J. Fac. Appl. Biol. Sci.,
Hiroshima Univ. (1981), **20**: 87 – 98

The Regional Morphology of the Infundibulum of the Hen's Oviduct with Special Reference to the Mechanism of the Engulfing of the Ovulated Ovum

Shunsaku FUJII, Yukinori YOSHIMURA, Toshikazu OKAMOTO and Tatsudo TAMURA

Faculty of Applied Biological Science, Hiroshima University, Fukuyama

Received: October 15, 1981
(Figs 1–23)

When ovulated, the ovum is engulfed by the oviduct through the infundibulum. The mechanism of engulfing the shed ovum is a particularly intersting subject of study in hens with enormously large ovum. So that, it has aroused much attention since a long time ago. WARREN and SCOTT (1934[1], 1935[2]) observed by means of biopsy under anesthesia that the shed ovum usually fell into the ovarian pocket and then was picked up by the infundibulum. It is a generally accepted opinion that the shed ovum may not enter the oviduct of its own accord, but may be engulfed actively by the oviduct through the infundibulum. This opinion is based upon the structure of the infundibulum itself which is mainly responsible for the engulfing of the ovum. Although a large number of authors[3–7] have described the structure of the oviduct in detail, only a few have reported the morphology of the infundibulum.

The present study was carried out to elucidate the mechanism of engulfing the shed ovum from the morphological point of view of the infundibulum. Observations were made on the general structure, the blood supply, and the innervation of the infundibulum.

MATERIALS AND METHODS

The materials used were all collected from the mature White Leghorn hens in laying. According to the different purposes, the following methods were used.

For the general morphology

The general morphology was examined by macroscopy, microscopy, and scanning electron microscopy. Hens were killed by decapitation under anesthesia with ketamine hydrochloride. After examination by the naked eye, the infundibulum was removed from the oviduct and processed for histological observation. For light microscopy, small blocks of tissues were fixed in a 10% formalin or Zenker's fluid and made into paraffin sections by the conventional method. These sections were stained with hematoxylin and eosin or by azan staining. For scanning electron microscopy, pieces of tissues were fixed in a 2.5% glutaraldehyde solution (pH 7.4). Then they were dehydrated in ethanol, soaked in amyl acetate, and dried by the critical point drying method with carbon dioxide. They were coated with gold and examined by a Hitachi S-410 scanning electron microscope.

For the blood supply

The vascular injection method was used in this study. Immediately after killing the hen in the same way as mentioned above, the thoracic cavity was opened to visualize the vascular arrangement of the cavity. After complete irrigation of blood with physiological saline via the descending aorta, 30% solution of gutta percha (for dental use) in chloroform was injected slowly. After this injection, the whole oviduct was removed from the abdominal cavity together with its associated ligaments and fixed in a 10% formalin. The infundibulum was cut off from it, cleared through glycerol, and examined by the dissecting microscope.

For the innervation

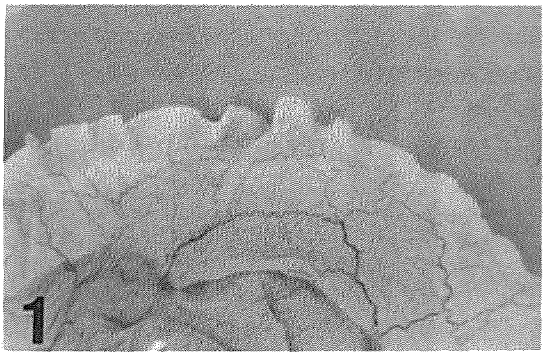
The innervation of the infundibulum was examined in the whole mount specimen prepared in the following manner. The infundibulum is too thin to work on with paraffin or frozen sections. On the other hand, it is too thick for stretching preparations. Therefore, when the whole infudibulum was removed immediately after killing, its mucosal surface was sealed downward around a polyethylene funnel. The funnel was bent by heating in order to fit the shape of the organ. Then the organ was stretched out with the fingertips into a membrane, as thin as possible. After drying for a little while, it was fixed for over a month in 20% neutral formaline, together with the holder. The membranous preparation was cut into pieces and stained by the Bielschowsky's silver impregnation method for the nervous tissue. The stained pieces were mounted on glycerin-gelatin and examined.

OBSERVATIONS

General morphology

Macroscopically, the infundibulum was formed in a thin-walled, funnel-shaped structure. It consisted of two portions without any distinct demarcation. One portion was a cranial thin-walled, expanded structure, and the other a cuadal neck region with a rather thick, tube-like structure. The infundibulum was suspended, pressed dorsoventrally, in the peritoneal cavity by the aid of a dorsal and a ventral ligament with its slit-like abdominal ostium facing the ovary. The dorsal angle of the infundibulum was attached to the vicinity of the 4th rib by a thickened ligament lining the cranial margin of the dorsal ligament. The ventral angle was attached to the uterovaginal junction by a thickened, cord-like ligament lining the cranial margin of the ventral ligament.

The most outstanding structure of the infundibulum was the abdominal ostium which was edged by a well-defined thicknened wall about 1.5–2.0 mm in width (referred to as the fimbrial lip). The fimbrial lip had wavy wrinkles at somewhat regular intervals



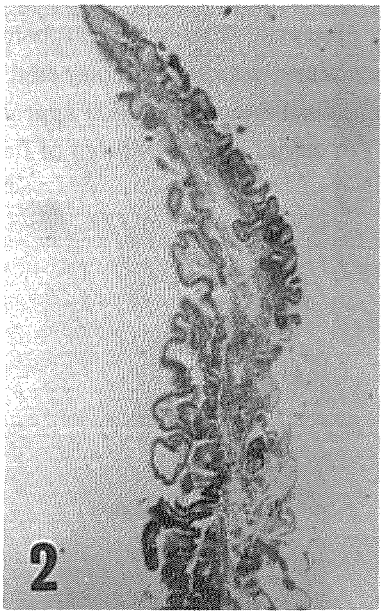


Fig. 1. The cranial part of the infundibulum. The free margin is edged by an opaque, wrinkled zone named the fimbrial lip.

Fig. 2. Vertical section of the cranial portion of the infundibulum. The cranial wall with a double-layered mucosa is the fimbrial lip. Hematoxlin and eosin staining. X70.

(Fig. 1). These wrinkles were characteristically conspicuous in the organ which had been fixed in strong fixatives or had been collected at the time of rigor mortis.

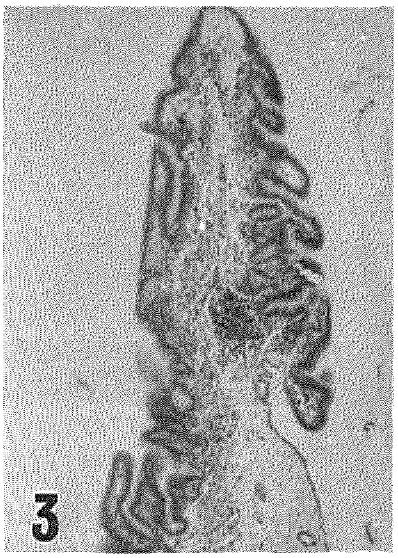
Microscopically, the infundibulum, like any other segment of the oviduct, consisted of four layers, mucosal, submucosal, muscular, and serosal, from inside to outside. The mucosa was thrown into low, longitudinal folds, unlike any other segment of the oviduct (Fig. 6). Cranially, it became lower and more irregular in arrangement. Caudally, it became higher and converted into high folds of the magnum. Surprisingly, the fimbrial lip was covered with two layers of the mucosal epithelium, visceral and parietal (Figs. 2 and 3). In it, the visceral mucosa extended over its free edge to the parietal side, depending on the width of the lip (Figs. 2, 3, and 7). The parietal mucosa merged abruptly into the serosa, forming a sharp angle (Figs. 3, 4, and 7). In the parietal side, the mucous folds lost their regularity and became round in shape (Fig. 7). The thickening of the lip was due to the formation of the double-layered mucosa.

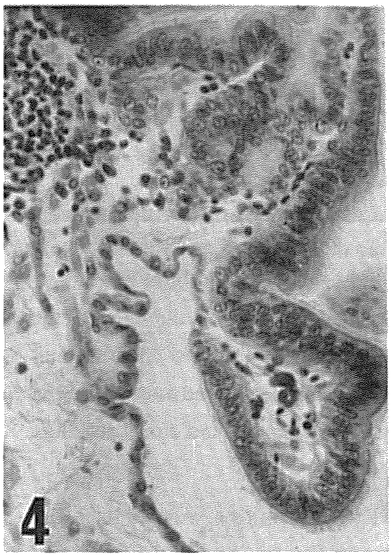
The mucosal epithelium of the infundibulum was generally composed of ciliated and nonciliated columnar cells forming a single layer. The fimbrial lip and its vicinity, however, was covered exculusively with ciliated cells with long and dense cilia (Figs. 8 and 9). Approaching the neck region, nonciliated cells increased in number. In the neck region, both types of cells were distributed alternately in even number.

The submucosa was composed of loose connective tissue. It was very poor in the fimbrial lip (Figs. 2 and 3). Lymphocytes and mast cells often scattered in it.

The infundibulum had a musculature less developed than the rest of the oviduct, although it presented a characteristic arrangement of muscle fibers (Figs. 2 and 3). Particularly, the fimbrial lip contained small amounts of muscle fibers, which ran vertically or obliquely to the plane of the abdominal ostium (Fig. 5). No circular musculature was present. The wall just below the lip had a considerably developed circular musculature, which was composed of thin, sheet-like bundles of fibers (Fig. 3). The longitudinal musculature first appeared near the neck region.

The serosa was constituted of flattened, polyhedral cells (Fig. 9).





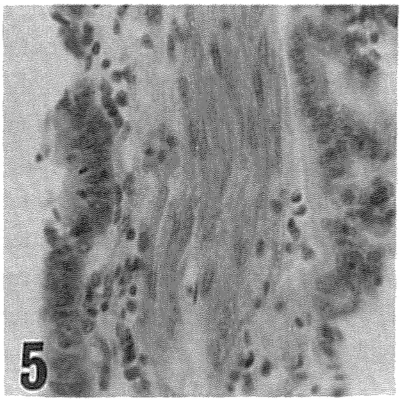
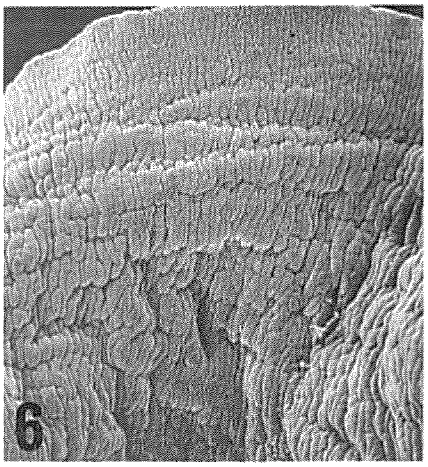
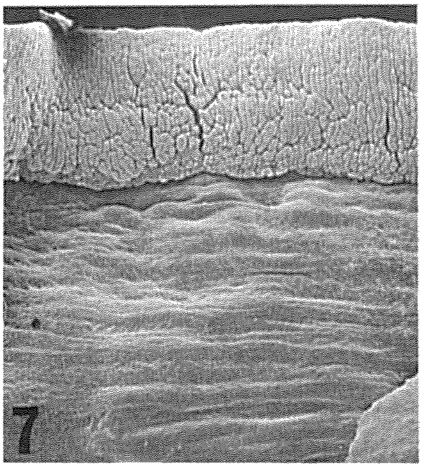


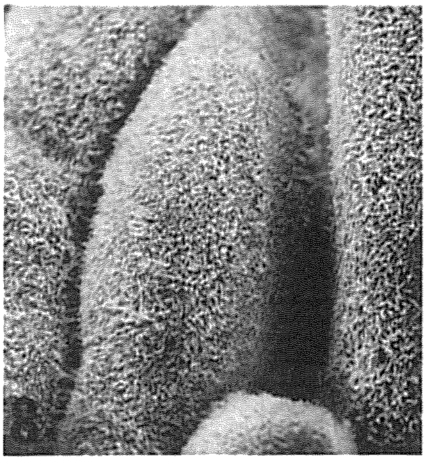
Fig. 3. Vertical section of the fimbrial lip. Between the mucosal layers, there is loose connective tissue containing a small amount of muscle bundles. The fimbrial lip is wide, since it has been cut obliquely. Hematoxylin and eosin staining. X 120.

Fig. 4. High-power magnification of Fig. 3. The transition from parietal mucosa to serosa is abrupt at an acute angle. Hematoxylin and eosin staining. X 400.

Fig. 5. Vertical section of the fimbrial lip. The muscle bundles are arranged longitudinally. Hematoxylin and eosin staining. X 400.







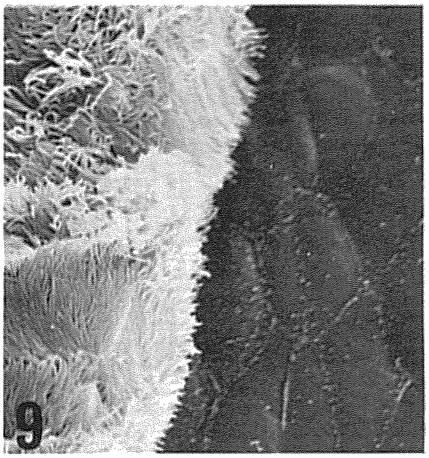


Fig. 6. The inner surface of the cranial part of the infundibulum. The mucosa is thrown into longitudinal folds. These folds become low and narrow cranially and high and wide caudally. ×25.

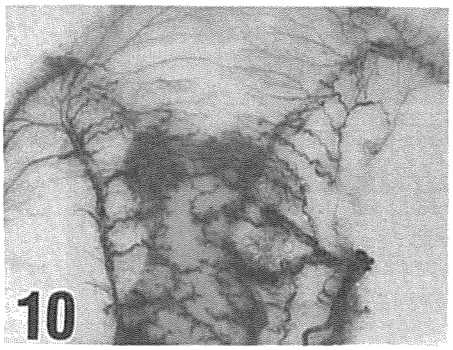
Fig. 7. The parietal surface of the cranial part of the infundibulum. The free margin is covered with a mucosal zone. This zone is the fimbrial lip. Mucosal folds are somewhat irregular. ×25.

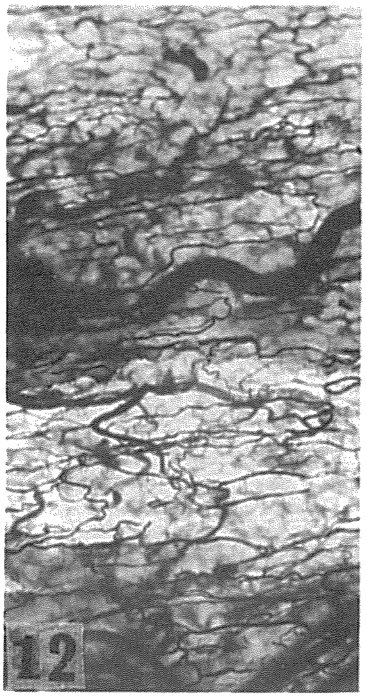
Fig. 8. High-power magnification of the cranial part of Fig. 6. The mucosal epithelium exclusively consists of cells with dense and long cilia. ×800.

Fig. 9. The transitional region from parietal mucosa to serosa. The mucosa is covered with ciliated cells only. The serosa is covered with polyhedral flat cells. ×2,000.

Blood supply

The blood supply to the oviduct has been reviewed by many authors[4-7],yet the descriptions usually were restricted to the general supply of large blood vessels. Detailed examination was reported only on the uterus by FREEDMAN and STURKIE (1963)[8] and HODGES (1965)[9], and on the uterovaginal segment by GILBERT and REYNOLDS et al. (1968)[10]. No available studies have been made on the blood supply of the infundibulum.





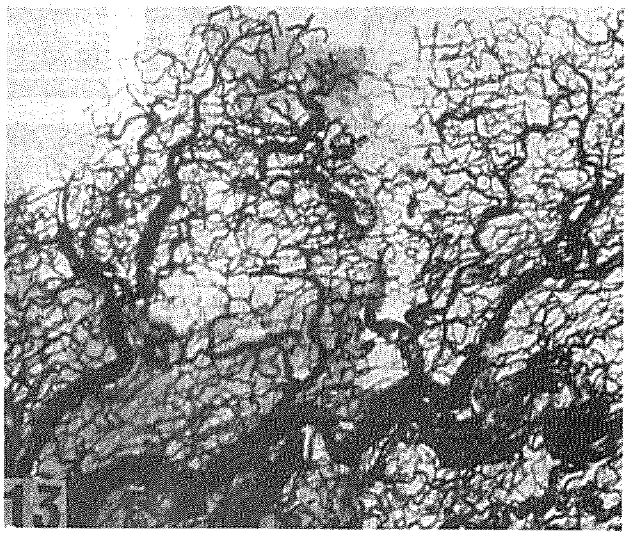


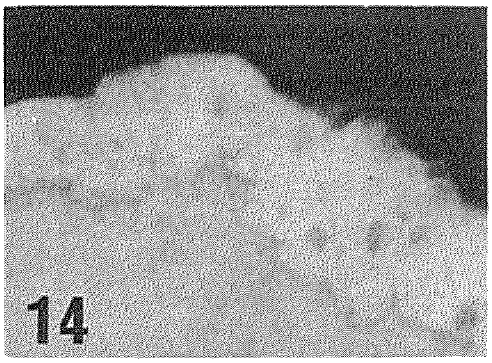
Fig. 10. The blood supply of the infundibulum. The infundibulum is supplied by branches from the marginal artery. The branches enter the infundibulum at somewhat regular intervals and run parallel to the line of the abdominal ostium.

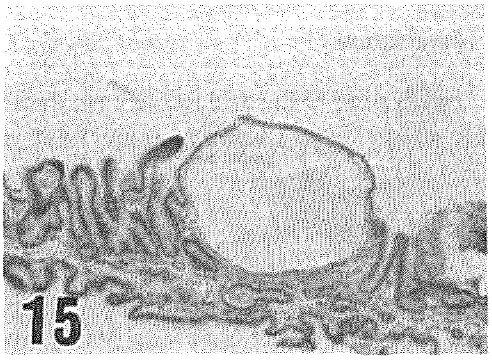
Fig. 11. Networks of blood vessels in the cranial region, including the fimbrial lip. The fimbrial lip is supplied ascending blood vessels found at somewhat regular intervals. ×20.

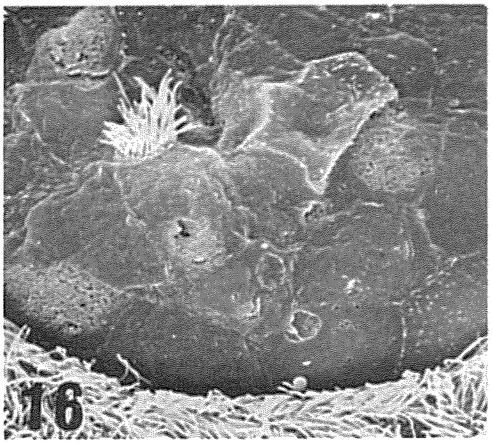
Fig. 12. High-power magnification of the networks of blood vessels in the region below the fimbrial lip. This region has relatively sparse networks of blood vessels. ×50.

Fig. 13. High-power magnification of the networks of blood vessels in the fimbrial lip. The lip has extensively dense networks of blood vessels. Compare with Fig. 12. ×50.

In the present study, the infundibulum was supplied by the anterior oviducal artery (HODGES, 1974)[5]. This artery passed through the dorsal ligament and was divided into the two main arteries, the anterior and the posterior one. The anterior oviducal artery ran upward along the infundibulum (the marginal artery), giving off a few small arteries to the infundibulum in its course (Fig. 10). After entering the infundibulum, these arteries ran crosswise to the long axis of the infundibulum, giving off lateral branches. These lateral branches anastomosed with one another, as well as with neighboring blood vessels, to form a relatively dense network of capillaries in the greater part of the infundibulum (Fig. 12). The uppermost cranial branche from the marginal artery ran along the lower edge of the fimbrial lip, giving off lateral branches towards the lip at regular intervals (Fig. 11). Again these ascending small arteries branched repeatedly to form a dense network of capillaries around the abdominal ostium (Fig. 13). Some of the







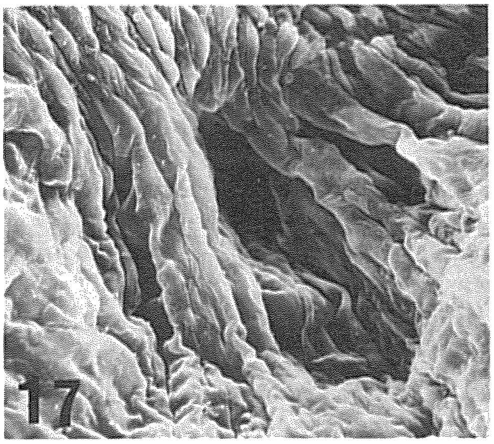


Fig. 14. Lymphocyst-like bulges appearing in the parietal mucosa of the fimbrial lip. They are various in size.

Fig. 15. Cross section of a lymphocyst-like bulge. It is enclosed by the mucosal epithelium and its lumen is scanty. Hematoxylin and eosin staining. ×120.

Fig. 16. A small-sized lymphocyst-like bulge enclosed by deciliated epithelial cells. ×2,200.

Fig. 17. Cut plane of a lymphocyst-like bulge. A lymph vessel-like canal is seen in its bottom. ×400.

branches from the marginal artery went directly across the infundibulum and formed the ventral marginal artery (Fig. 10). The arteries which supplied the infundibulum showed a typical coiled or curved form (Fig. 22).

On the other hand, the fimbrial lip and its vicinity appeared to be furnished richly with lymph vessels, although no direct evidence for that couled be given from the present study. In the fimbrial lip, lymphocyst-like protrusions varying in number and size bulged out from the parietal mucosal surface, when ovulation drew near (Fig. 14). They tneded to occur near both angles of the fimbrial lip. They were covered with a deciliated epithelium, and their lumen was scanty (Figs. 15 and 16). When their cross-section was observed, lymph vessel-like canals were often found in the wall (Fig. 17). Probably, the protrusions may have been formed by excessive engorgement of the vascular system.

Innervation

Innervation to the oviduct has been studied by a considerable number of researchers[4–7)], who usually made, however, only brief reports on the large bundles of nerve fibers.

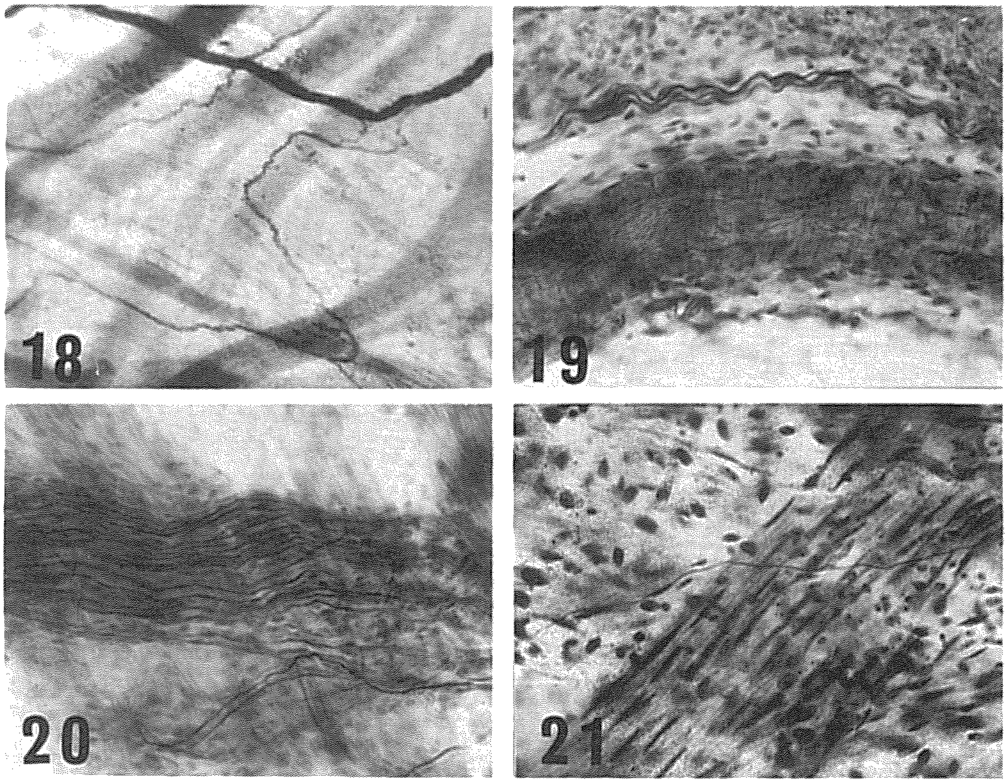


Fig. 18. Nerve bundles passing through the dorsal ligament of the oviduct. Bielschowsky's silver staining. ×50.

Fig. 19. A small nerve bundle running along a blood vessel in the infundibulum. Bielschowsky's silver staining. ×400.

Fig. 20. A large nerve bundle running in the tissue of the infundiblum. Bielschowsky's silver staining. ×400.

Fig. 21. A single nerve fiber ascending to the fimbrial lip. Bielschowsky's silver staining. ×400.

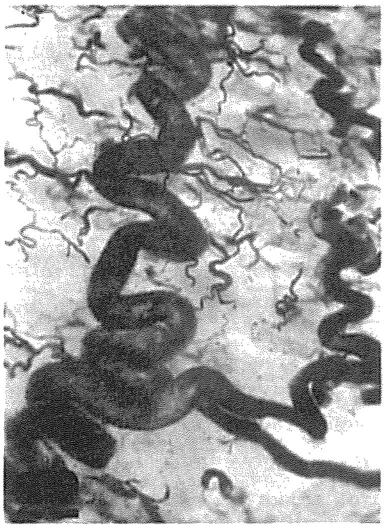
FREEDMAN and STURKIE (1963)[12] described the sympathetic innervation of the uterus in detail, and GILBERT and LAKE (1968)[13] that of the uterus and the vagina. Yet few mention was made of the innervation of the infundibulum.

The present study showed that the infundibulum was innervated well. A large number of nerve bundles, which probably have their origin in the ovarian plexus (MAUGER, 1941)[11], entered the infundibulum, passing through the dorsal ligament (Fig. 18). They ran together with the branches of the anterior oviducal artery mentioned above. After reaching the infundibulum, they ran chiefly just beneath the serosa with large blood vessels and divided repeatedly into small bundles in the course of their running (Figs. 19 and 20). Finally, they divided into single fibers. Some single fibers ran towards the fimbrial lip (Fig. 21). The present study could not demonstrat, however, nerve fibers terminating in the fimbria lip.

DISCUSSION

The mechanism of engulfing the shed ovum has not fully been determined until today. It is believed, however, that the movement of the infundibulum may play an important role in this mechanism. In the present morphological study, it was found that the infundibulum had several structural specifities which may have concern with the engulfing of the shed ovum.

Firstly, the free edge of the abdominal ostium of the infundibulum, which consists of a very thin and flexible wall, was surrounded by the fimbrial lip with a thickened and wrinkled wall. The presence of the fimbrial lip had been already detected by some



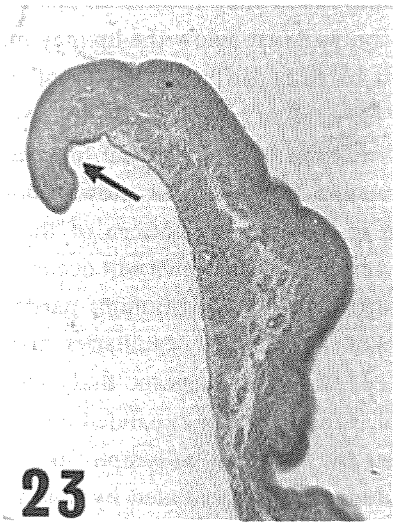


Fig. 22. A typical coiled artery appearing in the infundibulum.

Fig. 23. The cranial oviduct of 13-week-old pullet. The rudiment of the fimbrial lip has been formed. On the right is visceral mucosa. Arrow shows parietal mucosa. ×60.

workers[4,7]. Particularly, EITKEN (1971)[4] showed it in a photograph in his book. No previous workers, however, paid much attention to this structure.

As mentioned above, the fimbrial lip was composed of a double-layered mucosa, containing abundant blood vessels and few muscle bundles among them. This stange arrangement of the mucosa suggests the possibility that the fimbrial lip may grow in a rapid growing process of the oviduct before laying, but the rudiment of this lip had already been presented in 13-week-old pullets (Fig. 23). Therefore, it should be regarded as a native structure. The thickening of the fimbrial lip was due to the presence of a double-layered mucosa. It may serve to strengthen the flexible opening and to perform the delicate movement described below.

Secondly, the mucosa of the cranial infundibulum, including the fimbrial lip, was covered exclusively by ciliated cells with long and dense cilia. MIMURA (1937)[14] reported that the ciliary movement of the oviduct was vigorous and directed downward to the cloaca. Accordingly, the powerful ciliary movement of the ciliated cells around the abdominal ostium may help the shed ovum to be engulfed.

Thirdly, the oviduct is generally enclosed by an inner circular and an outer longitudinal musculature. In the fimbrial lip, however, only few muscle bundles ran vertically or obliquely to the plane of the abdominal ostium. No circular musculature was present. The infundibular wall below the level of the fimbrial lip had a well developed circular musculature forming sheet-like bundles.

Judging from the running pattern of the musculature, it is suggested that the fimbrial lip may move delicately to the direction of the long or oblique axis of the fimbrial lip, that this movement may involve an upward extension or transverse propagtion of the lip, and that the wall just below the lip may move transversely to constrict the infundibulum. These two or three different modes of movement that occur in the abdominal ostium may help the oviduct to engulf the shed ovum.

The wrinkling of the fimbrial lip and the transition with an acute angle from the parietal mucosa to the serosa shown above are considered to be brought about by the difference in the running pattern of the musculature. In other words, this aspect may represent the conditions which will occur in the stage of constriction of the infundibulum.

In addition, the infundibulum, particulary the fimbrial lip, was highly vascular. It had a dense network of capillaries and seemed to be rich in lymph vessels. This vascularized structure suggests that, when the infundibulum becomes engorged, the abdominal ostium may be expanded owing to severe strain. The strain of the ostium may be induced by the stasis of lymph fluid. The muscle movement and blood flow of the infundibulum may be regulated by neural control, since the infundibulum is well innervated, as mentioned above.

As for the mechanism of engulfing the shed ovum, EITKEN (1971)[4] described in his book that the infundibulum became extremely active at the time of ovulation, when the fimbriae surrounding the abdominal ostium were extended as a result of vascular engorgement aided by contraction of muscle fibers in the fimbriae and in the ventral ligament.

Although the precise mechanism of engulfing the shed ovum is not yet known, there is no doubt, however, that the movement of the infundibulum plays an essential role in the mechanism. The present findings may provide information on the behaviour of the infundibulum by the time when the shed ovum is engulfed. Ovulation occurs, however, at any site of the ovary. So that, how the movement of the infundibulum is oriented to the shed ovum remains an unsolved problem.

From the findings mentioned above, it can be concluded that the infundibulum, especially its fimbrial lip, plays a paramount role in the mechanism of the engulfing of the shed ovum. At the time of ovulation, the ostium of the infundibulum becomes larger by the engorgement of the vascular system. Simultaneously, it begins repeatedly to present two modes of movement; one is the extension and recession movement in the longitudinal direction, and the other is the wave-like movement in the transverse direction. When the shed ovum comes in contact with the fimbrial lip, the fimbrial movement extends to the surface of the ovum. Once the ovum is grasped partly by the fimbrial lip, thereafter it is engulfed progressively into the infundibulum by the constriction movement of the circular musculature.

SUMMARY

The infundibulum of the hen's oviduct was examined morphologically in connection with the action of engulfing the ovulated ovum. It was a funnel-shaped, thin-walled structure. Its abdominal ostium was edged by a specialized structure named the fimbrial lip. It was well-defined and had an enlarged wall 1.5–2.0 mm thick, consisting of a double-layered mucosa. In the ostium, the infundibular mucosa turned over the free margin of the fimbrial lip to the parietal side and merged into the serosa.

The mucosa of the fimbrial lip and its vicinity was thrown into low, longitudinal folds lined by ciliated epithelial cells only. Nearing to the neck region, mucous folds increased in height and nonciliated cells began to appear. The musculature of the infundibulum looked poorly developed, although its arrangement was characteristic. The fimbrial lip contained a few muscle bundles running parallel or obliquely to the long axis of the infundibulum, but no circular musculature was seen. The infundibular wall below the level of the fimbrial lip had a considerable amount of circular muscle fibers arranged in sheet-like bundles.

The infundibulum was abundantly supplied by blood vessels that originated in the ovarian artery. The fimbrial lip had a particularly dense network of capillaries and seemed to be furnished well with lymph vessels. The infundibulum was richly innervated by nerve bundles deriving from the ovarian plexus. On the bais of these structural findings of the infundibulum, discussions were held on the mechanism by which the ovulated ovum was engulfed by the oviduct through the infundibulum from a morphological point of view.

This work was supported in part by Grant-in-Aid for Scientific Research 00556186 from the Ministry of Education, Science and Culture of Japan.

REFERENCES

1) WARREN, D.C. and SCOTT, H. M. : *Science,* **80**, No. 2091, 461–462 (1934).
2) ——————: *Poult. Sci.,* 14, 195–207 (1935).
3) BRADLEY, O.C. and GRAHAME, T. : The Strucure of the Fowl, 4th Ed., 67–71, Oliver and Boyd, Edinburgh (1961).
4) AITKEN, R. N. C. : *In* "Physiology and Biochemistry of the Domestic Fowl" (Bell, D. J. and Freeman, B. M. eds.), Vol. 3, 1237–1289, Academic Press, London and New York (1971).
5) HODGES, R. G. : The Histology of the Fowl, 347–359, Academic Press, London, New York and San Francisco (1974).
6) KING, A. S. : *In* "Sisson and Grossman's The Anatomy of the Domestic Animals" (Getty, R. ed.), Vol. II, 1935–1951, Sauders Co., Philadelphia (1975).
7) GILBERT, A. B. : *In* "Form and Function in Birds" (King, A. S. and Mclelland, J. eds), Vol. I, 304–355, Academic Press, London, New York, Tront, Sidney and San Francisco (1979).
8) FREEDMAN, S. L. and STURKIE, P. D. : *Am. J. Anat.,* **111**, 1–7 (1963).
9) HODGES, R. D. : *J. Anat.,* **99**, 485–506 (1965).
10) GILBERT, A. B., RAYNOLDS, M. E., and LORENZ, F. W. : *J. Reprod. Fert.,* **17**, 305–310 (1968).
11) MAUGER, H. M. Jr. : *Am. J. vet. Res.,* 2, 447–452 (1941).
12) FREEDMAN, S. L. and STURKIE, P. D. : *Anat. Rec.,* **147**, 431–437 (1963).
13) GILBERT, A. B. and LAKE, P. E. : *J. Reprod. Fert.,* 5, 41–48 (1963).
14) MIMURA, H. : *Folia anat. jap.,* **15**, 287–259 (1937).

鶏の卵管漏斗部の局所構造，とくに卵子の取り込み機構との関連において

藤井俊策・吉村幸則・岡本敏一・田村達堂

排卵卵子は卵管腹腔口を通って卵管に取り込まれるのであるが，その機構はほとんど知られていない。本研究は鶏卵子が卵管内に取り込まれる機構を形態学的観点から明らかにするために，卵管漏斗部の構造を調べた。所見は以下のとおりであった。

1. 卵管近位端の漏斗部は狭義の漏斗部と基部の2部分に区別された。狭義の漏斗部はラッパ状に拡張し，極めて薄い壁構造を呈していた。漏斗部遊離端は約1.5～2㎜幅の漏斗采と名付けられる肥厚して皺の多い壁によって額取られていた。この采部は2重の粘膜を具えており，臓側の粘膜が遊離端を越えて漿膜側に伸びて形成されていた。
2. 采部の粘膜は低くい縦走ヒダによって被われていた。粘膜ヒダは漏斗基部に移行するにつれて幅と高さを増した。粘膜上皮は卵管の他の部とは異なり，繊毛細胞のみから成っていた。さらに，采部の粘膜下織は疎性の結合組織であって，少量の筋線維束を含んでいた。筋線維は漏斗部の長軸と平行に，あるいは斜め方向に走っていた。
3. 卵管漏斗部には卵巣動脈に由来する前卵管動脈が分布していた。前卵管動脈からの分枝は漏斗采部に極めて密性な毛細血管網を形成していた。また，采部には豊富なリンパ管の分布を示唆するリンパ様嚢胞がしばしば認められた。このリンパ様嚢胞は排卵前の漏斗部に多く認められる傾向があった。
4. 卵管漏斗部は卵巣神経叢に由来する豊富な神経によって支配されていた。上記の卵管漏斗部とくに漏斗采の構造的特徴に基いて，卵子の取り込み機構が漏斗部の形態学的見地から論議された。