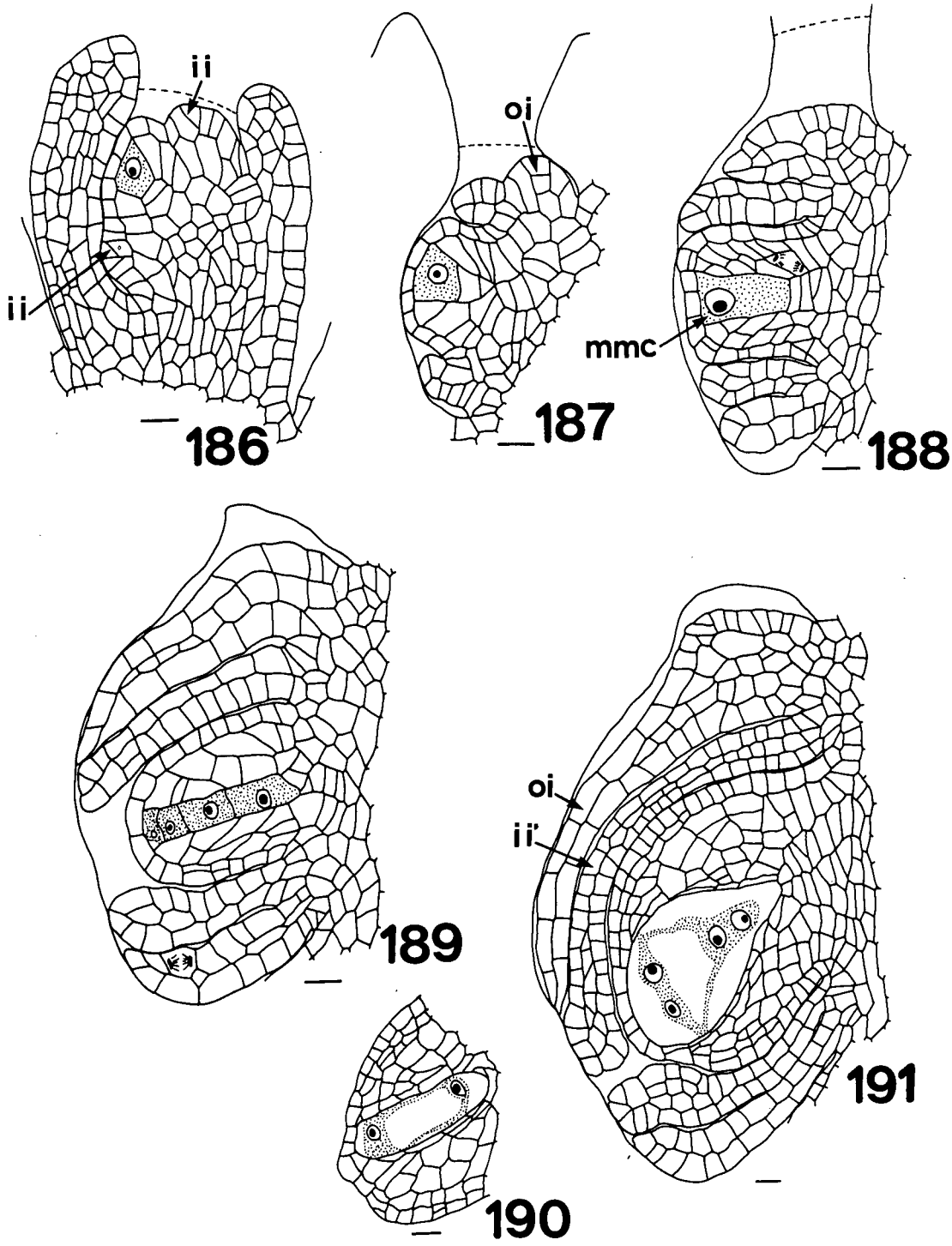
FIGS. 186 - 191. Ovule and embryo sac development in O. micrantha. Fig. 186, inner integument on upper and lower side. Fig. 187, outer integument see on upper side. Fig. 188, megaspore mother cell stage. Fig. 189, megaspore stage. Fig. 190, 2-nucleate embryo sac and surrounding nucellus. Fig. 191, 4-nucleate. All lines represent 0.01 mm.; ii, inner integument; mmc, megaspore mother cell; oi, outer integument.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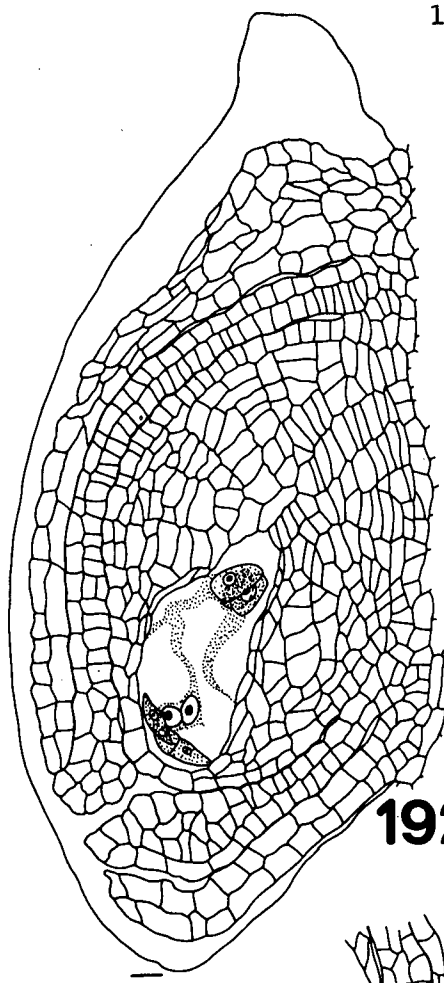
FIGS. 192 - 196. Stages in embryo sac development in O. micrantha. Fig. 192, 8-nucleate stage, before differentiation of egg and synergids. Fig. 193, 8-nucleate stage with differentiated egg and synergids. Fig. 193a, egg from same embryo sac as Fig. 193. Fig. 194, egg apparatus, polar nuclei about to fuse, surrounding nucellus and integuments prior to fertilization. Fig. 195, post-fertilization. Fig. 195a, fertilized (?) egg and synergids; Figs. 195 and 195a are from the same embryo sac. Fig. 196, 2-cell proembryo stage. All lines represent 0.01 mm.; e, egg; es, starch granules in egg; pt, pollen tube; sn, chromatin-like bodies.



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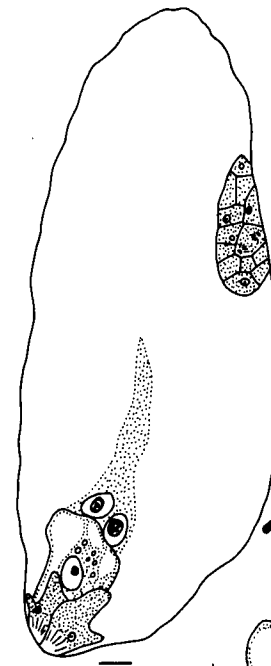

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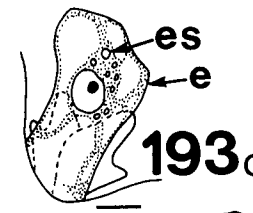

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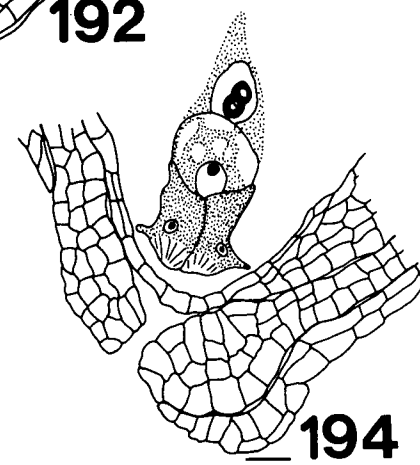

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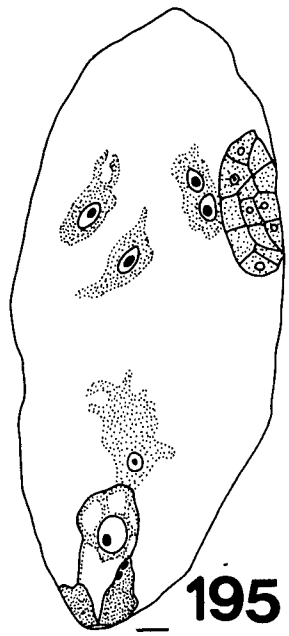

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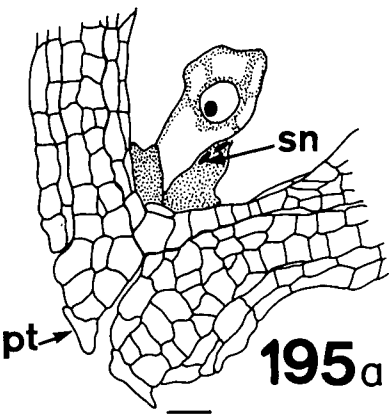

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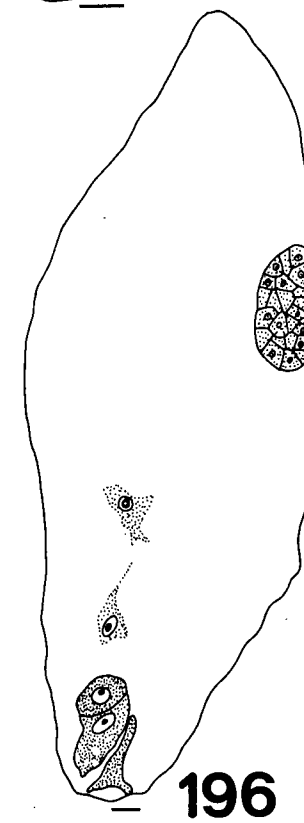

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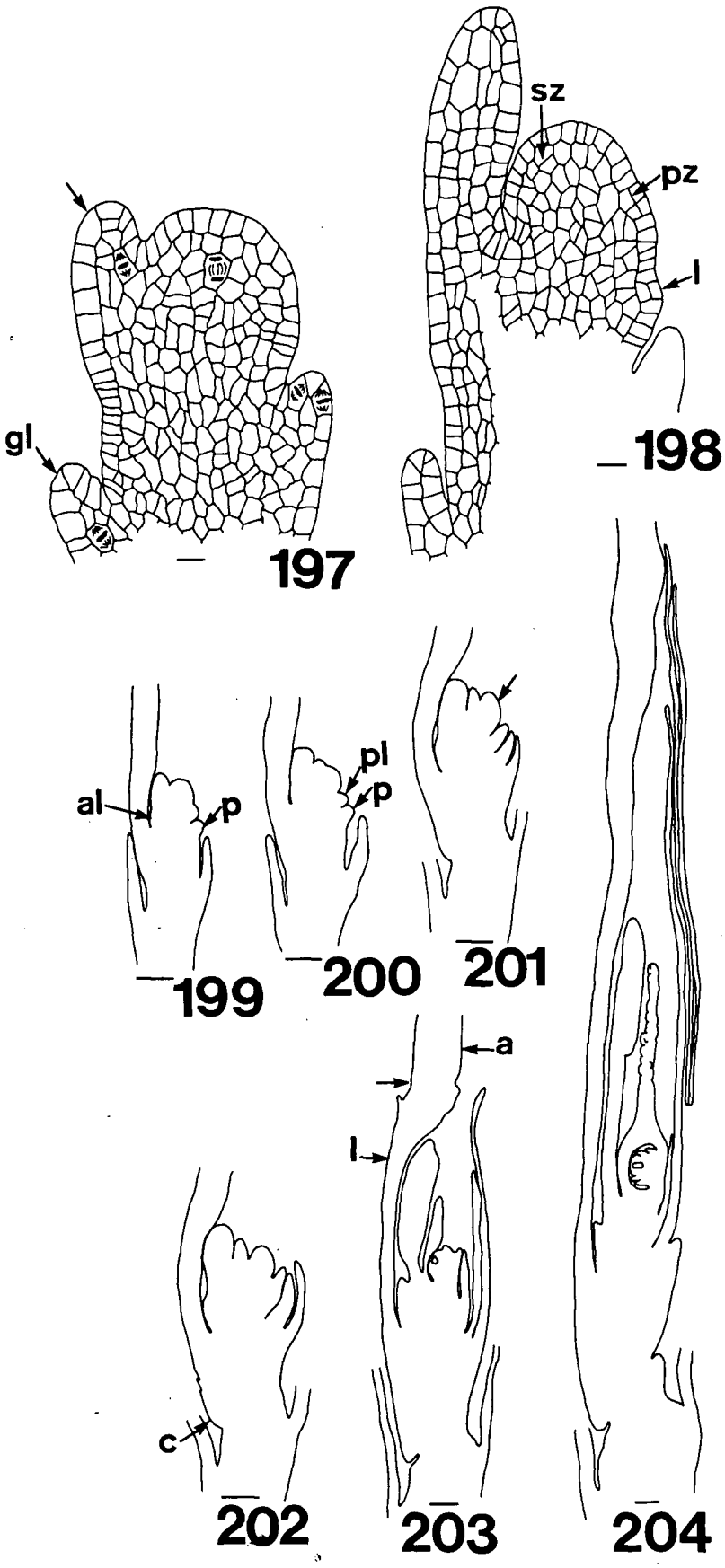
FIGS. 197 - 204. Stages in floret development in O. kingii. Fig. 197, spikelet at early awn-lemma growth (unlabeled arrow). Fig. 198, spikelet at palea and stamen initiation. Figs. 199 - 204, outline diagrams of whole florets; fig. 199, early growth of lodicules; fig. 200, at initiation of anterior gynoecial wall (unlabeled arrow); fig. 201, at initiation of posterior portion of gynoecial wall (unlabeled arrow); fig. 202, prior to integument initiation; fig. 203, at inner integument initiation, unlabeled arrow indicates awn-lemma junction; fig. 204, megaspore mother cell stage. Lines in figs. 197, 198 represent 0.01 mm., all other lines represent 0.05 mm.; a, awn; al, anterior lodicule; c, callus; gl, glume; l, lemma; p, palea; pl, posterior lodicule; pz, site of palea initiation; sz, site of stamen initiation.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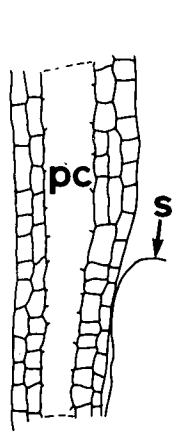
FIGS. 205 - 211. Stages in awn-lemma development in O. kingii. Lines represent 0.01 mm.; unlabeled arrows indicate junction between awn and lemma; pc, procambium; st, stamen; vt, vascular tissue.



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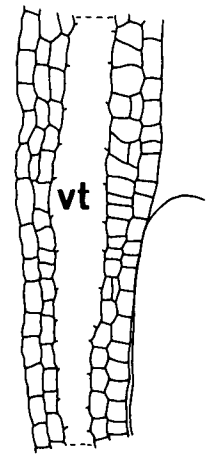

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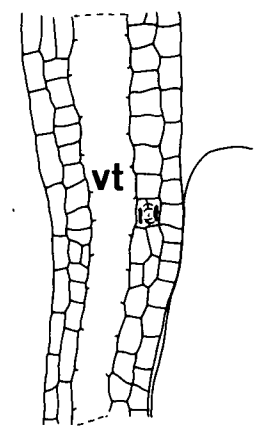

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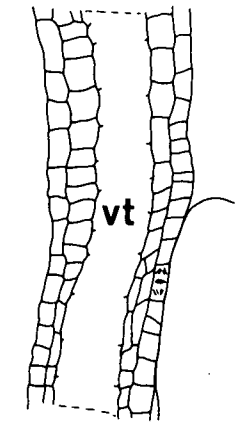

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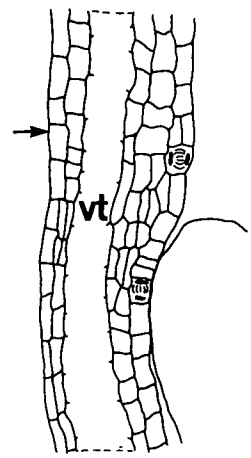

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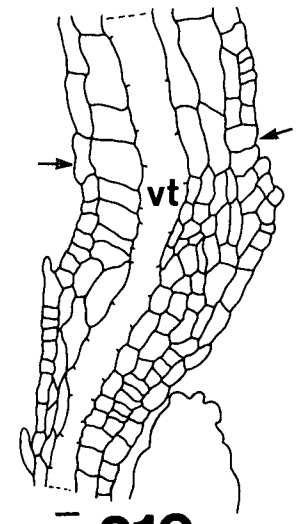

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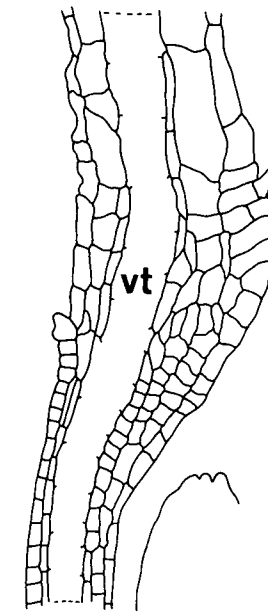
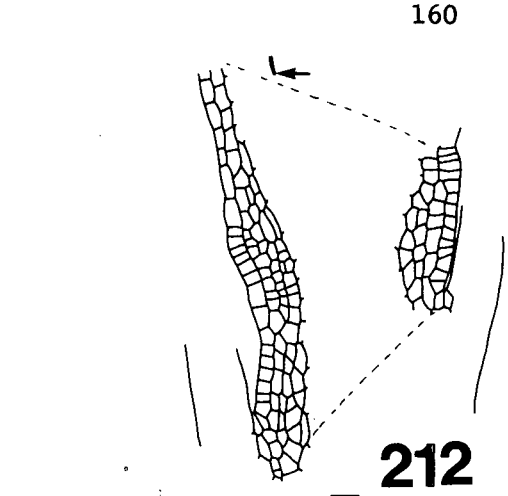


211

FIGS. 212 - 218. Stages in callus development in O. kingii. Figs. 212 - 217 are drawings of calluses; fig. 218 is a drawing of the posterior side of the rachilla immediately below the attachment of the floret. Lines represent 0.01 mm.; unlabeled arrows indicate axils of lemma; t, tabloid cells; vt, vascular tissue.



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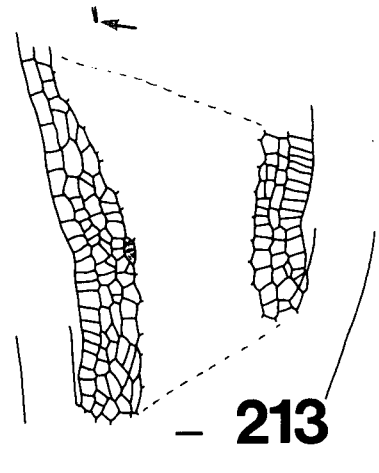

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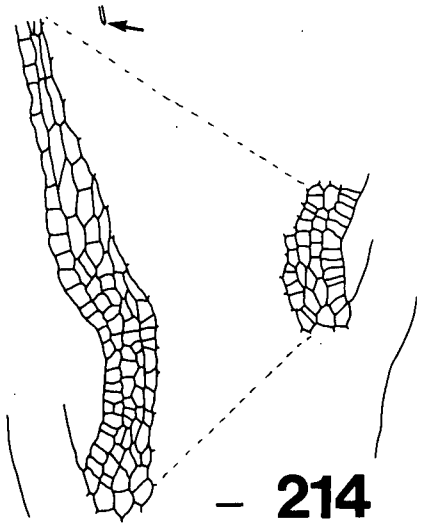

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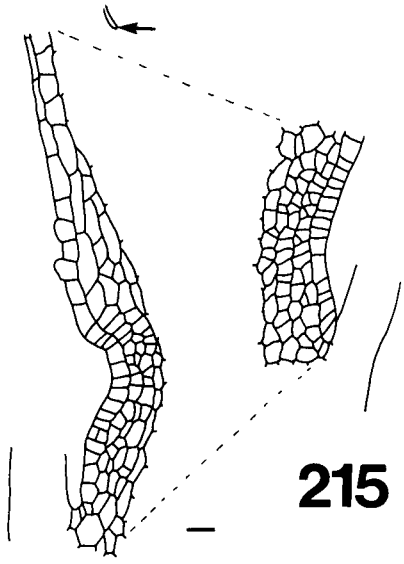

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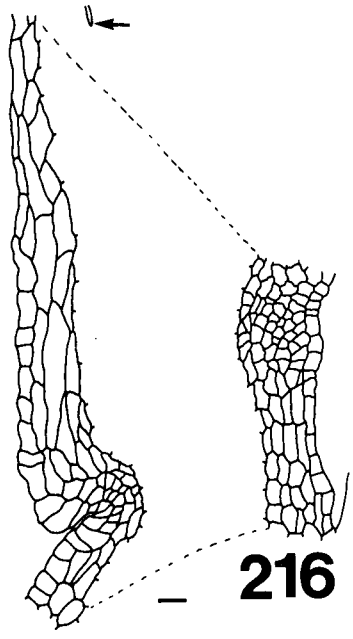

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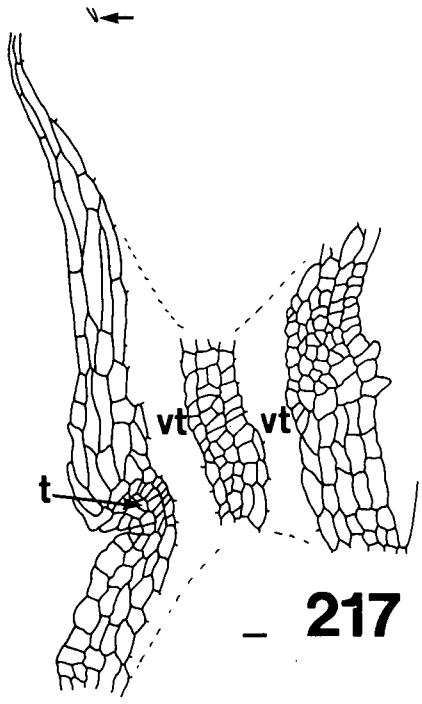

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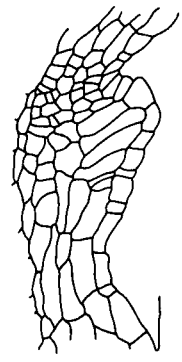
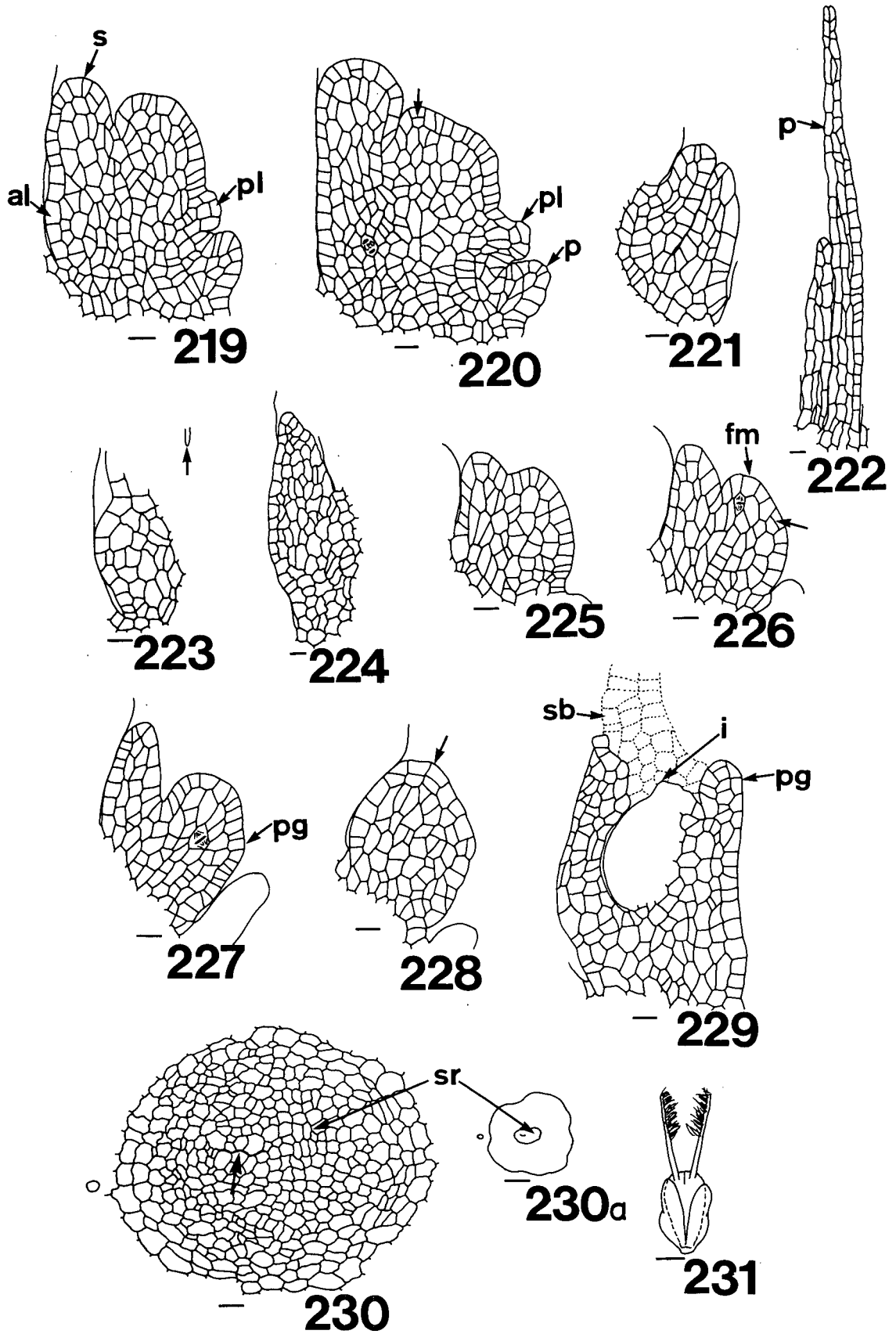


218

FIGS. 219 - 231. Stages in floret development in O. kingii. Fig. 219, young flower and palea. Fig. 220, young flower and palea at initiation of anterior gynoecial wall (unlabeled arrow). Figs. 221, 222, posterior lodicule and palea. Figs. 223, 224, anterior lodicule; unlabeled arrow in fig. 223 indicates axil of anterior stamen. Figs. 227, 228 are adjacent serial sections; fig. 227, growth of posterior gynoecial wall; fig. 228, arrow indicates growth of lateral portion of gynoecial wall into a style branch. Fig. 229, young gynoecium. Figs. 230, 230a show the same cross-section; fig. 230, 'stylar core' region at top of ovary, heavy line (indicated by unmarked arrow) shows 'closure' of ovarian locule; fig. 230a, ovary; circle in both figs. represent anterior axis of floret. Fig. 231, anterior lodicules and ovary, abaxial view. Line in fig. 230a represents 0.1 mm.; in fig. 231, 0.05 mm.; all other lines represent 0.01 mm.; al, anterior lodicule; fm, floret apical meristem; i, integument; p, palea; pg, posterior gynoecial wall; pl, posterior lodicule; s, stamen; sb, style branch; sr, 'stylar core' region.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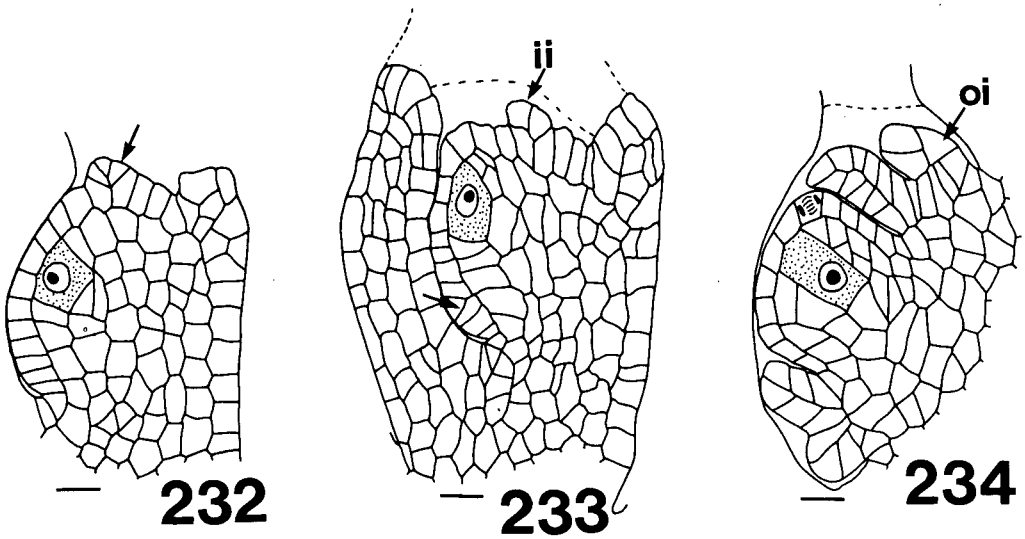
FIGS. 232 - 239. Ovule and early embryo sac development in O. kingii. Fig. 232, inner integument initiation on upper side (unlabeled arrow). Fig 233, inner integument initiation on lower side. Fig. 234, outer integument on both upper and lower sides. Fig. 235, megaspore stage. Fig. 236, functional megaspore, solid black indicates aborted megaspores. Fig. 237, 2-nucleate. Fig. 238, 2-nucleate stage with 3 persistent megaspores, embryo sac outlined with heavy black line. Fig. 239, 4-nucleate. Lines represent 0.01 mm.; ii, inner integument; oi, outer, integument; pm, persistent megaspores.



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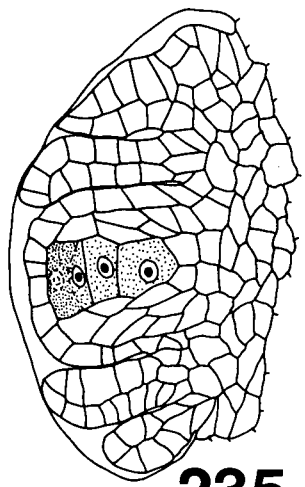

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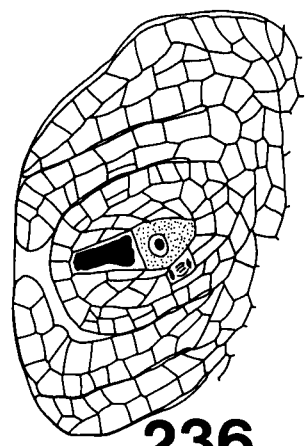

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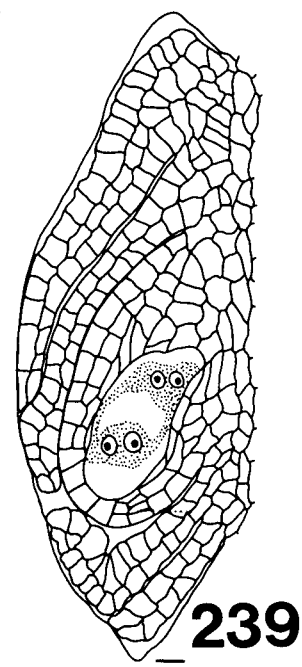

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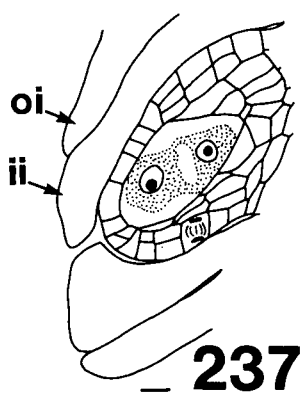

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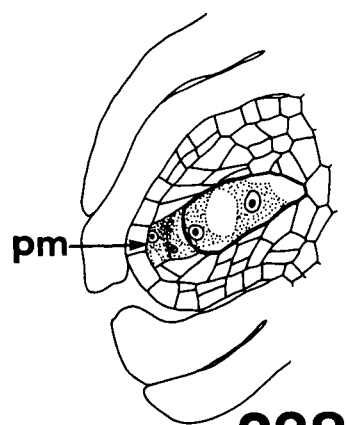

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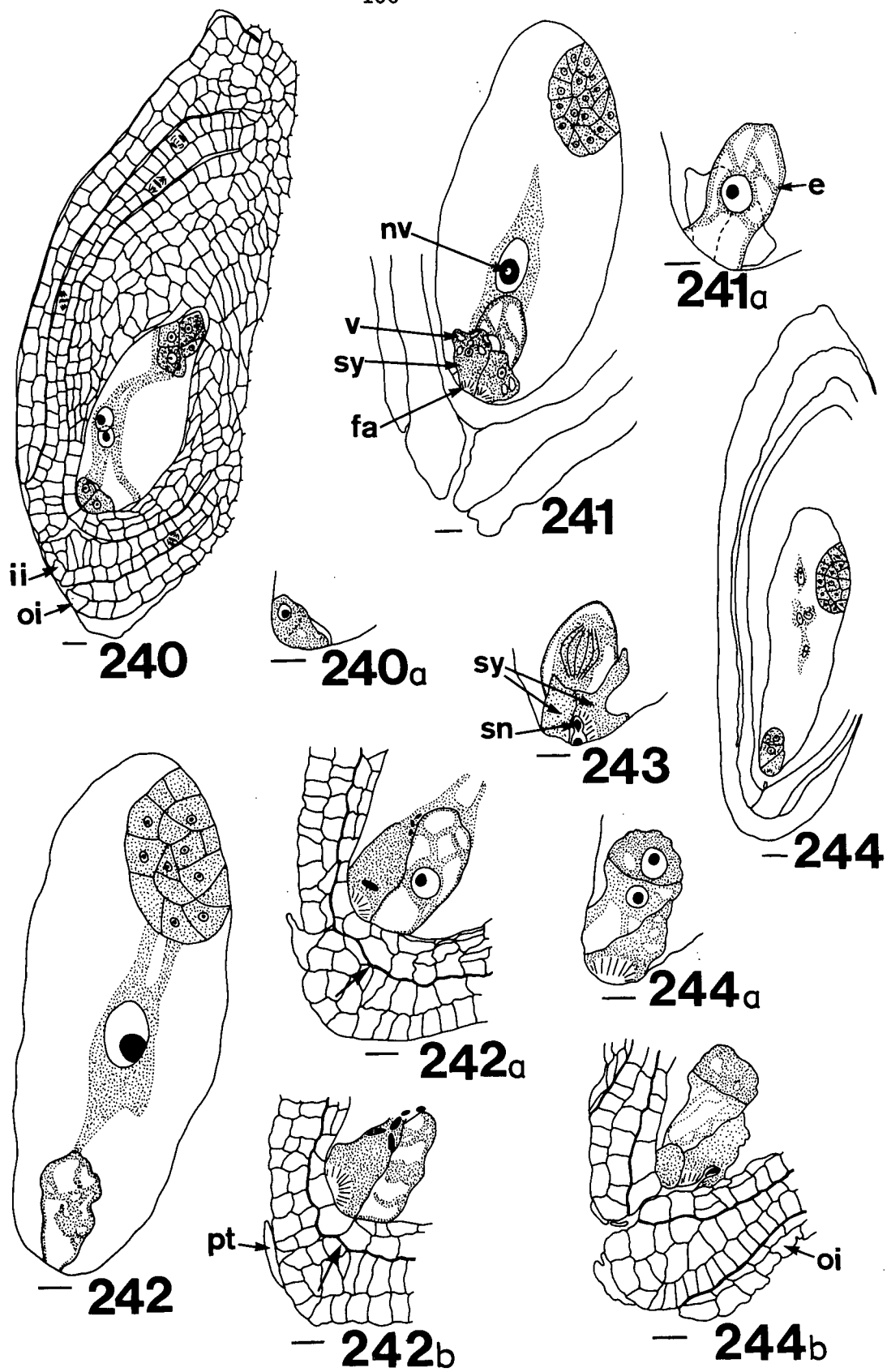
FIGS. 240 - 244. Stages in embryo sac development in O. kingii. Fig. 240, ovule. Fig. 240a, egg, from the same embryo sac shown in fig. 240. Fig. 241, embryo sac with fused polar nuclei. Fig. 241a, egg, from same embryo sac shown in fig. 241. Figs. 242, 242a, 242b, adjacent serial sections 7 μ apart, at fertilization; fig. 242, embryo sac; figs. 242a, 242b, egg, one synergid, and surrounding nucellus and inner integument; heavy line (arrow) indicates boundary between nucellar protoderm and inner integument. Fig. 243, zygotic division and two synergids. Figs. 244, 244a, 244b, adjacent serial sections 7 μ apart at 2-cell proembryo stage. Lines indicate 0.01 mm.; e, egg; fa, filiform apparatus; ii, inner integument; nv, nucleolar vacuole; oi, outer integument; pt, pollen tube; sn, nuclear-like material; sy, synergid; v, vacuole.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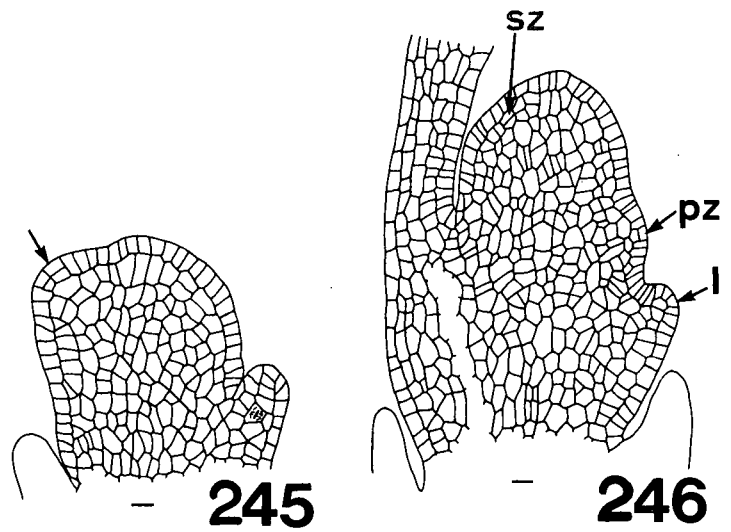
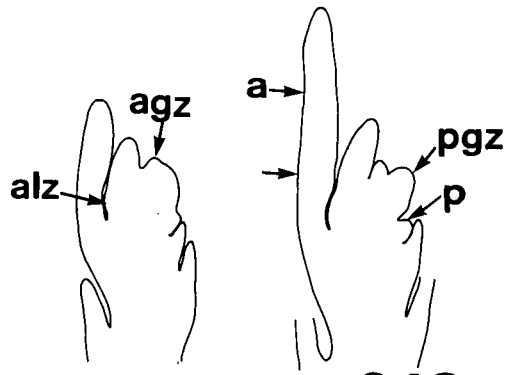
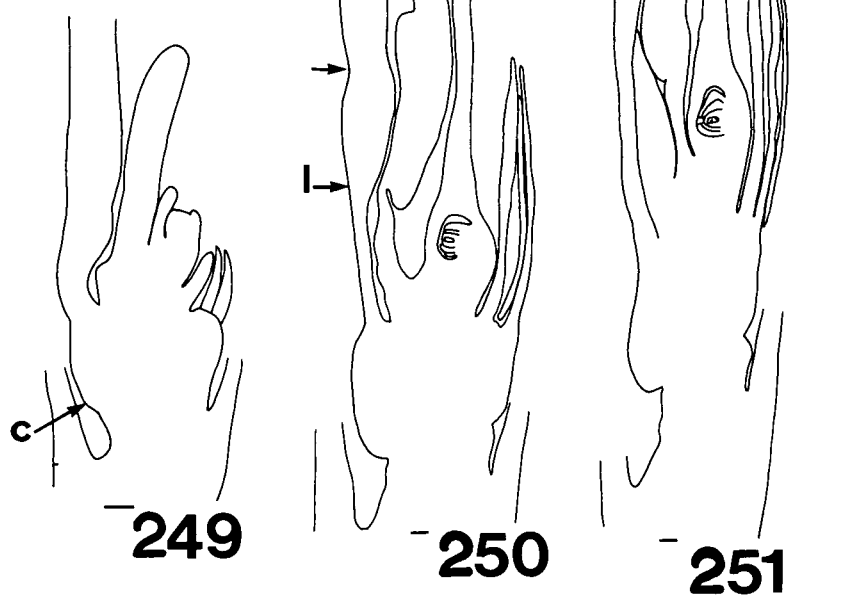
FIGS. 245 - 251. Stages in floret development in O. asperifolia. Fig. 245, awn-lemma initiation (unlabeled arrow). Fig. 246, palea and stamen initiation. Figs. 247 - 251, outline drawings of entire florets; fig. 247, at initiation of anterior gynoecial wall and anterior lodicule; fig. 248, at initiation of posterior gynoecial wall,,unlabeled arrow indicates awn-lemma junction; fig. 249, prior to integument initiation; fig. 250, at megaspore mother cell stage, unlabeled arrow indicates awn-lemma junction; fig. 251, 4-nucleate stage. Lines in figs. 245, 246 represent 0.01 mm., all other lines represent 0.05 mm.; a, awn; agz, initiation site of anterior gynoecial wall; alz, site of anterior lodicule initiation; c, callus; l, lemma; p, palea; pgz, initiation site of posterior gynoecial wall; pz, site of palea initiation; sz, site of stamen initiation.



245 246

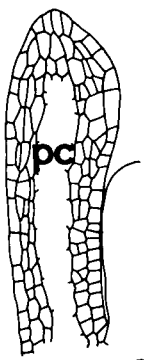


247 248

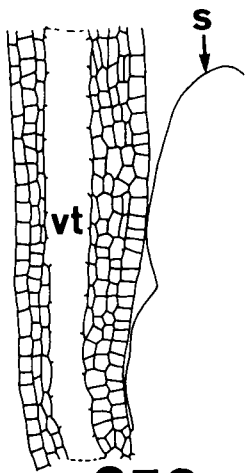


249 250 251

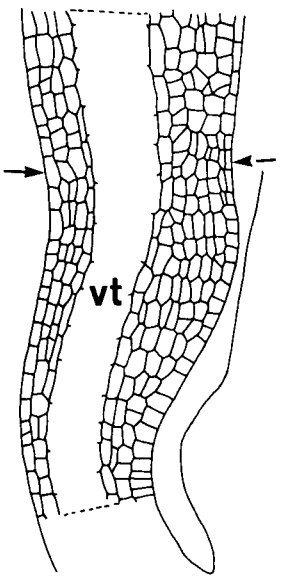
FIGS. 252 - 257. Stages in awn-lemma development in O. asperifolia. Lines represent 0.01 mm.; unlabeled arrows mark junction of awn and lemma; pc, procambium; s, stamen; vt, vascular tissue.



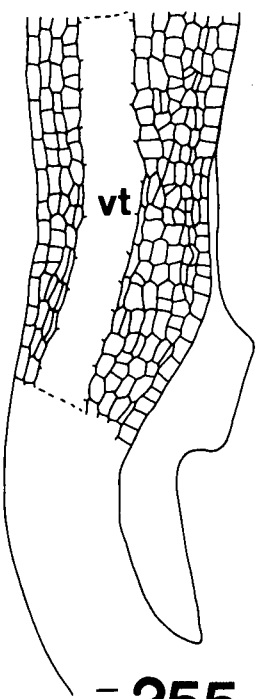
252



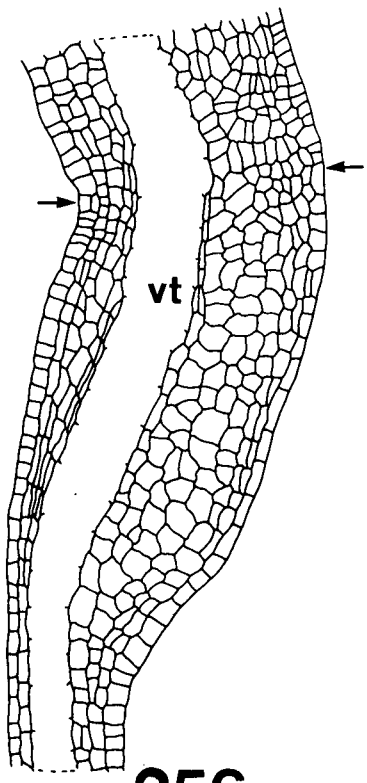
253



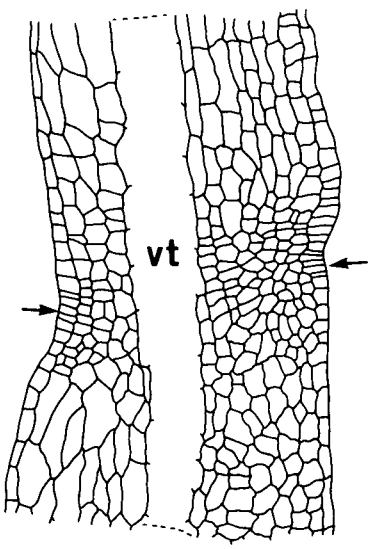
254



255

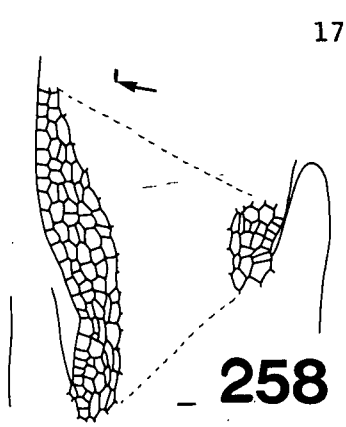


256

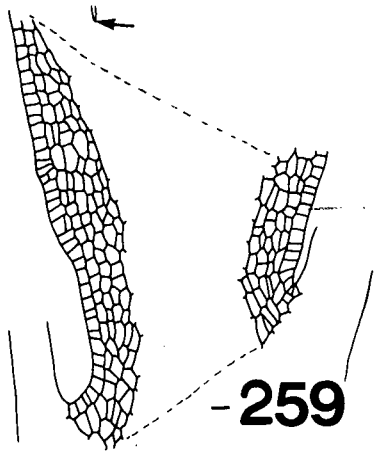


257

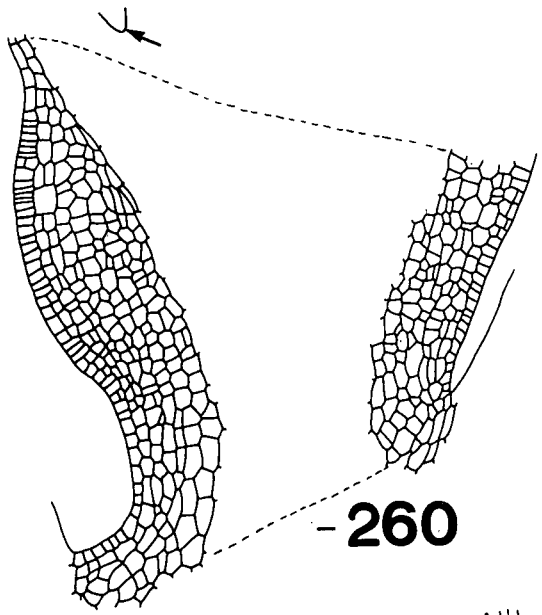
FIGS. 258 - 265. Stages in callus development in O. asperifolia. Figs. 262 and 265 are the posterior sides of the callus shown in figs. 261 and 264 respectively. Lines represent 0.01 mm.; unlabeled arrows denote axils of lemma.



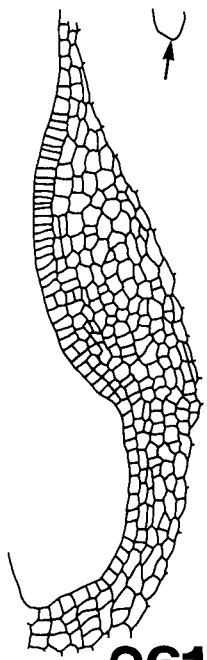
258



259

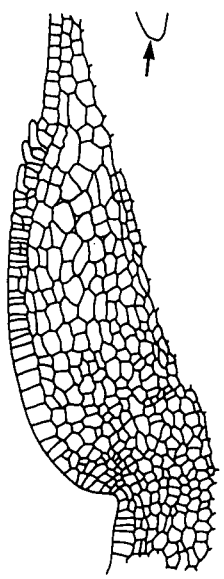


260

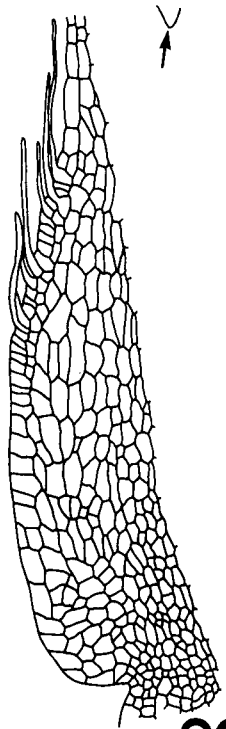


261

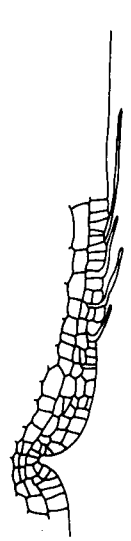
262



263

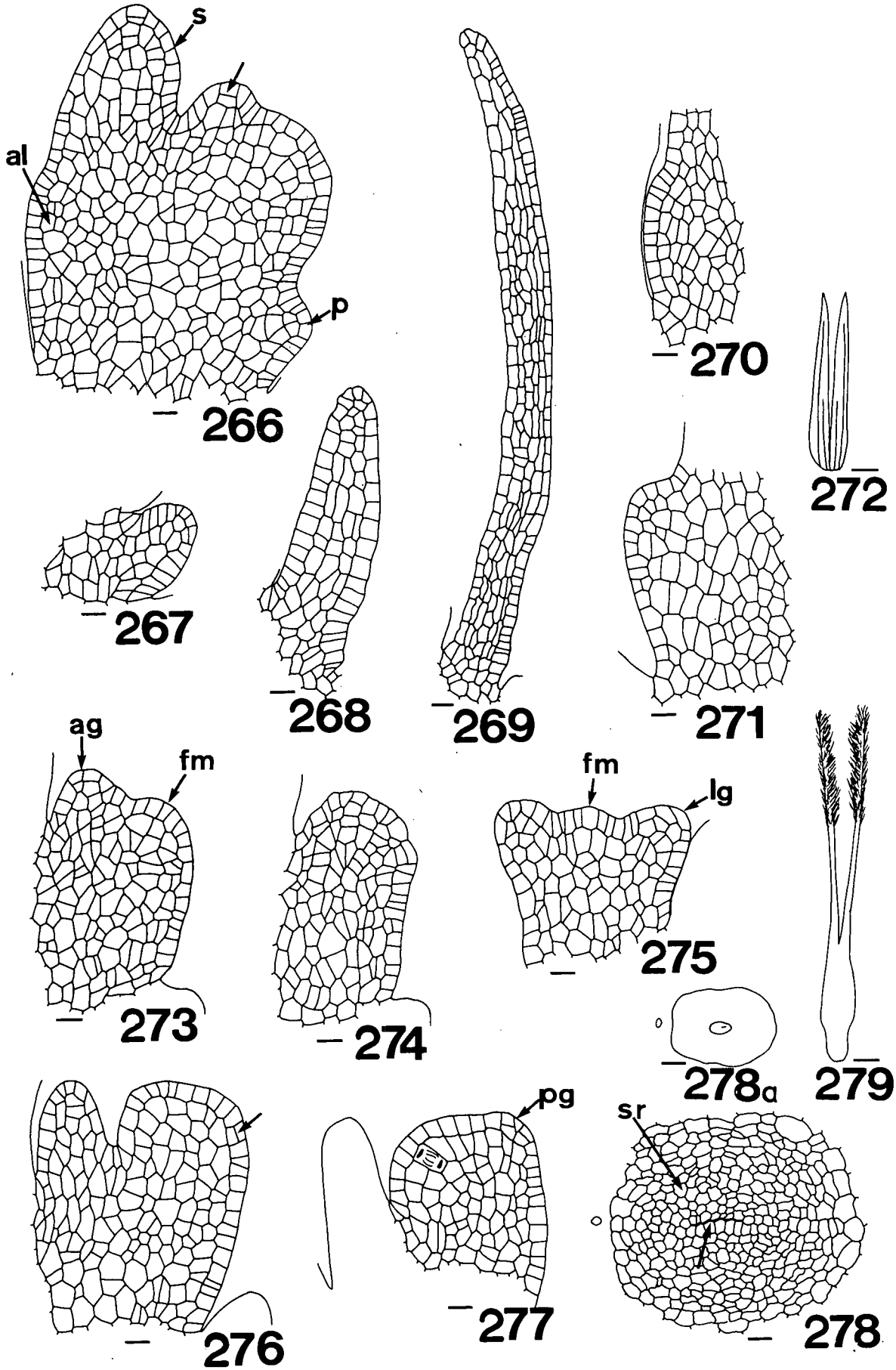


264

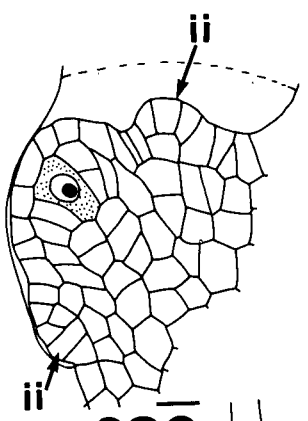


265

FIGS. 266 - 279. Stages in floret development in O. asperifolia. Fig. 266, flower and palea at initiation of anterior gynoecial wall (unlabeled arrow). Figs. 267, 268, 269, palea development. Figs. 270, 271, anterior lodicule development. Fig 272, anterior lodicules, whole structures, abaxial view. Fgis. 273, 274, adjacent serial sections of young gynoecium. Fig. 275, frontal section of young gynoecium. Fig. 276, initiation of posterior gynoecial wall (unlabeled arrow). Fig. 277, growth of posterior gynoecial wall. Figs. 278, 278a, same cross-section of top of ovary; fig. 278, 'stylar core' region, contact of inner margins indicated by heavy line (arrow); fig. 278a, ovary; circle in both figs. indicates anterior axis of floret. Fig. 279, ovary. Line fig. 278a represents 0.1 mm., lines in figs. 272, 279 represent 0.5 mm., all other lines represent 0.01 mm.; ag, anterior gynoecial wall; al, anterior lodicule; fm, floral apex; lg, lateral gynoecial wall; p, palea; pg, posterior gynoecial wall; s, stamen; sr, 'stylar core' region.

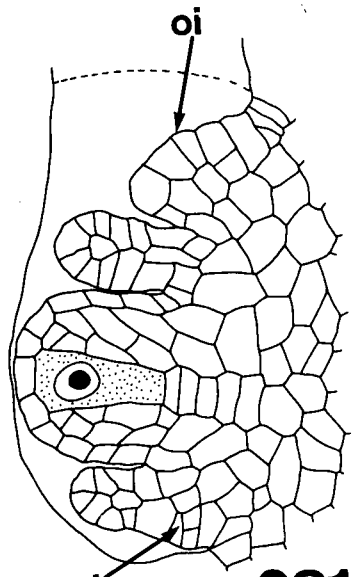

s
al
p
266
267
268
269
270
271
272
ag
fm
273
274
fm
lg
275
278a
279
276
pg
277
sr
278

FIGS. 280 - 284. Ovule and early embryo sac development in O. asperifolia. Figs. 280, 280a are of the same section; fig. 280, ovule; fig. 280a, gynoecium. Fig. 281, megaspore mother cell stage. Fig. 282, megaspore stage. Fig. 283, functional megaspore; solid black indicates aborted megaspores. Fig 284, 2-nucleate stage. Line in fig. 280a represents 0.05 mm., all other lines represent 0.01 mm.; b_1, first bump; b_2, second bump; ii, inner integument; oi, outer integument.

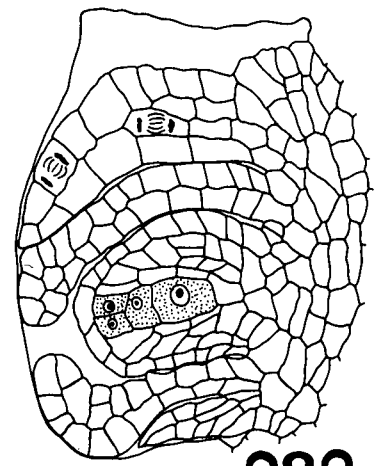


280

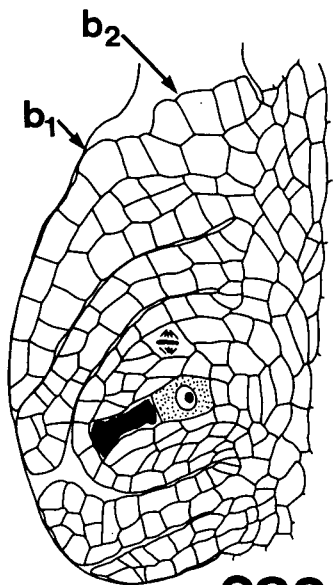
280a



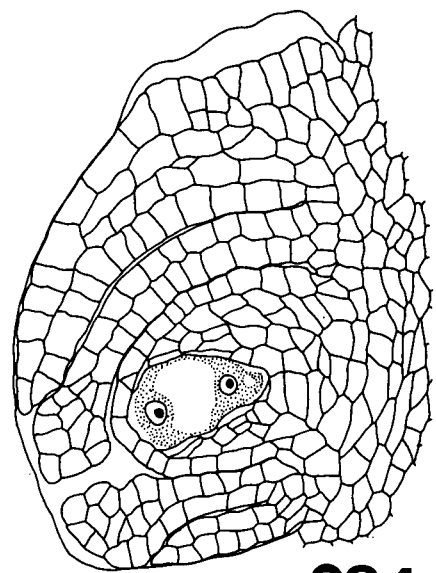
281



282

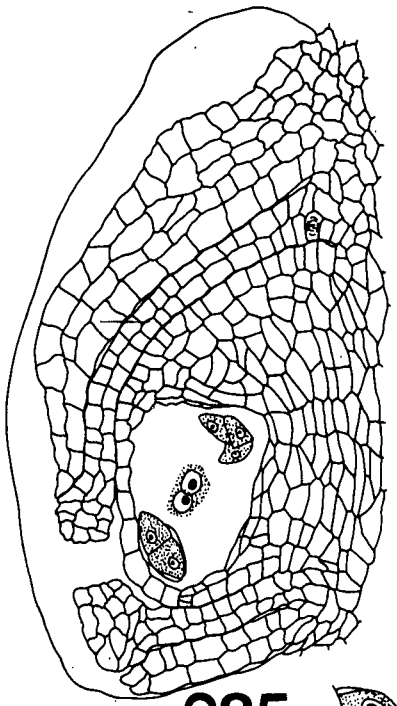


283

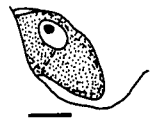


284

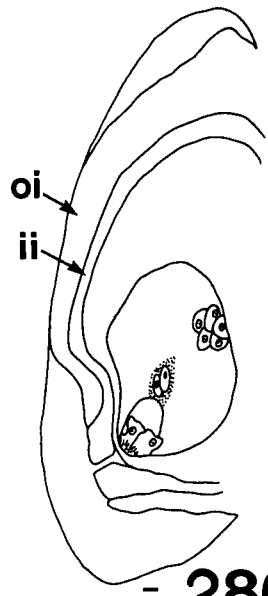
FIGS. 285 - 288. Stages in embryo sac development and fertilization in O. asperiflolia. Fig. 285, 8-nucleate stage. Fig. 285a, egg, from the same embryo sac as fig. 285. Figs. 286, 286a, 286b, 8-nucleate stage, prior to fertilization, all from the same embryo sac; fig. 286, ovule; fig. 286a, embryo sac; fig. 286b, egg. Fig. 287, egg at fertilization. Figs. 288, 288a, 288b, 2-cell proembryo stage, from the same embryo sac; fig. 288, ovule; figs. 288a, 288b, 2-cell proembryo, synergid and surrounding nucellus and integuments. Line in fig. 288 represents 0.05 mm., all other lines represent 0.01 mm.; an, antipodals; e, egg; es, starch granules in egg; h, homogenous dense staining material; ii, inner integument; oi, outer integument; pe, proembryo; pt, pollen tube; sn, nuclear-like material; sy, synergid.



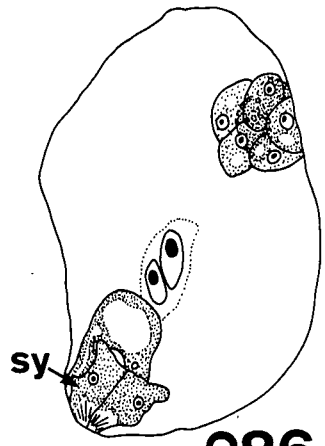
285



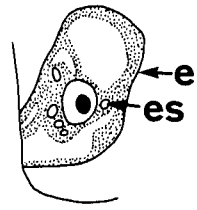
285a



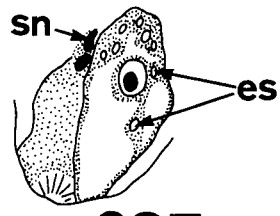
286



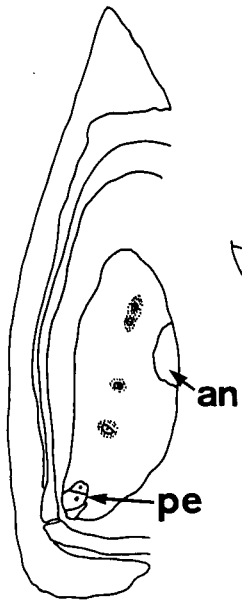
286a



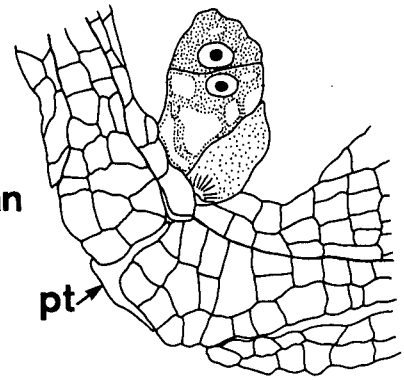
286b



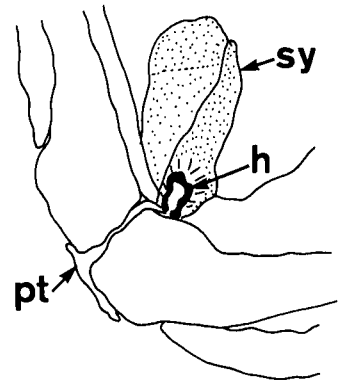
287



288



288a

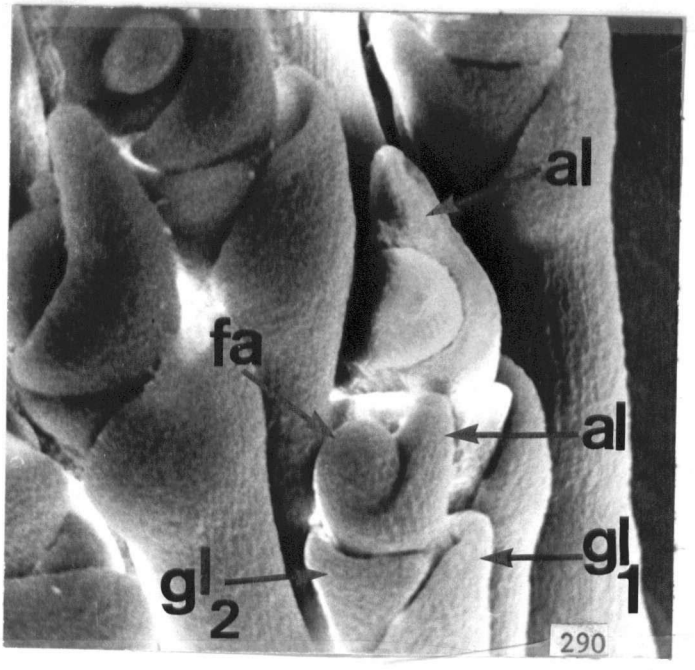


288b

FIG. 290. Scanning electronmicrograph of young florets of Oryzopsis virescens, during early growth of the awn-lemma. 260 x.

FIG. 291. Scanning electronmicrograph of young florets of O. virescens, prior to initiation of the gynoecium. 125 x.

Abbreviations for both figures: a, awn; al, awn-lemma; fa, floret apical meristem; gl_1, first glume; gl_2, second glume; l, lemma.


al
fa
al
gl 1
gl 2
290

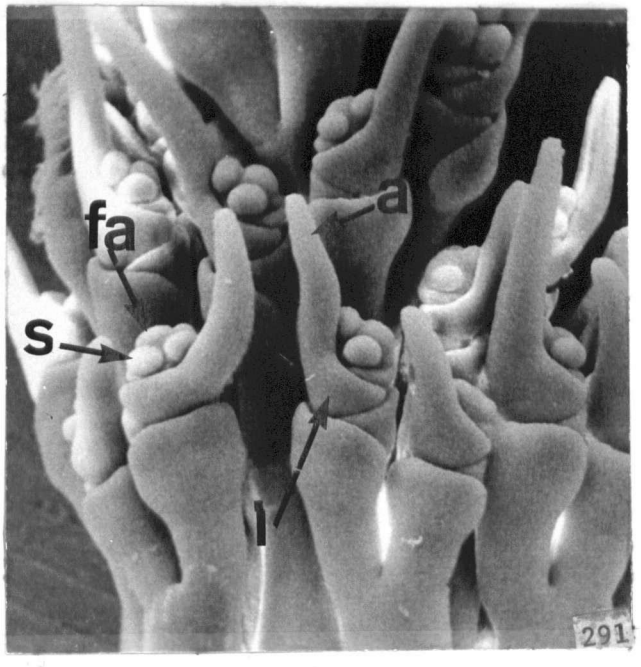

a
fa
S
l
291

FIG. 292. Scanning electronmicrograph of young florets of Oryzopsis virescens, during growth of the anterior portion of the gynoecial wall. 260 x.

Abbreviations: a, awn; ag, anterior portion of gynoecial wall; as, anterior stamen; l, lemma; p, palea; pl, posterior lodicule.

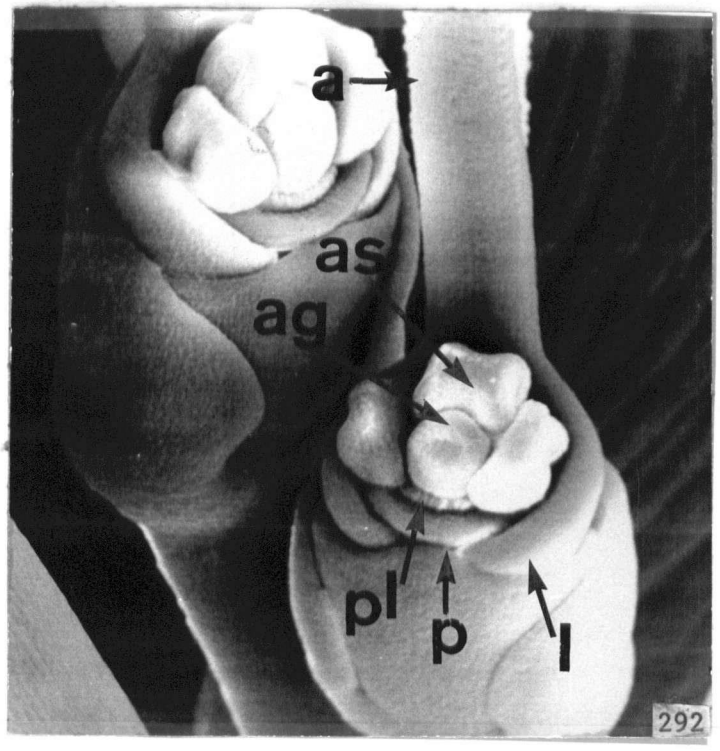

a
as
ag
pl
p
l
292

FIG. 293. Sagittal section of part of a young floret of Oryzopsis virescens, during growth of the anterior portion of the gynoecial wall. 440 x.

Abbreviations: ag, anterior portion of gynoecial wall; fa, floret apex; p, palea; pl, posterior lodicule.

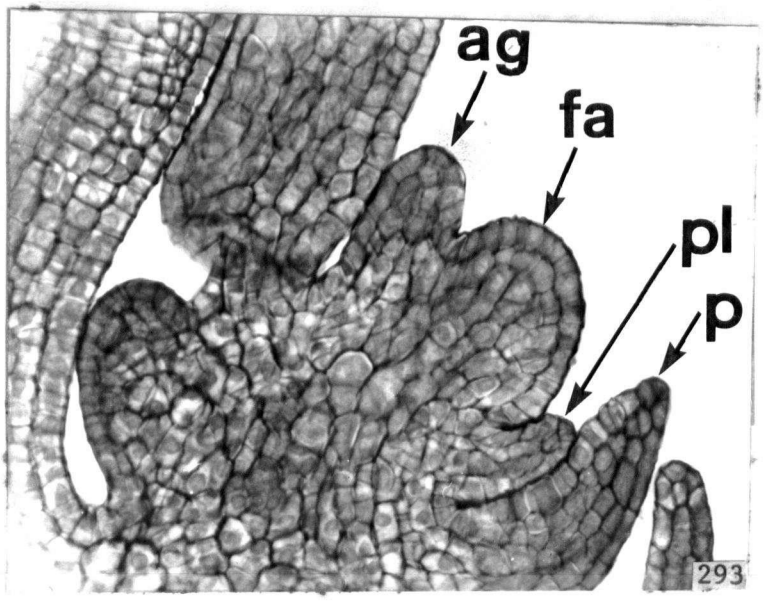
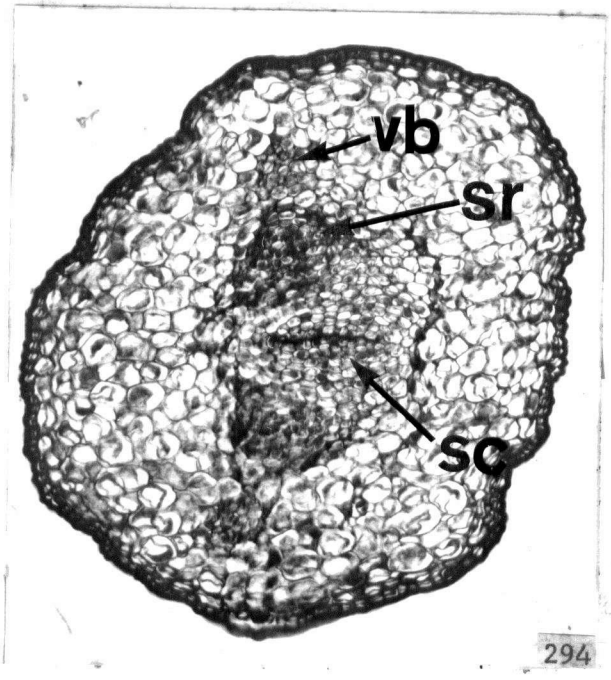
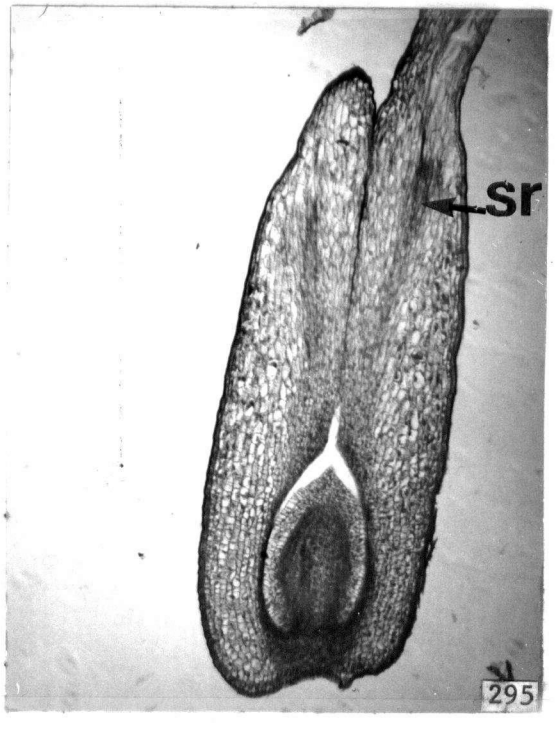

ag
fa
pl
p
293

FIG. 294. Transverse section at top of ovary in Oryzopsis hymenoides at anthesis. 225 x.

FIG. 295. Frontal longitudinal section of ovary of O. hymenoides at anthesis. 65 x.

Abbreviations for both figures: sc, 'stylar core' region; sr, stigmatoid tissue; vb, vascular bundle.


vb
sr
sc
294


sr
295