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Histological Studies on the Gametogenesis and Reproductive Cycle of the Hard Clam, *Meretrix lusoria*

Ju Ha Lee

School of Life Science, College of Natural Science and Engineering, Jeonju University, Jeonju 560-759, Korea

= 국문요약 =

백합, *Meretrix lusoria*의 생식세포형성과정 및 생식주기에 관한 조직학적 연구

이 주 하

전주대학교 이공대학 생명과학부

전북 김제시 심포에서, 1994년 1월부터 12월까지 월별로 채집된 백합 *Meretrix lusoria*의 생식세포형성과정 및 생식주기를, 조직학적으로 조사한 결과는 다음과 같다.

백합은 자웅이체이고 난생을 하며, 생식소는 내장낭의 간중장선의 하부로부터 족부의 근육부근까지 분포하며, 성숙되면 팽대되지만 방란, 방정 후에는 위축된다. 생식소는 많은 난자형성여포들과 정자형성여포들로 구성되어 있다. 여포에는 호산성 세포와 미분화간충직들이 들어 있는데, 이들은 초기 생식세포의 영양물질로 제공되고 있으며, 생식소가 발달함에 따라 점차 소실된다. 초기 활성기의 난원세포는 직경 10 μm 내외이며, 초기 난모세포는 난병을 여포벽에 부착한 채 성장을 하여 70 μm 내외의 완숙란으로 된다. 정원세포가 성장을 하여 정모세포, 정세포를 거쳐 변태를 마친 정자는, 정자형성소낭의 중앙 내강에 정자속을 형성한다. 방란, 방정을 마친 생식소는, 일부 미방출된 생식세포가 퇴화 흡수되면서 비활성기를 지나 이듬해 수온상승과 더불어 새로운 발달을 시작한다.

생식주기는 연속적인 5단계로 구분할 수 있는데, 초기 활성기(1-3월), 후기 활성기(2-5월), 완숙기(4-8월), 부분 방출기(6-9월), 퇴화 및 비활성기(9-2월)로 구분할 수 있다. 산란은 6월(22℃)부터 9월(25℃)까지 지속되지만, 산란성기는 7월(27℃)-8월(28℃)이다. 생식소지수는 1월에 0.58을 나타내며 5월에 4.60으로 최대값을 나타낸 후, 6월부터 점차 감소하기 시작하여 12월과 1월에는 1.0 미만에 머무른다.

Key words: ***Meretrix lusoria,*** **Gametogenesis, Reproductive cycle**

INTRODUCTION

M. lusoria is one of the commercially important edible bivalves and the very important aquatic living resources inhabiting in silty sand in the tidal flats and subtidal zones of Korea, Japan, China, and is found in depths up to 10 to 20 meters from the estuary to foreshore (Ikuta, 1988a).

Previously, there have been many studies on the mortality (Chang *et al.*, 1976), artificial fertilization and development (Choi and Song, 1974), early embryonic development and growth (Choi, 1975), effects of crude oil ingredients on the development and oxygen uptake (Lee *et al.*, 1975), acute toxicity tests on some heavy metals (Ikuta, 1988a, b), oxygen consumption and nitrogen excretion (Lee and Chin, 1986), nitrogen metabolism (Lee, 1989), environmental survey on the cultivation ground (Lee and Kim, 1991), effects of some hazardous substances on the physiological function (Lee, 1991), and the spawning season (Taki, 1949; Choi and Song, 1974; Ikuta, 1988a). However, I could not find out any histological study on the gonad development, the gametogenesis, and the reproductive cycle of this species.

Because of the marine pollutions and changes of the marine environments, the annual production of this species in the vicinity of Simpo, Kimje coast has been gradually decreased since the early 1970's. And because of a exploitation of the tidal flats, the habitats of the species have been also gradually decreased. Therefore, as a basic biological study for maintenance and control of natural resources on the hard clam, *M. lusoria*, the gametogenesis, the reproductive cycle, the spawning season, and the gonad index of the species were investigated by histological observations and morphometric data.

MATERIALS AND METHODS

Specimens of *M. lusoria* were collected monthly from natural intertidal population in the vicinity of Simpo, Kimje coast, Chollabukdo in Korea from January to December 1994 (Fig. 1). The materials were used monthly 30 to 40 individuals for this study. The collected samples were transported alive to the laboratory, and then shell height, shell length, total weight, meat weight, and shell weight of all the specimens were measured. And then the gonadal portion located at the visceral cavity of each specimen was cut into 5 to 7 mm in thickness and fixed in Bouin's solution for histological examination. The fixed specimens were subjected to

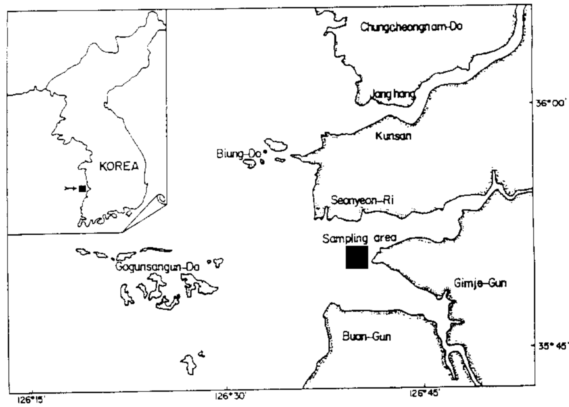

Fig. 1. Map showing the sampling site.

standard histological methods (dehydration in ethyl alcohol and embedding in paraffin). The embedded specimens were serially sectioned into 5 to 6 μm in thickness with a microtome. The serial sections were counterstained with Bohmer's hematoxylin and 1% alcoholic eosin for light microscopic observations.

RESULTS

1. Position and structure of the gonads

M. lusoria is oviparous and dioecious in sex. The gonads are situated between the lower part of mid-intestinal glands and connective tissues of the foot (Fig. 2).

When the gonads were fully ripe, the volumes of the gonads were expanded and the external features of female and male gonad portions showed milky white in color, therefore, it was hard to distinguish their sexes by the external features. After spawning, they were shrunken. The gonads are composed of a number of oogenic and spermatogenic follicles.

2. Gonadal phase and reproductive cycle

On the bases of the monthly changes of the morphological features and the sizes of the germ cells during gametogenesis in the gonads, gonadal phases of *M. lusoria* can be classified into five successive phases: early active, late active, ripe,

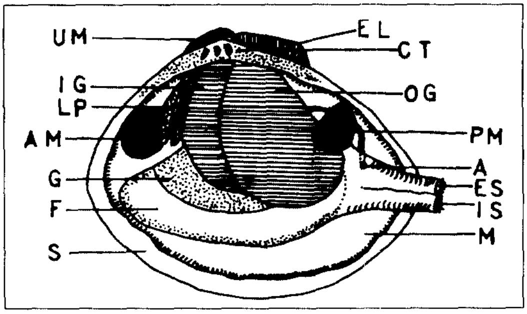

Fig. 2. Anatomy of *M. lusoria* with left shell removed.
A: Anus, AM: Anterior adductor muscle, CT: Cardinal tooth, ES: Exhalant siphon, EL: External ligament, F: Foot, G: Gonad, IG: Inner gill, IS: Inhalant siphon, LP: Labial pulp, M: Mantle, OG: Outer gill, PM: Posterior adductor muscle, S: Shell, UM: Umbo.

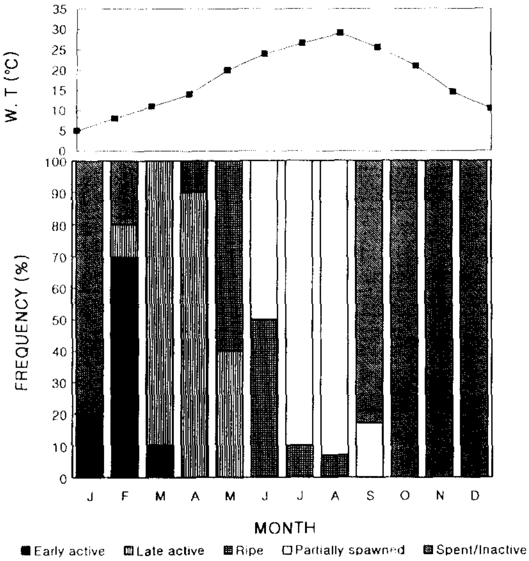

Fig. 3. Frequency of gonadal phases for *M. lusoria* and monthly changes of mean seawater temperature from January to December 1994.

partially spawned, and spent/inactive stages as shown in Fig. 3.

1) Early active stage

In females, oogonia actively multiply on the follicular wall, and every oogonium measuring about 10 μm in diameter has a distinct nucleus containing a nucleolus in its center. The oogonia grow into the early oocytes, while the cytoplasm of the early oocytes is very poor. At this time, a great number of undifferentiated mesenchymal tissues and eosinophilic cells can be also seen near the follicular walls (Pl. I-Fig. 1).

In males, the spermatogonia actively multiply on the follicular wall. The spermatogonia grow into the spermatocytes. At this time, undifferentiated mesenchymal tissues, and eosinophilic cells can be seen on the follicular wall. As already shown in the oogonium, spermatogonium also has a large nucleus containing a nucleolus in its center (Pl. II-Fig. 7).

In both females and males, the individuals in the early active stage appear from January to March.

2) Late active stage

In females, as the growth of the follicular walls advances, many oocytes are attached to the follicular walls by an egg-stalk. At this time, an oocyte has larger cytoplasm than that of early active stage, and the nucleus enlarges and becomes a germinal vesicle with a small nucleolus. The germinal vesicle has the conspicuous amphinucleolus, basophilic plasmosome and eosinophilic karyosome (Pl. I-Fig. 2).

In males, as the growth of the follicular walls advances, the spermatogonia grow into the spermatocytes, and then the spermatocytes grow into the spermatids and move toward the central lumen. At this time, most of spermatogenic cells, that is, spermatogonia, spermatocytes, and spermatids are seen in the follicles (Pl. II-Fig. 8).

In both females and males, the individuals in the late active stage appear from January to May.

3) Ripe stage

In females, a ripe oocyte measuring about 70 μm in diameter becomes round or oval in shape, and each follicle is filled up the mature oocytes in the center of the lumen (Pl. I -Fig. 3). At this time, the follicular walls become very thin, and the undifferentiated mesenchymal tissues and eosinophilic cells are very fewer than those of late active stage. Ripe oocyte has a number of yolk granules (Pl. I -Fig. 4).

In males, spermatocytes and spermatids are very decreased in number, while the spermatozoa which finished up the spermiogenesis are uniform in size and fill up the lumen of the follicle (Pl. II -Figs. 9 and 10). At this time, the follicular walls become very thin, and the undifferentiated mesenchymal tissues and eosinophilic cells are very fewer than those of late active stage.

In both females and males, the individuals in the ripe stage appear from April to August.

4) Partially spawned stage

In females, as spawning occurs, a few ripe undischarged oocytes remain in the follicles, while the lumina of the follicles become empty. After spawning, the undischarged oocytes in the lumen are subjected to the cytolysis. But the late growing oocytes are still on the follicular walls (Pl. I -Fig. 5).

In males, as the spawning occurs, most of spermatozoa in the lumina of the follicles are discharged into the surrounding environment, therefore the lumina of the follicles become considerably empty. But a number of spermatozoa, spermatids, and spermatocytes are still remained in the lumina (Pl. II -Fig. 11).

In both females and males, the spawning occurs from June to September above 22℃, and the main spawning appears from July (27℃) to August (28℃).

5) Spent/Inactive stage

In females, after spawning, the undischarged oocytes in the lumen of the follicle undergo the cytolysis, and each follicle is also contracted and degenerated. And then the newly formed follicles appear in the ovary, and the oogonia, the eosinophilic cells, and the undifferentiated mesenchymal tissues also appear in the follicular walls (Pl. I-Fig. 6).

In males, the undischarged spermatozoa in the lumen of the follicle are subjected to the cytolysis, and each follicle is also contracted and degenerated. The early spermatogonia, the eosinophilic cells, and the undifferentiated mesenchymal tissues appear in the newly formed follicular walls(Pl. II -Fig. 12).

In both females and males, the individuals in the spent/inactive stage appear from September to February of the next year.

3. Monthly changes of the gonad index

On the bases of the histological observations (Hillman, 1993), the monthly changes in the gonad indices appear 0.58 in January, and then gradually increase and reach the maximum value (4.60) in May (Fig. 4). Thereafter, their values gradually decrease from June to August, and then the values abruptly decrease below 1.0 from August to January of the next year.

DISCUSSION

Boolootian *et al.* (1962) reported that the breeding habits of molluscs divide into three large categories, that is, year-round breeders which spawn throughout the year, winter breeders which spawn from the end of fall to the beginning of spring of the following year, and summer breeders which spawn from the end of spring to the beginning of fall. In present study, it seems that *M. lusoria* belongs to the summer breeder by the histological observations.

The nutritive materials concerning with gonad development in marine invertebrates were reported by many authors (Holland and Giese, 1965; Chatylmne, 1969; Lee, 1980; Chang and Lee, 1982;

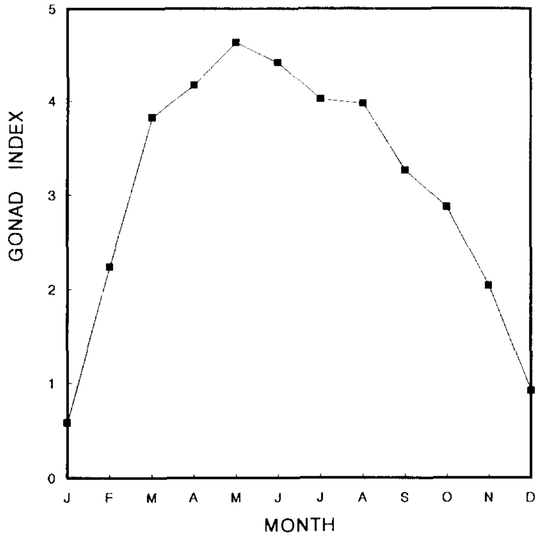

Fig. 4. Monthly changes of mean gonad indices (GI) for *M. lusoria* from January to December 1994.

Chung *et al.*, 1988).

The eosinophilic cells and undifferentiated mesenchymal tissues abunduntly appear on the walls of oogenic and spermatogenic follicles in the early active stage, and then gradually disappear with the further gonad developments, Chang and Lee (1982) described that these cells and tissues could be considered to be a kind of nutritive materials. Because the same results as above appeared in the present study, I also consider them the nutritive materials concerning with formation and development of the gametogenesis during the early phases.

The nucleus of oocyte in the late egg-stalk stage, that is, late active stage has the amphinucleolus (plasmosome and karyosome). After the amphinucleolus formation, karyosome is separated from it and extruded into the germinal vesicle, then into the cytoplasm (Nishikawa *et al.*, 1967). And the nucleus of oocyte in late active stage enlarges and has amphinucleolus involving in vitellogenesis. Especially, karyosome is stained uniformly with eosin, which separated from amphinucleolus, and extruded into the cytoplasm through the nuclear envelope (Chung *et al.* 1994). Results in the present study are also similar to the authors above mentioned. Yamamoto (1956) reported that the karyosome which is extruded into the cytoplasm involve indirectly in vitellogenesis.

Loosanoff (1962) stated that in some marine shellfishes which are fertilized outside the body, their gonad passes into the spent/inactive stage after spawning, and the germ cells are not found any more in the gonad at this stage. While many authors stated (Webber and Giese, 1969; Hayashi, 1980; Lee, 1980) that the gonads of abalones immediately pass into recovery stage without the spent/inactive stage. Especially, Ikuta (1988b) reported that in the Japanese *M. lusoria*, there is the difference between the female and the male, namely, the former has the recovery stage, but the latter the resting stage. In the present study, after spawning, the undischarged germ cells in the gonads of *M. lusoria* are gradually degenerated, and the oogenic and spermatogenic follicles withered too. After the spent/inactive stage, the walls of the newly formed oogenic and spermatogenic follicles are activated again, and then the newly formed germ cells appear on the follicular walls. Therefore, the species seems to pass into the spent/inactive stage after the spawning.

Many factors for gametogenesis and spawning in mollusks have been discussed. Taki (1949) described that the low specific gravity of seawater suppresses the spawning of *M. lusoria*. Griffiths (1977) reported that the breeding seasons of marine bivalves are closely related to the abundance of food for adults and their planktotrophic larvae. Kennedy and Krantz (1982) described that the duration of spawning varies geographically, that is, long duration of spawning are shown at lower latitude localities and short duration of spawning at higher latitude localities. And Webber and Giese (1969) and Brousseau (1995) reported that the role of seawater temperature in triggering release of gametes and gonad developments seems not to be clear.

While several authors (Chang and Lee, 1982; Chung *et al.*, 1988, 1994; Chung and Kim, 1994) reported that in the relations between the environmental seawater temperature of the habitat and the gonad development, the gonad development is closely related to the raise of the temperature. In the present study, the gonad maturation of the species is accompanied with rising temperature, the spawning occurs from June (22℃) to September (25℃), and the main spawning appears from July (27℃) to August (28℃). These results are similar to many reports above mentioned. Therefore, it is assumed that the spawning season and gonad development are closely related to the seawater temperature. As shown in Table 1, the spawning of *M. lusoria* occurs once a year, but some variations of the spawning periods and main spawning seasons among the various localities seem to be mainly related to the geographical differences of the water temperature, specific gravity of seawater, abundance of food, latitude, and some other environmental factors during a year in given localities.

Brousseau (1995) reported that the gonad indices of *Crassostrea virginica* reach the maximum value during the ripe stage and decrease precipitously during the spawning phase. The indices of *Haliotis diversicolor aquatilis* (Okuno *et al.*, 1978) and *Turbo* (*Batillus*) *cornutus* (Yamamoto and Yamakawa, 1985) were also similar to *Crassostrea virginica*. In the present study, the gonad indices gradually increase and reach the maximum value (4.60) in May, and then the value gradually decrease from June (4.40) to September (3.26). Therefore, it is assumed that the spawning season is from June to September, and monthly changes in the indices nearly correspond with the gonadal phases.

SUMMARY

M. lusoria is oviparous and dioecious in sex. The gonads are located between the lower part of mid-intestinal glands and the connective tissues of the foot. When the gonads are ripe, they extend their volume and after spawning, they are shrunken. The gonads are composed of a number of zoogenic and spermatogenic follicles.

The eosinophilic cells and undifferentiated mesenchymal tissues in the follicles function as nutritive materials for germ cells in the immature phases. With the further development of gonad, these cells and tissues gradually disappear.

The oogonia during early active stage are about 10 μm in diameter. The growing oocytes with their egg-stalk attach to the follicular wall, and then they grow into ripe eggs of nearly 70 μm in diameter. Spermatogonia gradually grow into spermatocytes and spermatids, and then sperms finished spermiogenesis migrate toward the center of the lumen and they form the sperm bundles in the lumen.

After spawning, undischarged oocytes and sperms in the lumen are degenerated and absorbed, and oogenic and spermatogenic follicles are also shrunken and degenerated.

Reproductive cycle of *M. lusoria* can be classified

Table 1. Comparison of the spawning seasons and seawater temperature in each locality for *M. lusoria*.

Spawning seasons			W.T (℃)	Locality	Author
Initiation	Peak	Termination			
Jun.	Jul.	Oct.	20-30	Haneda, Tokoy Bay (Japan)	Taki, 1949
Jun.	Aug.	Oct.	26-30	Chiba, Tokoy Bay (Japan)	Taki, 1949
Jun.	Jul.	Aug.	24-29	Anmyn Island (Korea)	Choi and Song, 1974
Jun.		Aug.	23-28	Seto Inland Sea (Japan)	Ikuta, 1988a
Jun.	Jul. & Aug.	Sep.	22-28	Kimje (Korea)	Present study

into five successive phases: early active (January to March), late active (February to May), ripe (April to August), partially spawned (June to September), and spent/inactive (September to February).

The spawning occurs from June (22℃) to September (25℃), and the main spawning appears from July (27℃) to August (28℃).

Monthly changes in the gonad index values exhibit 0.58 in January, the peak 4.60 in May, and then their values gradually decrease from June. The values exhibit below 1.0 between December and January.

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EXPLANATION OF PLATES

Plate I

Fig. 1. Section of the oogenic follicles in the early active stage. X 400. Note the multiplying small oogonia on the follicular walls, early oocytes, eosinophilic cells, and undifferentiated mesenchymal tissues.

Fig. 2. Section of the oogenic follicles in the late active stage. X 400. Note the growing oocytes and egg-stalk of oocytes attaching to basement membranes of the follicles. Nucleus contains the conspicuous amphinucleolus, basophilic plasmosome and eosinophilic karyosome.

Fig. 3. Section of the oogenic follicles in the ripe stage. X 200. The follicular lumina are filled with the mature oocytes.

Fig. 4. Section of the oogenic follicles in the same stage as above. X 400.

Fig. 5. Section of the oogenic follicles in the partially spawned stage. X 100. Note a few undischarged oocytes and residual substances in the follicles after spawning.

Fig. 6. Section of the oogenic follicles in the spent/inactive stage. X 200. Note the gradual disappearance of the follicles.

Plate II

Fig. 7. Section of the spermatogenic follicles in the early active stage. X 400. Note a number of small spermatogonia, undifferentiated mesenchymal tissues, and eosinophilic cells appeared along the follicular walls.

Fig. 8. Section of the spermatogenic follicles in the late active stage. X 100. Note the follicles contained spermatogenic cells in various stages of the development.

Fig. 9. Section of the spermatogenic follicles in the ripe stage. X 100. The follicles contain a great number of ripe spermatozoa.

Fig. 10. Section of the spermatogenic follicles in the same stage as above. X 200.

Fig. 11. Section of the spermatogenic follicles in the partially spawned stage. X 200. Note a number of undischarged spermatozoa and residual substances in the follicles.

Fig. 12. Section of the spermatogenic follicles in the spent/inactive stage. X 200. Note the disintegrating tissues and follicles of the testis.

PLATE I

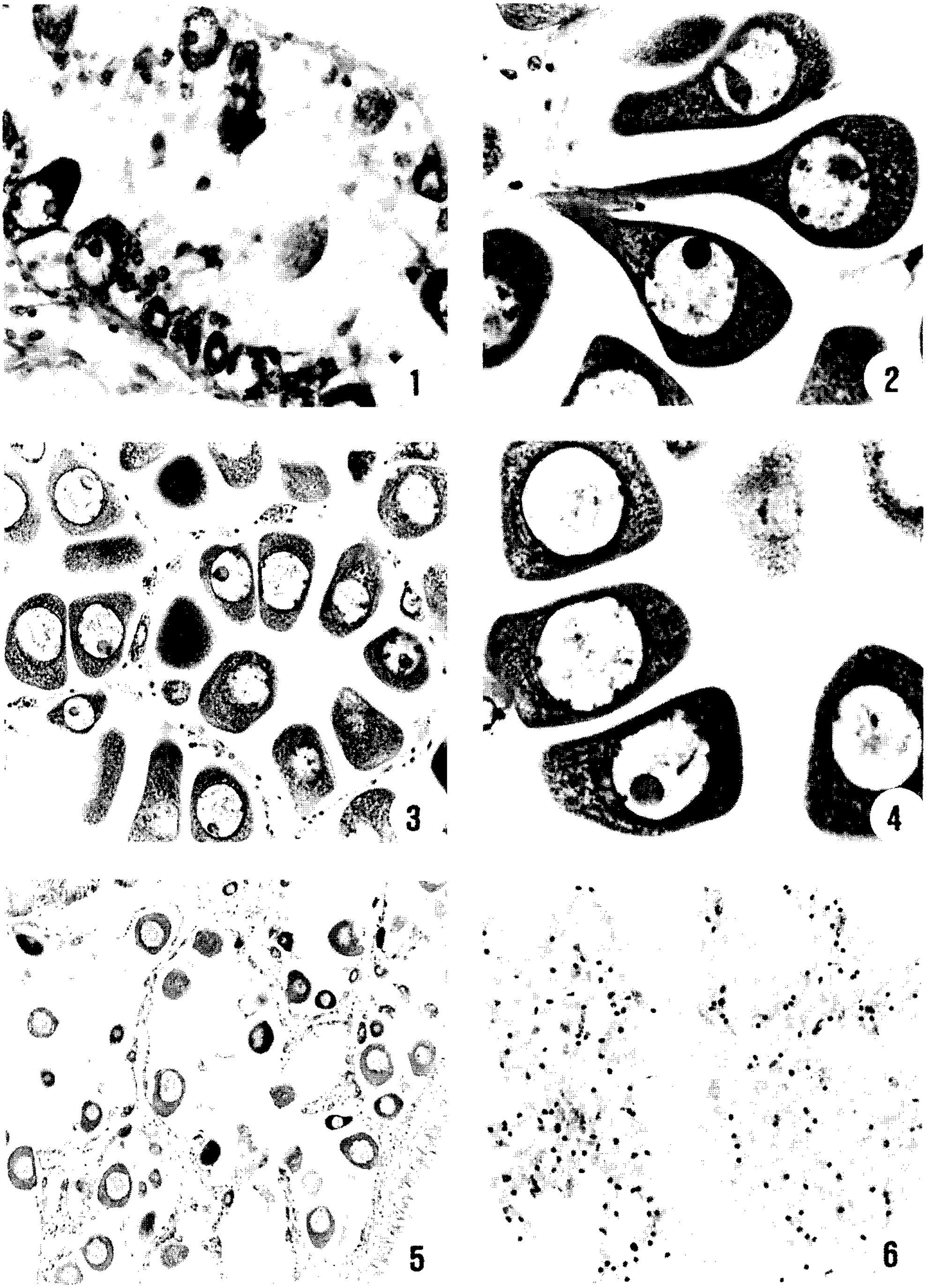

PLATE II