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Eyjólfur Friðgeirsson

Observations on spawning behaviour and embryonic development of the Icelandic capelin

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By

EYJÓLFUR FRIÐGEIRSSON

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Introduction

The behaviour of the capelin at beach spawning has been described in detail e.g. by TEMPELMAN (1948). The behaviour of the capelin at offshore spawning is less known, but most of the capelin spawning in the Barents Sea — (MÖLLER and OLSEN 1962 and PROKHOROV 1965), at Iceland — (VILHJÁLMSSON 1968 and 1974) and part of the spawning at Newfoundland — (TEMPLEMAN 1948 and PITT 1958) takes place offshore.

In this paper the author attemps to add to the knowledge regarding the offshore spawning capelin by describing observations on spawning of the Icelandic capelin in an aquarium.

POZDNJAKOV (1960) describes in detail the development of the Barents Sea capelin. The embryological descriptions in this paper are similar, but possibly more detailed in some aspects, and it is hoped that they will add to the knowledge of the capelin.

The division into periods and stages that has been adopted is, in the author's view, the clearest and most accurate and most common to all the teleost fishes and can be recommended in ichtyoplanktonic and embryological descriptions.

Material and methods

The studies on capelin described in the present paper were carried out at the Aquarium in Vestmannaeyjar from late February to the beginning of May 1974 and 1975.

The behaviour of the capelin was observed in the Aquarium's display tanks. These tanks measure 1.50×1.75 m. with a water level of 1 m. The front side is made of plexiglass. Half the bottom of the tank was covered with lava sand, which is common substrate inside the 50 m. depth level at the S-coast of Iceland and half of it was covered with lava boulders. Sea water was obtained from a 30 m. deep well near the Aquarium. The sea water had a constant temperature of 7.2°C and the salinity was about 29.5‰. The capelin in the Aquarium were brought in from purse seiners fishing in the vicinity.

For embryological studies the author used dry fertilized eggs that were made to stick to the bottom of Petri dishes. The Petri dishes containing eggs were then kept in running sea water of 7.2°C constant temperature and 29.5‰ salinity in the laboratory of the Aquarium.

Series of eggs fertilized on 1—2 March 1974 were studied intensively. Studies were also carried out on a batch of eggs fertilized somewhat later (19—20 March). In 1975 the studies were concentrated on eggs fertilized from 5—7 March. In both years eggs from spawning that took place in the display tanks of the Aquarium were also studied.

It is known that the capelin spawn at S-, SW- and W-Iceland and spawning also occurs at N- and NE-Iceland, (H. Vilhjálmsson 1968, 1974 and H. Vilhjálmsson and E. Friðgirsson 1975). At the S- and SW-coast of Iceland the salinity during the spawning season of the capelin is about 35‰. The environmental conditions of the spawning have not yet been investigated sufficiently. Therefore it is impossible to say whether spawning takes place under natural conditions at such low salinity as in the Aquarium, but it might be so since at spawning the capelin move into shallower waters containing considerable runoff from land.

At the Aquarium the capelin spawned successfully at 29.5‰ salinity and no effect of this low salinity could be traced on the development of the eggs. In 1974 one series of eggs was kept in sea water brought in from the coast with normal salinity (about 35‰) and constant temperature of 7.2°C. Comparison with the series kept in 29.5‰ salinity showed no difference in development. In view of this it is here taken for granted that salinity of 29.5‰ does not affect the development of the capelin eggs.

Drawings of eggs and larval stages were made both in 1974 and 1975, but the photographs were all taken in 1975.

Spawning behaviour of the capelin

In 1974 observations on the capelin in the Aquarium started on 20 February. The capelin were at that time kept in two display tanks, 100—150 in each. Both sexes were equally represented, i.e. the ratio was about 50:50. When observations began, the capelin had been kept for two weeks in one tank but for three weeks in the other. All phases of the spawning could be observed among these capelin.

In 1975 capelin could not be obtained until 3 March. About 50 fish were kept in one tank, only 10 of which were females. On capture these capelin were on the point of spawning and first spawning occurred on 4 March. Intensive observations on these capelin were carried out and at the same time these were filmed for further studies later on.

The spawning behaviour of the capelin can be divided into four distinct phases: 1. Migration behaviour. 2. Behaviour at preparation for spawning. 3. Spawning behaviour. 4. Behaviour after spawning.

1. Migration behaviour.

This phase could be observed in 1974, but in 1975 it was over already. When observations began in 1974 the capelin seemed quite at ease and to have recovered from the changes in environment during and after transportation. The capelin formed shoals and swam slowly in clockwise circles occupying all the space in the

Capelin in tank. Males and a few females at interwal between spawning periods.

display tanks. No irregularities in the distribution were observed. At a sudden light or other unexpected stimuli the shoal dispersed and this reaction was exhibited without exeption by all the individuals. In phases 2, 3 and 4, reaction to such effects was clearly variable and individual. Occasionally the capelin were scattered but mostly they were in shoals.

The main character of this phase is random mixture of both sexes, formation of shoals and migration.

Morphological characters: increasing maturity of both sexes, increasing spawning ridges of the male and light (pelagic) colour.

2. Behaviour during preparation for spawning.

Three days before the first spawning it was noticed that the males left the shoal one by one or in small groups and swam searchingly along the bottom without touching it but after a while returning to the shoal. This behaviour gradually became more frequent until spawning began. As a result of this the shoal gradually broke up and finally dispersed. The females retained some semblance of a shoal, but it was obvious that they were already ripe and swam heavily. If the females lost balance or stopped swimming they sank. The swimming in circles (migration) gradually stopped and the fish created a formless group. Until spawning the separation of the sexes gradually became more obvious and finally complete.

The main character of this phase is the gradual separation of the sexes, the breakdown of the shoal formation and the end of migration.

Morphological character: ripeness of both sexes, full development of spawning ridges on the male, enlargement of the anal fin and darkening of the sides of his head and back.

3. Spawning behaviour.

In 1974 first spawning occurred on 1 March and continued until 8 March. In 1975 spawning started on 4 March and lasted to 14 March.

The male is the active part in the spawning. Spawning began when the males assembled just above the bottom and started looking for ready females. The females stayed above the males. One by one the females swam into the group of males. One of the males made for her, thrust himself up to her sideways and then in a sense held her to his side. The distended abdomen of the female fits quite well into the concave side of the male formed by his spawning ridge and the lower half of his abdomen. After mating and during copulation male and female were joined and looked like one fish. They moved rapidly digging their abdomen ½ to 1 cm into the bottom by rapid movements. In this way they moved along the bottom, whirling sand and eggs outwards and upwards on both sides. The eggs were evenly spread over a 10 to 15 cm wide stretch of the bottom. The importance of the big anal fin of the male in dispersing the eggs was obvious. Copulation lasted only 1 to 2 seconds and in that time the couple did not care if they ran into a hindrance and thus the spawning process continued even though a stone on the bottom blocked the way. After copulation the mating couple separated. The female was spent and thin, but in appearance the male looked like before the copulation. The female swam up from the bottom without direction, but the male soon returned to the group of males and resumed spawning behaviour.

Obviously the female spends all her roe in one copulation, but the male seems to be able to mate more than once.

In the Aquarium spawning took place in spawning periods. A spawning period — active search for a ripe female — lasted in most cases 10 or 15 minutes and then gradually subsided. In each spawning period 1 to 3 matings took place. In between the capelin behaved as in phase two and the sexes kept apart. Occasionally a spawning period could be initiated by squeezing sperm from 1 or 2 males into the tank.

In 1975 mating of one female and two males was observed, but this never occurred in 1974 when the initial sex ratio was even.

During the spawning periods the backs of the males and the sides of their heads turned pitch-black becoming somewhat lighter soon afterwards.

The main character of this phase is complete separation of the sexes, the spawning periods of the males and mating.

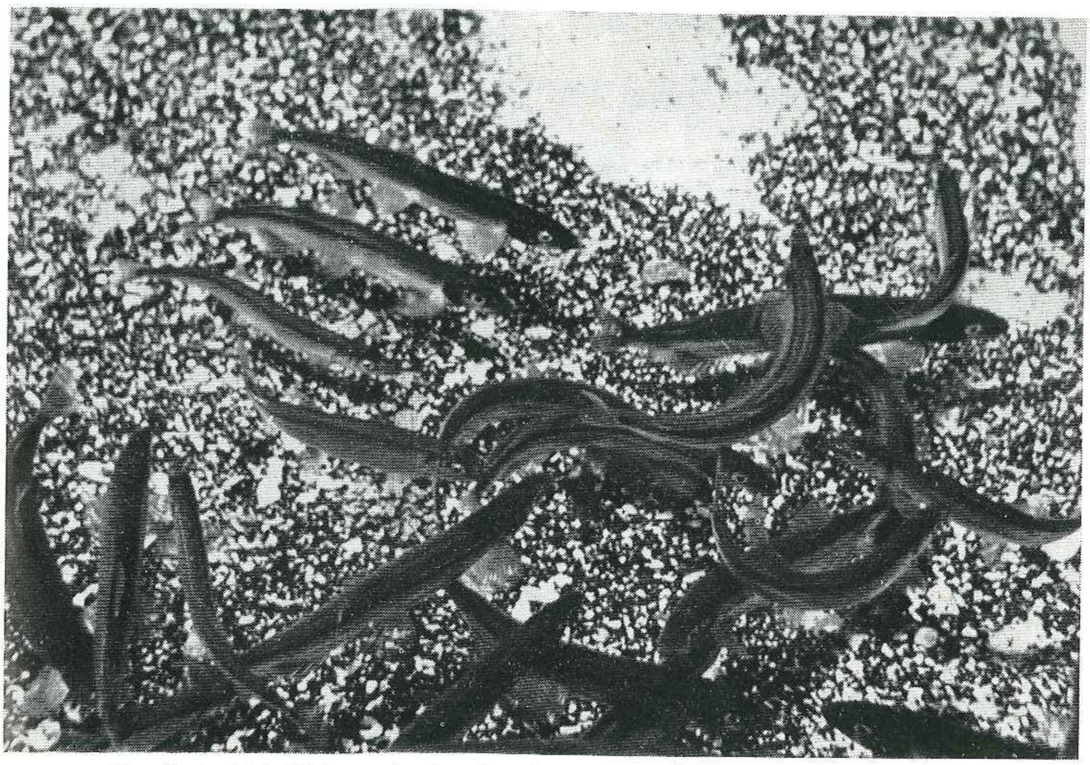
Morphological character: Blackness of the backs of the males and the sides of their heads during spawning periods.

4. Behaviour after spawning.

The general behaviour of the males did not change after the spawning stopped. The spawning periods ceased, however, most likely because the male was not stimulated by the presence of ripe females.

After spawning the females swam randomly in the tank and most likely they leave the spawning grounds soon after spawning.

After copulation the capelin were often wounded. Most frequently the lower half



Capelin in tank. Males and a few females at interwal between spawning periods.

of the head was wounded on both sexes and besides that the male's pectoral, pelvic and anal fins were injured. These wounds, which obviously were the result of scraping the bottom during copulation, did not heal and resulted in numerous deaths.

In both 1974 and 1975 the death rate was higher among males than females. The males were on the whole more extensively wounded than the females and their expenditure of energy at spawning was also much higher. Of a total of 200—250 capelin at the onset of spawning in 1974 only 10 females remained alive by 10 May. These females were fit and ate well the fishmeal and roe they were fed on. In 1975 36 males and 10 females were in the tank after spawning. Of these only 6 females remained by 16 April and 4 by 3 May. Thus no males survived spawning in the Aquarium but some of the females did.

Observations on males after spawning showed no signs of reversal from mating dress to the normal form before maturity. It is therefore concluded that the morphological changes of the male at maturity are final and irreversible and that the males remain on the spawning grounds until they die. The females, on the other hand, leave the spawning grounds and, despite the wounds that some of them incur during copulation, no physiological changes prevent them from surviving the spawning.

☆

VILHJÁLMSSON (1974) reports that varying sex ratios were observed in capelin catches during the spawning season, depending on time and location of the catches. Thus at the beginning of the season off E-Iceland the ratio was equal or near to 50:50. When the capelin moved inshore at SE-Iceland the sex ratio changed and was often 45:55 males/females. At the onset of spawning the sex ratio increased even further to 24:76 males/females. At the end of the spawning the sex ratio changed again and the percentage of males increased to nearly 100% on the spawning grounds. On the other hand, almost 100% spent females have been found in research vessel catches at E- and W-Iceland some distance from the actual spawning grounds.

The author investigated a couple of thousand dead capelin that had been washed ashore in Vestmannaeyjar at the end of March 1975. All these fish were males.

The above observations on capelin in their natural surroundings correspond quite closely to their behaviour as observed in the Aquarium's tanks and has just been described.

Embryological development of the capelin

THE CAPELIN EGG

Table 1 shows the size frequency and average size of 100 capelin eggs at the end of early organogenis, about 5 days after fertilization. Measurements are from 19 March 1975.

TABLE 1

Diameter Ocular micrometer units	Frequency	Diameter mm
4,55	1	1.045
4.60	1	1.057
4.65	4	1.069
4.70	12	1.080
4.75	17	1.091
4.80	23	1.103
4.85	22	1.115
4.90	12	1.126
4.95	6	1.137
5.00	1	1.149
5.05	1	1.160

No - 100
Average diameter: 1.104 mm

An analysis on the chemical contents of capelin eggs, taken from ripe females just before spawning, was carried out by the Icelandic Fisheries Laboratories, Reykjavík, in March 1975. It shows that the eggs contained 70% water, 14.2% protein (N×6.25), 5.7% fat, 1.1% salt (NaCl), 1.5% ash.

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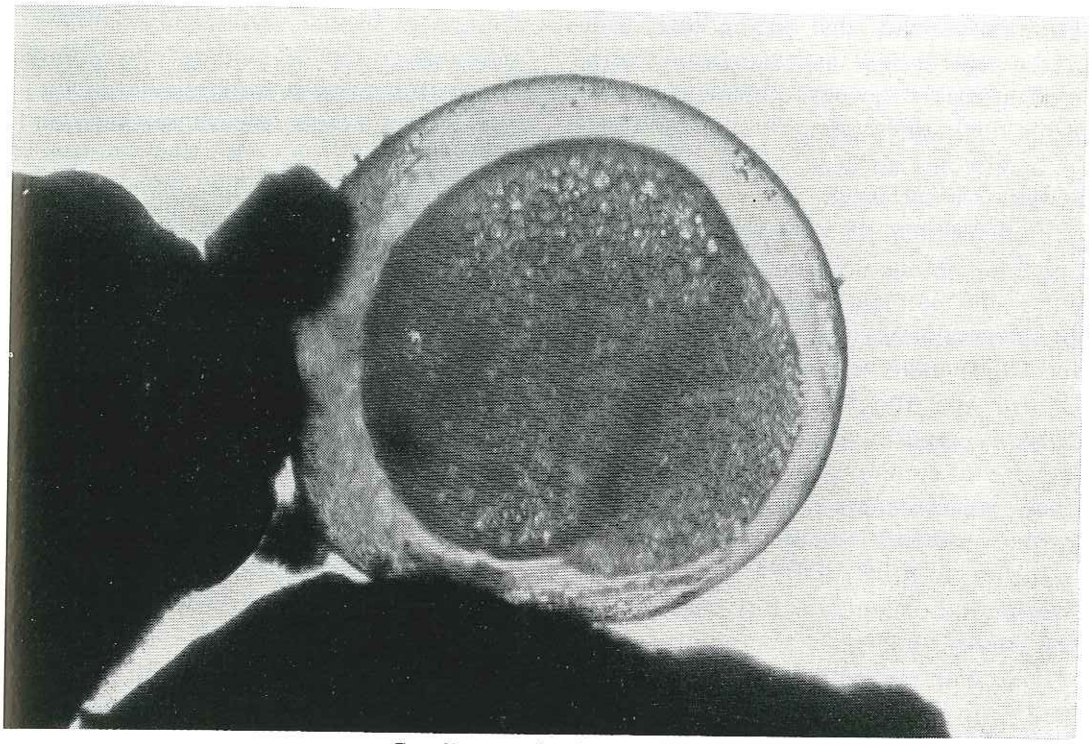
The capelin egg (Plates 1—7, Fig. 1.1.) is pale-grey in colour, but a small content of carotin gives it a faint yellow and orange hue. The yolk contains numerous small oil globules that render the inner part difficult to discern. The egg membrane (the first membrane) is thick and on its upper half (the animal pole) is the microphyle. The microphyle itself is tiny and invisible, but lies in a depression surrounded by a thickening of the membrane (Fig. 1.2.). This structure can be clearly distinguished on many of



Capelin egg glued to stones.

the photographs. The second membrane covers the first and consists of an adhesive material. This sticky layer is very thin except on the lower half of the first membrane (on the vegetative pole). There it forms a thick layer that covers about ⅓ of the inner membrane. POZDNJAKOV (1960), in agreement with RASS (1949), calls this glue-layer a pigment-layer. The present author cannot accept this terminology, since he believes this substance to be pure glue containing no pigment at all.

Immediately after the egg comes in contact with the water it starts distending (Plates 1—2). The main distension takes place in 2 minutes time. As soon as the egg comes into contact with water the glue becomes sticky. The glue is effective for one hour and then gradually becomes less sticky until it is almost inactive and has hardened in two hours. Until hatching, however, the egg remains a little sticky. Both fertilized and unfertilized eggs distend and become sticky at the touch of water, but eggs obtained from a female that has been dead for some hours become distended while the glue remained ineffective.

When the eggs in the display tanks were studied after spawning it appeared that they were evenly distributed all over the bottom of the tanks but only occasionally stuck together. They had settled with the glue-layer down. They adhered to stones on the bottom and frequently a lot of small sand particles stuck to the glue-layer forming something like a sand-bowl on the lower half of the egg. It was an exception if anything stuck to the eggs outside the area of the thick glue-layer.

SOME DEFINITIONS

In describing the development of the capelin reference is made to periods, stages and moments, in accordance with the theories of VASHNETHOV (1946, 1948 and 1953) and KRYSHANOVSKY (1953 and 1956). According to their definition a *period* is a portion of time including many stages with common inner characters and some environmental factors that have leading influence throughout the period.

In the early life of fishes we find two such periods: namely embryonic and larval periods.

The main characters of the embryonic period are intensive development and that food is obtained from reserves that originate from the mother. Leading environmental factors are the quantity of oxygen and predators.

The embryonic period can, and this is true for the capelin, end at hatching. Hatching before the end of it is, however, more common (fish of the cod family and many others). In the latter case we subdivide the period into subperiods, i. e. when the embryo is inside the egg membranes and that of a free embryo.

The main characters of the larval period are temporary organs and that food is obtained from the outside. A decisive environmental factor is the quantity of food. The larval period ends at metamorphosis when the temporary organs vanish and the fish becomes a juvenile with the appearance of the adult.

Stage is a short time of growth and with slow changes, but no principal changes in structure, physical conditions or behaviour that will change the attitude of the fish to environmental factors. Changes of stages are sharp, fast and complete.

Moment is the duration of any small step in development.

THE EMBRYONIC PERIOD

1. stage. Concentration of the plasma — Preparation for cleavage.

The distension of the egg takes 2 to 3 minutes (Plates 1—2). The space between the egg itself and the membrane (perivitalline space) is rather large in the capelin egg or about $2/10$ (200 μ) of its total diameter. When distension is complete, the cytoplasm that covers the yolk as a thin layer, begins to concentrate on the animal pole of the egg and forms a little cap — the blastodisk (Fig. 1.2, Plates 3—7).

The concentration of the cytoplasma takes about 3 hours.

Soon after the formation of the blastodisk a deformation of the yolk starts. This is typical for the capelin egg. This deformation is continuous (it only stops for a while just before cleavage) until the end of gastrulation. It is visible on most of Plates 7 to 38.

Most likely this deformation is caused by differential and changing tension in the cytoplasm that covers the yolk and its function is to disturb the liquid in the perivitalline space and thus make circulation of oxygen from the membrane to the egg more effective. Similar phenomenon is known in the egg of the stickleback.

2. stage. Cleavage of the blastodisk.

Moment of 2 blastomeres. Fig. 1.3, Plates 8—10, 4 hours old. (Timing is from the moment of fertilization).

This stage is characterized by an increasing number of cells but at the same time differentiation of cells takes place.

Cleavage is continuous at an interval of approximately 2 hours.

Moment of 4 blastomeres. Fig. 1.4, Plates 11—12, 6 hours old.

Moment of 8 blastomeres. Fig. 1.5, Plates 13—22, 8 hours old.

Moment of 16 blastomeres. Fig. 1.6, Plates 23—29, 10 hours old.

Plates 23—29 show that the cells start to concentrate to form a cap at the top of the yolk.

Moment of 32 blastomeres. Fig. 2.1, Plate 30, 14 hours old.

Formation of morula can be observed on Plates 31—36.

This stage ends about 1 day and 15 hours after fertilization with the formation of the blastula.

3. stage. Formation of basic embryonic tissue layers — Gastrulation.

At the beginning of gastrulation, the embryo is a little cap at the animal pole of the yolk. The gastrulation — the formation of the three basic tissues of the embryo — is the most important item at this stage in development. At the same time as the blastula starts to gastrulate it also starts to grow and extend in all directions, in the process gradually covering the whole yolk. The end of these two processes does not, in most cases, occur at the same time. The difference in size of the yolk and the blastula is responsible for this. The blastula of the capelin egg is large compared with the yolk and therefore the growth of the blastula around the yolk is completed before the three tissue layers of the embryo have formed.

On photographs 37 to 43 the formation of the embryonic tissue layers is shown.

Moment of beginning gastrulation. Fig. 2.4, 1 day and 20 hours old.

Moment of late gastrulation. Fig. 2.5, 2 days old.

Moment of blastopore. Fig. 2.6, 2 days and 8 hours old. At this moment all deformation of the yolk stops.

Moment of end of gastrulation. Fig. 3.1, 3 days and 12 hours old.

The three basic tissue layers of the embryo originate from different groups of cells in the blastula.

Endoderm (inner layer) is formed from two cell group. The first lies on the yolk under the blastula. These cells form tissue that at first breaks the yolk into food for the embryonic body, but later forms part of the embryonic gut. The other group of cells is in the thick lower half of the blastula. This group of cells makes up tissue that forms the spinal cord and the lining of the mouth.

Ectoderm (outer layer) originates from cells covering most of the outside of the blastula. This tissue forms the outside of the yolksac and the embryonic body, the nervous system etc.

Mesoderm (intermediate layer) is made of cells from the thick lower half of the blastula. From this tissue originate the blood system, muscles, skeleton and the surface of the inner organs. Part of the mesodermal cells migrate between the ecto- and endoderm of the yolksac to form the heart, some of the blood vessels and blood corpuscles.

It is difficult to follow the formation of the tissue layers in the capelin egg and the end of their formation can only be seen by the occurrence of the embryonic thickening. Fig. 3.1, Plates 42—43.

4. stage. Formation of pre-organs — Organogenis I.

During this stage the head and part of the embryonic body are formed as well as rudimentary organs of the central nervous system, main nerves, spinal cord, myotomes and the gut in that part of the body which already has been formed. Plates 44—50.

Three basic sections of the brain are formed from part of the neural tube. These are the forebrain (prosencephalon), midbrain (mesencephalon) and hindbrain (rombencephalon). The forebrain bulges at both sides and rudimentary eyes, the optic bulbs, appear. A crack appears on the outer side of the optic bulbs. It grows larger as the outer part of the optic bulbs folds inwards and a double cup is formed. At the same time the surface ectoderm folds invards and developes into eye lenses. The formation of the eye is completed during this stage, but like all other organs it still has to develop much further before it becomes functionary.

In front of the optic cups the nose primordium appears. The ear primordium lies behind the optic cups and at the end of this stage tiny otholits appear in the primordia.

The first somite appears at the middle of the embryonic body by cleavage of the somatic mesoderm that lies on both sides of the chordum. The first three somites appear, then one somite forms on each side increasing the number to 5, then 7 and so on until all the somites of the existing body have been laid down.

The mid-gut forms beneath the embryonic body.

The formations of the organs can be observed only roughly in the capelin egg.

Moment of occurence of optic bulbs. Fig. 3.2, Plate 46, 4 days old.

Moment of crack of optic bulbs. Fig. 3.3, Plate 47, 5 days old.

At this moment the nose primordium, ear primordium and the first three somites have appeared, but in the capelin egg they are invisible under an ordinary microscope.

Moment of end of organogenis I. Fig. 3.5, Plate 50, 6 days old.

By the end of this stage the hind gut and anus have formed in most species of fish but in the capelin embryos it has not. In that respect the capelin is an exception.

5. stage. Full development of main organs — Organogenis II.

At the beginning of this stage a major change in the life of the embryo takes place as it starts to move.

The development during this stage can be observed in photographs 51 to 61.

Moment of first movement. Fig. 3.6, Plate 51, 7 days old.

Weak movements of the embryonic body can be seen. Eyes, inner ear and olfactory organs have been formed. Hind part of the embryonic body developes, new somites appear as the body grows in length. The growing embryo forces the upper part of the yolk into two separate sacs.

Moment of first beating of the heart. Fig. 4.1, Plates 52—54, 8 days old.

Rudimentary heart has formed from mesoderm cells that have gathered on the yolksac at the left side of the head. The heart, which has the form of a bell shaped tube, beats slowly. Red corpuscles (with haemoglobin) have not formed, nor will they appear during the embryonic period. Movement of the blood can soon be observed in the aorta dorsalis together with movements of blood corpuscles other than the red ones. The capelin embryo has no special embryonic breathing organs.

Moment of occurence of pigment in eyes. Fig. 4.2, Plates 55—59, 9 days old.

The formation of the embryonic body, except the tail, is complete with hind gut and anus and the embryo has acquired the full number of body somites. Black pigment (melanophor) is present in the eyes. The movements of the embryo are more intense and stronger than at the beginning of the stage.

Moment of appearance of hatching cells. Fig. 4.3, Plate 60, 10 days old.

The developmental stage at hatching is fixed for each species of fish, but can be rather different for the various species. Preparation for hatching begins with the apperance of hatching cells. The time from their appearance to hatching is usually considered a separate stage in development. In the case of capelin, however, we do not separate it as a stage, though it could be done, since there is still another important stage to be completed before hatching.

On both sides of the embryonic body numerous hatching cells have appeared. These cells secrete a chemical that weakens the membrane and thus helps the embryo to break out of the egg. These cells disappear after hatching.

Moment of end of later organogenis. Fig. 4.4, Plate 61, 11 days old.

All the main organs have formed, but the tail is still developing. At the end of this stage the tail is already formed on most species of fish. The capelin, however, is an exception.

6. stage. Formation of mouth — Preparation for independent feeding.

Moment of beginning of separation of the head from yolksac. Fig. 4.5, Plate 62, 12 days old.

The anteriour of the head separates from the yolksac, indicating the beginning of mouth, front gut and a rudimentary mouth skeleton development. A single row of black pigment cells (melanophores) has appeared under the hind half of the gut between the yolksac and anus. Hatching cells have appeared on the head and their number has increased on both sides of the embryo and on its tail. All parts of the brain have developed.

Moment of more intense pigmentation of eye. Fig. 4.6, Plate 63, 14 days old.

6 or 8 days remain until hatching and the development can be seen on Plates 64 to 70.

The main events during development up to hatching are as follows:

The head which has been lying bent across the yolk rises to lie in line with the body. The mouth opens, gill openings appear and a rudimentary cartilage of the mouth and gill skeleton appears. The front part of the gut is formed and opens into the mouth. The pectoral fins, which appear like lobes with the lower part joined horizontally to the embryonic body, enlarge and move until they have taken up the normal vertical position. At their base a cartilaginous cleitrum is formed. The eyes have well developed muscles and are thus capable of adjustment. They have a steel-blue and yellow hue indicating that at hatching they are already functional.

The embryo acquires pigmentation that does not change during the subsequent larval period: a single row of pigments under the gut from yolksac to anus (on herring larva this row is double). On both sides of the gut there is also a row of large single pigment cells from yolksac to anus. At the lower side of the tail lie further pigment cells. Yellow (carotinoid) pigment is only present in the eyes.

At the beginning of the development of the embryo the oil globules in the yolk are small and numerous. During development the oil globules gradually join each other. They grow bigger and become fewer in numbers and at hatching there is only one big blob left in the yolksac and possibly a few small ones. This blob of oil then takes up more than half of the yolksac space. The rate of absorption of fat seems to be slower from the yolk than that of other components. Thus, higher contents of oil than other components in the yolksac after hatching will make the larva lighter in the water.

If kept at constant 7.2°C temperature during development hatching starts on the 20th day after fertilization. Most of the embryos hatch on the 21st and 22nd day and the remainder on the 23rd day after fertilization.

LARVAL PERIOD

7. stage. Hatching — Mixed feeding.

Moment of hatching. Fig. 5.1, shortly after hatching, length 7.2 mm.

Pozdnjakov (1960) states that the larvae are 4.8 to 7.5 mm at hatching. The relatively few measurments carried out by the present author are within this size range.

Pozdnjakov (1960) gives a detailed description of the hatching and behaviour after hatching and to this the author has nothing to add.

Well developed mouth, eyes and gut, small yolksac, vertical pectoral fin supported by cleitrum and the behaviour of the larvae — high level of activity, horizontal position and positive reaction to light, — all this points in the same direction, i.e. that the embryonic period is over at hatching and the larva is able to catch and utilize food from outside.

At this stage the only changes in the larva are due to the growth increment.

Length 7.2 mm. Fig. 5.2, 1 day and 12 hours after hatching.

Length 7.6 mm. Fig. 5.3, 3 days after hatching.

Length 7.7 mm. Fig. 5.4, 6 days after hatching.

8. stage. Independent feeding.

Length 7.7 mm. Fig. 5.5, 8 days after hatching.

The yolk is almost finished and the larva completely depends on the food it can obtain from the environment. During complete starvation the yolk will disappear in 8 to 10 days and in further 1 to 2 days the larvae die. If the larvae catch some food during the first 8—10 days the yolk will last longer.

At the beginning of this stage the larva is about 8 mm long. Pozdnjakov (1960) gives 7.2 to 8.2 mm.

Ecology of spawning and eggs

The main part of the mature stock of capelin migrates southwards off the east coast of Iceland to the south coast for spawning. During the southwards migration the gonads of both sexes gradually develop and so do the spawning ridges of the male. The development is at first slow but accelerates when the capelin move into the warmer waters at the southeast coast and the westward migration begins.

It has been shown (VILHJÁLMSSON 1974) that the spawning migration usually enters the coastal Atlantic waters off SE-Iceland when the weight of the ovaries of the females has reached 8—9% of its total body weight. After a few days in these warmer waters this ratio has increased to more than 10% and then increases gradually to reach some 20% a few days before spawning. At this point there is a sudden, sharp increase to 25% or even up to 30% of the total body weight when spawning finally commences.

Changes in behaviour pattern from phase 1 to phase 2, which is described earlier, occur undoubtedly at this sudden increase in gonad weight. The migrating capelin have reached their destination, they arrive at the spawning grounds and start preparing for the spawning.

The preparation of spawning seems to take only about 3 days. Then spawning begins — phase 3.

The most important factors during spawning are: the disturbance of the substrate, even distribution of eggs and short spawning periods with long intervals. Besides, the structure of the eggs is of major importance. All the above mentioned facts lead to the conclusion that the most suitable spawning substrate is sand or fine gravel that the capelin can easily disturb during copulation.

The eggs spread upwards and outwards from the copulating capelin and remain long enough in the water before touching the bottom to settle with the lower, heavier, glue-covered part facing downwards, where the eggs stick to the particles they touch. The particles of the substrate which are shoveled up from the bottom by the copulating pair mix with the eggs. Although covering the eggs these particles do not stick to them as there is no glue present on the upper half of the eggs. Thus the eggs are stuck to the bottom while the top half of them is free and thus can more easily absorb sufficient oxygen.

When the first spawning period is over the eggs will not be disturbed for several hours. In that time the glue hardens and the eggs are permanently glued to the particles they have tauched and thus they remain stuck during the following spawning periods.

The adhering particles will cause the eggs to resettle on the bottom if they are disturbed at continued spawning, or if they drift off by current or wave action.

As the layer of egg and gravel mixture is looser and lighter than the undisturbed bottom it will be easily whirled up at next spawning, and consequently the next couple can disturb new layers of undisturbed substrate under the existing egg and gravel mixture. By continued spawning at the same locality a thick layer of egg and gravel mixture can be formed. BAKKE and BJÖRKE (1971) found the layer of egg and gravel mixture to be up to 4 to 5 cm thick at the main spawning grounds at Norway.

At the bottom of the 4—5 cm layer of egg and gravel mixture oxygen uptake will be difficult. The non-sticky two thirds of the egg surface and the transformations of the yolk in the three first stages of development are adaptations that will help a great deal but, in fact, the embryo has no special adaptive organs for increasing oxygen uptake which we would expect to find if aeration were extremely poor.

Towards the end of the spawning process in a certain locality, the sex composition usually changes drastically. Thus, during a few days of each fishing season, the catches consist practically of males only (VILHJÁLMSSON, 1974). When all the females in the tanks were spent, spawning periods stopped. It was, however, obvious that the males were still active and ready and they remained so until they became exhausted and died.

After copulation the role of the female is over and she moves out of the spawning grounds leaving the still active males behind.

VILHJÁLMSSON (1974) reports that the increase of the female component on the East Coast grounds that is sometimes observed during the period 1—15 April is due to the fact that apart from immature female capelin, a substantial number of spent females may be present. The latter have apparently made their way back east after spawning and as far as can be ascertained were in active search of food.

Acknowledgements

The author is indebted to Mr. Friðrik Jesson director of the Vestmannaeyjar Aquarium for providing laboratory facilities and the opportunity to use the display thanks at will. His assistance in carrying out this investigation was most valuable. Thanks are also due to Mr. Halldór Dagsson for setting up the photographic equipment and filming the behaviour of the capelin.

The author also wishes to thank Mr. Jakob Jakobsson and Mr. Hjálmar Vilhjálmsson for helpful advice and criticism of the manuscript.

Íslenskt ágrip

Frá febrúar til maí árin 1974 og 1975 rannsakaði höfundur fósturþroska og hrygningarhegðun loðnu, sem hrygndi í búrum Sædýrasafnsins í Vestmannaeyjum. Tilgangur rannsóknanna var að auka þekkingu okkar á íslensku loðnunni. Fylgst var með hegðun loðnunnar í búrum bæði árin og jafnframt var loðnan kvikmynduð 1975, og kvikmyndirnar athugaðar síðar.

Í hegðun loðnunnar má greina 4 stig:

1. Gönguhegðun, sem einkennist af torfumyndun, jafnri blöndun kynjanna og stigvaxandi þroska kynfæra. Þetta ástand varir alla göngu loðnunnar suður með austurlandi og gönguna í hlýja sjónum vestur með suðurströndinni, þar til gangan stöðvast.
2. Undirbúningur að hrygningu, sem einkennist af leit hænga að heppilegum hrygningarstað, en við það hættir torfumyndun smátt og smátt og kynin aðskiljast í æ ríkara mæli. Þetta ástand varir aðeins um 3 daga og á þessum tíma vex hrognaþungi hrygnanna skyndilega mjög mikið.
3. Hrygning. Hængurinn er leiðandi aðili hrygningarinnar. Hængarnir halda sig í hópum við botninn og hrygningin hefst með ákafri leit þeirra að reiðubúnum hrygnum. Ein og ein hrygna syndir inn í hængahópinn og einhver hængur gefur sig að henni og þrýstir henni upp að hliðinni á sér og festir hana við sig. Parið þýtur síðan eftir botninum með kviðinn ½ til 1 cm niðri í sandinum og þyrlar frá sér frjóvguðum hrognum, sandi og smásteinum. Pörunin stendur aðeins í 1—2 sekúndur og síðan losnar parið í sundur. Hrygnan, sem hefur losað sig við öll hrognin í einni pörun, syndir stefnulaust í burtu, en hængurinn samlagast aftur hængahópnum og virðist geta tekið þátt í fleiri en einni pörun. Paranir fara fram í hrygningarlotum, sem eru 2—3 á dag og vara aðeins í 10—15 mínútur.
4. Hegðun eftir hrygningu. Mikið bar á meiðslum hjá loðnunni eftir hrygningu, þó meira á hængunum. Hængarnir halda sig reiðubúnir til pörunar á hrygningarstaðnum, þar til þeir örmagnast eða deyja af sárum, en hrygnurnar leita burt frá hrygningarstaðnum strax að lokinni pörun.

Við endurtekna hrygningu á sama stað getur myndast 4—5 cm þykkt lag af blöndu eggja, malar og sands.

Eggin hvíla aðskilin og límast sjaldnast saman. Neðsti þriðjungur þeirra er þakinn þykku límlagi, sem límir eggið við smásteina og sandkorn, en ⅔ hlutar eggsins eru auðir og auðveldar það egginu að ná til sín nægu súrefni úr sjónum.

Fullþroska lirfa klekst úr egginu eftir um það bil 21 dag og leitar hún þá fljótlega upp í sjó og getur strax farið að afla sér fæðu.

Í fullu svelti endist kviðpokinn lirfunni í 8—10 daga og þær deyja á 10.—12. degi, ef þær ná ekki í fæðu eftir klak.

Teikningar og ljósmyndir aftan við texta eru af fósturþroska loðnunnar.

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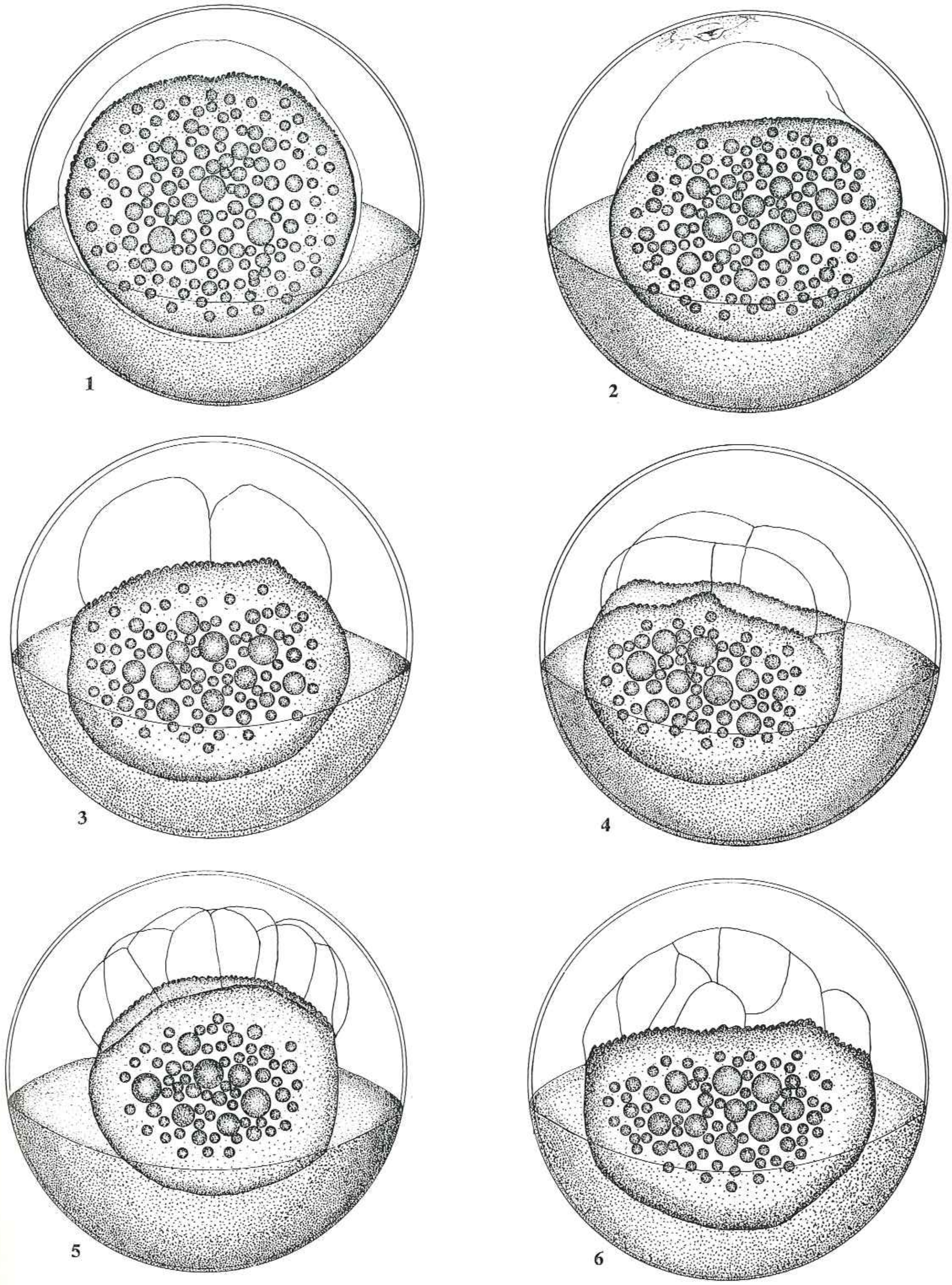

Figure 1.

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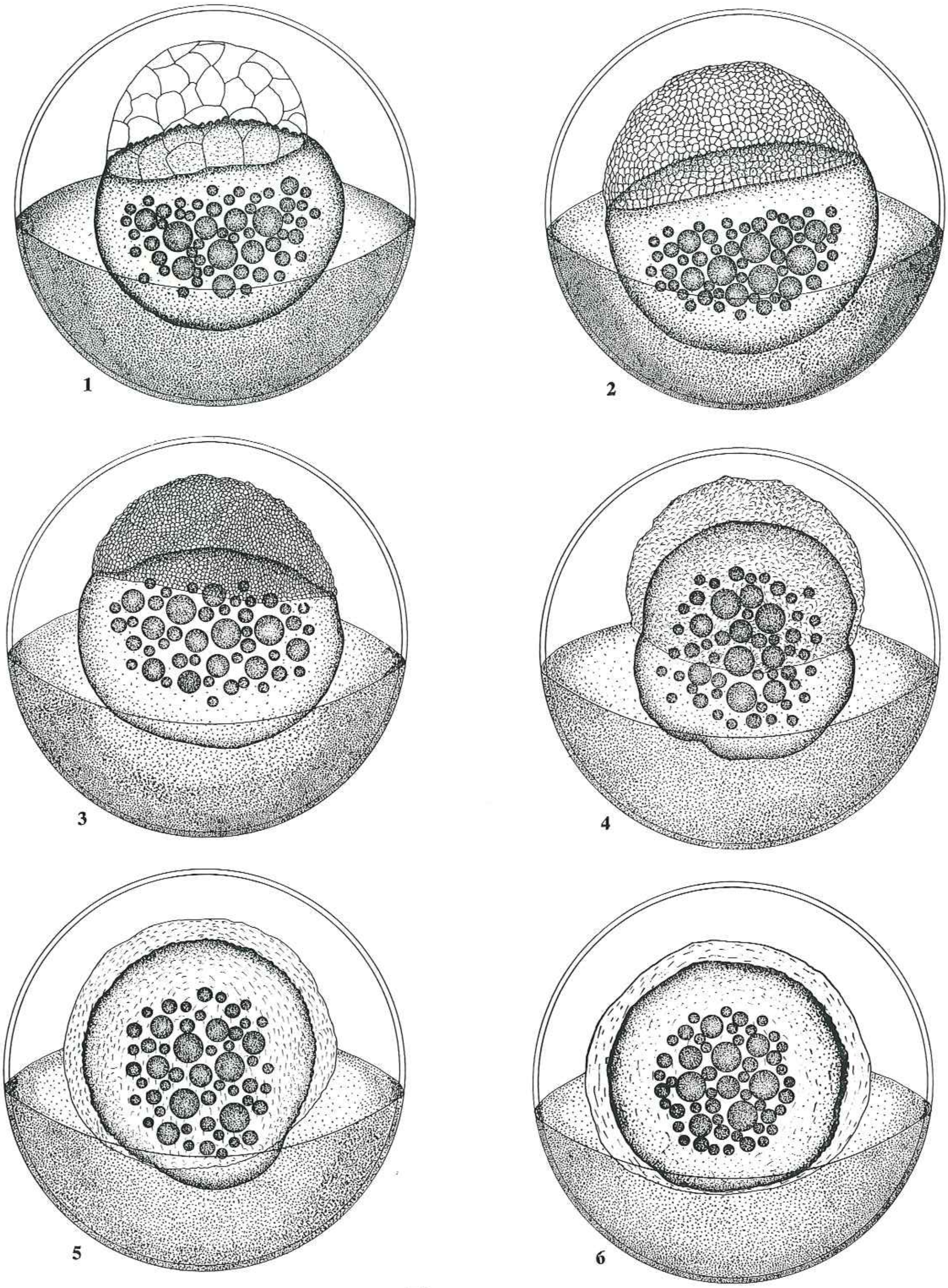

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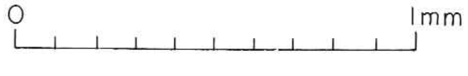

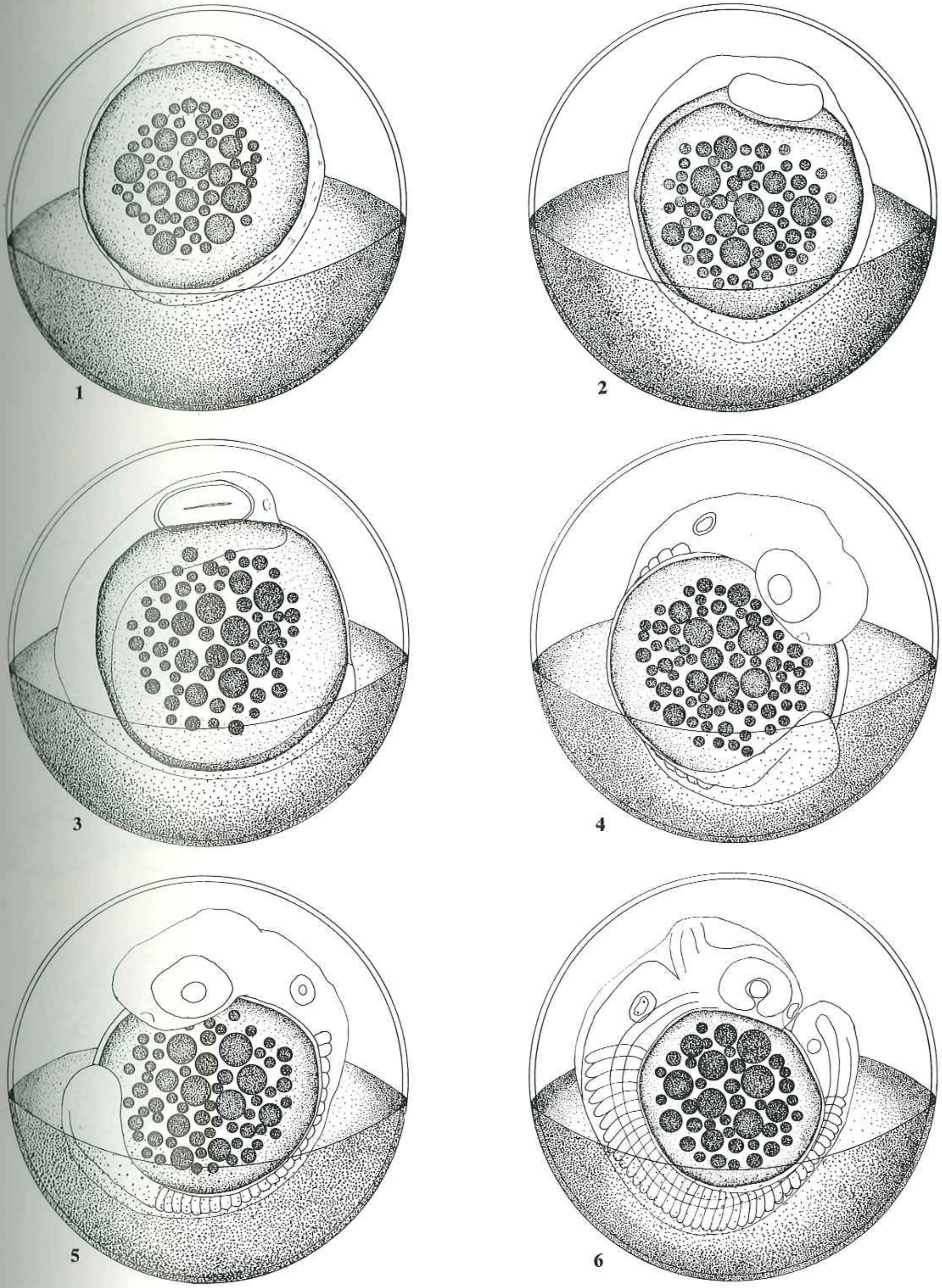

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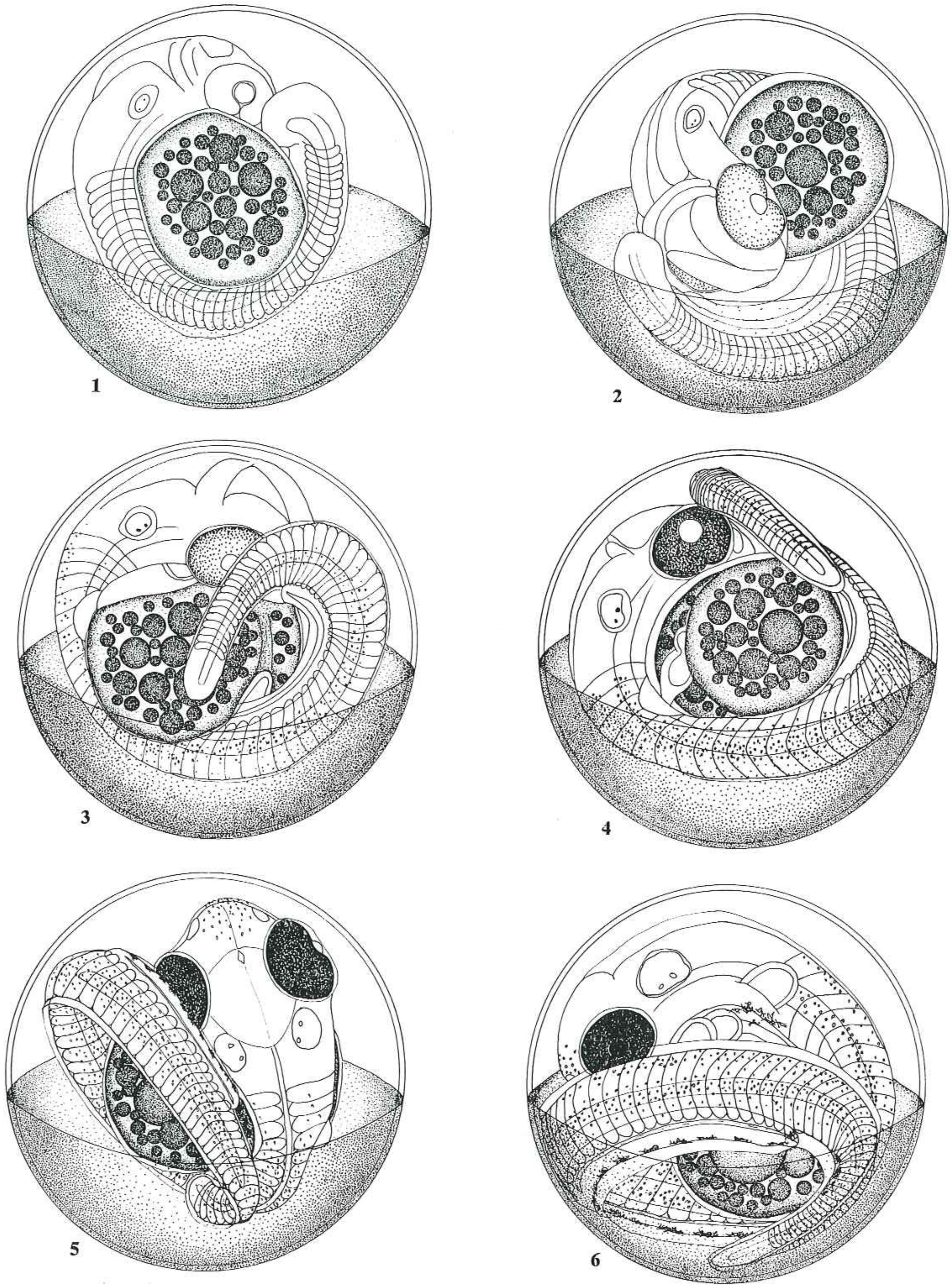

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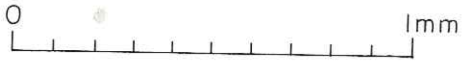

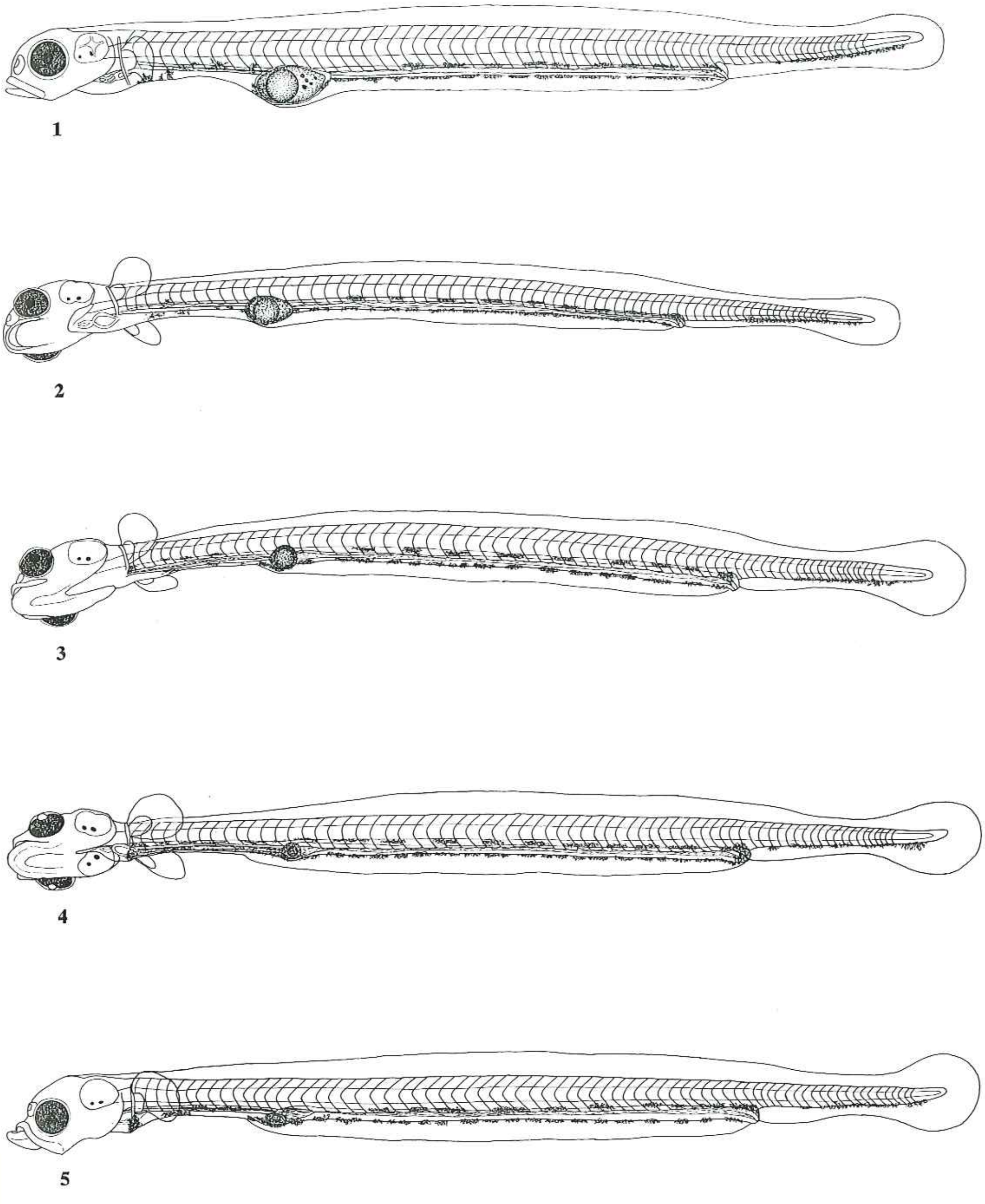

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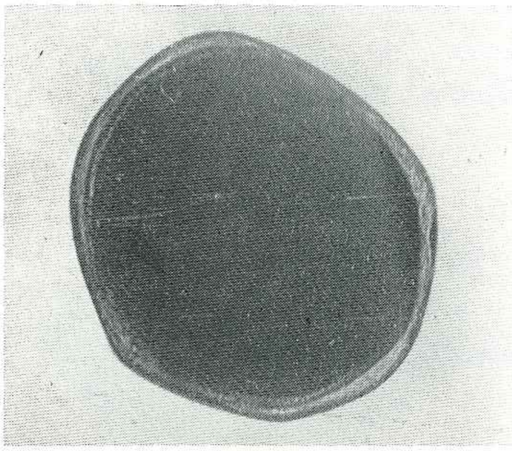
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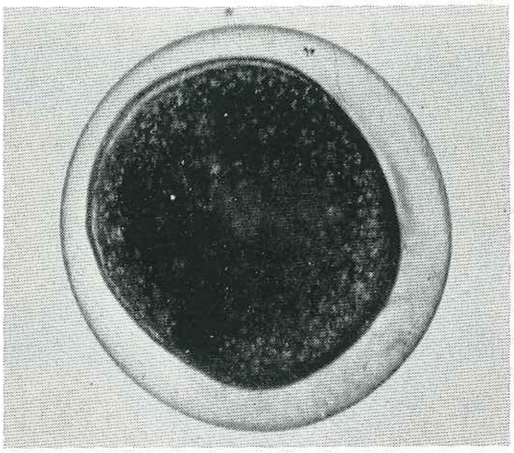
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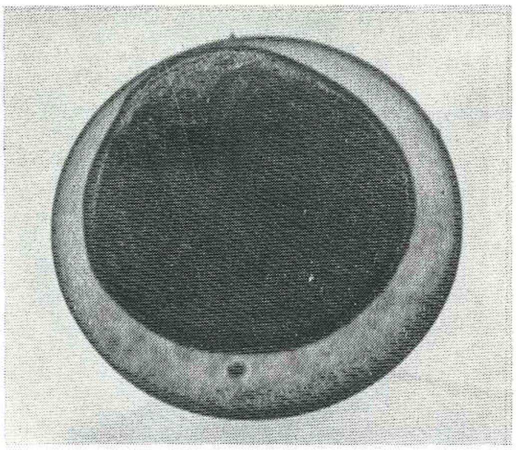
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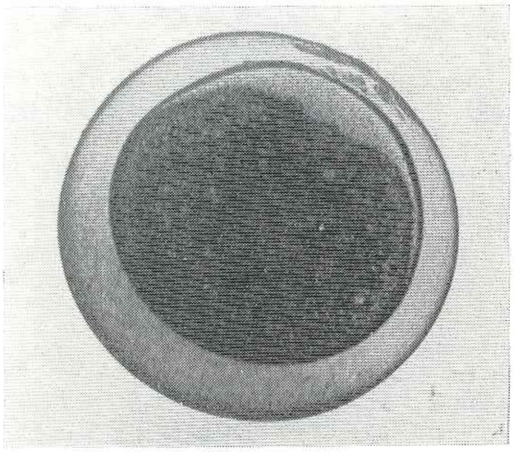
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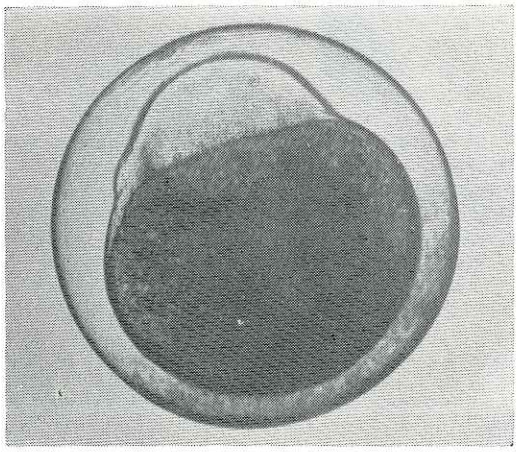
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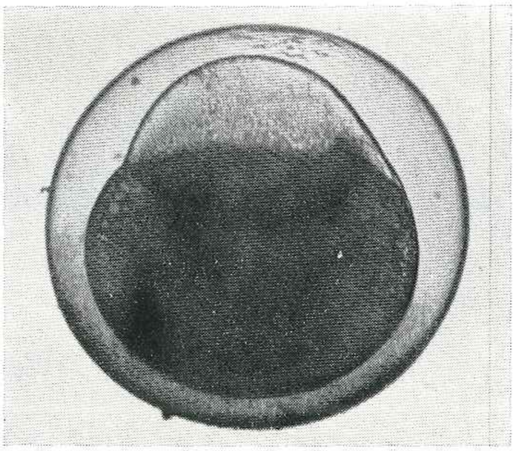
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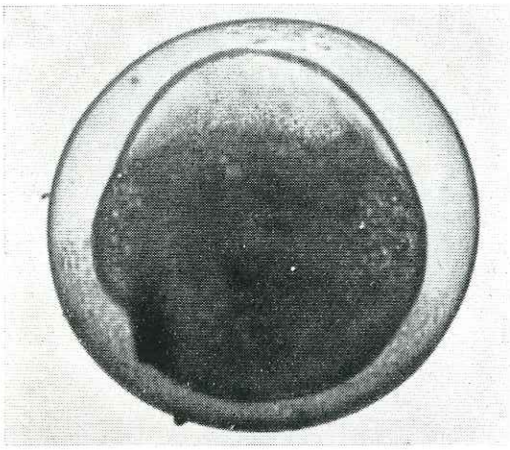

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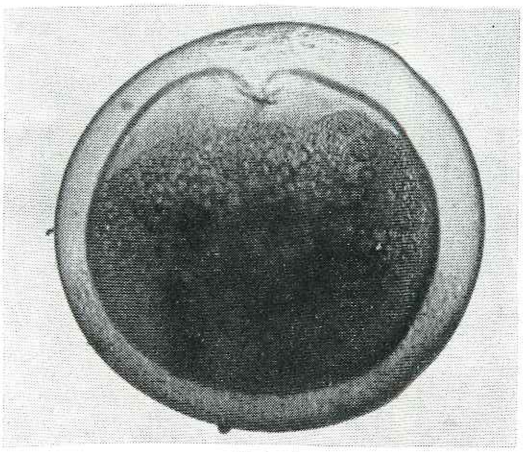

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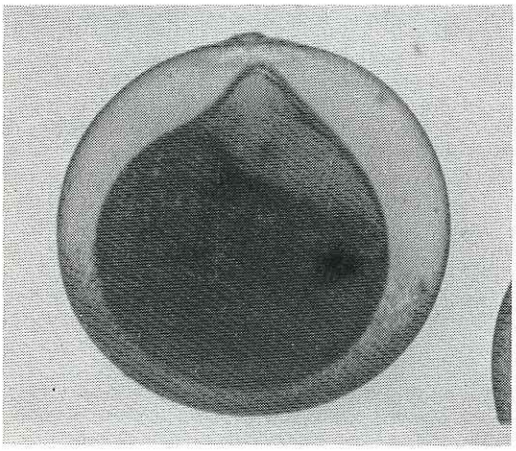

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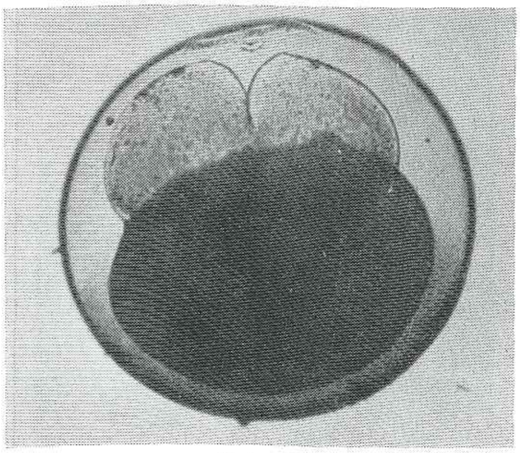

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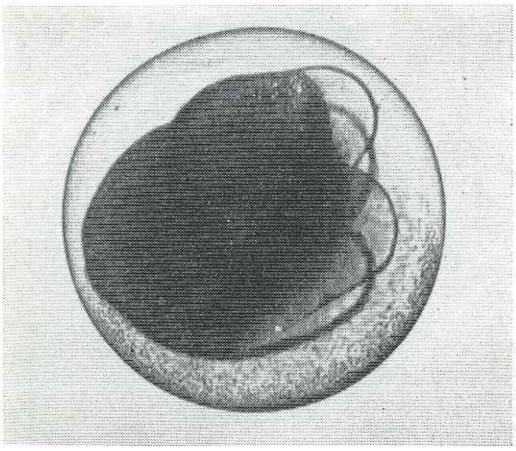

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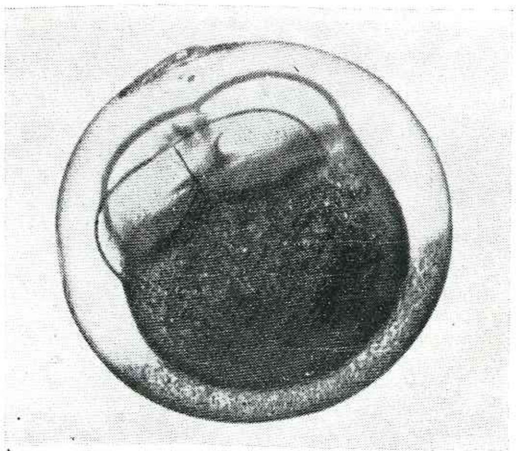

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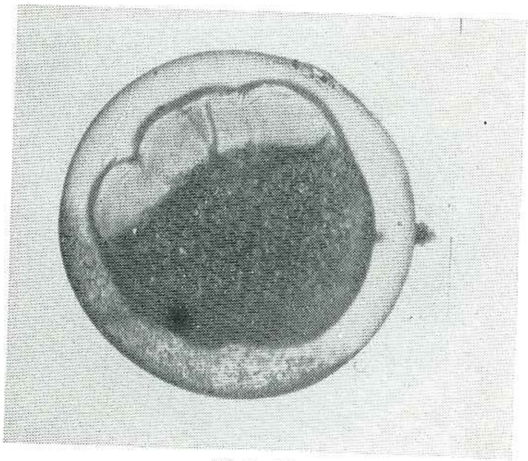
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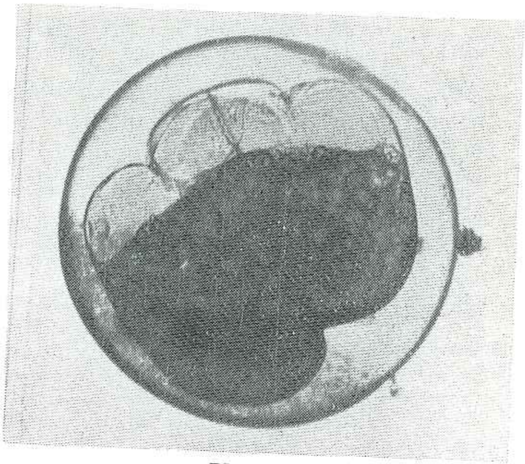
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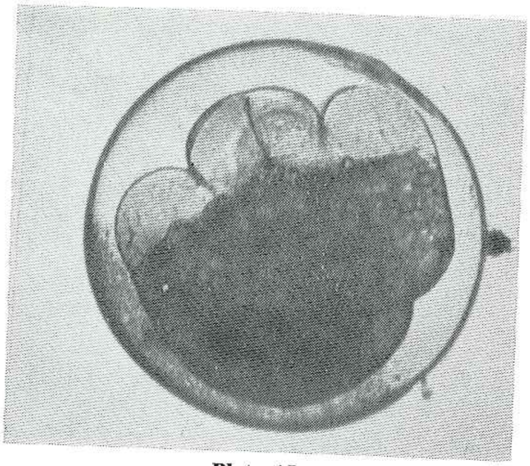
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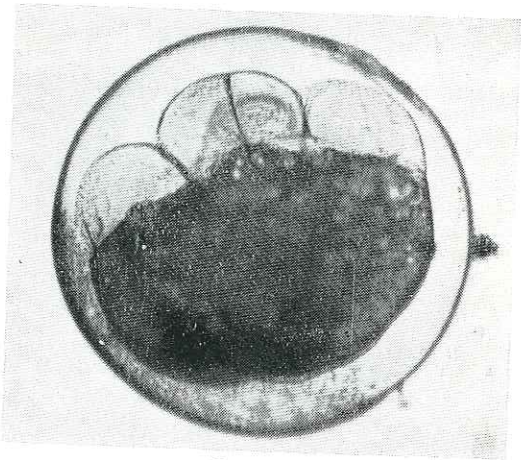
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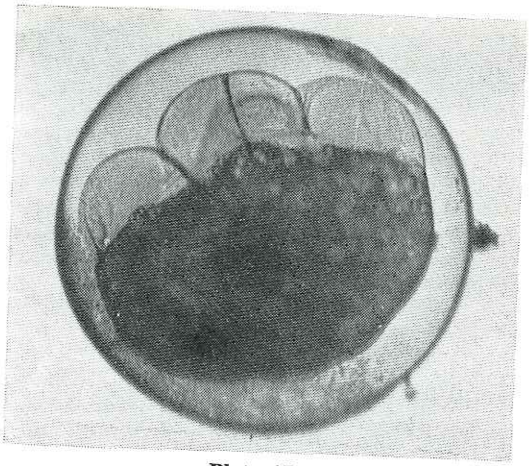
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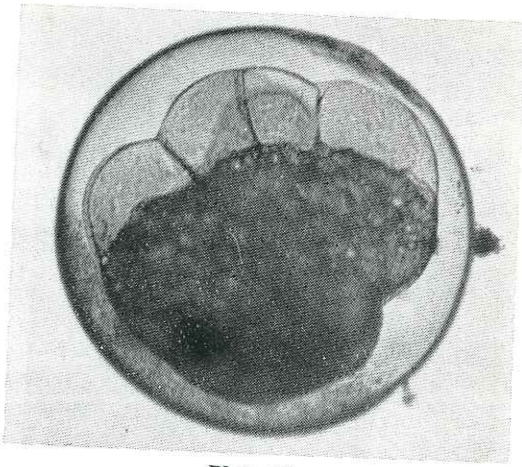
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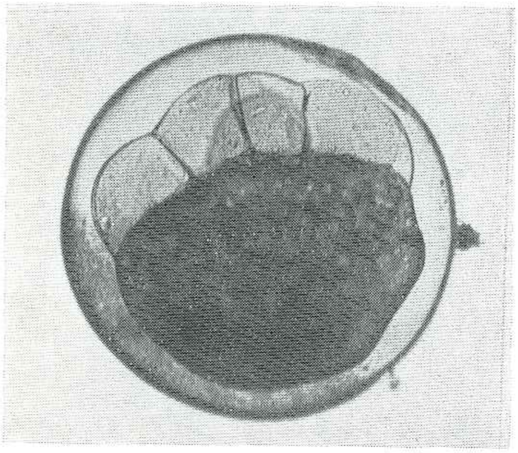

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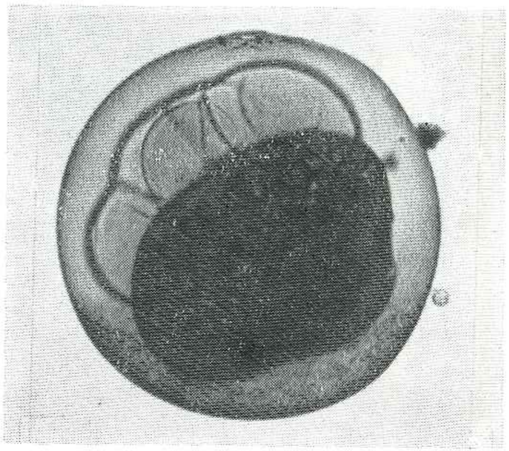

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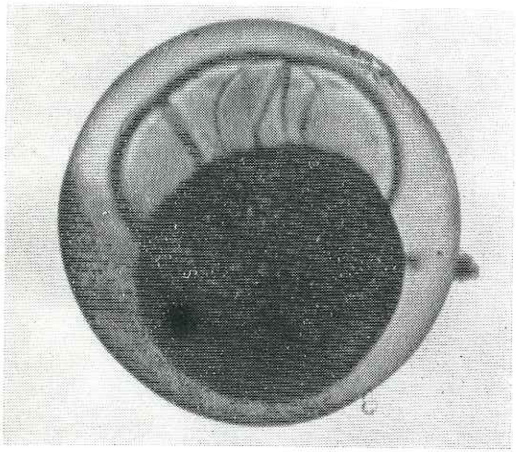

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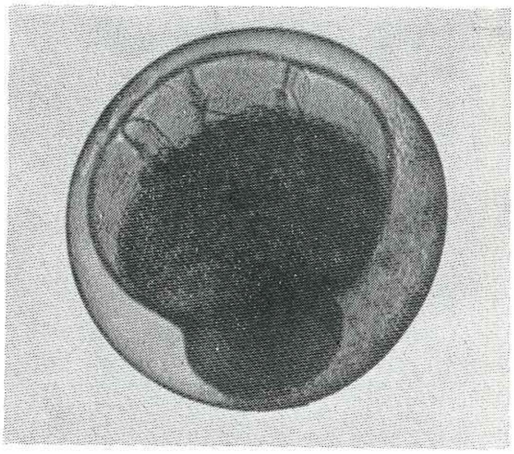

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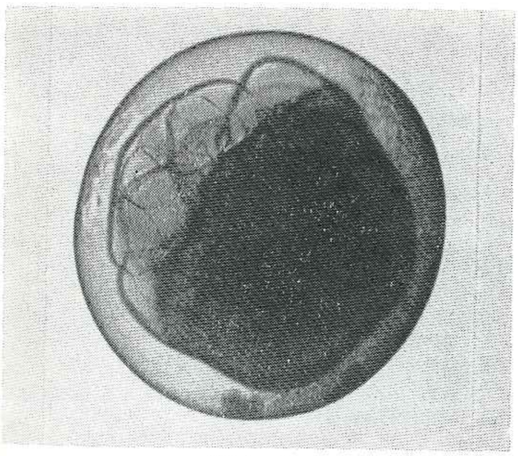

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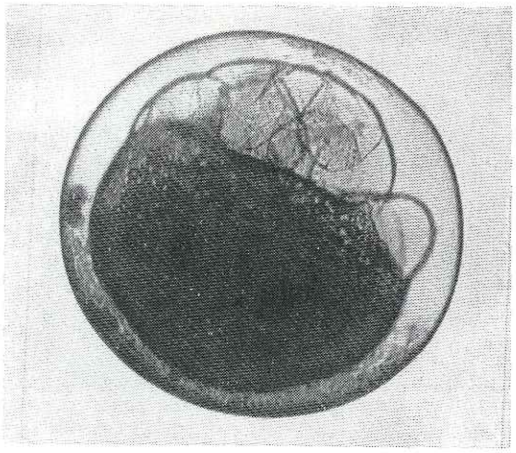

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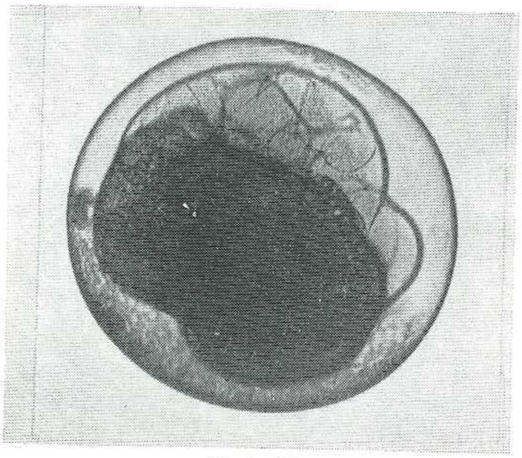
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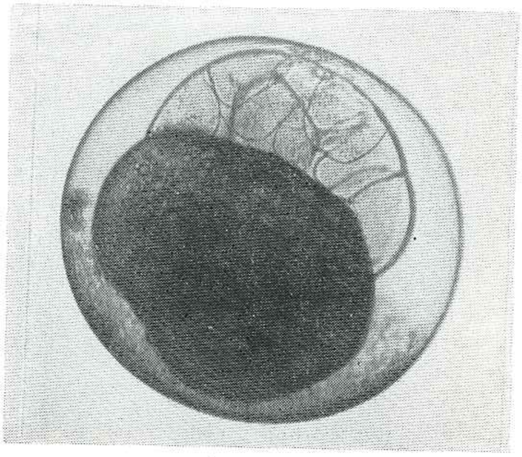
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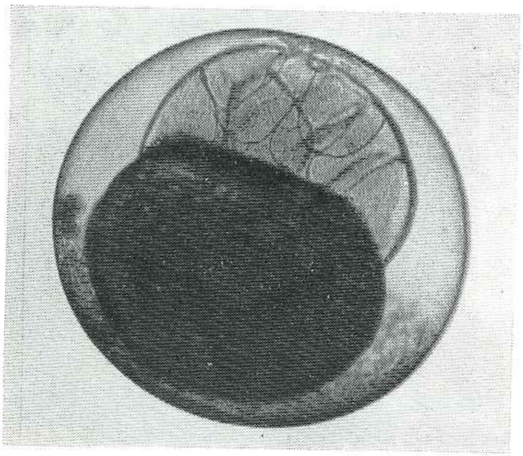
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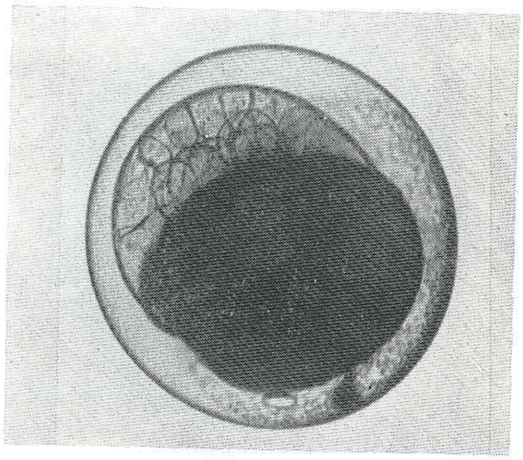
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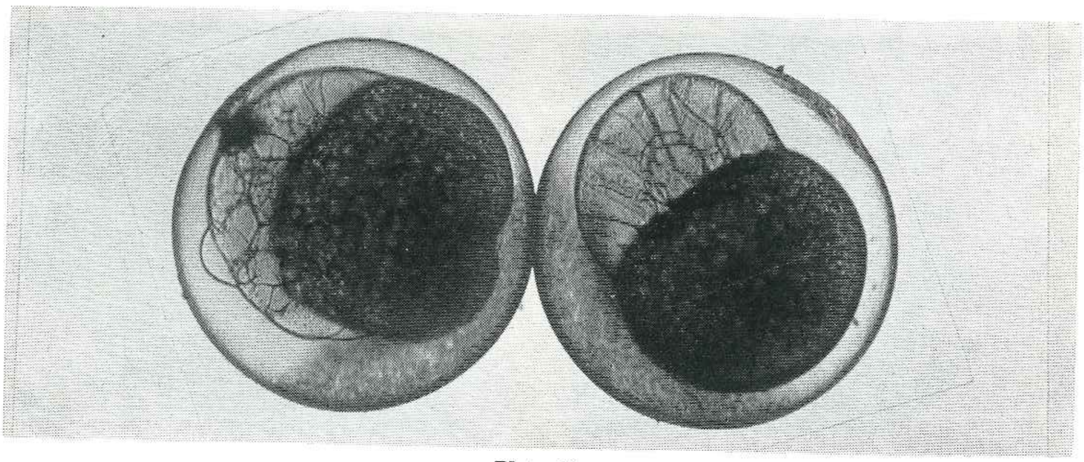
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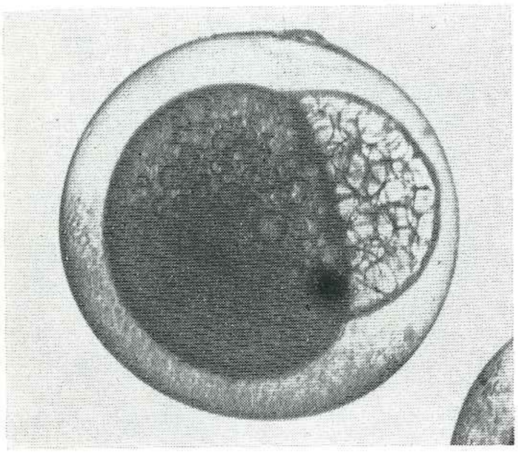

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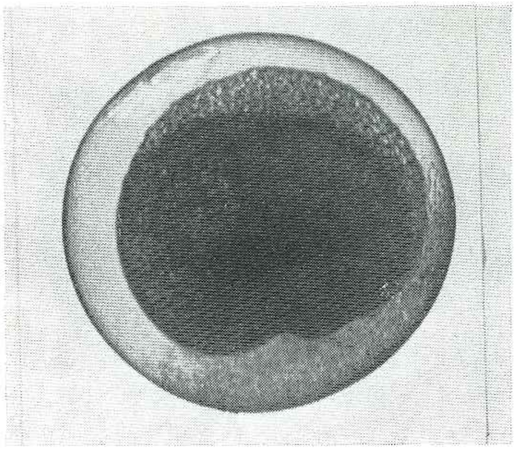

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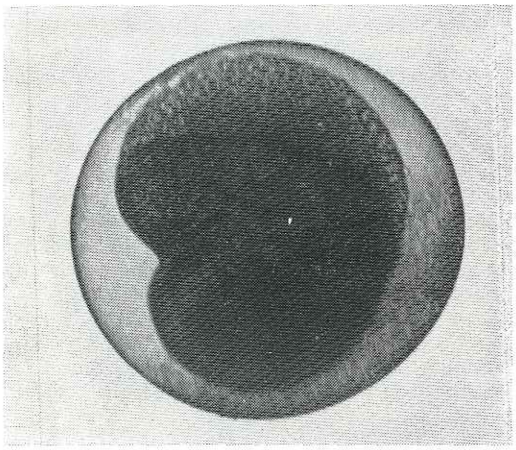

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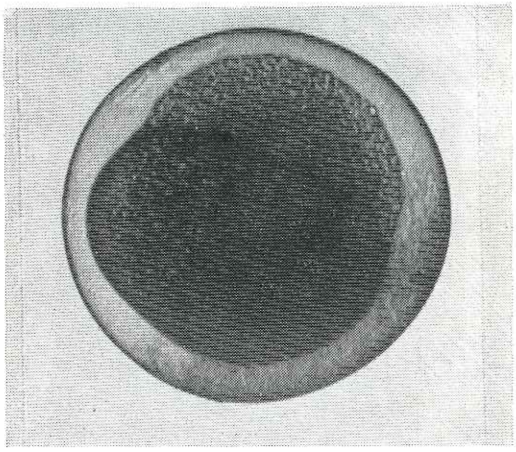

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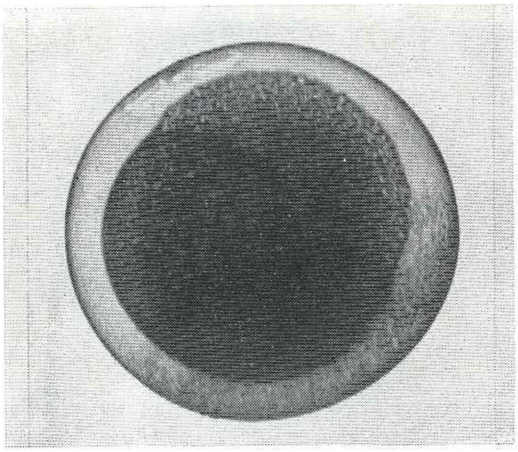

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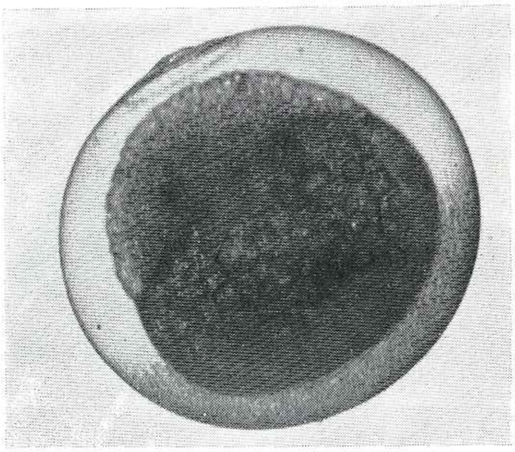

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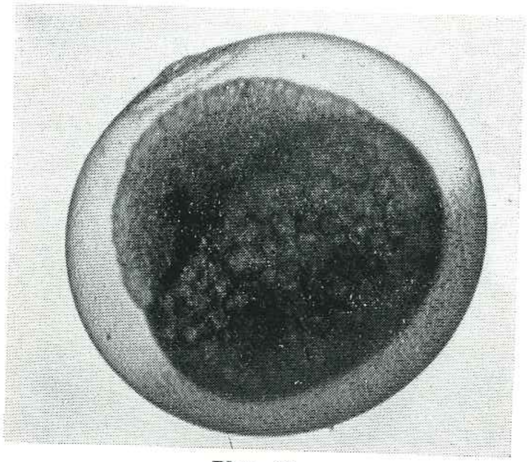

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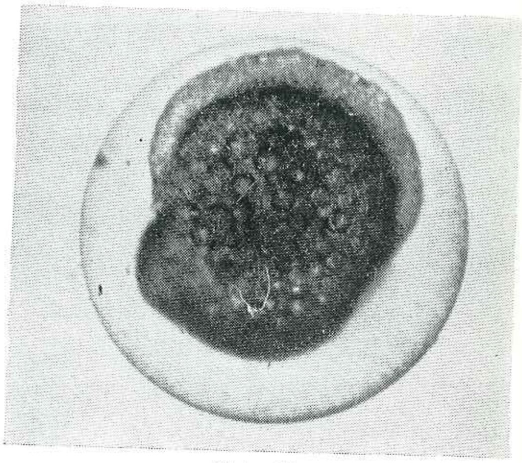

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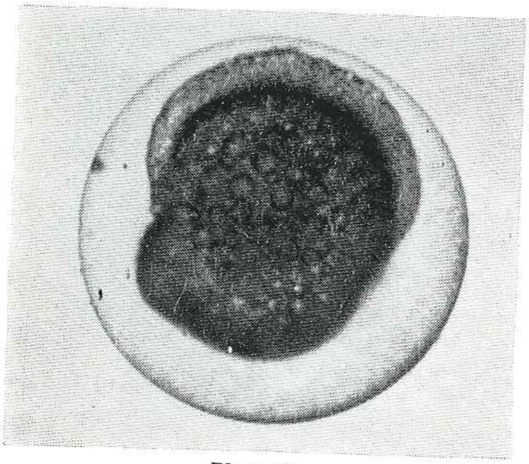

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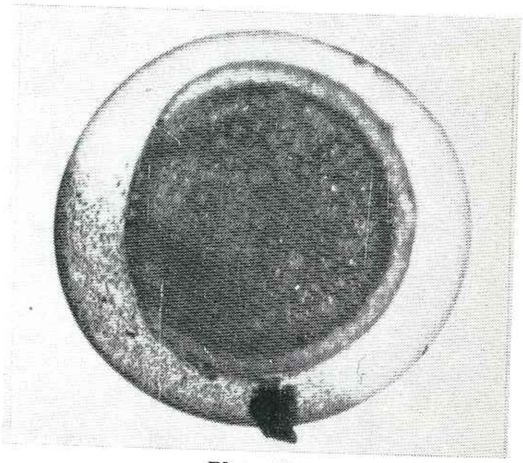

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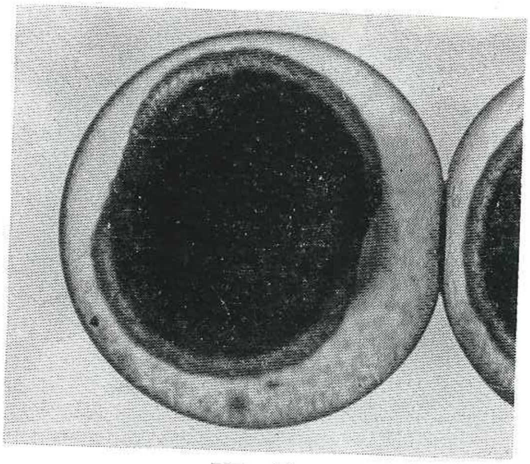

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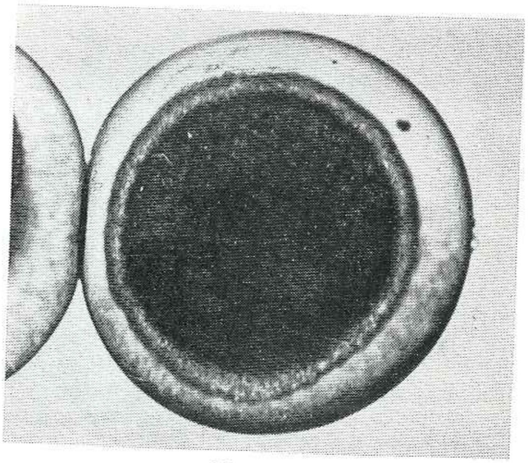

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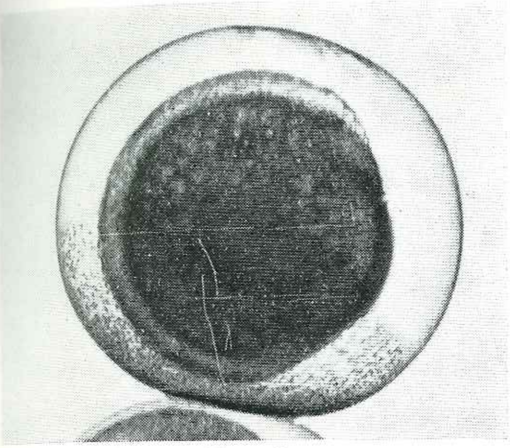

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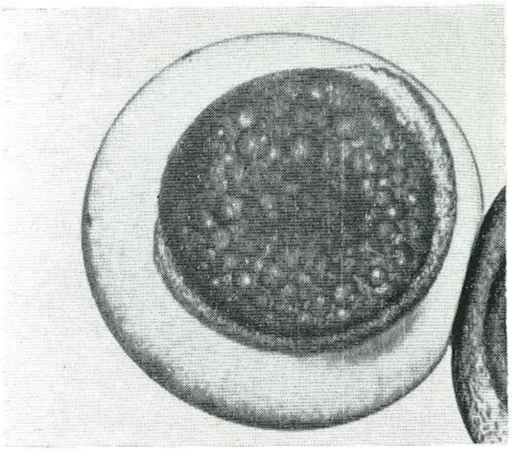

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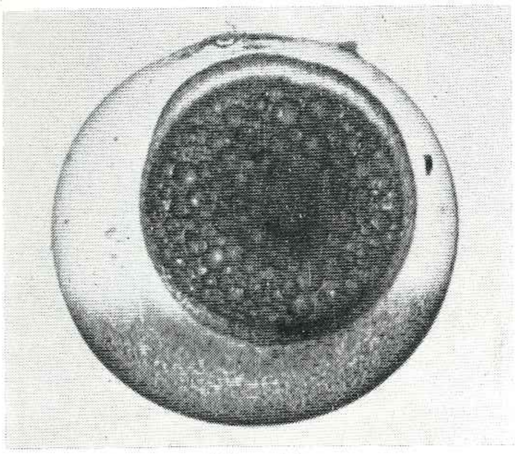

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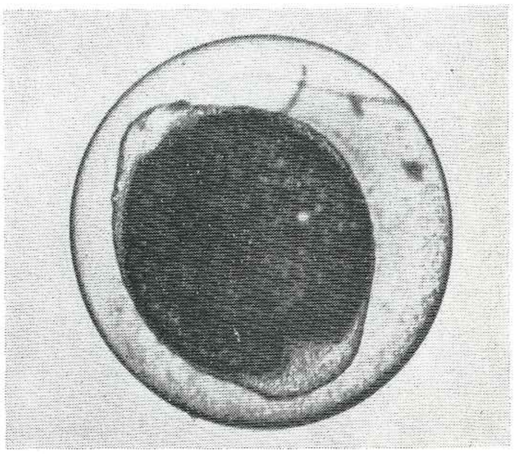

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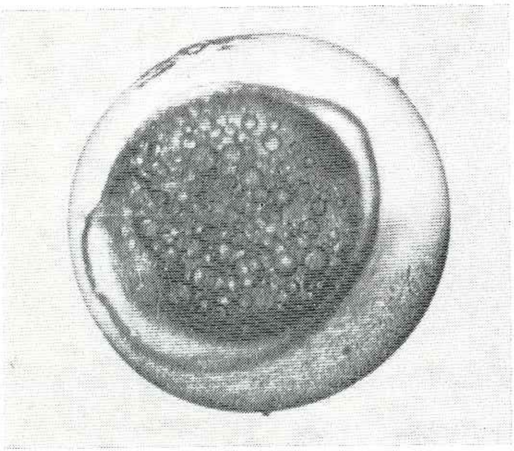

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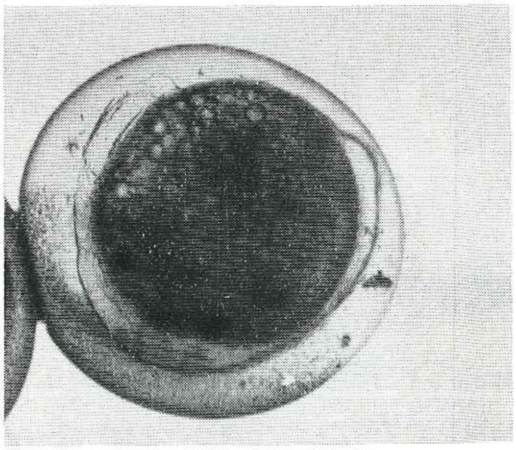

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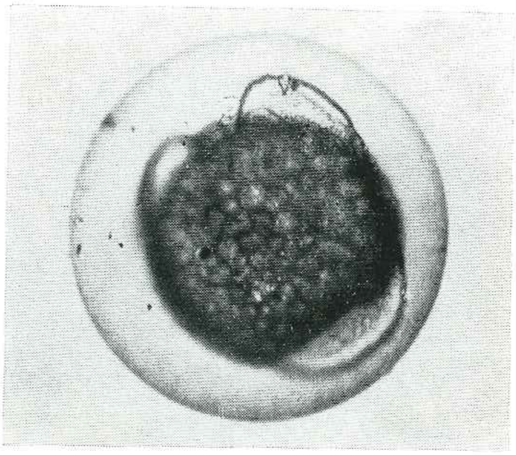

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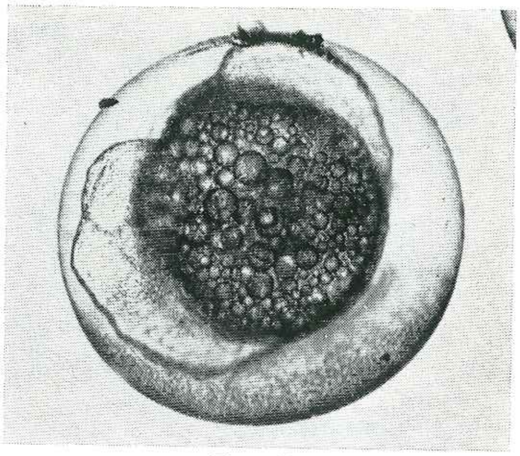

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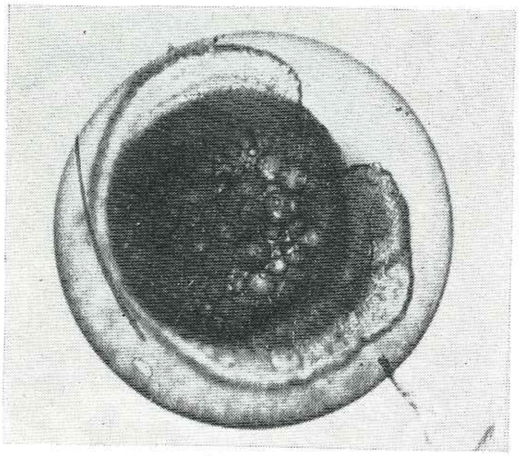

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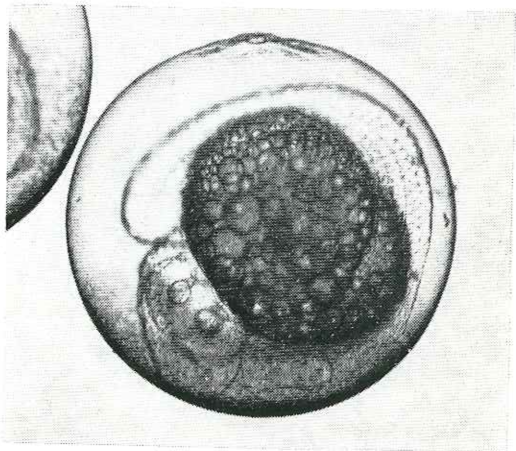

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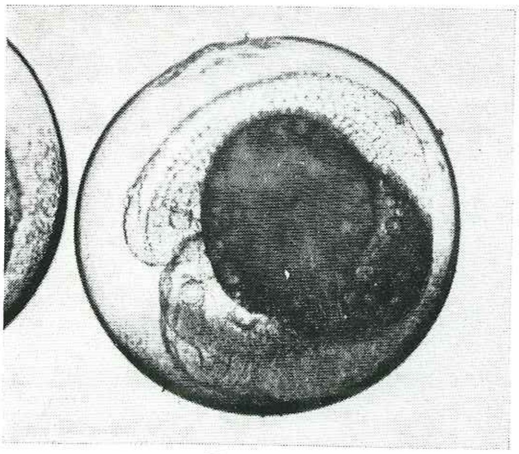

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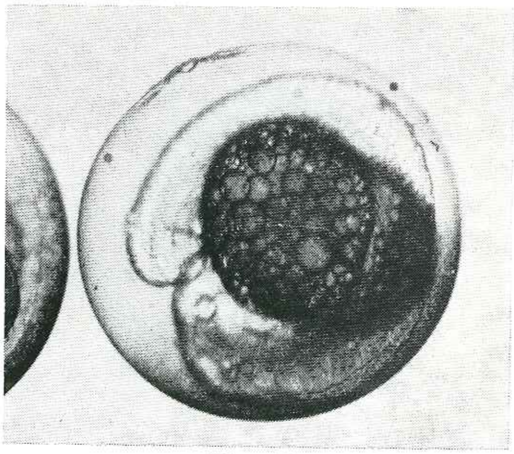

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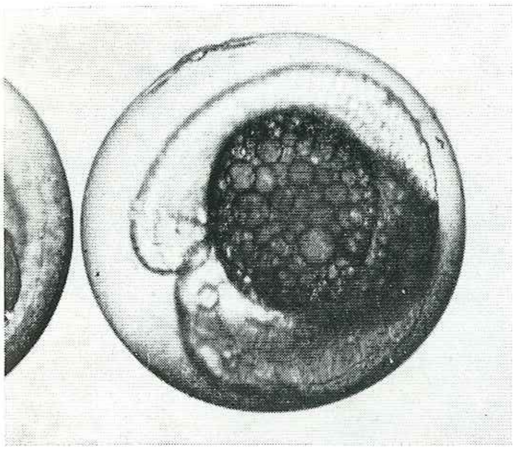

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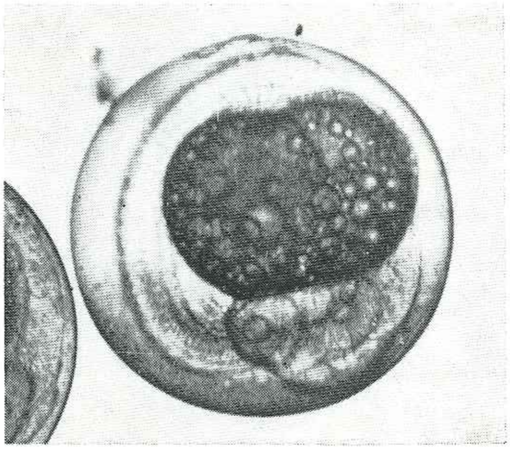

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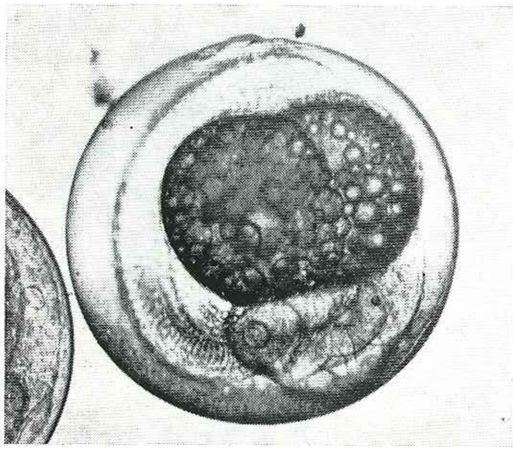

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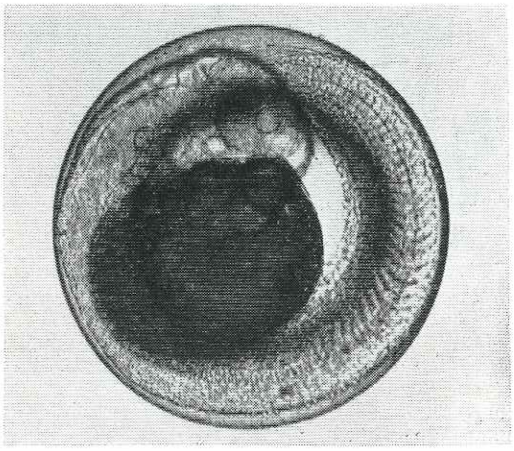

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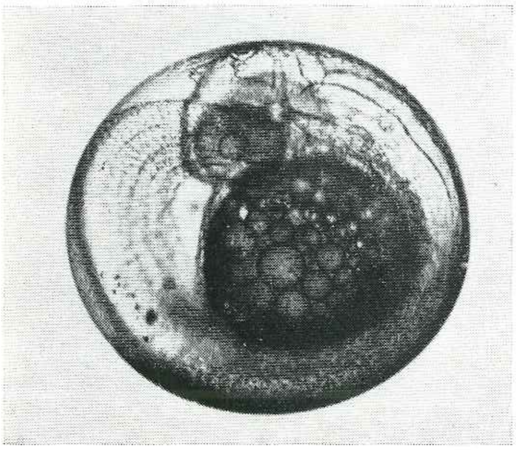

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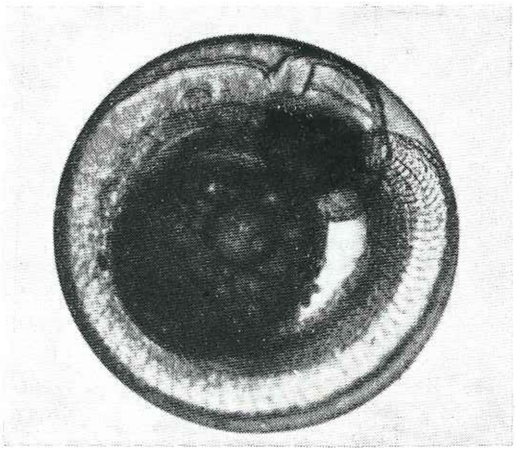

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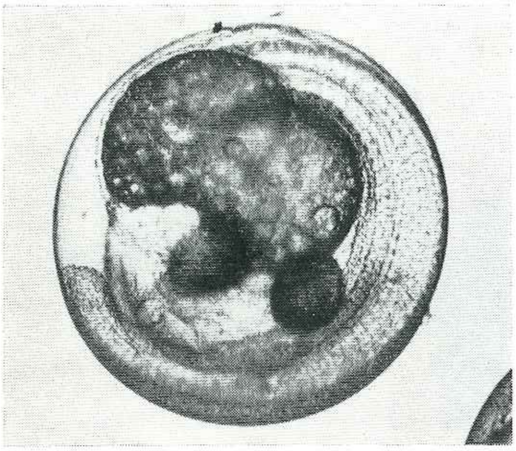

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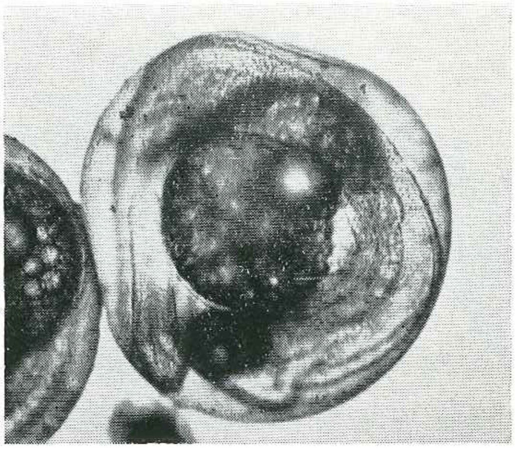

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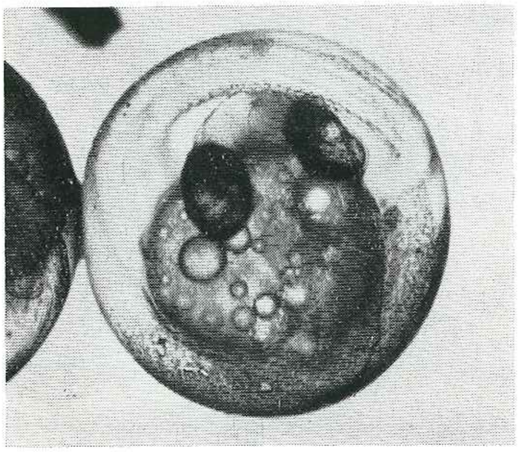


Plate 62[1].

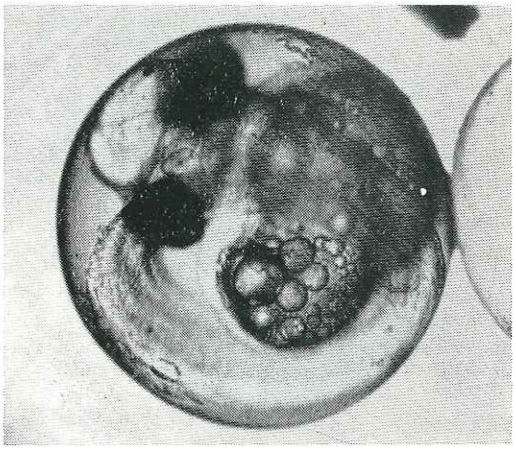
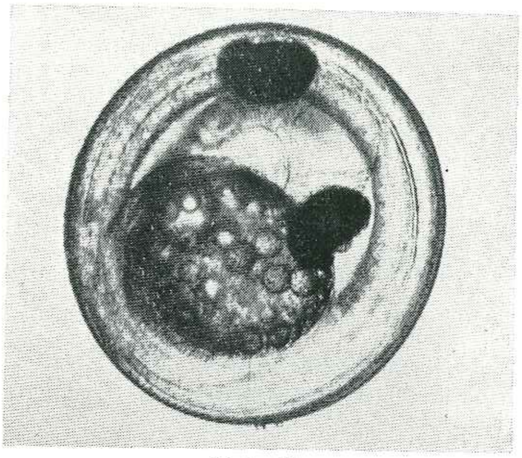


Plate 62[2].

Plate 63.

Plate 64.



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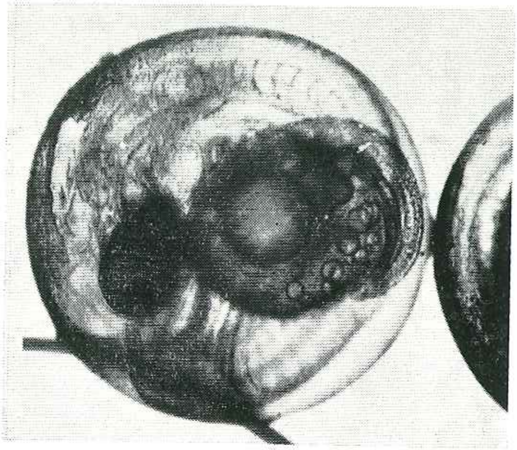

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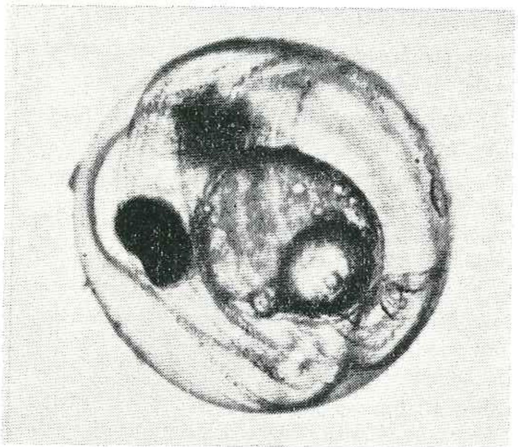

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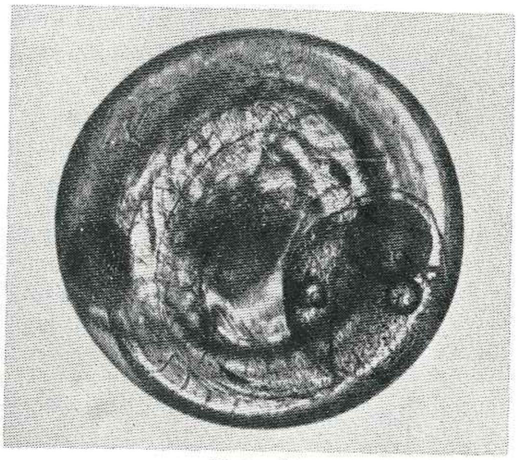

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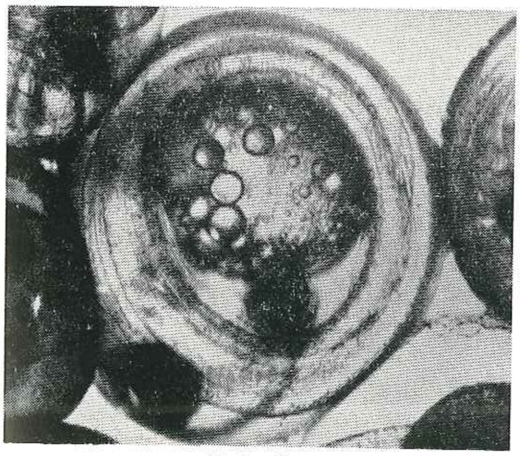

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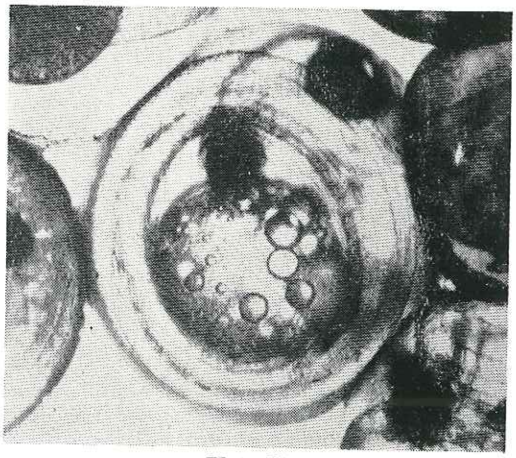

Plate 70.