THE FIBRINOID CAPSULE OF THE RAT PLACENTA AND THE DISAPPEARANCE OF THE DECIDUA

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From the time of Duval's comprehensive work (1891) there have been several morphological investigations of the rat placenta. In some of these the descriptions have not been complete, nor have the interpretations placed upon the changes in the decidual cells always been justified. A more detailed account of some features, amplified where possible by histochemical findings, may help to clarify some of the problems involved.

MATERIAL AND METHOD

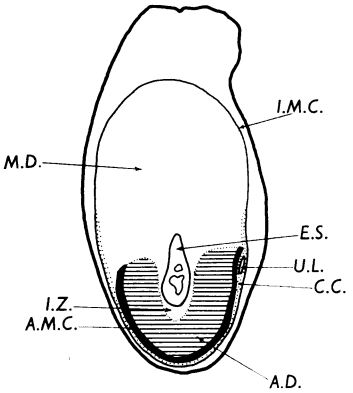
The material consisted of rat placentae of between 9 and 19 days, fixed in neutral formalin or acetic alcohol formalin for 24 hr. Series of sections, 5 μ thick, throughout the entire placental region were stained by the methods described in previous publications (Bulmer & Dickson, 1960; Dickson & Bulmer, 1960). In addition, sections were stained with Mallory's phosphotungstic acid-haematoxylin (Lillie, 1954) after mordanting with mercuric chloride (Peers, 1941), by the methyl green-pyronin technique (Pearse, 1960), by methyl green alone with the solution used by Alfert (1952), by the fast green method for nuclear histone (Alfert & Geschwind, 1953), by the chromalum-gallocyanin method (Pearse, 1960), with the azur B solution used by Flax & Himes (1952), by the acid solochrome cyanin technique (Pearse, 1957) and by the methods for bound lipid described by Berenbaum (1958). Tryptophan was demonstrated by the DMAB-nitrite method of Adams (1957) and reticulin fibres were impregnated by the techniques of Long (1948) and Gomori (Lillie, 1954).

OBSERVATIONS

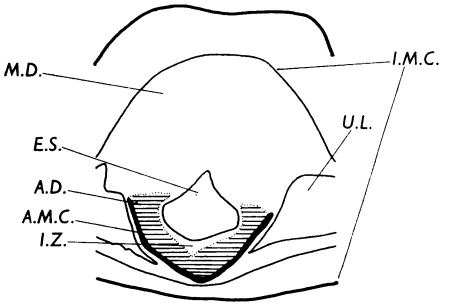
The antimesometrial decidua

At the 9-day stage the antimesometrial decidua is clearly distinguished by the cytoplasmic basiphilia of almost all its cells, and is already less extensive than the more recently arisen mesometrial decidua (Text-fig. 1(*a*)). It bulges into the lumen of the proximal and distal inter-implantation regions and completely occludes the lumen in the implantation region.

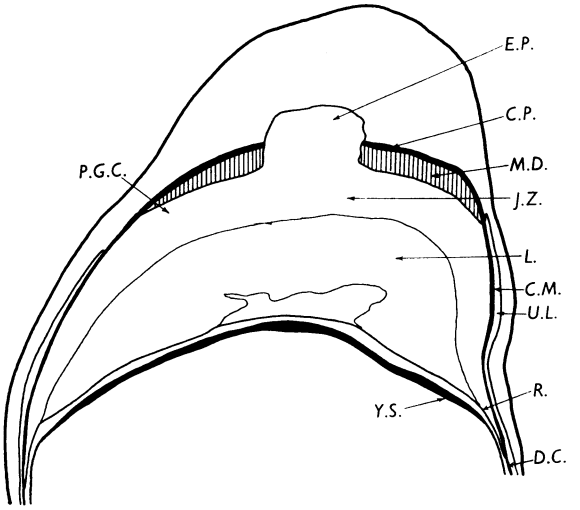
Text-fig. 1. Diagrammatic sections of 9- to 19-day rat placentae. (*a*), (*c*), (*d*) and (*e*) are at right angles to the long axis of the uterus, while (*b*) is parallel to the long axis. *I.M.C.* inner muscle coat, *M.D.* mesometrial decidua, *E.S.* embryonic sac, *A.M.C.* antimesometrial capsule, *A.D.* antimesometrial decidua, *I.Z.* implantation zone, *U.L.* uterine lumen, *C.C.* cellular condensation in the plane of the uterine lumen, *M.C.* mesometrial capsule, *J.Z.* junctional zone, *L.* labyrinth, *R.* Reichert's membrane, *Y.S.* yolk sac, *C.Z.* central zone, *C.P.* paracentral capsule, *C.M.* marginal capsule, *P.G.C.* placental giant cells, *D.C.* decidua capsularis in apposition with Reichert's membrane, *E.P.* endovascular plasmodium, *R.D.C.* remnant of decidua capsularis at placental margin.



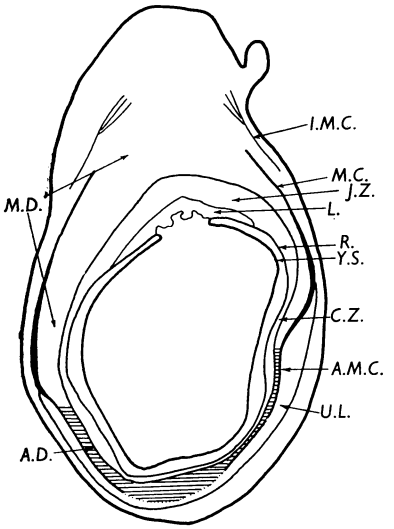
(*a*) 9-day placenta



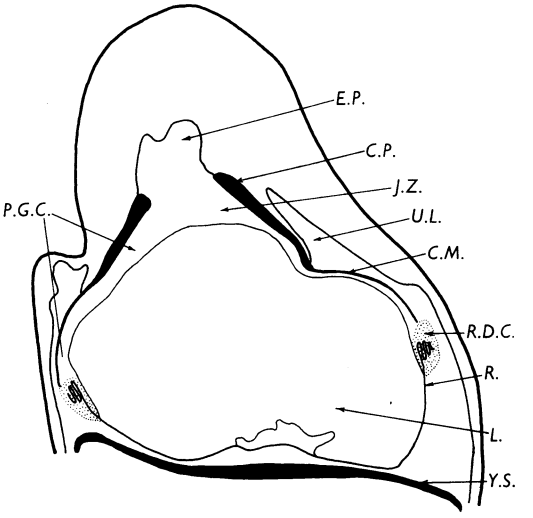
(*b*) 10-day placenta



(*d*) 15-day placenta



(*c*) 12-day placenta



(*e*) 19-day placenta

For legend see foot of facing page.

Various cell types may be distinguished. In the implantation zone (Krebheil, 1937), around the antimesometrial pole of the embryonic sac and extending mesometrially as a thin layer on either side of the sac, degenerating decidual cells lie in a mesh of vascular spaces with the foetal giant cells of the central zone (Everett, 1935) or Durchdringungszone (Grosser, 1927) immediately internal to them. The decidual nuclei here are of irregular shape, some small with their chromatin clumped in relatively large granules and some fragmented. In sections stained with a basic thiazine dye this zone is clearly distinguished by the absence of cytoplasmic basiphilia (Pl. 1, fig. 1).

Elsewhere the antimesometrial decidua is formed principally of large cells, often binucleate and with the nuclei large and open-faced. These cells are similar to those which occur in the corresponding situation in deciduomata, and which Sachs & Shelesnyak (1955) considered to be polyploid. The cytoplasm is markedly basiphilic, more so in some cells than in others and generally more in the inner layers, just outside the implantation zone, than in the outer layers. Mitoses are restricted to the more peripheral layers. Among the decidual cells is an extensive network of small vessels, lined by large endothelial cells with densely staining cytoplasm and compact nuclei. Limiting the antimesometrial decidua externally is the layer of condensed tissue which may be termed the capsule (Bulmer & Dickson, 1960). This stains a deep brown colour in trichrome preparations and with phosphotungstic acid-haematoxylin there are irregular patches of deep-blue staining. It contains numerous nuclei, smaller than those of the decidual cells and larger than those of the surrounding stroma, but along its inner margin nuclei can be identified which are intermediate in appearance between the decidual and capsular nuclei (Pl. 1, fig. 2). This antimesometrial capsule was noted by Grosser (1927) as a layer of degenerating connecting tissue and by Holmes & Davies (1948) as a layer of flattened decidual cells. A similar condensed band was observed in deciduomata by Velardo, Dawson, Olsen & Hisaw (1953). Immediately external to the capsule is a fairly dense condensation of stromal cells which indicates the plane of, and is in part split by, the new uterine lumen (Text-fig. 1(*a*)). Outside this is the inner muscle coat of the uterus.

At the 10-day stage the antimesometrial decidua still forms a thick layer (Text-fig. 1(*b*)). The capsule lies inside the stromal zone of the uterine lumen and now stains intensely with the picric acid differentiator in trichrome preparations. Many of the antimesometrial decidual cells have a yellow-staining cytoplasm, others stain a deep brown colour, while there is a discontinuous layer of large cells, just internal to the capsule, with cytoplasm which is unstained in trichrome preparations (Pl. 1, fig. 3). It is notable that these latter cells are the only antimesometrial decidual cells to show mitotic figures at this stage.

Despite the absence of basic staining with haematoxylin the capsular matrix shows a marked basiphilia with azur A and pyronin (Pl. 1, fig. 4). This is abolished by previous extraction for 15 min. at 90° C. with 5% trichloracetic acid, but unlike the cytoplasmic basiphilia of the antimesometrial decidual cells is not markedly reduced by a prior digestion with ribonuclease (Pl. 1, fig. 5). While the capsule is moderately PAS-positive, stains faintly with Gomori's aldehyde fuchsin and red in acid solochrome cyanin preparations, it stains orthochromatically with azur A and

does not stain with alcian blue. It does, however, stain metachromatically with the azur B solution of Flax & Himes (1952) and binds chromalum-gallocyanin at pH 1·64. It is possible that the basiphilia of the capsule, therefore, is due to the presence of ribonucleic acid in a form more resistant to nuclease digestion after formalin fixation than the ribonucleic acid of the decidual cells. The capsule stains strongly with the coupled tetrazonium technique, moderately with the methods for bound lipid described by Berenbaum (1958) and shows a strong reaction with the DMAB-nitrite method, of similar intensity to that of fibrin. With phosphotungstic acid-haematoxylin it gives a deep blue colour, and the cytoplasm of many of the anti-mesometrial decidual cells now reacts similarly with this technique. Silver impregnation methods for reticulin demonstrate sparse argyrophil fibres in the capsule and outline the walls of the numerous small vessels within it.

The capsular nuclei stain only very faintly with haematoxylin in trichrome preparations, often with a yellowish tinge, and show a reddish colour with acid solochrome cyanin. Many are of irregular shape and some appear fragmented. They are strongly basiphilic with azur A, Feulgen-positive and methyl green-positive and stain well with the fast green method for nuclear histone (Pl. 1, fig. 6). While the nuclei of the internal layers of the antimesometrial decidua, including those of the implantation zone, stain strongly with the fast green method, staining is much fainter in the outer layers, particularly in the nuclei of the large cells which form a discontinuous layer just within the capsule.

At the 12-day stage most of the antimesometrial decidua forms a thin decidua capsularis, though the penetration of the new uterine lumen is not yet complete (Text-fig. 1(*c*)). An outer condensed layer, with staining reactions similar to those of the capsule at the 10-day stage, is present laterally and now extends mesometrially outside the marginal portion of the mesometrial decidua. It is difficult to define precisely where the junction lies between antimesometrial decidua and mesometrial decidua, but there is no doubt that the capsule and, to a lesser extent, the uterine lumen, have now come into relation with the periphery of the mesometrial decidua. The mesometrial decidua, therefore, as well as the antimesometrial decidua, contributes to the decidua capsularis.

Around the antimesometrial pole the decidua capsularis consists of up to about a dozen layers of degenerating cells (Pl. 2, fig. 7). The nuclei are irregularly shaped or fragmented, but stain strongly with the fast green method and are Feulgen- and methyl green-positive. They are contained in a matrix which gives a moderate diastase-fast PAS reaction and, in contrast to the earlier stages, shows occasional granules of glycogen. Phosphotungstic acid-haematoxylin produces an orange colour, with patches of intense blue staining, and there are extensive accumulations of basiphilic material which can be removed by ribonuclease digestion. In the regions around the antimesometrial pole which are not penetrated by the uterine lumen a thin capsular band separates the degenerating decidua from the stromal zone. Where the uterine lumen is present, however, the capsule is usually deficient and the degenerating tissue is exposed to the lumen. Laterally, where the capsule forms a well-defined band, a few layers of degenerating cells may lie inside it, but the whole decidua capsularis is very much thinner here than in the region of the antimesometrial pole, and sometimes consists of the capsule alone. Near the margin of the

chorio-allantoic placenta the degenerating cells are replaced by healthy cells, similar in structure to those of the decidua basalis. Internally, the decidua capsularis lies adjacent to the rich vascular bed of the central zone. Many of the foetal giant cells of this zone are now beginning to degenerate, with flattening, elongation and vacuolation of the nuclei—a process similar to that occurring at a rather later stage in the placental giant cells (Dickson & Bulmer, 1960). There are accumulations of leucocytes in the central zone, in the decidua capsularis and in the uterine lumen.

At the 13-day stage degeneration of the antimesometrial decidua is almost complete and the capsule is mainly restricted to the mesometrial decidua. Where it is related to the uterine lumen its outer surface is often covered with a low cubical epithelium (Pl. 2, fig. 8). Antimesometrially, between Reichert's membrane and the uterine epithelium and among the maternal vessels of the central zone, are a few layers of giant cells, most of them degenerate, with a few small nuclear remnants of decidual cells and leucocytes external to them.

At the 15-day stage (Text-fig. 1(*d*)), only a very thin layer separates Reichert's membrane from the uterine epithelium antimesometrially. Nuclear remnants of decidual cells, giant cells or leucocytes are very rare, except near the margin of the chorio-allantoic placenta (*v. infra*).

The mesometrial capsule

It has been mentioned that at the 12-day stage the capsular layer of the antimesometrial decidua extends mesometrially. It forms a thin band outside the marginal part of the decidua basalis (Pl. 2, fig. 9), and immediately external to it there is a thin layer of stroma, containing occasional metrial gland cells, which separates it from the inner muscle coat of the uterus. The capsule is deficient over a large area across the base of the mesometrium (Text-fig. 1(*c*)), where the decidua is separated from the mesometrial triangle only by the fibres of the inner muscle coat, intermingled with numerous metrial gland cells. The mesometrial capsule resembles the antimesometrial capsule in its appearance and staining reactions. It binds the picric acid of trichrome preparations, and the intense orthochromatic basiphilia with azur A is resistant to ribonuclease digestion. It contains small, dense nuclei which stain strongly with the Feulgen, methyl green and fast green methods, but faintly and with a yellowish tinge in trichrome preparations. The capsular matrix stains intensely blue with phosphotungstic acid-haematoxylin, there is faint staining with aldehyde fuchsin and alcian blue, and a strong reaction with the DMAB-nitrite technique.

Text-fig. 1(*d*) will serve to illustrate the main features of the 14- and 15-day stages. The capsule is a well-marked structure, considerably thicker than at 12 days. It extends further across the base of the mesometrium, but does not form a complete investment for the decidua basalis. The aperture remaining at the mesometrial pole is traversed by the endovascular plasmodium lining the maternal arteries of the placenta (Dickson & Bulmer, 1961). At the margin of the chorio-allantoic placenta the capsule is continuous with the decidua capsularis, which here consists of an amorphous mass with a few small nuclear remnants lying outside an interrupted

layer of central zone giant cells, many of which are degenerating. This mass is continuous with the very narrow remnant of the antimesometrial part of the decidua capsularis, which has been noted above.

The uterine lumen extends mesometrially around the marginal part of the chorio-allantoic placenta, and here the 'marginal' part of the capsule forms a thin layer internal to the lumen (Pl. 2, fig. 10). In some regions a low cubical or squamous epithelium clothes its outer surface (Duval, 1891). Immediately adjacent to it internally are the foetal giant cells, and the layer of decidua which separated this portion of the capsule from the giant cells at the 12-day stage has either disappeared or been incorporated into the capsule. Though the marginal part of the capsule is rather thicker, presumably because of the incorporation of more tissue in its inner layers, it closely resembles the mesometrial capsule of the 12-day placenta in appearance, staining reactions and nuclear content.

Beyond the mesometrial limit of the uterine lumen, between it and the central aperture of the capsule, a thin layer of decidua separates the 'paracentral' part of the capsule from the foetal giant cells. In contrast to the marginal portion, the paracentral portion of the capsule shows little sign of degeneration. It is traversed by vascular channels, and is distinguished from the stroma outside and the decidua inside by its deeper brown staining in trichrome preparations (Pl. 2, fig. 11). The nuclei are of regular shape, closely packed and stain well. The matrix is basiphilic, though less markedly so than that in the marginal portion, and the basiphilia is more readily removable with ribonuclease digestion.

It can be seen that the uterine lumen and the capsule extend further mesometrially around the chorio-allantoic placenta at this stage, though this may be due in part to antimesometrial growth of the placenta itself. The size of the central aperture in the capsule is actually less at the 14-day than at the 12-day stage, and the paracentral portion of the capsule appears to be a new formation. In the 12-day placenta, however, the decidual cells in the position occupied by the paracentral portion of the capsule at the 14-day stage are smaller than those lying internal to them, and are flattened along a line continuous with the capsule (Pl. 2, fig. 12). It is likely that the paracentral portion of the capsule arises from these cells.

With further development the capsule retains its position. Degenerative changes, which at the 12- to 15-day stages are confined to the marginal portion, also occur in the inner layers of the paracentral portion. The layer of decidua basalis between the paracentral portion and the foetal giant cells becomes reduced, and the cytoplasm of its cells stains a deep blue colour with phosphotungstic acid-haematoxylin. By the 17-day stage this decidual layer has effectively disappeared (Dickson & Bulmer, 1960). In some areas, either immediately adjacent to the capsule or incorporated in its inner layers, are masses of closely packed degenerate nuclei, apparently remnants of decidual cells. Elsewhere the capsule is in immediate contact with the foetal giant cells, many of which are degenerate and incorporated within its substance (Pl. 2, fig. 13).

At the 19-day stage (Text-fig. 1(*e*)) the uterine lumen has extended still further mesometrially, so that the placenta is attached by a relatively narrow pedicle. The marginal portion of the capsule incorporates many degenerate giant cells as well as decidual nuclei. Paracentrally, the capsule is very much thicker. Though

degenerative changes, with clumps of nuclear remnants, occur in the inner layers, the outer layers consist of closely packed and deeply staining cells (Pl. 2, fig. 14). The central aperture of the capsule is still evident, though the outgrowth of endovascular plasmodium is now degenerating. In addition to the thickening of the paracentral part of the capsule, there is an extensive proliferation of small, deeply staining stromal cells at the base of the mesometrium, in the region of the metrial gland.

One further point may be mentioned. The mesometrial capsule lies between the decidua basalis and the stromal zone which is eventually largely split by the uterine lumen. In two of our specimens, one at the 15-day and one at the 17-day stage, there is a further band of condensed tissue at the periphery of this stromal zone, outside, and roughly parallel to, the paracentral part of the capsule. This band, which from its staining reactions appears to be collagenous, does not cross the mesometrial triangle, but can be followed antimesometrially into continuity with a dense connective tissue layer immediately beneath the uterine epithelium.

DISCUSSION

The capsule which we describe, first appearing in relation to the antimesometrial decidua and persisting as a feature of the mesometrial decidua, has not been reported in detail by previous workers. Bridgman (1948) described a dense connective tissue layer around the entire decidua from the 9th day onwards, and the subsequent splitting of this layer by the extension of the new uterine lumen. It is difficult to reconcile our findings with Bridgman's account. The dense connective tissue layer she described may correspond with the stromal zone which forms the plane of extension for the new lumen. This is a fairly dense, cellular condensation at the 9-day stage, though it then contains no demonstrable collagen fibres and is deficient mesometrially. In the later stages the mesometrial portion of this zone, beyond the extending uterine lumen, is a very loose tissue, and it is difficult to believe that this could be the structure which Bridgman described as a dense connective tissue layer, separating the decidua basalis from the myometrium. It would appear that Bridgman must have been referring to the mesometrial portion of the capsule which we describe. If this is so, her account of a dense connective tissue layer seems misleading, and her identification of the capsule as the plane of the uterine lumen inaccurate. The mesometrial portion of the capsule in the later stages of gestation was noticed by Holmes & Davies (1948), who described the compression of the decidua basalis into a narrow band, except for a persistent tuft around the central artery. Despite the description by Duval (1891) of the disappearance of the decidua basalis, he made no mention of the mesometrial part of the capsule.

The capsule of the antimesometrial decidua may originate in part from the layer of stromal cells which lies external to it, but the morphological appearances of the nuclei, particularly at the 9-day stage, suggest that decidual cells are incorporated into its internal layers. In the mesometrial decidua, the appearances at the 15-, 17- and 19-day stages indicate that degenerate decidual cells and giant cells are incorporated into the inner layers of the capsule, while the outer layers are formed by proliferation of stromal cells.

Grosser (1927) and Bridgman associated the function of the capsule with the subsequent formation of the uterine lumen. The plane of the capsule, however, is not the plane of extension of the lumen, though obviously the formation of the capsule may facilitate the spread of the lumen outside it. The degeneration in the inner layers of the paracentral part of the capsule by the 19-day stage may provide a plane for placental separation, and the proliferation of stromal cells in its outer layers and in the mesometrial triangle may be associated with the post-partum regeneration of the endometrium.

The nature of the capsular material presents a difficult problem. Its staining reactions may justify the term fibrinoid, though there are obvious differences, particularly in basiphilia, from those of fibrin. The intense basiphilia of the antimesometrial capsule and of the degenerate part of the mesometrial capsule may be due to an accumulation of ribonucleic acid, presumably derived from the degenerate cells which they incorporate. The staining with gallocyanin at low pH suggests the presence of either nucleic acid or acid mucopolysaccharide. The lack of appreciable staining with alcian blue, the orthochromasia with azur A and the removal of the basiphilia with hot trichloracetic acid might be taken to exclude the presence of acid mucopolysaccharide (Swift, 1955). On the other hand, there is a very marked resistance to nuclease digestion, and nucleic acid would be expected to stain blue with acid solochrome cyanin (Pearse, 1957). The lack of basic staining with alum haematoxylin in trichrome preparations is an interesting feature, and the staining with picric acid, both in the capsular material and in the nuclei, suggests the accumulation of a basic protein which, like the protein of red blood cells, binds picric acid in preference to the plasma stain. The degeneration process must be associated with the freeing of a large number of stainable groups, both basic and acidic, and also with the presence of a relatively high tryptophan content.

Degenerative changes and fragmentation occur in the nuclei of the antimesometrial capsule from the 10-day stage onwards, and in the nuclei of the marginal portion of the mesometrial capsule from the 12-day stage. The degenerating nuclei retain their affinity for methyl green, though recent opinion (Alfert, 1952; Rosenkranz & Bendich, 1958) indicates that methyl green stainability is not, as Kurnick (1950) suggested, a simple index of the degree of polymerization of desoxyribonucleic acid. The significance of the staining differences in the antimesometrial decidua demonstrated with the fast green method is obscure. The rat placenta, with the occurrence of polyploidy (Sachs & Shelesnyak, 1955) followed by degenerative changes in decidual cells and the appearance and subsequent degeneration of polyploid giant cells would seem to offer a fertile field for microspectrophotometric studies.

The degeneration and disappearance of both antimesometrial and mesometrial decidua is a striking feature of the rat placenta. While appearances suggest that the external layers of each are incorporated into the capsule, other factors must also be involved. The degeneration of the decidua capsularis may be due, as Young (1956) suggested, to an impairment of its vascular supply, though Everett (1935) found that the vessels of the central zone contain actively circulating blood at the 13- to 14-day stage. The work of Velardo *et al.* (1953) on deciduomata, where there is a similar degeneration of the antimesometrial decidua with the appearance of a

condensed zone surrounding it, implies that capsule formation and decidual degeneration are not dependent upon the presence of an expanding embryonic sac. Sachs & Shelesnyak suggested that the abnormal reproductive mechanism associated with the appearance of polyploidy in deciduomata may be responsible for the subsequent degeneration, and such an explanation could also be applicable to the decidual degeneration of pregnancy.

Phagocytosis by the foetal giant cells has been held to be largely responsible for the removal of the degenerate decidual tissue (Bridgman). Morphological evidence that this is an important mechanism in the removal of the decidua capsularis is doubtful and unconvincing, and we have recorded a similar opinion on the removal of the decidua basalis (Dickson & Bulmer, 1960). The leucocytosis, which occurs in both the decidua capsularis and decidua basalis, may be involved in the removal of the degenerate tissue. There may be autolysis of the decidua, as Duval suggested for the decidua capsularis, and absorption of the products of autolysis by the large vessels of the decidua basalis, the vessels of the central zone or the uterine epithelium.

SUMMARY

1. A capsule appears by the 9-day stage, limiting the periphery of the antimesometrial decidua. The basiphil cells of the antimesometrial decidua degenerate, and by the 15-day stage the decidua capsularis has effectively disappeared.

2. At the 12-day stage the capsule extends around the mesometrial decidua, though it never reaches the mesometrial pole. The mesometrial decidua gradually disappears, in part by incorporation into the capsule.

3. The histochemical features of the capsule and of the degenerating decidual tissue are described and discussed. The capsular matrix is probably justifiably termed fibrinoid.

4. There is no convincing morphological evidence that the foetal giant cells phagocytose degenerate decidual tissue.

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REFERENCES

ADAMS, C. W. M. (1957). A *p*-dimethylaminobenzaldehyde-nitrite method for the histochemical demonstration of tryptophane and related compounds. *J. clin. Path.* **10**, 56–62.

ALFERT, M. (1952). Studies on basophilia of nucleic acids: the methyl green stainability of nucleic acids. *Bull. biol.* **103**, 145–156.

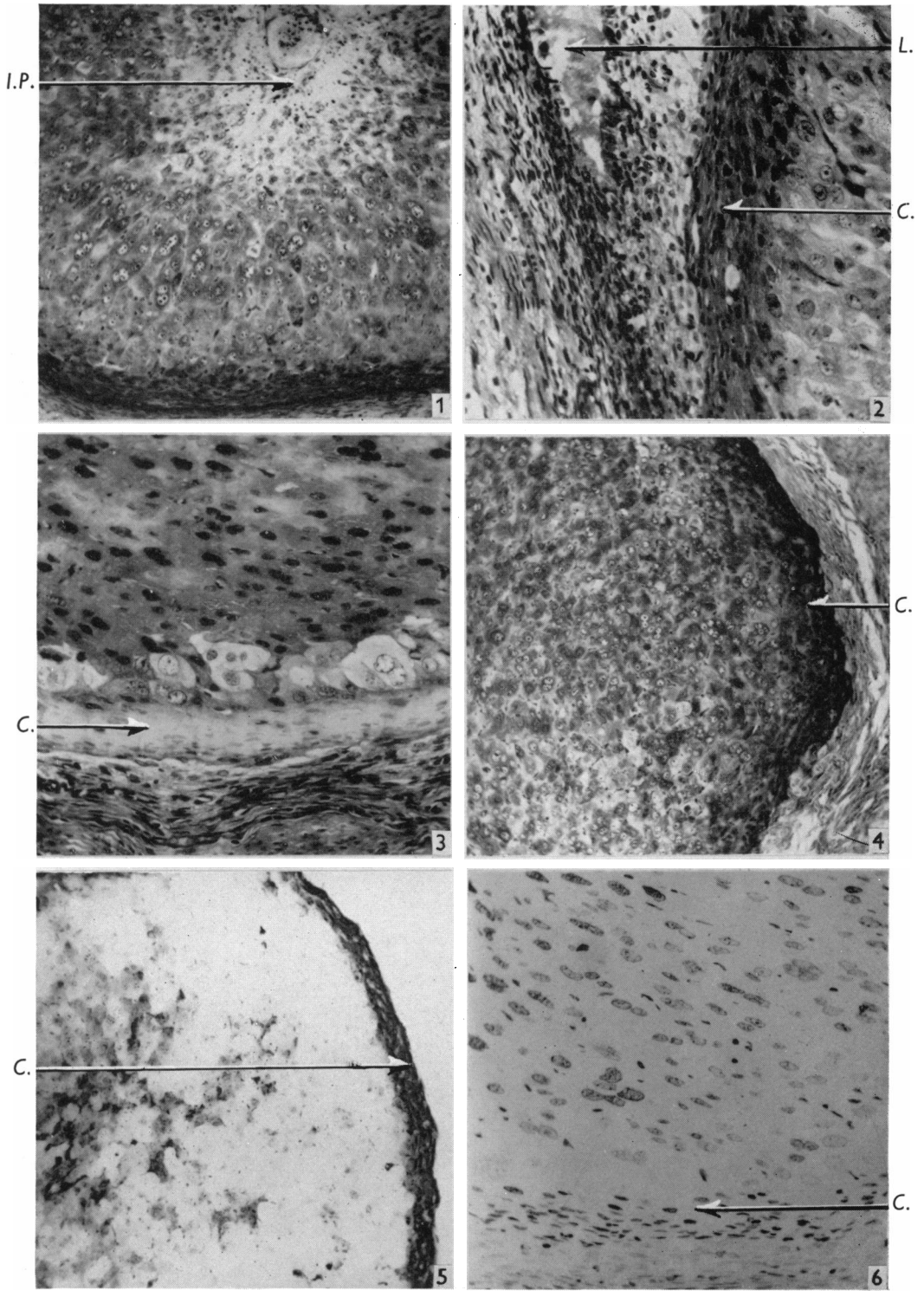
ALFERT, M. & GESCHWIND, I. I. (1953). A selective staining method for the basic proteins of cell nuclei. *Proc. nat. Acad. Sci., Wash.*, **39**, 991–999.

BERENBAUM, M. C. (1958). The histochemistry of bound lipids. *Quart. J. micr. Sci.* **99**, 231–242.

BRIDGMAN, J. (1948). A morphological study of the development of the placenta of the rat. I. An outline of the development of the placenta of the white rat. *J. Morph.* **83**, 61–85. II. An histological and cytological study of the development of the chorio-allantoic placenta of the white rat. *J. Morph.* **83**, 195–223.

BULMER, D. & DICKSON, A. D. (1960). Observations on carbohydrate materials in the rat placenta. *J. Anat., Lond.*, **94**, 46–58.

DICKSON, A. D. & BULMER, D. (1960). Observations on the placental giant cells of the rat. *J. Anat., Lond.*, **94**, 418–424.



BULMER AND DICKSON—FIBRINOID CAPSULE OF THE RAT PLACENTA

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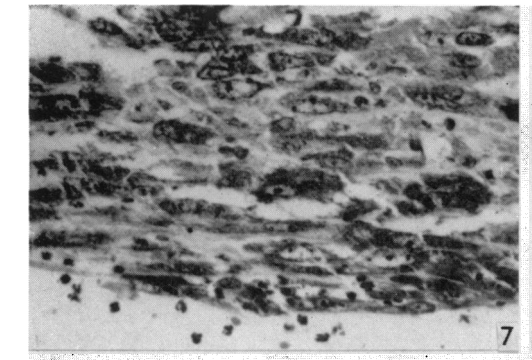

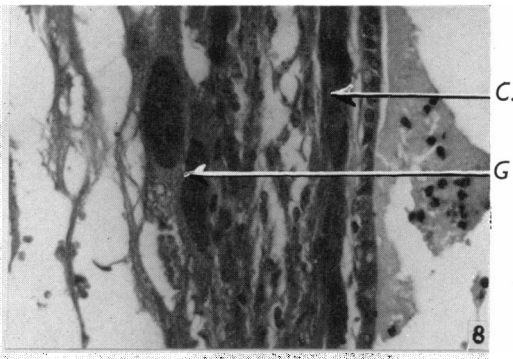

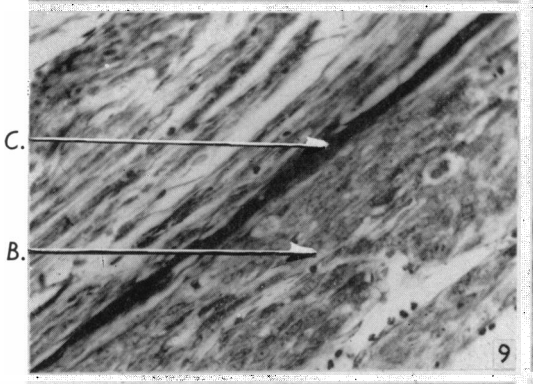

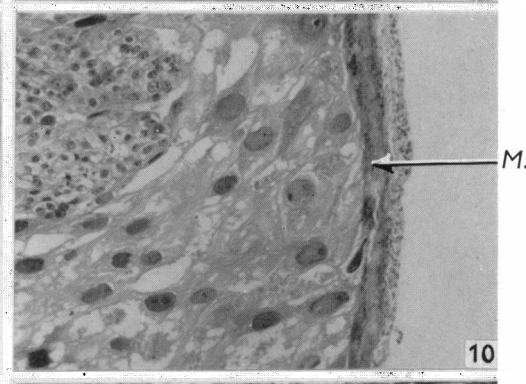

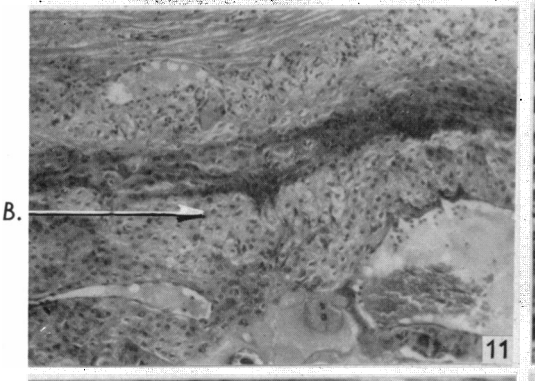

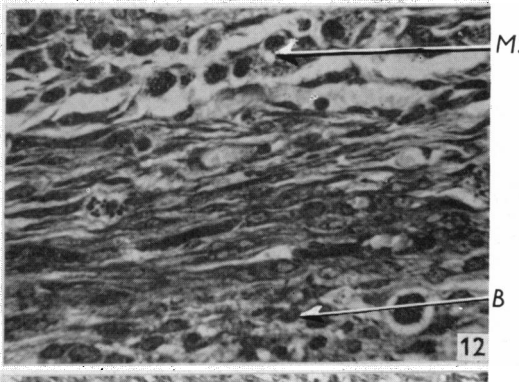

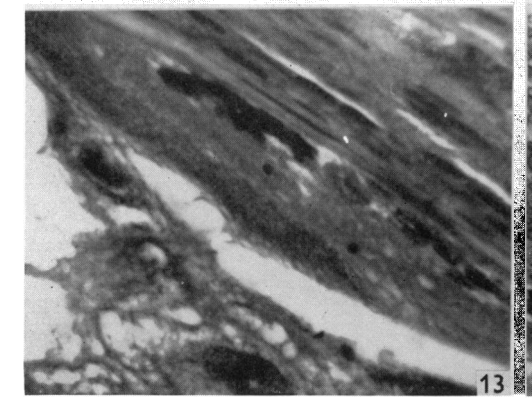

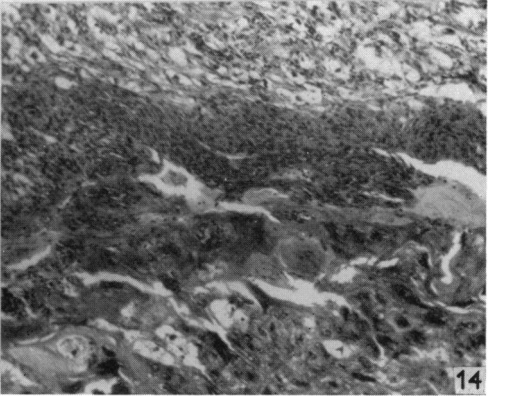

BULMER AND DICKSON—FIBRINOID CAPSULE OF THE RAT PLACENTA

DICKSON, A. D. & BULMER, D. (1961). Observations on the origin of metrial gland cells in the rat placenta. *J. Anat., Lond.*, **95**,

DUVAL, M. (1891). Le placenta des rongeurs. III. Le placenta de la souris et du rat. *J. Anat., Paris*, **27**, 24–96, 344–395, 515–612.

EVERETT, J. W. (1935). Morphological and physiological studies of the placenta in the albino rat. *J. exp. Zool.* **70**, 243–284.

FLAX, M. H. & HIMES, M. H. (1952). Microspectrophotometric analysis of metachromatic staining of nucleic acids. *Physiol. Zool.* **25**, 297–311.

GROSSER, O. (1927). *Fruhentwicklung, Eihautbildung und Placentation.* Munich: Bergmann.

HOLMES, R. P. & DAVIES, D. V. (1948). The vascular pattern of the placenta and its development in the rat. *J. Obstet. Gynaec. Brit. Emp.* **55**, 583–607.

KREBHEIL, R. H. (1937). Cytological studies of the decidual reaction in the rat during early pregnancy and in production of deciduomata. *Physiol. Zool.* **10**, 212–234.

KURNICK, N. B. (1950). Methyl green-pyronin. I. Basis of selective staining of nucleic acids. *J. gen. Physiol.* **33**, 243–264.

LILLIE, R. D. (1954). *Histopathologic Technic and Practical Histochemistry.* New York and Toronto: The Blakiston Company Inc.

LONG, M. E. (1948). Differentiation of myofibrillae, reticular and collagenous fibrils in vertebrates. *Stain Tech.* **23**, 69–75.

PEARSE, A. G. E. (1957). Solochrome dyes in histochemistry with particular reference to nuclear staining. *Acta histochem.* **4**, 95–101.

PEARSE, A. G. E. (1960). *Histochemistry, Theoretical and Applied.* London: J. and A. Churchill, Ltd.

PEERS, J. H. (1941). A modification of Mallory's phosphotungstic acid-hematoxylin stain for formaldehyde-fixed tissues. *Arch. Path. (Lab. med.)*, **32**, 446–449.

ROSENKRANZ, H. S. & BENDICH, A. (1958). On the nature of the DNA-methyl green reaction. *J. biophys. biochem. Cytol.* **4**, 663–664.

SACHS, L. & SHELESNYAK, M. C. (1955). The development and suppression of polyploidy in the developing and suppressed deciduoma in the rat. *J. Endocrin.* **12**, 146–151.

SWIFT, H. (1955). Cytochemical techniques for nucleic acids. In Chargaff & Davidson, *The Nucleic Acids*, Vol. II. New York: Academic Press Inc.

VELARDO, J. T., DAWSON, A. B., OLSEN, A. G. & HISAW, F. L. (1953). Sequence of histological changes in the uterus and vagina of the rat during prolongation of pseudopregnancy associated with the presence of deciduomata. *Amer. J. Anat.* **93**, 273–305

YOUNG, A. (1956). The vascular architecture of the rat uterus during pregnancy. *Trans. roy. Soc. Edinb.* **63**, 167–184.

EXPLANATION OF PLATES

PLATE 1

Fig. 1. Antimesometrial decidua of a 9-day placenta. The implantation zone is shown at *I.P.* Azur A, ×75.

Fig. 2. Periphery of the antimesometrial decidua of a 9-day placenta. *C.* indicates the capsule and *L.* the uterine lumen. Trichrome, ×200.

Fig. 3. Periphery of antimesometrial decidua of a 10-day placenta, showing large subcapsular cells with unstained cytoplasm. Trichrome, ×200.

Fig. 4. Capsule and antimesometrial decidua of a 10-day placenta. Azur A, ×75.

Fig. 5. A similar section to that shown in Fig. 4, but which has been subjected to ribonuclease digestion. Azur A, ×75.

Fig. 6. Nuclei of antimesometrial decidua and capsule stained by alkaline fast green method. *D*, antimesometrial decidua. ×200.

PLATE 2

Fig. 7. Degenerate decidua capsularis in the region of the antimesometrial pole at the 12-day stage. Methylene blue, ×250.

Fig. 8. Decidua capsularis close to margin of chorio-allantoic placenta at the 13-day stage. The surface of the capsule is covered by a low cubical epithelium. Central zone giant cells are indicated at *G.* Trichrome, ×200.

Fig. 9. The mesometrial capsule at the 12-day stage, outside the decidua basalis, ***B.*** Methylene blue, × 200.

Fig. 10. The marginal portion of the capsule (***M.***) at the 14-day stage. Trichrome, × 75.

Fig. 11. The paracentral portion of the capsule at the 14-day stage. Trichrome, × 75.

Fig. 12. The paracentral area at the 12-day stage. The flattened cells between the decidua basalis and the region of the metrial gland (***M.G.***) indicate the future paracentral part of the capsule. P.T.A.H., × 400.

Fig. 13. The paracentral portion of the capsule at the 17-day stage. The decidua basalis in this region has disappeared, and a degenerate giant cell nucleus is incorporated into the capsule. Trichrome, × 200.

Fig. 14. The paracentral portion of the capsule at the 19-day stage, showing the proliferation of stromal cells in its outer layers. Trichrome, × 75.