The Formation of the Ootheca by *Periplaneta americana*

I. The Micro-anatomy and Histology of the posterior part of the Abdomen

*By P. C. J. BRUNET*

*(From the Department of Zoology and Comparative Anatomy, University Museum, Oxford)*

**SUMMARY**

The ootheca is of interest because it is composed of quinone-tanned protein. No detailed account of the secretory processes leading to the production of structural protein and tanning agents exists, and this paper is intended as an introduction to such a cytological and histochemical account; it contains a description of the general anatomy of the organs concerned with the formation of the ootheca. These organs are located round the vestibulum, a large intucking of the posterior part of the abdomen.

The colleterial glands open into the vestibulum and secrete most of the protein and tanning agent. The structure of each type of secretory cell of which the gland is composed is outlined.

A new organ, taking the form of a large invagination of the dorsal wall of the vestibulum, is described. The walls of this invagination are secretory, and it is notable that the secretion-product accumulates and is stored within the substance of a modified layer of the endocuticle.

Two types of massed dermal gland cells are described. One type is present mostly on the ventral walls of the ovipositor, and the other towards the posterior end of the vestibulum. The former may not be directly concerned with ootheca formation, while the latter probably secretes the alkali-resistant outer layer of the ootheca.

The relations between the ovipositor and the 'horned die' of Kramer and Wigglesworth are discussed.

**INTRODUCTION**

LIKE all blattids, the cockroach produces an ootheca, which serves to protect the eggs, probably as much from members of its own species as from any other predator. It then attempts to bury the ootheca, and often plasters upon it suitable environmental debris, using saliva for the purpose (Haber, 1920).

Pryor (1940a) has described the ootheca as being shaped like a carpet bag, which is essentially a cylinder, more or less rounded anteriorly and posteriorly, and split along the dorsal midline; the two lips of the slit, which form the crista, are raised and notched in a characteristic way, and remain cemented together in the interval between oviposition and eclosion.

The protecting membranes of an insect egg are secreted partly by the follicular cells of the ovary and partly from within the egg (Beament, 1946). In many families of Orthoptera there are additional substances which are derived from accessory glands and are concerned with protection of the egg: locustids glue their eggs together with such a secretion, and the egg-masses, with the...
surrounding earth which adheres to them, form cocoon-like structures (Waloff, 1950); phasmids lay their eggs singly, each with a tightly fitting outer case to the egg—an individual ootheca (Wigglesworth and Beament, 1950; Moscona, 1950). Blattids and mantids form oothecae characteristic of the species: in mantids it is often of considerably larger volume than the female which produces it, and consists of a tough, frothy substance; in blattids the ootheca forms a closely fitting, hard, brown outer case around the eggs, which usually number sixteen—one from each ovariole—in Periplaneta. In most blattids the ootheca is set free from the body and left while the eggs develop, but in some species it is retained, partly projecting from the body, while the eggs develop within (Shelford, 1912).

The discovery of the biochemical nature of the ootheca by Pryor (1940a) led to a wider understanding of the methods of stabilizing proteins found in nature. It was known that the ootheca contained no chitin, and Pryor showed that it was composed of a structural protein, the hardening and stabilizing of which occurred as the result of the addition of a quinonoid substance which acted by cross-linking the protein molecules. Certain similar properties of both the ootheca and the integument of arthropods suggested that quinone-tanned protein might be the agent conferring rigidity, and resistance of the integument to the environment. Pryor confirmed this in the case of a number of insects (1940b), showing that rigidity was due to tanning of the protein within the chitin-protein complex of which the integument is composed; and the occurrence of quinone tanning has since proved to be widespread in invertebrates: in Protozoa (Brown, 1950); in platyhelminth eggs (Stephenson, 1947; Nurse, 1950); in annelid chaetae (Brown, 1950; Dennell, 1949); in the periostracum and byssus of Mollusca (Brown, 1950); in crustacean cuticle (Dennell, 1947b); in insect cuticle (Wigglesworth, 1948; Dennell, 1946, 1947a) and eggs (Beament, 1946). Quinone tanning occurs also in the egg-cases of selachians (Brown, 1950). The subject has been reviewed by Brown (1950).

In the case of the ootheca, Pryor confirmed previous work which had shown that the protein used in forming the ootheca was derived from the left colleterial gland, and he showed that the right gland secreted the precursor of the ω-quinone, in the form of an ω-dihydroxyphenol derivative, which was enzymatically oxidized to the quinone. The precursor was later shown to be ω-dihydroxybenzoic acid (Pryor, Russell, and Todd, 1946).

It seemed likely that the colleterial glands would provide better material than epidermal cells for a cytological and histochemical approach to the problems of the secretion of protein and diphenol; for secretion of these substances is continuous in the colleterial gland, while, in the epidermis, secretion is of relatively brief duration and is complicated by the concurrent secretion of other substances, e.g. chitin and cuticular lipoids. It became evident in the course of the work that other undescribed accessory sexual glands were present, the location and description of which would not be possible without a brief anatomical survey of the whole genital region. In consequence, this
paper takes the form of such a survey, and it is to be followed by another at a cytological and histochemical level of investigation.

**Historical Survey**

The fact that the material used in making the ootheca was derived from the accessory or colleterial glands was known to Dufour (1841) and Milne-Edwards (1870). Duchamp (1878) discovered the crystals present in both the ootheca and the colleterial glands. Kadyi (1879) showed that these crystals were of calcium oxalate, and he noted that the left and right colleterial glands were unlike one another in structure and content. He described ootheca-formation, as did Wheeler (1889). Miall and Denny's monograph on the cockroach (1886) added no new material in this context. Bordas (1909) capably described the histology of the colleterial glands, but his work did not cover all the types of cell that go to make up the colleterial glands; he wrongly described the secreted crystals as calcium carbonate. Ito (1924) reviewed the accessory glands of the Orthoptera, but added little to what Bordas had said previously. Voy (1949) described the whole accessory genital system and added a considerable amount of new material. His work on the colleterial glands is, however, misleading, since his description of the right gland applies to the left, and vice versa. Other historical references are to be found in Bordas, Ito, and Voy.

**The Vestibulum**

The ootheca of *Periplaneta* is about 7 mm. long, and is thus large in relation to the size of the body. In consequence one finds special adaptations of the abdomen. Snodgrass (1933) gives a clear account of the external anatomy of the abdomen of *Blatta*, and includes a list of terms applicable to the genital region. These terms, listed on pp. 45-47 of his paper, have been used wherever possible in this paper. Fig. 1A shows the fundamental arrangement of the posterior segments of the insect abdomen; it can be seen that the oviduct, the colleterial glands, and the spermatheca open ventrally in this region, and that the valvulae of the ovipositor occur in association with these openings. The oviduct opens in the eighth (abdominal) segment, of which the first valvula (gonapophysis) is a modified limb-base. The accessory or colleterial glands open on the ninth segment, between the second valvulae. The spermatheca opens in a specialized sclerite between the eighth and ninth segments (but in some other cases on the eighth).

In most insects this pattern is found to have been modified: the portion of the eighth sternum which lies anterior to the gonopore is produced posteriorly so as to form a small genital atrium, which is a pocket in the eighth sternum, opening posteriorly, and enclosing the gonopore and the opening of the spermatheca. The cockroach shows even more modification from the fundamental plan (fig. 1C). Posterior to the genital atrium there is a larger cavity known as the vestibulum. Anteriorly it is in connexion with the genital atrium. Its ventral wall represents the intersegmental membrane between seventh and
Fig. 1. Diagrams of the posterior segments of the insect abdomen, cut by sagittal section. A. Fundamental arrangement of posterior abdominal segments. B. Comparable figure, showing modifications found in Periplaneta americana. C. Enlargement of fig. 1b, with lettered key beneath, showing levels at which the transverse sections, constituting fig. 2, are cut. A solid line represents the surface of a tissue cut by the sagittal section; a broken line represents tissue not lying in the median plane. Terga are shown by Arabic numerals, sternae by Roman.
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eighth sterna. Posteriorly, and tending dorsally, the membrane becomes folded so that in transverse section it presents approximately the shape of a W (fig. 2A). It is in this posterior end of the vestibulum that the ootheca is held during its formation, at which time the folds are fully extended. The outer walls of this most posterior region, the so-called terminal lobes of the seventh sternum, connect anteriorly with the unmodified part of the same sternum. The dorsal wall of the vestibulum is formed by the ventral parts of the ninth and tenth segments. Since the bases of the second and third valvulae meet in the middle line, there is no room for the sternum of the ninth segment and it is absent; the roof of the vestibulum in this region is formed from the ventral walls of the second and third valvulae (fig. 2J). There is no clearly demarcated sclerite on the tenth segment representing its sternum. It is in that part of the roof of the vestibulum that is formed from the second valvulae that the openings of the two colleterial glands occur. There is a further invagination in the roof of the vestibulum between the opening of the colleterial glands and the spermatheca; for this invagination the term vestibular organ is proposed (fig. 1C). To compensate for these modifications of the ventral wall of the body, the terga of segments eight and nine are reduced in antero-posterior length and telescoped under the seventh.

The Ovipositor

Three pairs of valvulae and two pairs of valvifers constitute the ovipositor. These are said to represent modified limb-bases of the eighth and ninth segments (Snodgrass, 1931). Each of the two pairs of limb-bases develops one or two elongate processes, known as valvulae. The term valvifer is used to denote the limb-base itself, forming part of the body-wall, from which the valvulae project. A pair of valvulae constitutes a valve of the ovipositor.

The first valvifers, those of the eighth segment, bear the first valvulae; the second valvifers, those of the ninth segment, bear the second and third valvulae. In the case of the cockroach it is difficult strictly to apply the terms valvifer and valvula since there is no distinct line of demarcation; they define regions rather than sclerites.

All three pairs of valvulae are finger-like processes, directed posteriorly from their valvifers on the ventral body-wall; their posterior ends lie freely in the vestibulum (fig. 2B-C). The first valvifers form the dorso-lateral wall of part of the vestibulum (fig. 1R), and the valvulae are attached at their anterior ends to the valvifers; at the level of fig. 2L they become free. They lie, for the most part, ventrally and laterally to the other two pairs of valvulae.

The second valvulae are smaller than the others, and lie within the third pair, being united to them by their outer lateral walls (fig. 2D; and anteriorly). The third valvulae are attached by their lateral walls to the body (from the level of fig. 2L, and anteriorly), this region of attachment representing the second valvifer.

In addition to these lateral fusions, median dorsal fusions occur between members of the second pair of valvulae (cf. fig. 2G, 2H), and between members
FIG. 2A-L. Diagrams of transverse sections through the posterior part of the abdomen of Periplaneta americana. The letters on each figure, indicating the level at which the section was cut, correspond with the key beneath fig. 1c.
of the third (cf. fig. 2E, 2F). These fusions result in the formation of two anteriorly directed apophyses projecting into the haemocoel (fig. 2K, anterior and posterior apophyses), the walls of which serve as attachments for muscles. A similar condition has been found by Janet (1898) to occur in Hymenoptera.

The Valvulae

The integument of the first valvulae and valvifers consists for the most part of normal cuticle, strengthened in certain regions by the formation of an exocuticle. The epidermal cells beneath are normal (fig. 3A), and become greatly reduced in height a few days after the last moult. However, in a region situated dorsally on the inner walls of the valvifers (fig. 2M–T), the epidermal cells are modified for carrying out a secretory function; they resemble those of the vestibular organ (fig. 3C), and will be later described under that heading. There is a possibility that other patches of epidermal cells which occur over scattered regions of the vestibulum and valves also retain a secretory function: they appear as normal epidermal cells except for the fact that they are clustered around infoldings of the inner surface of the cuticle (fig. 3B), and that they appear to diminish in size after the last moult less than do the majority of epidermal cells.

Much of the integument of the second and third valvulae and their valvifer consists of normal epidermal cells, but the specialized nature of both valves leads to the occurrence of many modifications. The larger, third valvulae fuse dorsally (fig. 2F), and anterior to this point they go to form the posterior apophysis (fig. 2K), which amounts to being a horned knob within a cavity connected to the vestibulum. This is undoubtedly the 'horned die' described by Wigglesworth and Beament (1950), the function of which is to mould the inner surface of the crista of the ootheca, leaving therein an air space, which connects with the specialized respiratory region of the egg below. Sections show the presence of oothecal protein in this cavity where shaping of the inner walls of the crista evidently occurs in advance of the main body of the ootheca which lies farther back, within the terminal lobes of the seventh sternum.

The dorsal tips of the third valve appear to be lined with epidermal cells, not particularly modified, but retaining a secretory function probably connected with the moulding process. The lateral walls of the third valve have a characteristic structure: their inner walls give rise to large infoldings (fig. 3B), and much of the space within the valvulae is occupied by these infoldings. The function of the cells lining these folds is not known: their nature would suggest that they do not carry out a skeletal function, and it may be either that they are acting as a reserve of cells for the dorsal secretory portion of the third valve (no mitosis occurring in this region after the last moult), or that they are themselves secreting, and their products diffusing along the substance of the infoldings and out through the cuticle.

The dorsal wall of the posterior apophysis, part of the integument of the ninth segment, is penetrated by small intuckings of the cuticle which bears fine bristles, and the epidermal cells beneath appear to be secreting a product...
FIG. 2M–X. Diagrams of transverse sections through the posterior part of the abdomen of *Periplaneta americana*. The letters on each figure, indicating the level at which the section was cut, correspond with the key beneath fig. 1C.
which is stored, as in the integument of the vestibular organ, within the cuticle in the form of globules.

The outer and ventral surfaces of the third valvulae are penetrated by the ducts of many dermal gland cells which lie beneath (fig. 2M–O). Similar regions of dermal glands line the inner ventral walls of the second valvulae anterior to their dorsal union (fig. 2N). In 1949 Voy described these ‘cellules polyédriques . . . dans lesquelles on trouve de nombreux canalicules intracellulaires’ as occurring in the median vertical slit which forms a channel between the second valvulae (fig. 2K). There is no doubt that in this region a veritable organ is present, composed of orthodox dermal glands (fig. 3D). This type of dermal gland, acting as accessory sexual organ, is found in the adult female cockroach, and remains functional after the laying down of the cuticle. It represents a new type, not included in Konček or Stanislavskij’s classifications, as reported in Kramer and Wigglesworth (1950); and yet another type of dermal gland organ which is present in the vestibulum is described on p. 126.

It is into this channel, lying between the ventral and inner walls of the second valvulae, that the ducts of the colleterial glands open.

**The Colleterial Glands**

The colleterial glands consist of a pair of organs composed of many tubules, which lie freely in the haemocoel. Together the glands occupy much of the body-cavity of the posterior part of the abdomen. For the most part they lie antero-dorsally to the vestibulum and ventrally to the rectum (fig. 1C). Each gland has a main duct, which divides into two, and these branches again repeatedly divide. The left gland occupies many times the volume of the right, the tubules of which are more or less enveloped by those of the left. Since the tubules of the right gland are the shorter, the gland does not extend so far anteriorly as does the left.

It is the left gland that secretes the oothecal protein, and its lumen can be seen to be filled with a viscous, white fluid of the consistency of condensed milk. The right gland secretes a diphenol (Pryor, 1940a). This gland appears far more transparent than the left. Voy (1949) alone attributes protein secretion to the right gland. He is, without doubt, mistaken in this respect.

The main ducts of the two glands open separately. The opening of the left gland is posterior to that of the right, and occurs on a short, posteriorly directed papilla (fig. 2J), which abuts on to the dermal gland organ between the second valvulae. The external and internal cuticle of the papilla bears a dense covering of long, fine bristles, and such cuticle lines the main duct for part of its length. The cells beneath are of normal cubical epithelium (fig. 4, type I cells).

Anterior to this region, the main duct and all the tubules of the left gland are composed of two types of cell. The major part is made up of glandular epithelial cells (figs. 4 and 5C) attached to a basement membrane. Apically, abutting on the chitinous intima, are small conical chitinogenic cells,
characterized by their scarcity of cytoplasm. Outside the basement membrane in the region of the main ducts is a layer of circular muscle.

The glandular epithelial cells are based on the plan of the dermal gland cell. Each cell has an end-apparatus (the term vesicle, which has been much used, is not applicable), a chitin-lined intucking in the apical part of the cell into which the products of secretion are poured, whence they reach the lumen of the gland (figs. 4 and 5c, end-apparatus). There is, however, great diversity in the shape of these cells at different levels of the tubules, and of the end-apparatus.

In the greater part of the main duct of the left gland, and for some distance anterior to the first bifurcation, the glandular epithelium consists of cells which I have called type II cells (fig. 4). Most of their volume is occupied by the end-apparatus, which is urn-shaped and very thick-walled. Posteriorly, where the cells are short, the end-apparatus impresses itself on the nucleus, which becomes basin-shaped. These cells are actively secretory, and the products pass through the wall of the end-apparatus by way of minute radial canalicules. Previous workers on these glands of the cockroach, including Ito (1924), have failed to record this remarkable type II cell, although Ito figures a similar cell as occurring in *Mantis*. Type II cells have a weakly acidophil cytoplasm, and their end-apparatus is made clear by using Heidenhain’s iron haematoxylin or Altmann’s acid fuchsin. There is an increase in the height of the cells as the type III cell region is approached.

Type III cells are taller than the other cells of the left gland (fig. 5c). The end-apparatus is longer and has thinner walls than that of type II cells. The
chitinous intima is thinner. The cells have a basiphil cytoplasm, except for the fibrillar region at the base of each cell, which is faintly acidophil. The type III cells do not secrete into the lumen so actively as types II and IV, and may perhaps represent a transitional type.

Type IV cells constitute the bulk of the gland, and it is they that secrete the oothecal protein. Posteriorly the cells are taller and there is less secretion-product in the lumen; anteriorly the cells are shrunken and the lumen is full.

The cytoplasm of these cells, after formaldehyde-saline fixation, is strongly basiphil, while the protein secreted is acidophil. In addition to the protein, calcium oxalate is secreted (Kadyi, 1879), and is visible in the lumen in the form of large crystals.

The fact that the cells towards the posterior end of the gland recolour the leucobase of methylene blue, and that this reaction is inhibited by cyanide but not by azide, indicates that a diphenol oxidase, such as occurs in the cuticle (Dennell, 1947a), is secreted by this region of the left gland.

The right gland opens directly into the vestibulum, slightly anteriorly to the opening of the left gland, and there is no papilla (fig. 3M). The openings of the two glands are thus quite separate: each occurs slightly to its respective side of the middle line, and the right opening is situated anterior to the left (fig. 2L and M). Bordas (1909), Snodgrass (1933), and Ito (1924) have reported that there is but one opening. Miall and Denny (1886) were wrong in stating that the colleterial glands opened on the underside of the uterus. Since the publication of Bordas's paper it has been known that the glands opened on the
ninth segment, and Snodgrass correctly figured the opening as occurring between the second valvulae. Voy (1949) confirmed this, and described the papilla of the left gland (left and right are here used in the correct, and not his reversed, sense), but he held that the main duct of the right gland encircled the papilla of the left, which is not so.

The opening of the right gland leads out from the main duct, which is considerably narrower than that of the left. At its posterior end it consists of cubical epidermal cells beneath a thick chitinous intima (fig. 4). There is a thick layer of circular muscle surrounding the tubule. The remainder of the right gland is secretory and is composed of glandular epithelial and chitinogenic cells, as is the left. The end-apparatus throughout the gland, which is not easily colourable with dyes, is in the form of a thin tube.

Type II cells are tall, cylindrical cells, not unlike the tall type III cells of the left gland. They are characterized by the fact that the cell is packed with round granules of about 1 μ diameter, which leave little room for ground cytoplasm. The nucleus is basal, apparently itself displaced by the granular contents of the cell. These granules are acidophil, they are colourable with eosin and intensely so with acid fuchsin, but such cytoplasm as is present is basiphil.

In type III cells the nucleus is no longer basal. There is more ground cytoplasm and it is strongly basiphil; it has the appearance of a reticulum surrounding granules and vacuoles, the larger of which remain uncoloured by most dyes.

The argentaffine reaction shows that both the granules of type II and the granules and vacuoles of type III cells are, in part, composed of diphenolic substances, and an intensely positive reaction with McManus's (1948) periodic acid/Schiff routine indicates the presence of a substance containing an α-glycol or hydroxy-amino group. Since this reacting substance is not a lipoid, the reaction suggests that it is a polysaccharide or a precursor of the diphenolic secretion-product.

**The Vestibular Organ**

Between the openings of the colleterial glands and the spermatheca occurs an intucking of the dorsal wall of the vestibulum (fig. 1c). It forms a median cavity of considerable size dorsal to the spermathecal plate (fig. 2v), and bifurcates both anteriorly and posteriorly (figs. 2o and w and 5a). The walls of the organ are secretory, and the integument is highly modified (figs. 3c and 5b). The cells have the appearance of normal epidermal cells and show the usual decrease in height after moulting, during which time they secrete a considerable quantity of substance that accumulates within an especially modified endocuticle. Overlying the cells is a thin layer of laminated endocuticle, exterior to which is the storage layer, followed by an outer layer of endocuticle and the epicuticle. The storage layer, after fixation, generally appears as a tenuous network of fibrils, amongst which the globules of secretion-product accumulate. These are of various sizes up to 10 μ in diameter. The globules are colourable with acid dyes, in particular acid fuchsin, and by
Heidenhain's iron haematoxylin. They appear to be of protein nature, and to contain diphenols. The nature of the storage endocuticle is interesting in that it is composed of polysaccharide in the form of the sulphate ester. Pore-canals, of far larger size than are found elsewhere in the cockroach, carry the secretion-product to the exterior.

This specialized region of the cuticle is not limited to the vestibular organ, but occurs on the inner walls of the first valvifers, and on the lateral walls of the vestibulum (fig. 2R).

![Diagram](image)

**FIG. 5A.** Transverse section of the roof of the vestibulum (cf. fig. 2Q and R), showing the vestibular organ, dermal gland organ, and left and right colleterial glands. B. Section through the wall of the vestibular organ (cf. fig. 4c). C. Section through the left colleterial gland in region of type III cells, showing general disposition of cells.

No previous mention has been made of the occurrence of this organ in the cockroach, but a similar organ apparently occurs in the form of the 'chambre périvulvaire' of *Locusta* (Cappe de Baillon, 1920); it is of different shape, and Cappe de Baillon does not describe the storage globules, but mentions that there is a regular breakdown in the continuity between the hypodermal cells and the chitin which derives from them... the layer of homogeneous chitin (being) separated from the surface of the epithelium by a very loose network. In the cockroach the separation definitely occurs within the endocuticle and not between epidermis and cuticle, but the organs are clearly comparable. The 'renflement sus-oviductaire' (Voy, 1949) is probably a similar organ.

The vestibular organ and the specialized cells of the vestibular wall are in a position to coat the egg, as it passes through the vestibulum, with their secretion, and may well contribute to the substance which binds the eggs together within the outer casing of the ootheca.
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OTHER SECRETING REGIONS

Blattids and mantids produce a far more complex ootheca than other Orthoptera, where it is commonly found that one accessory sexual gland functionally replaces another; for instance, the colleterial glands are absent in acridiids but are replaced by the 'boyau calcial' (Voy, 1947), a diverticulum of the ovary. The cockroach, however, appears to have modified the entire vestibular and atrial regions for one or other purpose concerned with ootheca formation, and to possess a bewildering number of secretory tissues. The remaining secretory regions that have been observed are mentioned here, but there may even be others still to be described.

Fig. 2W and x shows that there is a region of dermal glands situated anterolaterally in the genital atrium. The cells are similar in all respects to those on the ventral walls of the second and third valvulae. Voy (1949) noted these, and also that the intersegmental membrane which lines the terminal lobes of the seventh sternum, and forms the posterior end of the vestibulum, bears dermal glands (fig. 2A). These indeed, form an organ of considerable size, a fact which he did not point out. The cells are disposed on the membrane in such a way that, at one time or another, they are in contact with the entire outer wall of the ootheca, except for the region of the dorsal crista. The chemical content of these posterior dermal glands differs from that of the other dermal gland cells, described above, which may not be concerned directly with the formation of the ootheca. The posterior cells may be responsible for the production of the thin outer membrane found to remain after dissolution of the ootheca with strong alkali (Pryor, 1940a).

Finally, the folds of the vestibular and atrial floor, between which the eggs pass (fig. 2W), secrete a lubricating substance from a bristled integument not unlike that of type I cells of the left colleterial gland (fig. 4).

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