RIT FISKIDEILDAR

V. BINDI – VOL. V

Nr. 6

Eyjólfur Friðgeirsson

Embryonic development of five species of gadoid fishes in Icelandic waters

HAFRANNSÓKNASTOFNUNIN

MARINE RESEARCH INSTITUTE

REYKJAVÍK 1978

RIT FISKIDEILDAR VOL. V – NR. 6

Embryonic development of five species of gadoid fishes in Icelandic waters

By

EYJÓLFUR FRIÐGEIRSSON

CONTENTS

Introduction

This work is a contribution to the study of the spawning of the most common gadoid fishes in Icelandic waters. It is a detailed observation on the embryonic development of 5 species of gadoid fishes and is meant to be a morphological basis for further studies of gadoid eggs and larvae in the field.

The embryonic development of the cod and other gadoids has been described by many authors, the work of professor A. Mock of the University of Durham in the twenties being of outstanding importance. Besides, a lot of experimental work has been done on these fishes and descriptions of eggs and larvae as well as works on ichtyoplankton are numerous. A number of these publications are listed in this paper but in addition the author wants to point out two detailed general references in the field, i.e. Blaxter (1969) and Russell (1976).

While the present paper is mainly intended as a guide to investigations in Icelandic waters the author hopes it will also be useful for researchers working on similar investigations elsewhere.

The description of the embryonic development, which is most detailed for the cod, is similar to the description of the embryonic development of the Icelandic capelin already published by the author (Friðgeirsson, 1976). The division into periods and stages, that has been adopted, is the same as that used in the description of the embryonic development of the capelin.

This division is thougt to be clear and accurate in the case of teleost fishes. It is recommended for ichthyoplanktonic and embryological descriptions, as it is based on a division of embryological development commonly in use in embryology.

In describing the development of the embryo, stages and moments are used 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 periods are intensive development and food obtained from reserves that originate from the mother. Leading environmental factors are the quantity of oxygen and predators.

In the case of the gadoids the embryonic period does not end at hatching as it does with the capelin. The embryonic period of gadoids will therefore, have to be divided into two subperiods: embryonic development inside the egg membrane and development of the free embryo.

The main characters of the larval period are temporary organs and food 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.

Material and methods

The present study of the embryonic development of the gadoid fishes was carried out at the Aquarium in Vestmannaeyjar, S.-Iceland, from late February to the beginning of May 1974 and 1975. The delay in publishing this material was mainly caused by a lack of adequate means by which to distinguish between haddock eggs and cod eggs. The distinction is still ambiguous.

The eggs were mainly obtained from ripe females in commercial catches, but also from catches of research vessels. The eggs were dry fertilized on board. The method used is described in the chapter on haddock. After fertilization the eggs were kept in ½ liter jars with seawater, that was changed once or twice a day. At the aquarium water is obtained from a 30 meter deep drilled well and has a constant temperature of 7,2°C and salinity of 29,5‰. The salinity of the water in the aquarium turned out to be too low to be used successfully for keeping eggs of the gadoids alive.

In the aquarium the jars containing the eggs were kept in constantly running water and thus at a constant temperature of 7,2°C.

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

Cod *(Gadus morhua morhua L.)*

EMBRYONIC PERIOD

Subperiod of egg or embryonic development inside the egg membrane.

1. stage. Fertilization — preparation for cleavage.

As soon as the cod egg touches the water at spawning its membrane (chorion) starts to distend (plate 1.1.). The egg itself distends less, and a perivitelline space is thus formed between the egg and the egg membrane. The perivitelline space is relatively small in the cod egg, or less than 1/10 of its total diameter. All living eggs fertilized and unfertilized that come in touch with water become distended.

When distension of the egg membrane is complete the cytoplasm that covers the yolk as a thin layer, begins to concentrate on the animal pole of the egg to form a little cap — the blastodisk (Fig. 1.1.). The gradual concentration of the cytoplasm moves the egg inside the membrane until it touches the membrane on all the vegital half of the egg and the perivitelline space surrounds only the sides of the blastodisk on the animal pole (see plates 1.9, 1.10 and figures 1.10, 1.11). This does not change the shape of the egg which is round or slightly oval.

After distension the egg is quite transparent. The egg membrane is thin and a small content of carotin gives the egg a very faint yellow hue. This, and the small size of the egg (see Table 1), makes it almost invisible to the naked eye in the water. The egg floats because of its high water content. Generally the water is up to 92% of the yolk in marine fishes (Soin, 1968). S. Greipsson of the Icelandic Fisheries Laboratories in Vestmannaeyjar measured the water content of two samples of cod eggs in april 1978. The water content of the samples was 92.7% and 92.8%. As the water content of the embryo is less the egg floats with the yolk up and the embryo hanging upside down underneath. When observing a cod egg or any pelagic egg under a microscope one usually looks at the embryo through the yolk. The embryo is in the upside down position until after hatching when the head sinus helps it to turn around. The cod egg floats at salinity above 32‰ and at salinity above 35‰ it floats at the very surface.

Table 1 shows the size frequency and average size of eggs from two females. One sample of 100 eggs was measured 2 days after fertilization and another of 104 eggs was measured 3 days after fertilization. The cod egg size was 1.3 to 1.5 mm (1.322 to 1.494 mm) in diameter. Ehrenbaum gives 1.16 to 1.60 mm and in the Baltic up to 1.89 mm.

Moment of one blastomere. Fig. 1.1, 2 hours after fertilization. (All timing is from the moment of fertilization).

TABLE 1

Size frequencies and average size of 204 eggs. One sample of 100 eggs 2 days old. The other of 104 eggs 3 days older.

Diameter Ocular micro-meter units	*Diameter mm*	*Frequency*	*Frequency*	*Frequency*
5.75	1.322	1		1
5.80	1.333	3		3
5.85	1.345	4		4
5.90	1.356	12	1	13
5.95	1.368	10	2	12
6.00	1.379	27	14	41
6.05	1.390	13	16	29
6.10	1.402	17	23	40
6.15	1.414	10	13	23
6.20	1.425	2	14	16
6.25	1.437	1	6	7
6.30	1.448		7	7
6.35	1.460		4	4
6.40	1.471		1	1
6.45	1.483		2	2
6.50	1.494		1	1
	No	100	104	204
Average diameter		1.382	1.411	1.397

2. stage. Cleavage of the blastodisk.

In this stage a one cell embryonic body becomes multicellular by repeated cleavages. During cleavage the embryonic cells do not grow to any extent and therefore become smaller with increasing number.

The two blastomeres that appear after the first cleavage are not equal in size. One of them is notably larger than the other. Later on, two of the four will be larger and consequently four of the eight. Later still one half of the morula and then the blastula will be larger than the other half. The head and most of the embryonic body will be formed from the larger half of the blastula. This obviously is a part of the differentation of cells into groups of cells that later on, during gastrulation, will differentiate into three basic embryonic tissue layers.

The sequence of cleavage is as follows:

Moment of 2 blastomeres. Fig. 1.2, 4 hours after fertilization.

Moment of 4 blastomeres. Fig. 1.3, 6 hours old.

Moment of 8 blastomeres. Fig. 1.4, plate 1.2, 8 hours old.

Moment of 16 blastomeres. Fig. 1.5, plate 1.3, 10 hours old.

Moment of 32 blastomeres. Fig. 1.6, plate 1.4, 12 hours old.

Moment of big cell size morula. Fig. 1.7, plate 1.5, 17 hours old.

Moment of moderate cell size morula. Fig. 1.8, plate 1.6, 1 day 2 hours old.

Moment of small cell size morula occurs at 1 day 7 hours after fertilization.

The blastomeres are all directly connected to the yolk until 16 blastomeres have formed, and the border blastomeres are connected to the thin layer of cytoplasm, which completely covers the yolk. At the occurrence of 32 blastomeres some of them will be completely separated from the yolk by horizontal cleavage. In one of the following cleavages uneven horizontal cleavage of the blastomeres, still connected to the yolk, will leave the blastomeres next to the yolk smaller than the rest. The small blastomeres fuse to form a thin continous cytoplasmic layer containing several free nuclei. This layer covers the yolk, and is the periblast, its nuclei taking part in breaking down the yolk and supplying its nutrients to the growing embryo. Expansion of the periblast plays an important role in the extension (epibolia) of the blastula at gastrulation. Soon after the formation of the periblast it starts to extend and its border goes beyond that of the morula. A part of the periblast extends beyond the edges of the morula to form a zone of periblast around it.

Moment of small cell morula with periblast zone. Fig. 1.9—1.10, plates 1.7—1.9, 1 day and 10 hours old.

The cleavage of the morula continues and at the same time changes in the shape of the morula can be observed. After the appearance of the periblast zone the morula gradually concentrates and becomes almost spherical. This results in its lower part being forced into the yolk. At this moment it is sitting on the top of the yolk like a ball in a bowl, the edge of the bowl being the zone of the periblast. The tension in the morula that is causing it to gather up into a ball gradually diminishes and eventually vanishes completely, resulting in the flattening down of the morula and its spreading in all directions. The morula is now a flat thin layer with poorly visible irregular borders. These changes in shape end with the formation of the blastula. Next the morula, having spread and covered the periblast entirely, shrinks and becomes in diameter similar to what it was before and thus the periblast zone reappears. The border of the morula thickens and forms a ring which becomes the germ ring of the blastula. Most of the nuclei of the periblast gather underneath the germ ring soon after the beginning of gastrulation. Inside the germ ring the blastula is elevated and free from the periblast leaving a cavity, the blastocoele.

Moment of concentrated morula. Fig. 1.11, plate 1.10. 1 day 20 hours old.

Moment of late morula. Fig. 1.12, plate 1.11, 2 days old.

Moment of blastula formation. Fig. 1.13, plate 1.12, 2 days and 3 hours old.

Moment of blastula. Fig. 1.14—1.15, plates 1.13—1.15, 2 days and 5 hours old.

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

This stage involves two processes — the formation of the three basic tissues of the embryonic body and the overgrowth of the yolk. The formation of the three basic tissues of the embryo ends as the formation of pre-organs begins, but this does not coincide with the completion of the overgrowth of the yolk in the eggs of cod and other gadoids. The end of those two processes occurs at the same time in the capelin eggs, but for example in salmonoid eggs the closure of the blastopore happens much later than the beginning of organogenesis which should be used as an indication of the end of gastrulation, rather than the closure of the blastopore.

The blastoderm overgrows the yolk by epiboly following epiboly of the periblast (Trinkaus, 1969).

The overgrowth of the blastoderm is dependent on the epiboly of the periblast. As the blastoderm overgrows the yolk, cells of the germ ring migrate dorsally and form gradually an oblong embryonic shield. The embryonic shield gives rise to the embryo. The head part of the embryonic shield is first laid down and as mentioned before is mainly formed from cells originating from the larger half of the blastula.

Moment of beginning gastrulation. Fig. 1.16, plates 1.16—1.17, 2 days and 12 hours old.

Moment of early gastrulation. Fig. 1.17—1.18, plates 1.18—1.19, 3 days old.

Moment of middle gastrulation. Fig. 1.19, plates 1.20—1.21, 3 days and 4 hours old.

4. stage. Formation of pre-organs — Organogenesis 1.

The first rudimentary organs that are formed and can easily be seen are the three basic sections of the brain and soon afterwards the optic bulbs. Formation of those rudimentary organs mark the end of the gastrulation and the beginning of organogenesis. 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 chord, notochord, somites and the gut.

Moment of occurence of optic bulbs. Fig. 1.20, plate 1.21, 4 days old. Forebrain, midbrain and hindbrain have formed. At both sides the forebrain has bulged out and formed the rudiment of the eyes — the optic bulbs.

Moment of formation of ear primordia. Fig. 1.21, plate 1.22, 4 days 1 hour old.

The ear primordia have formed and can be seen at both sides of the hindbrain.

Moment of closure of the blastopore. Fig. 1.22—1.23, plates 1.23—1.24, 4 days 10 hours old. The blastopore has closed so the yolk is now completely overgrown by the blastoderm. At the time of the closure of the blastopore the first pigmentation of the embryonic body begins. First segmentation of the somital mesoderm has taken place and first somites have been formed on the middle of the embryonic body. Further somites will appear in pairs on both sides of the first somites thus making them 3, then 5, 7 and so on until the whole number of the body somites is formed. The somites of the tail will appear as it grows.

Moments of optic cups. Fig. 1.24, plate 1.25, 5 days 4 hours old. The number of somites has increased to a full complement of body somites 18—20. The nose primordium has appeared and is clearly visible. The middle gut has formed. The outside of the optic bulbs has folded inwards to make the optic cup of the eye. The pigment cells have enlarged and taken the form of stars.

Moment of tailbud. Fig. 1.25, plate 1.25, 6 days old. Rudiments of all the main organs of the embryonic body have formed including all the somites of the body, the gut, anus and the tailbud which will soon start developing into a tail.

5. stage. Full development of main organs — Organogenesis 2.

During this stage organs and systems of organs become functionary one after another. In the beginning a major change in the life of the embryo takes place as it starts to move its body. Besides, this stage includes the development of the heart and blood system and development of all the main organs of the embryo.

Moment of the first movement. Fig. 1.26, plate 1.27, 6 days 2 hours old. The embryo has acquired the power of mobility and is performing weak body movements. Two tiny otoliths begin to form in the inner ear. Olfactory bulbs can be seen and the ectodermal lenses of the eye have appeared. The tail is developing. On both sides of the embryonic body the rudimentary pectoral fin lobes are taking shape.

Moment of development of heart. Fig. 1.27—1.28, plates 1.28—1.29, 6 days and 10 hours old. A growing mesodermal thickening lies under the left side of the head from where the heart is developing.

Moment of first beating of the heart. Fig. 1.29—1.30, plates 1.30—1.31, 7 days and 20 hours old.

Rudimentary heart has developed from mesodermal cells that have gathered under the head. The heart has the form of a bell shaped tube, and its beats are irregular and slow. Red corpuscles (with haemoglobin) have not formed, nor will they appear until at the end of the embryonic period. The embryo has no special embryonic breathing organs, and such organs are not found in any cod fish during the embryonic period. Under the frontal part of the gut a rudimentary liver appears. The tail is enlarging rapidly. Fin lobes are developing ventrally and dorsally on the tail and on the dorsal side of the embryonic body.

6. stage. Preparation for hatching.

The beginning of this stage marks the end of organogenesis. Formation of the embryonic body as well as the tail and main organs is over, but the body and the tail are still growing. The organs must still undergo development and growth before becoming fully functional.

Moment of first hatching cells. Fig. 1.31, plates 1.32—1.34, 8 days old. Hatching cells have appeared on the head of the embryo. 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. Black pigment has appeared in the eyes.

Moment just before hatching. Fig. 1.32, plate 1.35, 9 days old. The embryo is ready for hatching.

If the eggs are kept at constant temperature of 7.2°C the embryos will start hatching 9 days old but most of them hatch when they are 9 days and 12 hours to 10 days old.

SUBPERIOD OF FREE EMBRYO

7. stage. Hatching and formation of mouth.

The embryo frees itself from the egg membrane, but is still floating passively upside down at the surface of the water and it is still feeding on supply from its mother. Thus no major changes in the relation between the embryo and its environment have taken place.

Moment of hatching. Fig. 2.1, plates 2.1—2.3. Most of the embryos break through the membrane (chorion) head first with rapid movements of the body and tail.

The anterior of the head is free of the yolksac, indicating the beginning of the development of a mouth. The pectoral fins still appear like lobes with the proximal part joined horizontally to the embryonic body. The yolksac is large and the embryo is floating at the surface with it upward. The fin lobes above the head, the body and part of the tail are saclike and hollow filled with light liquid. This is the head sinus, *sinus cephalicus*. As the embryo grows the yolksac becomes smaller and its buoyancy decreases. This decreased buoyancy is compensated for by the growing head sinus. This not only keeps up the buoyancy of the embryo but moves the point of gravity so that the embryo gradually turns the dorsal side upwards. When the yolk is almost finished and the embryo starts to eat independently its normal position in the horizontal plane with the back upwards is gained.

Moment of mouth opening. Fig. 2.2, 1 day after hatching. The head of the embryo is now almost in line with the embryo's body. The mouth has opened out.

Moment of occurrence of sensual line cells. Fig. 2.3, 2 days after hatching.

Several changes connected with swimming and independent feeding can be noted. The mouth opening is enlarging and a rudimentary mouth skeleton is forming. Ten cells of the sensual line have appeared. These cells are situated symmetrically, 5 on both sides of the embryonic body. Two are above the posterior part of the eyes, two are just behind the pectoral fins and 6 of them are on the tail. These cells are at the surface of the embryonic body and are supplied with tiny nerves connected to a nerve that goes along both sides of the body mid laterally. The number of cells will not increase during the late embryonic and early larval periods. Similar cells are found in all gadoid larvae at this stage in development. Developing cleitrum can be seen, and the pectoral fin has begun to move from a horizontal to a vertical position. The developing swim bladder has appeared.

Moment of functionary eyes. Fig. 2.4, plate 2.4, 3 days after hatching.

Black pigment, which first appeared in the eyes at the beginning of 6. stage, has gradually been increasing and the eyes are now almost black. For the last two days guanin pigment has been concentrating in the eyes and now the whole eye has a steelblue and yellow hue. The eyes have well developed muscles and are thus capable of adjustment. All this indicates that the eyes are now becoming functional.

LARVAL PERIOD

8. stage. Mixed feeding.

The larva, which until now has been living on food reserves from its mother, now starts independent feeding. It still has some of the yolk left, so it is at first not totally dependent on food from outside.

Moment of first active eating. Fig. 2.5, 4 days after hatching. Length 5.5 mm.

Morphologically the larva is now prepared to catch and utilize external food. The mouth is fully formed and opens into the gut that has become rather big and its inner surface has increased as it has grown uneven. In connection with the gut is a relatively large liver and at its side the gallbladder. The eyes and the sensitive cells are now functional so the larva can find and orientate on food particles. The pectoral fins have enlarged and are now in an almost vertical position and supported by cartilaginous cleitrum.

The embryonic development is over and the larva will grow but not change very much in the near future.

Moment of active eating. Fig. 2.6, 5 days after hatching. Length 5.8 mm.

9. stage. Independent feeding.

Moment of independent feeding. Fig. 2.7, 6 days after hatching. Length 5.9 mm.

The yolk is almost finished and the larva is entirely dependent on food it can catch itself. During complete starvation the remains of the yolk will disappear in the next 1 or 2 days and in further 3 or 4 days the larvae will die.

From the sixth day after hatching *Artemia salina* was fed to some of the larvae hatched in the laboratory. Half of them obviously could not utilize the food and died about 5 days after first feeding, the rest usually died within 10 days. From that series is the larva on Fig. 2.8, 6 mm long, 15 days after hatching. During this feeding experiment it was noticed that often the larvae were having difficulties with the *Artemia,* they had been feeding on. Caught and swallowed *Artemia,* that had been more than an hour in the larva's stomach, were often still alive and even crawling around inside it. Furthermore, *Artemia* was observed to crawl out of a larva's anus not notably hurt and swim away. This shows that even if *Artemia* is small enough for the cod larvae to catch it they have difficulties in utilizing it, and *Artemia* for one reason or another is not suitable as food for cod larvae.

Haddock *(Melanogrammus aeglefinus (L))*

The haddock egg size is 1.3 to 1.5 mm (1.391 to 1.494) in diameter. Russel gives 1.20 to 1.70 mm. The results of measurement of 50 haddock eggs is shown in Table 2.

The haddock egg is almost identical to the cod egg and differences in size, morphology and colour are small. This makes them almost indistinguishable from cod eggs until pigmentation differences can be used as criterion. But even this should be used carefully because variation in pigmentation can be quite considerable. In one aspect, however, the morphology of the haddock egg differs considerably from the cod egg and eggs of other fish of the cod family. Where all other gadoid eggs have only one primary egg membrane, the chorion, the haddock egg has a secondary membrane of adhesive material covering the first membrane. The existence of this secondary membrane was first observed when haddock eggs were dry fertilized. Eggs and sperm were mixed dry in a jug. After pouring sea water into the jug and leaving it for one or two minutes to give time for fertilization to take place the water containing dead sperm was poured off, thus leaving the eggs almost dry, before pouring fresh sea water over them. When the fresh sea water had been applied to the fertilized eggs the eggs were in almost all cases glued together in a lump or layer leaving only a few eggs free floating. There was no doubt that the eggs were glued together, most probably by an adhesive layer on the egg. Under the microscope this adhesive layer could not be detected. An exception was that eggs from the same female did not stick together and, as said before, some eggs in most of the series did not stick to other eggs. The formation of lumps or layers of eggs could be avoided if the eggs were prevented from close contact by never letting them dry.

Turdakov (1963), Sadov (1963) and Soin (1968) state that the quantity of glue can differ on eggs from different females and also within a batch of eggs from the same female. Eggs with no glue at all are also found. Several efforts were made to expose the glue and make it visible by colouring it and breaking it up with chemicals to make the haddock eggs distinguishable from cod eggs but in vain.

Except in timing, the development of the haddock eggs does not differ very much from that of the cod, so the description of the cod egg development is valid for the haddock as well and will therefore not be repeated. The timing of the process is, however, described in a series of drawings and photographs.

TABLE 2

Size frequencies and average size of 50 haddock eggs at the moment of morula, 2 days old.

Diameter Ocular micro-meter units	*Diameter mm*	*Frequency*
6.05	1.391	4
6.10	1.402	9
6.15	1.414	6
6.20	1.425	11
6.25	1.437	6
6.30	1.448	5
6.35	1.460	3
6.40	1.471	1
6.45	1.483	3
6.50	1.494	2
Average diam.	1.430	50

EMBRYONIC PERIOD

Subperiod of egg or embryonic development inside egg membrane.

1. stage. Preparation for cleavage.

Moment of blastodisk. Fig. 3.1, plates 3.1—3.2, 3 hours old.

2. stage. Cleavage of the blastodisk.

Moment of 2 blastomeres. Fig. 3.2, plate 3.3, 5 hours old.

Moment of 4 blastomeres. Fig. 3.3, plate 3.4, 7 hours old.

Moment of 16 blastomeres. Fig. 3,4, plate 3.5, 13 hours old.

Moment of 32 blastomeres. Fig. 3,5, 15 hours old.

Moment of big cell size morula. Fig. 3.6—3.7, plates 3.6—3.7, 17 hours old.

Moment of moderate cell size morula. Fig. 3:8, plate 3.8, 1 day and 1 hour old.

Moment of periblast zone. Fig. 3.9, plate 3.9, 1 day and 6 hours old.

Moment of concentrated morula. Fig. 3.10, plate 3.10, 1 day and 10 hours old.

Moment of flat morula. Fig. 3.11, plate 3.11, 1 day and 12 hours old.

Moment of blastula. Fig. 3.12—3.13, plates 3.12—3.13, 1 day and 19 hours old.

The germ ring has formed. Figure 3.13 and plate 3.13 show a slit through the middle of the blastula. Under the blastula and extending its border is the periblast, the nuclei of which are almost all concentrated underneath the germ ring. The difference between the thickness of the two halves of the blastula is clearly illustrated in the drawing and photograph.

At this moment the haddock eggs will still stick together if they are dry or get into close contact with each other. This shows, that the glue is still active.

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

Moment of beginning of gastrulation. Fig. 3.14, plate 3.14, 3.15, 2 days and 3 hours old.

4. stage. Formation of pre-organs — Organogenesis 1

Moment of optic bulbs. Fig. 3.15, plate 3.16, 2 days and 18 hours old.

Moment of eye lens formation. Fig. 3.16, plate 3.17, 3 days and 4 hours old.

Moment of end of organogenesis 1. Fig. 3.17, plates 3.18—3.19, 4 days and 6 hours old.

Similar to the cod, pigmentation of the haddock's embryonic body occurs at the time of the closure of the blastopore. The pigmentation follows a similar pattern to that of the cod and it can therefore not yet be used to distinguish the haddock egg from cod egg.

5. stage. Full development of main organs — Organogenesis 2.

Moment of first movement. Fig. 3.18—3.19, plate 3.20, 4 days and 16 hours old.

Moment of first heart beats. Fig. 3.20, 5 days and 10 hours old.

Moment of end of organogenesis 2. Fig. 3.21, plate 3.21, 6 days and 4 hours old.

6. stage. Preparation for hatching.

Moment of occurrence of hatching cells. Fig. 3.22, 7 days and 5 hours old.

If the haddock eggs are kept at a constant temperature of 7.2°C hatching starts when the embryos are 8 days and 12 hours old, but most of them will hatch on the 10th day.

SUBPERIOD OF FREE EMBRYO

7. stage. Hatching and formation of mouth.

Moment of hatching. Fig. 4.1, 9 days after fertilization. Just after hatching.

Moment of mouth opening. Fig. 4.2, 1 day after hatching.

Moment of swim bladder. Fig. 4.3, 2 days after hatching.

Moment of functional eyes. Fig. 4.4, 3 days after hatching.

LARVAL PERIOD

8. stage. Mixed feeding.

Moment of first active feeding. Fig. 4.5, 4 days after hatching.

Moment of active feeding. Fig. 4.6, 5 days after hatching.

9. stage. Independent feeding.

Moment of independent feeding. Fig. 4.7, 6 days after hatching. Length 5.2 mm.

Fig. 4.8, 10 days after hatching. Length 5.2 mm.

Saithe *(Pollachius virens (L.))*

TABLE 3

Size frequencies and average size of 100 saithe eggs at first cleavage. 1 day old.

Diameter Ocular micro-meter units	*Diameter mm*	*Frequency*
9.00	1.051	2
9.05	1.058	1
9.10	1.064	2
9.15	1.070	7
9.20	1.075	8
9.25	1.081	5
9.30	1.087	8
9.35	1.093	9
9.40	1.099	9
9.45	1.105	7
9.50	1.111	10
9.55	1.116	6
9.60	1.122	4
9.65	1.128	3
9.70	1.134	3
9.75	1.140	5
9.80	1.146	3
9.85	1.151	3
9.90	1.157	2
9.95	1.163	1
10.00	1.169	2
Average diameter	1.104	100

The result of measurements of 100 saithe eggs is shown in Table 3. The saithe egg is morphologically similar to the cod egg but smaller 1.0 to 1.2 mm (1.051 to 1.169 mm) in diameter. Russell gives 1.03 to 1.22 mm.

EMBRYONIC PERIOD

Subperiod of egg or embryonic development inside egg mebrane.

1. stage. Preparation for cleavage.

Moment of blastodisk. Fig. 5.1, 3 hours old.

2. stage. Cleavage of the blastodisk.

Moment of 2 blastomeres. Fig. 5.2, 5 hours old.

Moment of 4 blastomeres. Fig. 5.3, 7 hours old.

Moment of 8 blastomeres. Fig. 5.4, 9 hours old.

Moment of 16 blastomeres. Fig. 5.5, 11 hours old.

Moment of 32 blastomeres. Fig. 5.6, plates 5.1—5.2, 13 hours old.

Moment of moderate cell size morula. Fig. 5.7, 23 hours old.

Moment of small cell size morula. Fig. 5.8, 1 day and 8 hours old.

Moment of periblast zone. Fig. 5.9, plate 5.3, 1 day and 8 hours old.

Moment of flat morula. Fig. 5.10, 1 day and 14 hours old.

Moment of blastula. Fig. 5.11, 1 day and 20 hours old.

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

Moment of beginning of gastrulation. Fig. 5.11, 2 days and 3 hours old.

Moment of early gastrulation. Fig. 5.12, plate 5.4, 2 days and 8 hours old.

Moment of end of gastrulation. Fig. 5.13, 3 days old.

4. stage. Formation of pre-organs — Organogenesis 1

Moment of optic bulbs. Fig. 5.14, 3 days and 4 hours old.

Moment of 5 somite. Fig. 5.15, 3 days and 9 hours old.

Moment of closure of the blastopere. Fig. 5.16, 4 days old.

The black pigmentation appears on the embryonic body at the time of closure of the blastopore.

Moment of eye lens formation. Fig. 5.17, 4 days and 2 hours old.

5. stage. Full development of main organs — Organogenesis 2

Moment of first movement. Fig. 5.18, 5 days old.

Moment of first heart beats. Fig. 5.19, 6 days and 5 hours old.

6. stage. Preparation for hatching.

Moment of occurrrence of hatching cells. Fig. 5.20, 7 days and 2 hours old.

If saithe eggs are kept at a constant temperature of 7.2°C, hatching will take place on the 8th day.

SUBPERIOD OF FREE EMBRYO

7. stage. Hatching.

At hatching the saithe embryo is less developed than that of the cod and haddock. As will be seen later the same is true for the Norway pout. The embryo of the saithe is at this moment floating immobile at the surface, as the tail is still bent and not in line with the body and therefore of little use for moving about. The head is bent down on the yolksac. Neither the pectoral fin nor the head sinus have yet started to develop.

Moment of hatching. Fig. 6.1, 7 days and 6 hours old. Just after hatching.

Moment of pectoral fin lobes. Fig. 6.2, 6 hours after hatching.

Moment of preparation for mouth formation. Fig. 6.3, 2 days after hatching.

Head and tail are now in line with the body. At this stage in development the embryo is comparable to that of the cod and haddock at hatching.

Moment of mouth cup. Fig. 6.4, 3 days after hatching. Length 4.5 mm.

Moment of mouth opening. Fig. 6.5, 4 days after hatching. Length 4.7 mm.

Moment of yellow pigment in eyes. Fig. 6.6, 5 days after hatching. Length 4.7 mm.

Moment of vertical pectoral fin. Fig. 6.7, 6 days after hatching. Length 4.8 mm.

Moment of functional eyes. Fig. 6.8, 7 days after hatching. Length 5.0 mm.

LARVAL PERIOD

8. stage. Mixed feeding.

Moment of first active feeding. Fig. 6.9, 8 days after hatching. Length 5.0 mm.

9. stage. Independent feeding.

Moment of independent feeding. Fig. 6.10, 10 days after hatching. Length 5.0 mm.

Norway pout *(Trisopterus esmarki* (Nilsson))

TABLE 4

Size frequencies and average size of 54 Norway pout eggs at moment of morula at the end of the first 24 hours of development.

Diameter Ocular micro-meter units	*Diameter mm*	*Frequency*
4.30	0.989	3
4.35	1.000	6
4.40	1.012	11
4.45	1.023	16
4.50	1.035	15
Average diameter	1.021	54

Size frequency and average size of 50 Norway pout eggs at organogenesis 1, 3 days old.

Diameter Ocular micro-meter units	*Diameter mm*	*Frequency*
3.20	0.994	1
3.25	1.010	3
3.30	1.025	6
3.35	1.041	13
3.40	1.056	15
3.45	1.072	11
3.50	1.088	0
3.55	1.103	1
Average diameter	1.049	50

Measurement of 104 Norway pout eggs is shown in Table 4. The Norway pout egg is morphologically similar to the cod egg but smaller 0.95 to 1.15 mm (0.989 to 1.103 mm) in diameter. Ehrenbaum gives 1.00 to 1.19 mm.

EMBRYONIC PERIOD

Subperiod of egg or embryonic development inside egg membrane.

1. stage. Preparation for cleavage.

Moment of blastodisk. Fig. 7.1, plate 7.1, 1 hour old.

2. stage. Cleavage of the blastodisk.

Moment of 2 blastomeres. Fig. 7.2, plate 7.2, 2 hours old.

Moment of 4 blastomeres. Fig. 7.3, plate 7.3, 3 hours and 30 minutes old.

Moment of 8 blastomeres. Fig. 7.4, 5 hours old.

Moment of 16 blastomeres. Fig. 7.5, 6 hours and 30 minutes old.

Moment of 32 blastomeres. Fig. 7.6, plate 7.4, 8 hours old.

Moment of big cell morula. Fig. 7.7, 10 hours old.

Moment of moderate cell morula. Fig. 7.8, plate 7.5, 12 hours old.

Moment of periblast zone. Fig. 7.9, plate 7.6, 14 hours old.

Moment of concentrated morula. Fig. 7.10, plate 7.7, 18 hours old.

Moment of formation of blastula. Fig. 7.11, plate 7.8, 22 hours old.

Moment of blastula. Fig. 7.12, plate 7.9, 1 day old.

3. stage. Formation of the basic embryonic tissue layers — gastrulation.

Moment of beginning of gastrulation. Fig. 7.13, plate 7.9, 1 day and 2 hours old.

Moment of end of gastrulation. Fig. 7.14, plate 7.10, 2 days and 1 hour old.

4. stage. Formation of pre-organs — organogenesis 1

Moment of optic bulbs. Fig. 7.15, plates 7.11—7.12, 2 days and 20 hours old.

As can be seen on the drawing (Fig. 7.15) and photograph (plate 7.12) the forebrain (prosencephalon) is unusually big and formed in such a way that the front of the embryonic head is high and steep. This makes the embryo of the Norway pout easily recognizable and different from other gadoid embryos.

Moment of cracks in the optic bulbs. Fig. 7.16, plate 7.13, 2 days and 22 hours old.

The formation of black pigment is rather late in the Norway pout's embryonic body, or after the closure of the blastopore. The pigmentation is at first rather weak.

Moment of first pigmentation. Fig. 7.17, plate 7.14, 3 days and 6 hours old.

5. stage. Full development of main organs — organogenesis 2

Moment of first movement. Fig. 7.18, plate 7.15, 3 days and 20 hours old.

Heart beats begin when embryo is 4 days and 18 hours old.

6. stage. Preparation for hatching.

Moment of hatching cells. Fig. 7.19, plate 7.16, 5 days and 1 hour old.

If the Norway pout eggs are kept at a constant temperature of 7.2°C hatching will take place during the later half of the sixth day and the first half of the seventh day.

SUBPERIOD OF FREE EMBRYO

7. stage. Hatching.

As the saithe the Norway pout embryo hatches early and is less developed than the embryos of cod, haddock and whiting.

Moment of hatching. Fig. 8.1, plate 7.17, just after hatching. 5 days and 20 hours old. Length 2.0 mm.

Moment of pigment in eye. Fig. 8.2, 1 day after hatching. Length 2.9 mm.

Moment of lifting of head. Fig. 8.3, 2 days after hatching. Length 3.7 mm.

Moment of mouth cup. Fig. 8.4, 3 days after hatching. Length 3.7 mm.

Moment of mouth opening. Fig. 8.5, 4 days after hatching. Length 4.3 mm.

Moment of yellow pigment in eyes. Fig. 8.6, 5 days after hatching. Length 4.0 mm.

Moment of functional eyes. Fig. 8.7, 6 days after hatching. Length 4.2 mm.

LARVAL PERIOD

8. stage. Mixed feeding.

Moment of first active feeding. Fig. 8.8, 8 days after hatching. Length 4.4 mm.

9. stage. Independent feeding.

Moment of independent feeding. Fig. 8.8, 9 days after hatching. Length 4.5 mm.

Length 4.6 mm. Fig. 8.10, 10 days after hatching.

Whiting *(Merlangius merlangus merlangus L.)*

TABLE 5

Size frequencies and average size of 50 whiting eggs at the moment of morula. 1 day old.

Diameter Ocular micro-meter units	*Diameter mm*	*Frequency*
4.40	1.012	3
4.45	1.023	9
4.50	1.035	17
4.55	1.046	13
4.60	1.058	4
4.65	1.069	3
4.70	1.081	1
Average diameter	1.039	50

Size frequencies and average size of 50 whiting eggs at organogenesis 1. 3 days old.

Diameter Ocular micro-meter units	*Diameter mm*	*Frequency*
3.40	1.056	1
3.45	1.072	1
3.50	1.088	18
3.55	1.103	22
3.60	1.119	6
3.65	1.134	1
3.70	1.150	1
Average diameter	1.100	50

Measurements of 100 whiting eggs is shown in Table 5. The higher karotin content of the whiting egg than of the cod egg gives it a faint yellow hue. Otherwise the whiting egg is similar to that of the cod except in size, which is 1.0 to 1.2 mm. (1.012 to 1.150 mm). Russell gives 0.97 to 1.32 mm.

EMBRYONIC PERIOD

Subperiod of egg or embryonic development inside egg membrane.

1. stage. Preparation for cleavage.

Moment of blastodisk. Fig. 9.1, 2 hours old.

2. stage. Cleavage of the blastodisk.

Moment of 2 blastomeres. Fig. 9.2, 3 hours old.

Moment of 4 blastomeres. Fig. 9.3, 5 hours old.

Moment of 8 blastomeres. Fig. 9.4, 7 hours old.

Moment of 16 blastomeres. Fig. 9.5, 9 hours old.

Moment of 32 blastomeres. Fig. 9.6, 11 hours old.

Moment of moderate cell size morula. Fig. 9.7, plate 9.1, 18 hours old.

Moment of periblast zone. Fig. 9.8, plate 9.2, 20 hours old.

Moment of concentrated morula. Fig. 9.9, plate 9.3, 1 day old.

Moment of blastula. Fig. 9.10, 1 day and 10 hours old.

3. stage. Formation of the basic embryonic tissue layers — gastrulation.

Moment of gastrulation. Fig. 9.11, plate 9.4, 1 day and 18 hours old.

4. stage. Formation of pre-organs — organogenesis 1.

Moment of optic bulbs. Fig. 9.12, plate 9.5, 2 days and 20 hours old.

Moment of first pigmentation. Fig. 9.13—9.14, plates 9.6—9.7, 3 days and 18 hours old.

The black pigmentation of the embryo, which occurs rather early or before the closure of the blastopore, is quite intense. It appears not only on the embryonic body but also on the yolksac and in that way the species differs from the rest of the codfishes described in this paper.

Moment of end of organogenesis 1. Fig. 9.15, plate 9.8, 4 days and 20 hours old.

5. stage. Full development of main organs — organogenesis 2.

Moment of first hearts beats. Fig. 9.16, plate 9.9, 5 days and 20 hours old.

At this moment a yellow karotinoid pigment appears on the embryo's body and yolksac. This is an exception for fishes of the cod family, but a yellow pigment is common for example on the embryonic body of many flatfish species.

6. stage. Preparation for hatching.

Moment of hatching cells. Fig. 9.17, plate 9.10, 6 days and 20 hours old.

If whiting eggs are kept at a constant temperature of 7.2°C hatching will take place on the 10th day.

SUBPERIOD OF FREE EMBRYO

7. stage. Hatching — formation of mouth.

Moment of hatching. Fig. 10.1, 9 days old. Length 3.0 mm.

The embryo in Fig. 10.1 is one of the first to hatch in the present series. At hatching the remaining embryos resembled however, more the embryo on Figure 10.2.

Moment of beginning of mouth formation. Fig. 10.2, 9 days and 20 hours old, 12 hours after hatching. Length 3.5 mm.

Moment of mouth cup. Fig. 10.3, 2 days after hatching. Length 3.5 mm.

Moment of mouth opening. Fig. 10.4, 3 days after hatching. Length 3.8 mm.

Moment of functional eye. Fig. 10.5, 5 days after hatching. Length 3.8 mm.

LARVAL PERIOD

8. stage. Mixed feeding.

Moment of first active feeding. Fig. 10.6, 6 days after hatching. Length 3.8 mm.

9. stage. Independent feeding.

Moment of independent feeding. Fig. 10.7, 7 days after hatching. Length 3.8 mm.

References

Ballard, W. W., 1966: Origin of the hypoblast in Salmon. J. Exp. zool., Vol. **161**, 211—220.

Blaxter, J. H. S., 1969: Development: eggs and larvae. Fish Physiology, **3**, 177—252.

Ehrenbaum, E., 1909: Eier und Larven von Fischen des Nordischen Planktons. Lipsius und Tischer, Kiel und Leipzig.

Friðgeirsson, E., 1976: Observations on Spawning Behaviour and Embryonic Development of the Icelandic Capelin. Rit Fiskideildar. Vol. **5**. no. 4.

Hubbs, C. L., 1943: Terminology of early stages of fishes. Copeia No. 4, 260.

Krysanovsky, S. G., 1956: Materiali po razvitiju seldevykh ryb. Tr. Instit. Morph. Siv. AN SSSR. Vyp. **10.**

Krysanovsky, S. G., Disler, N. N., Smirnova, E. A., 1953: Ekologomorphologicheskie zakonomernosti razvitija okunevidnykh ryb (percoidei). Tr. Instit. Morph. Siv. An SSSR. Vyp. **10.**

Messtorff, J., 1959: Untersuchungen über die Biologie des Wittlings Merlangius merlangus (L.) in der Nordsee. Ber. dt. wiss. Komm. Meeresforsch., **15**, (4), 277—334.

Orton, G., 1957: Embryology and evolution of the pelagic fish egg. Copeia No. 1, 56—58.

Russell, F. S., 1976: The eggs and planktonic stages of british marine fishes. Academic Press.

Sadov, A. I, 1963: Stroenie i formirovanie obolotsek jaits osetrovykh i nekotorykh predstavitelei kostistykh ryb. „Tr. In-ta morfol. zhivotnykh AN SSSR". Vip 38.

Soin, S. G., 1968: Prisposibitelnie osobennosti razvitija rib. Izd. Moskovskogo Universiteta.

Trinkaus, J. P., 1969: Cells into organs. Prenice-Hall.

Turdakov, A. F., 1963: Izmenenie svoistvo polovykh produktov therbathka na protjaschenii nerestovoga perioda. Mat. respubl. konf. molodykh biologov Kirgizii. Frunze.

Vasnetzov, V. V., 1946: Divergentzija i adaptzija v ontogenese. Zool. Surn., XXV, 3.

Vasnetzov, V. V., 1948: Etapi razvitija sistemy organov svjazanykh s pitaniem u lescha, vobly i sazana. Sbornik: Morph. osob. opredel. pitanija lescha, vobly i sazana na vsekh st. razv. AN SSSR.

Vasnetzov, V. V., 1953: Etapi razvitija kostistykh ryb. Ocherki po obsch. Vopr. ikhtiol. Izd-vo AN SSSR.

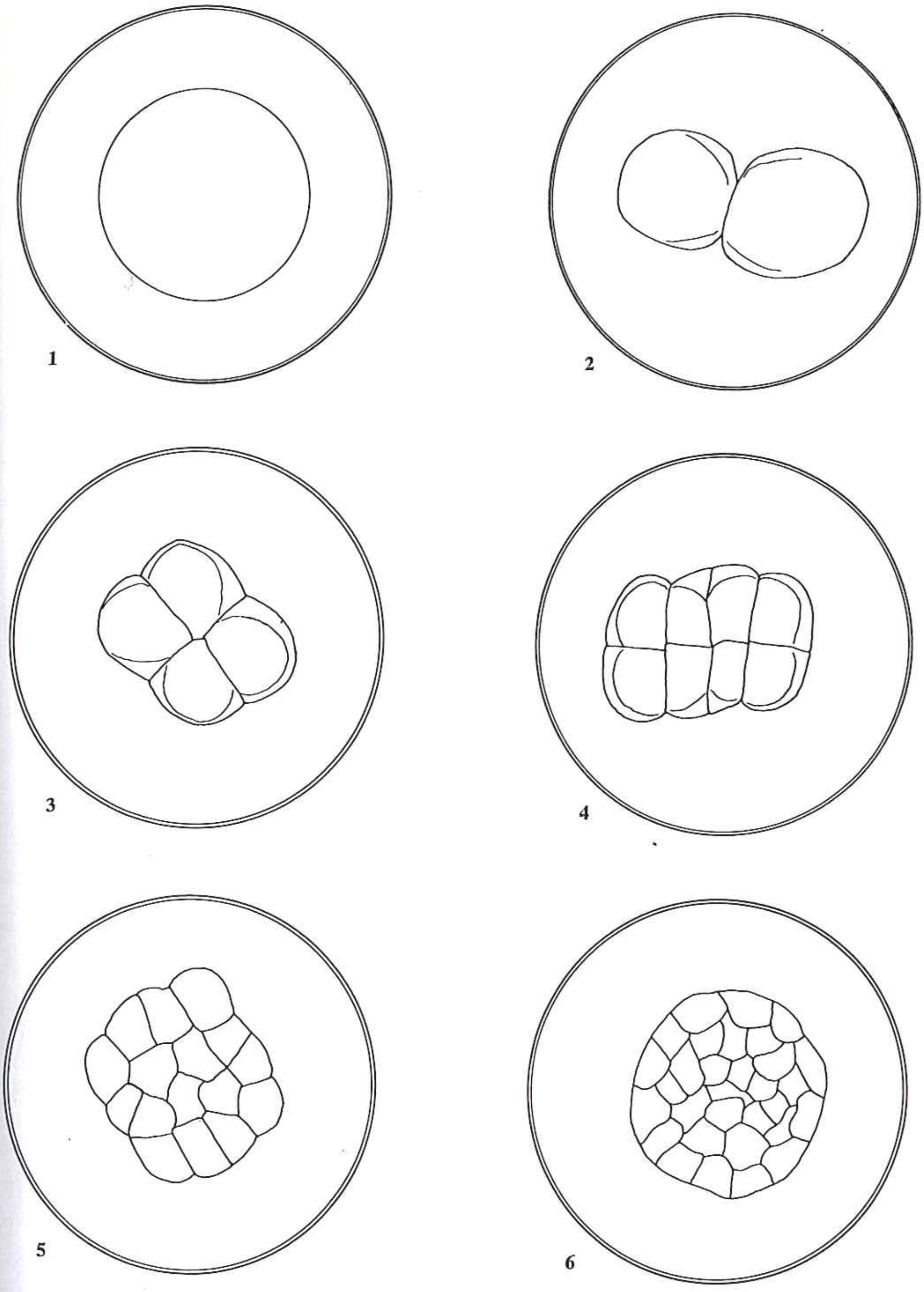


Figure 1

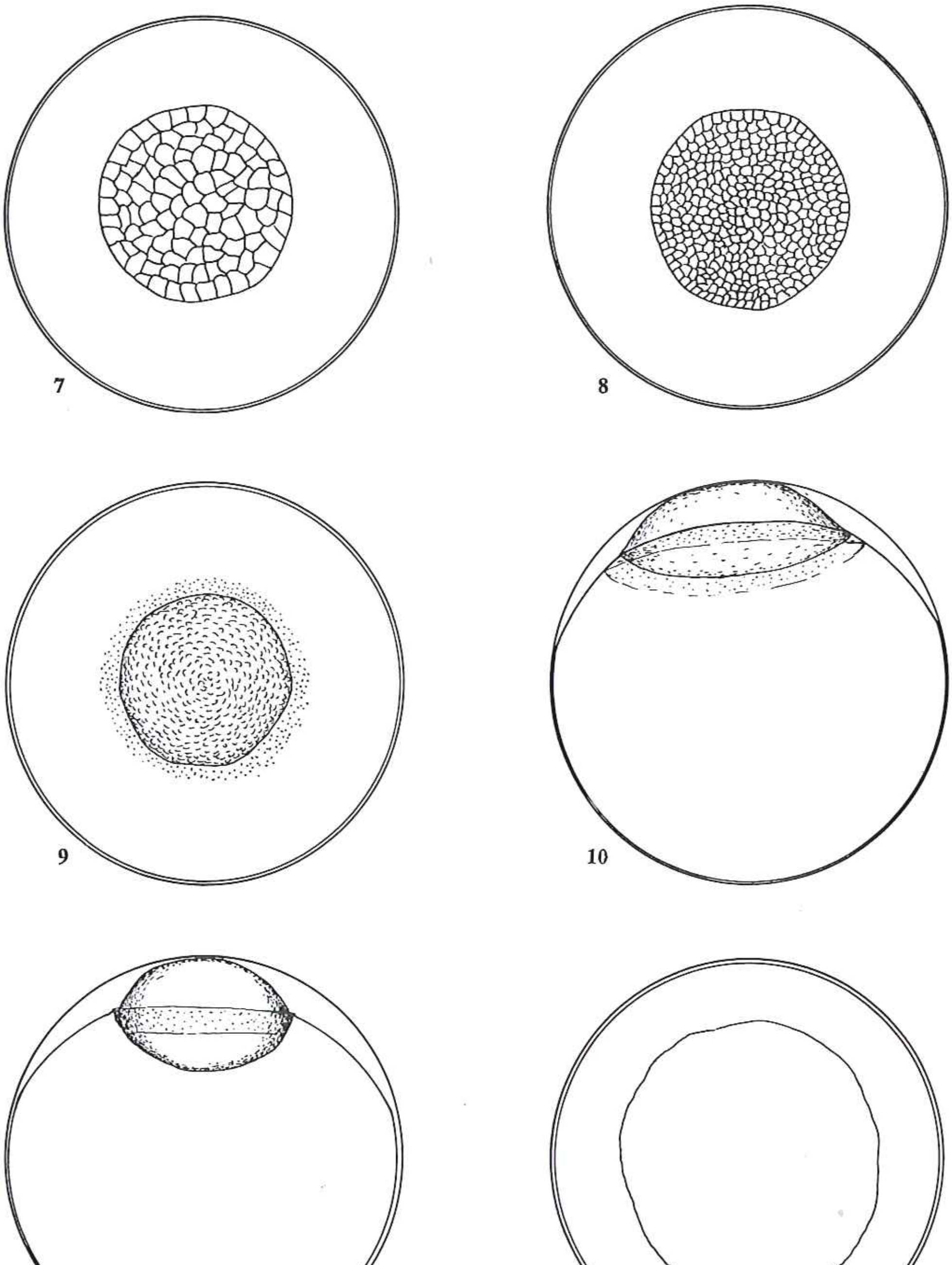


Figure 1

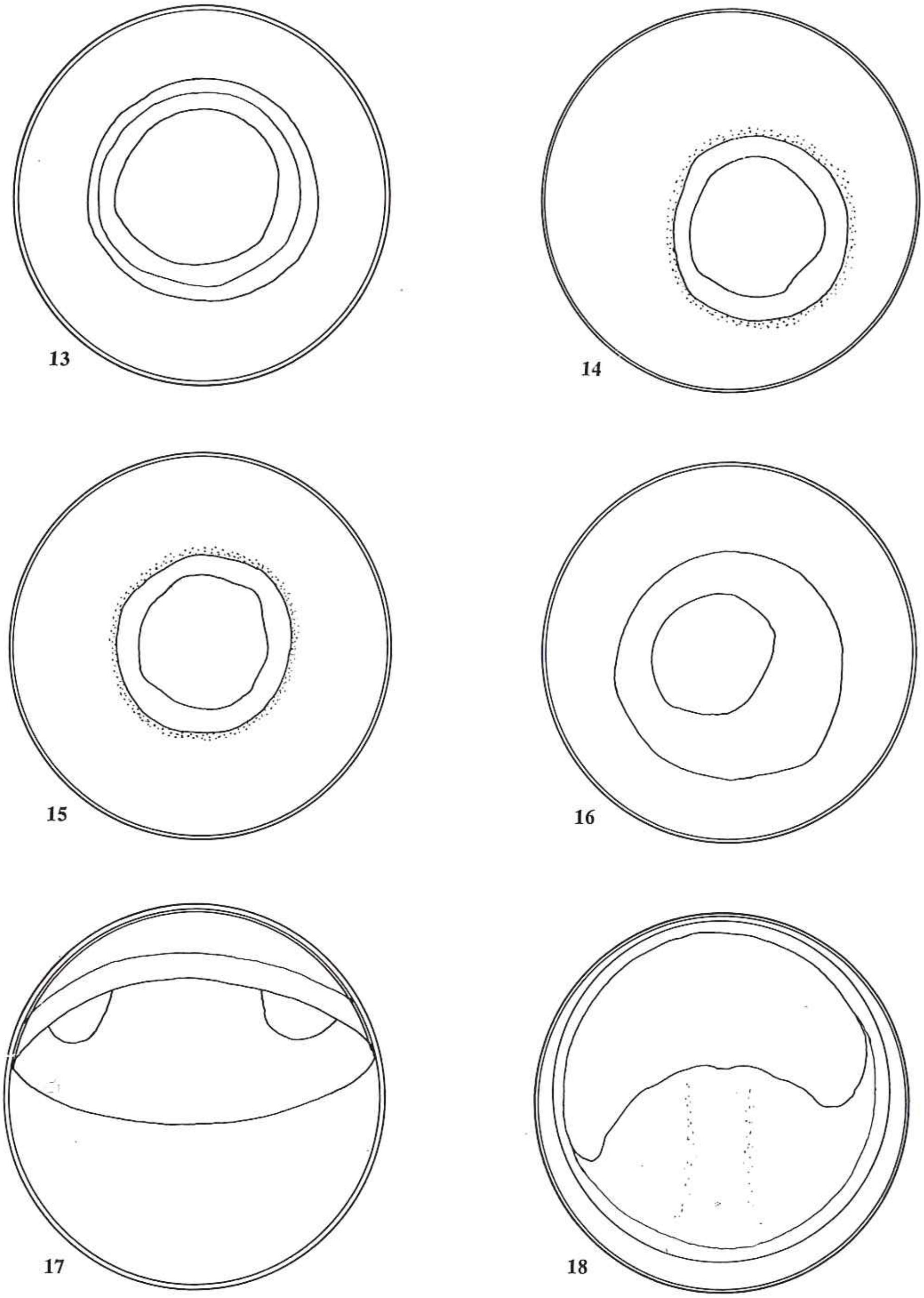


Figure 1

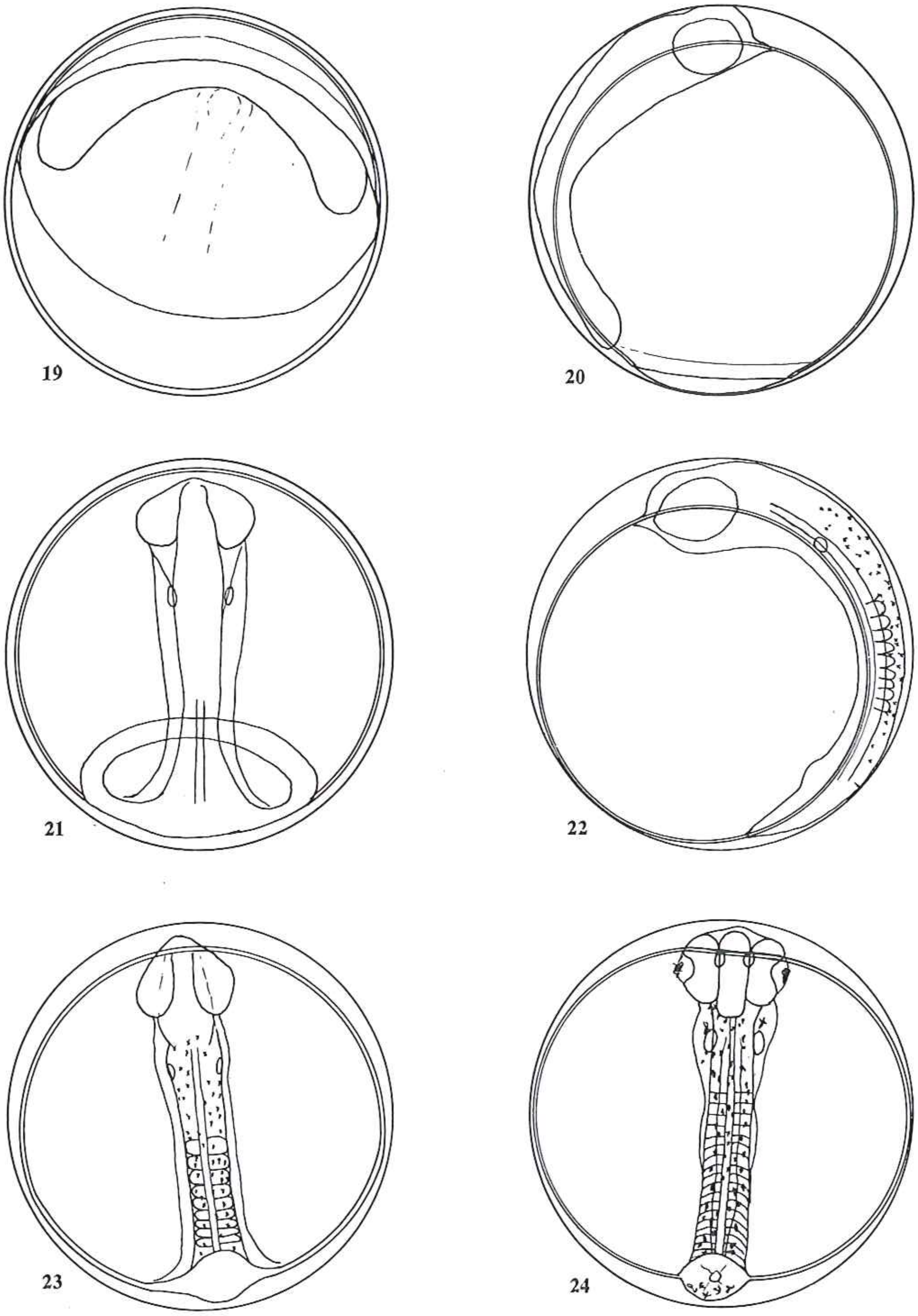


Figure 1

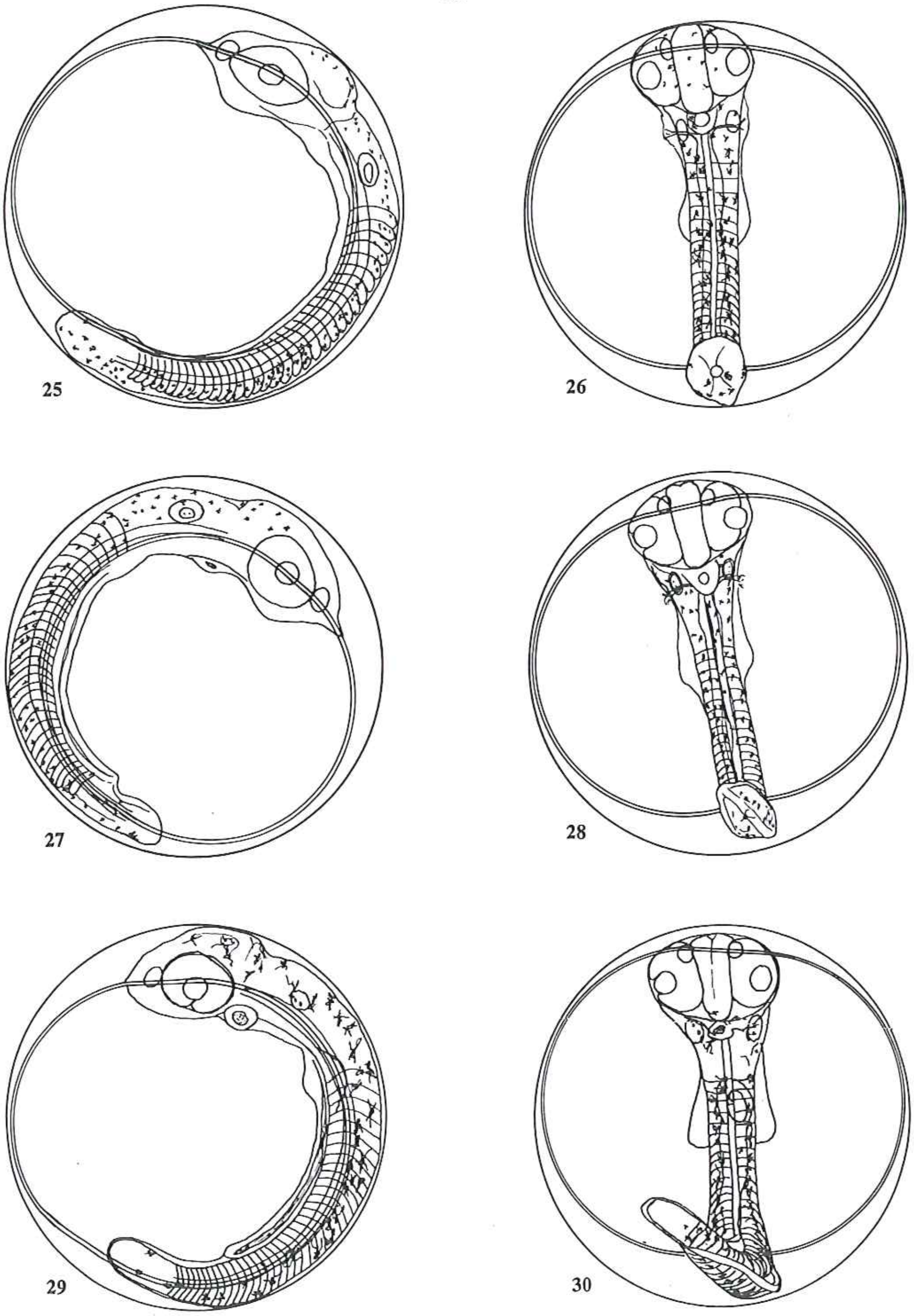
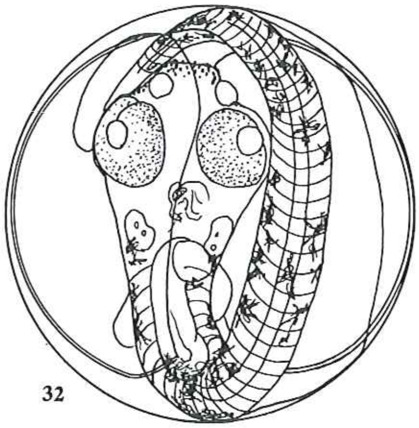


Figure 1

31



32

Figure 1

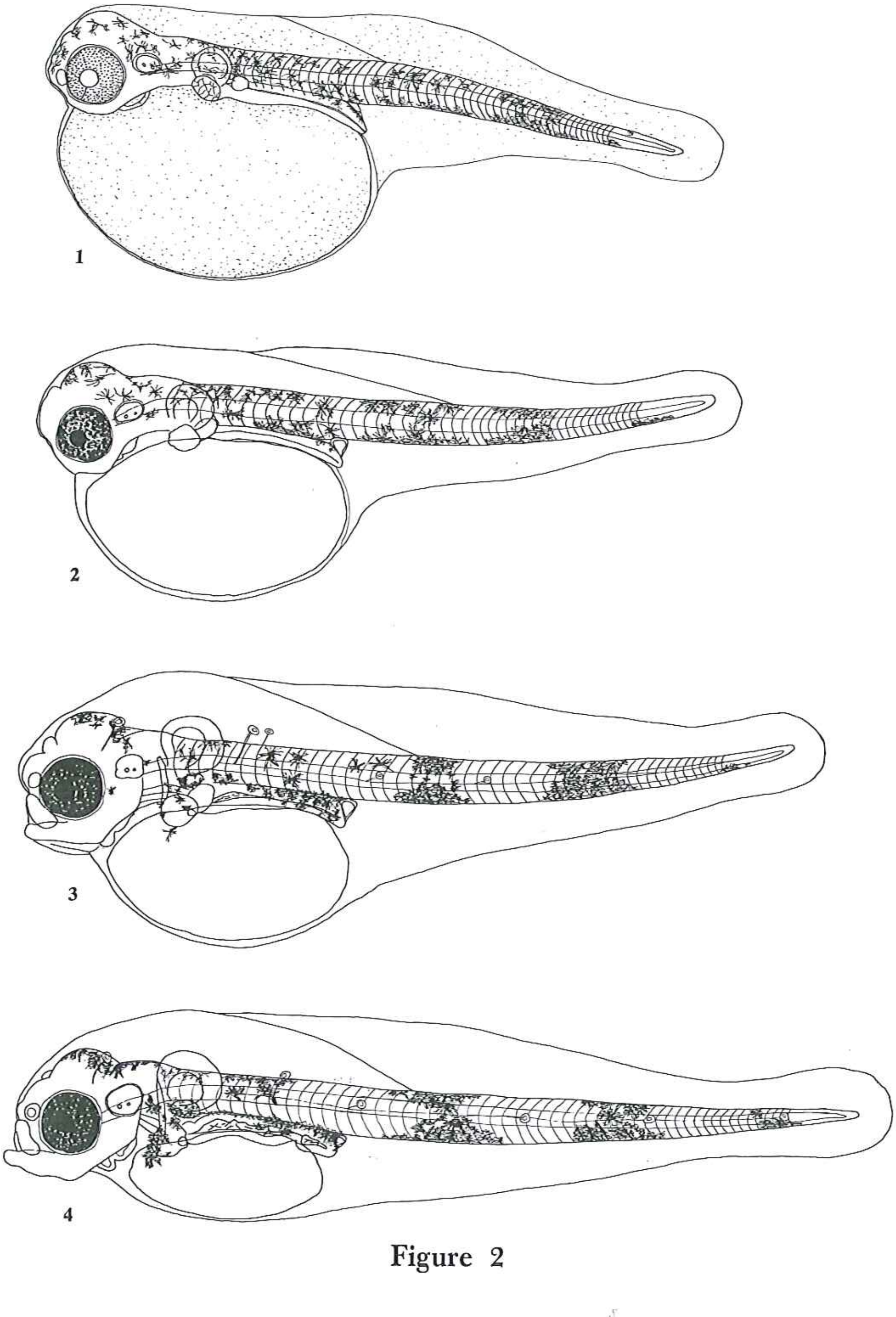


Figure 2

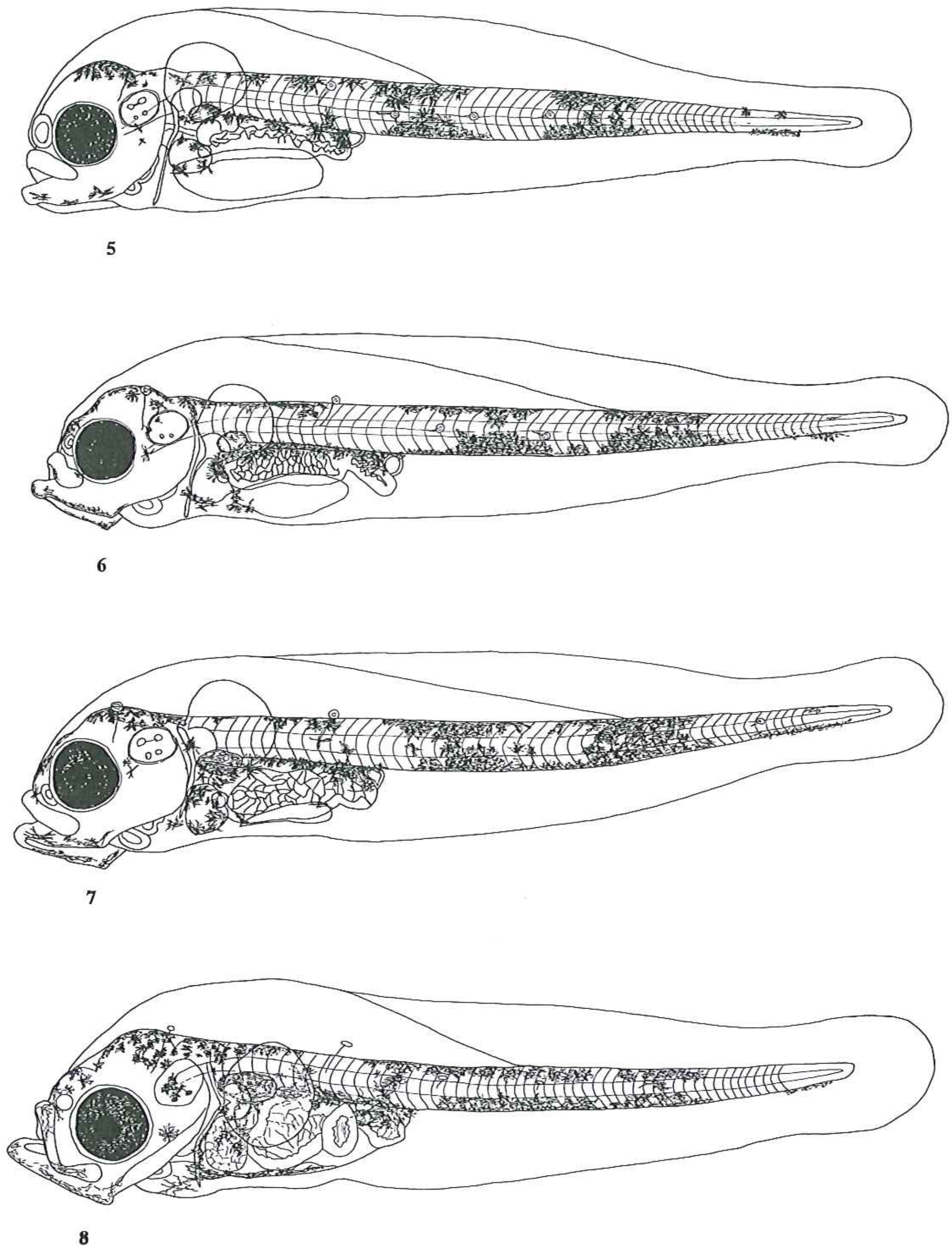


Figure 2

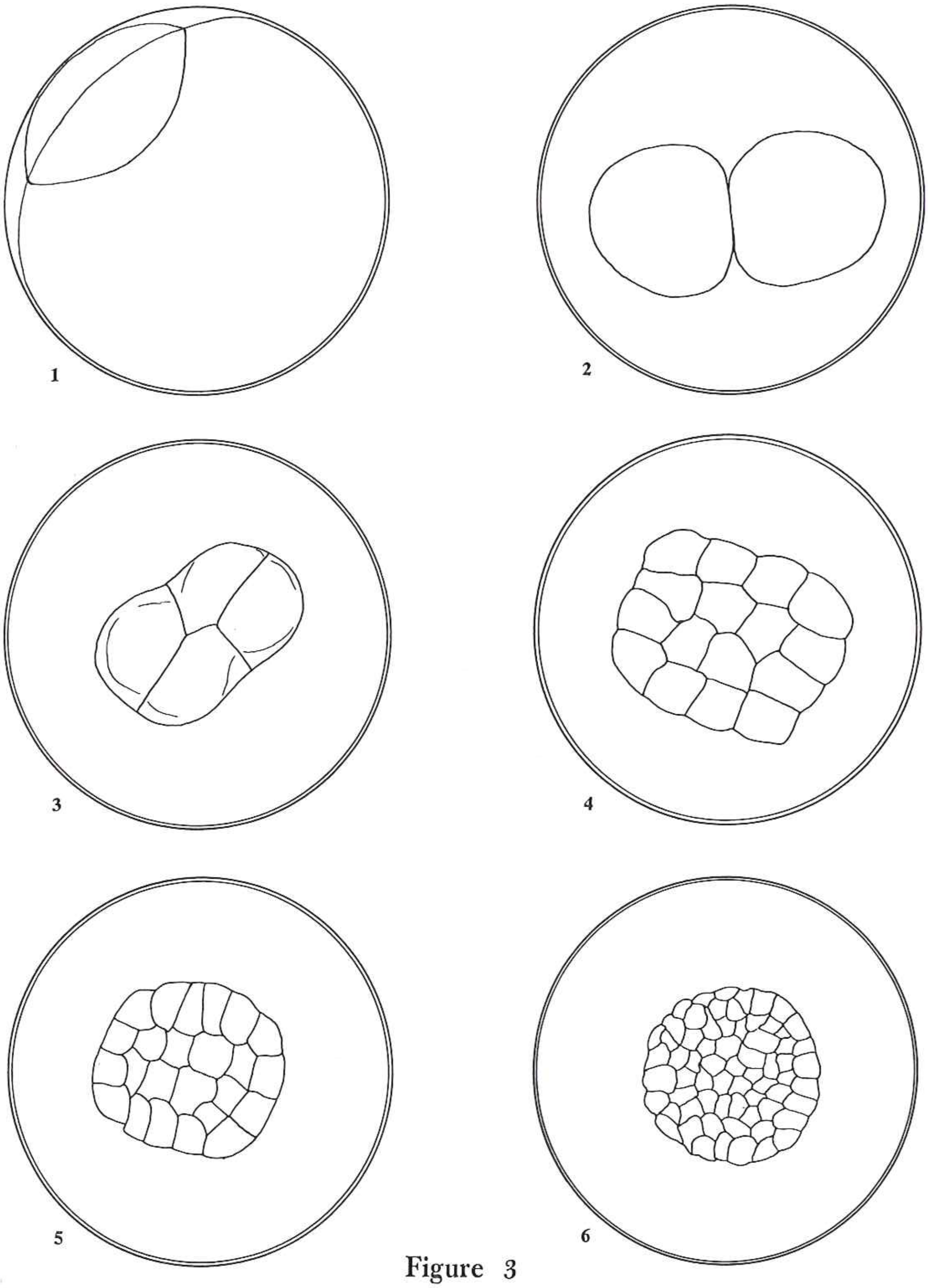


Figure 3

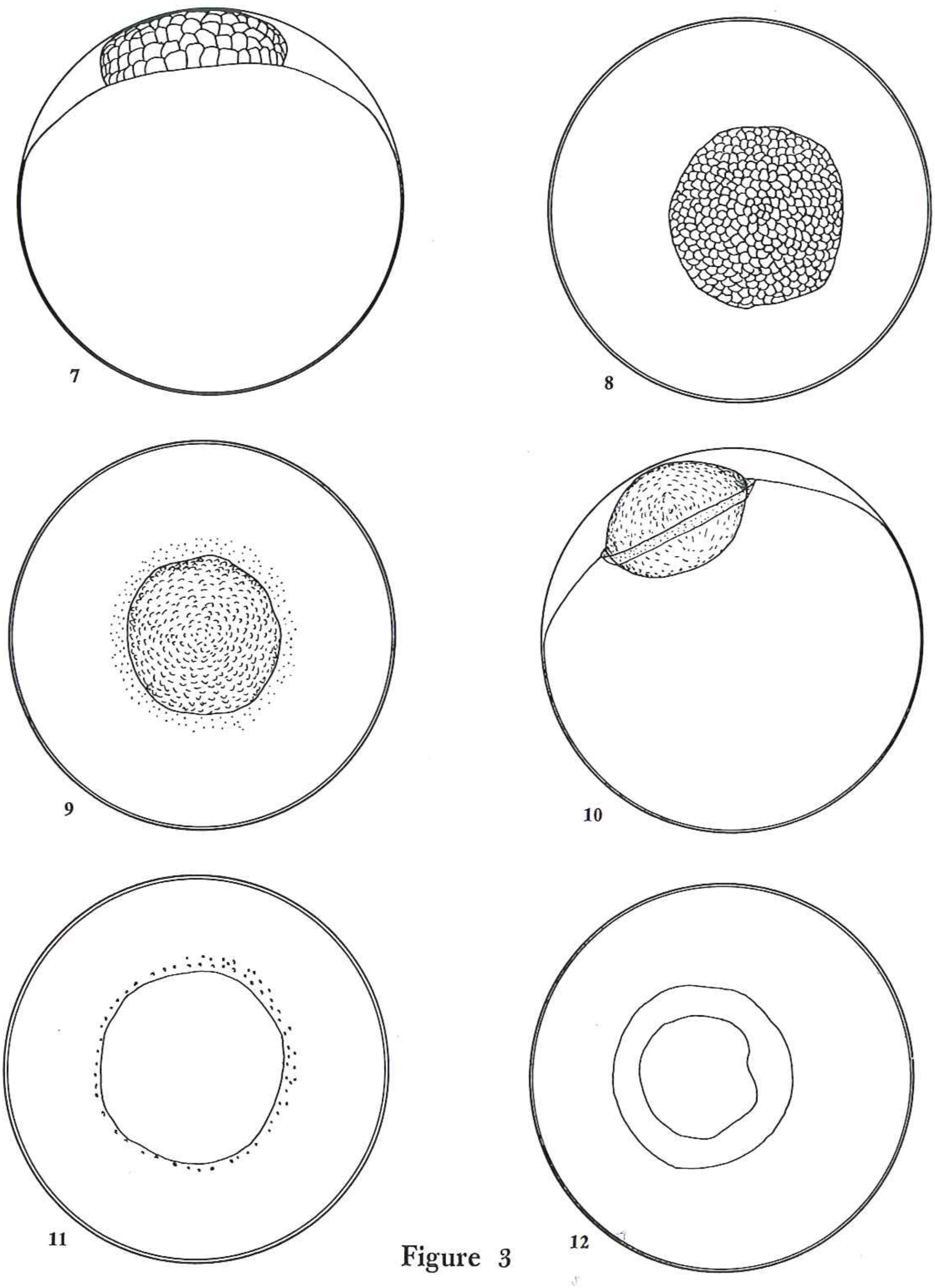


Figure 3

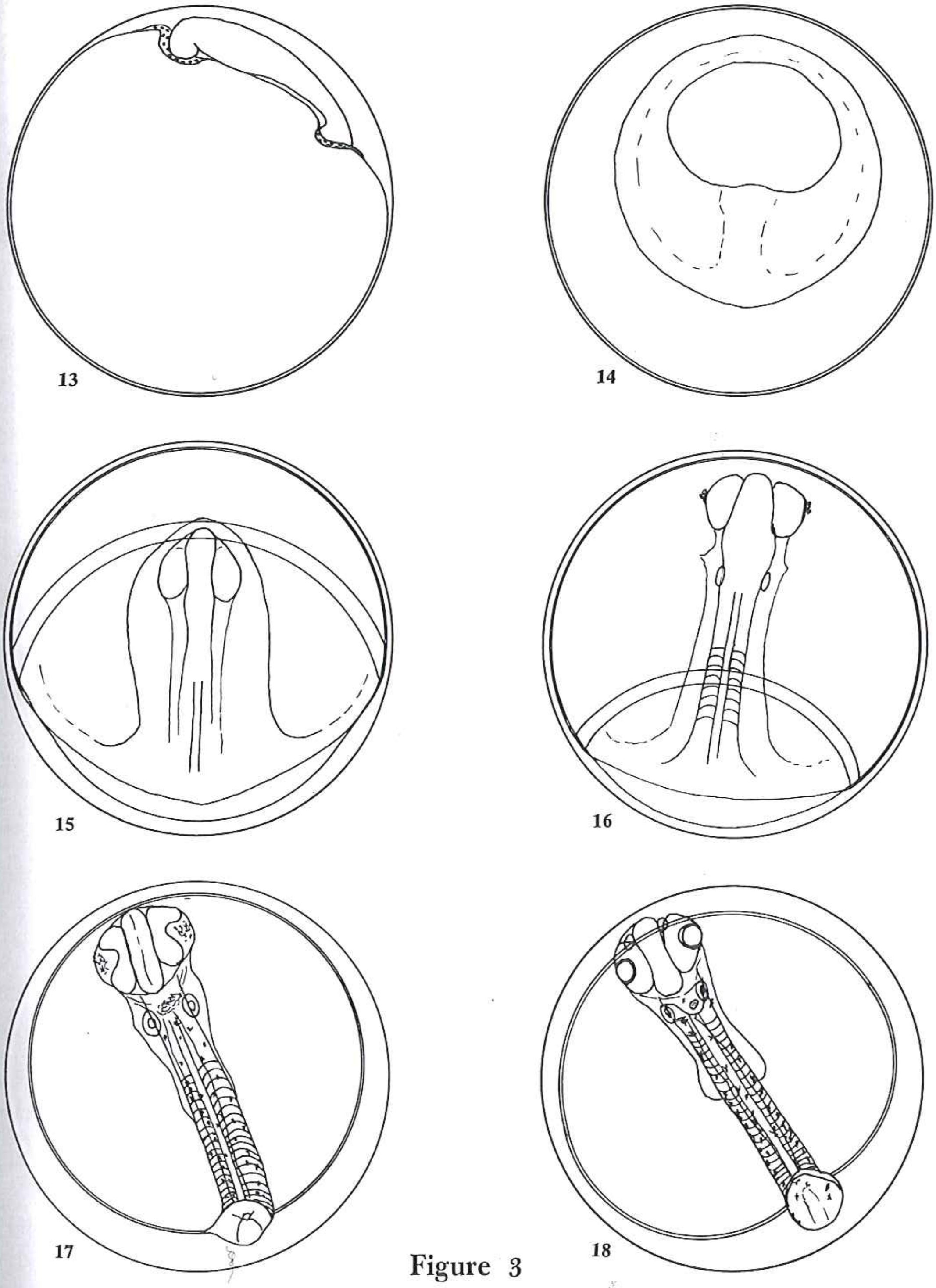


Figure 3

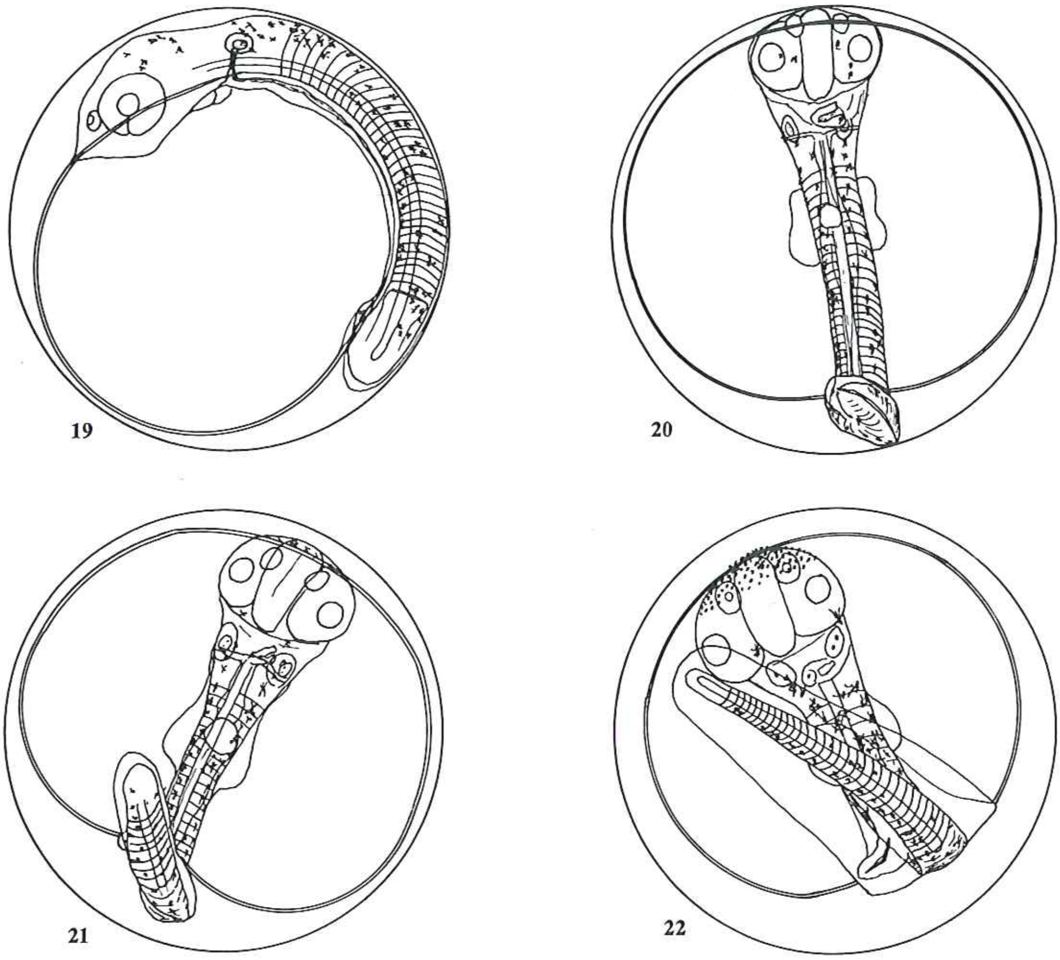
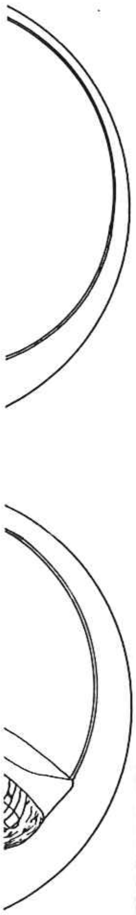


Figure 3



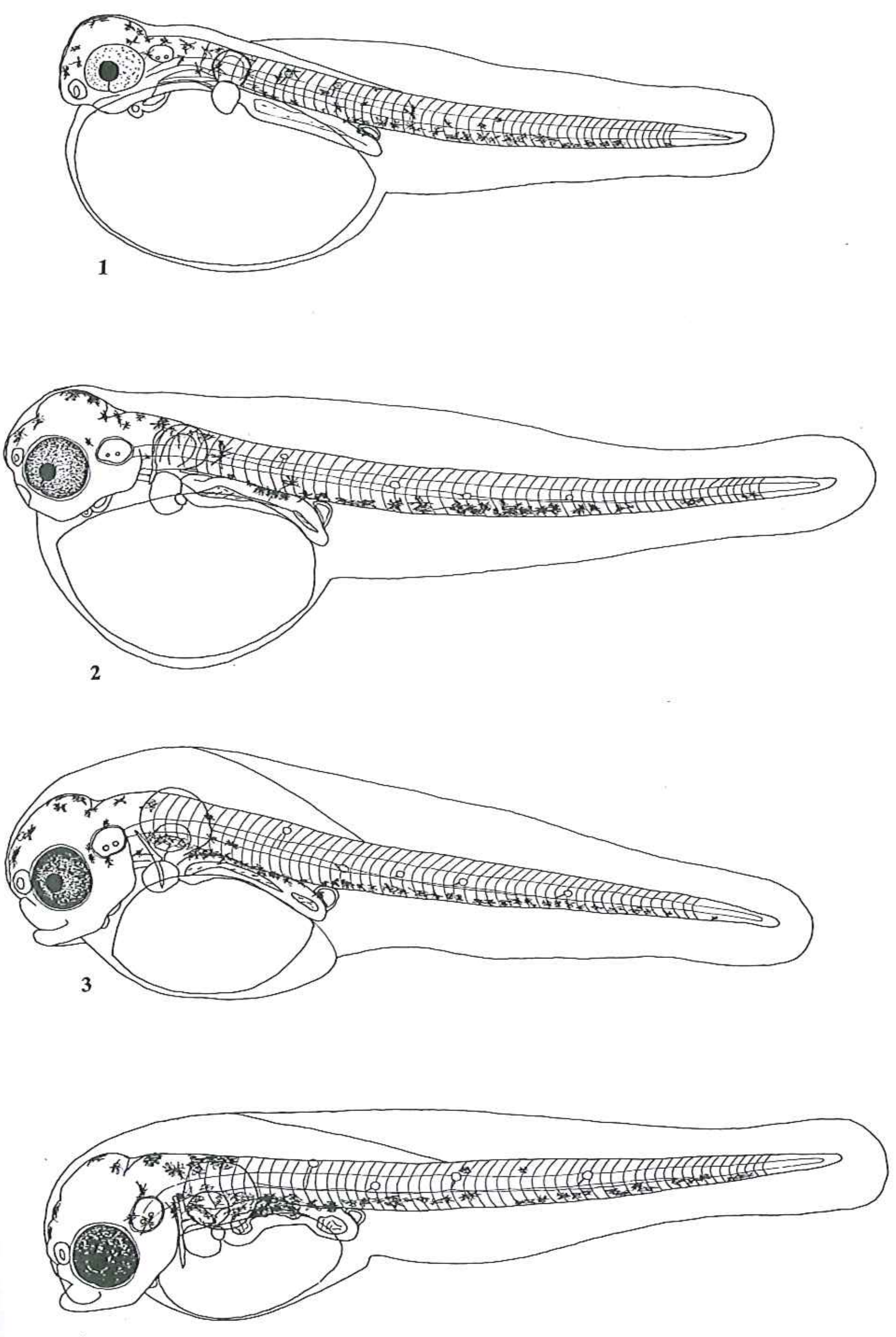


Figure 4

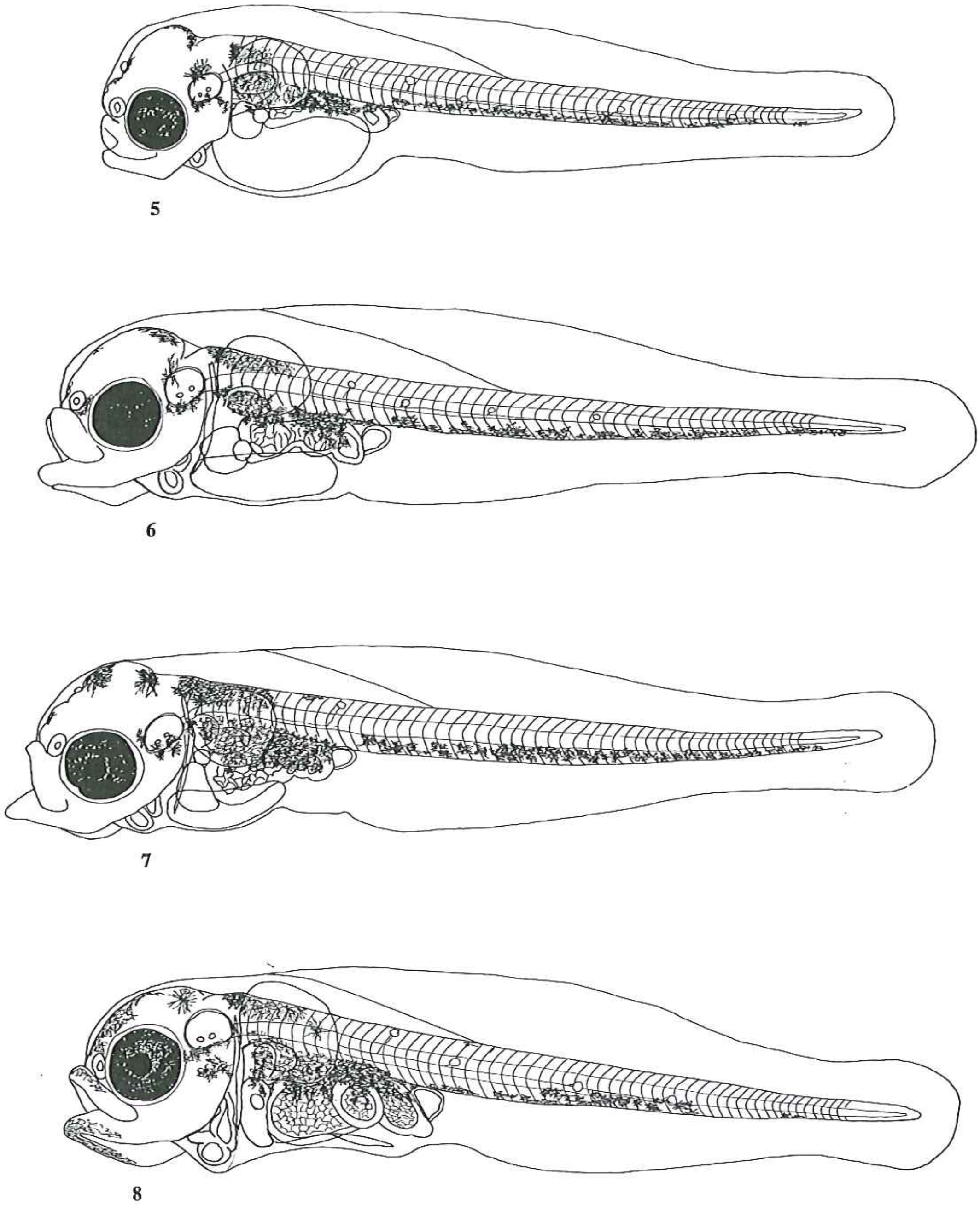


Figure 4

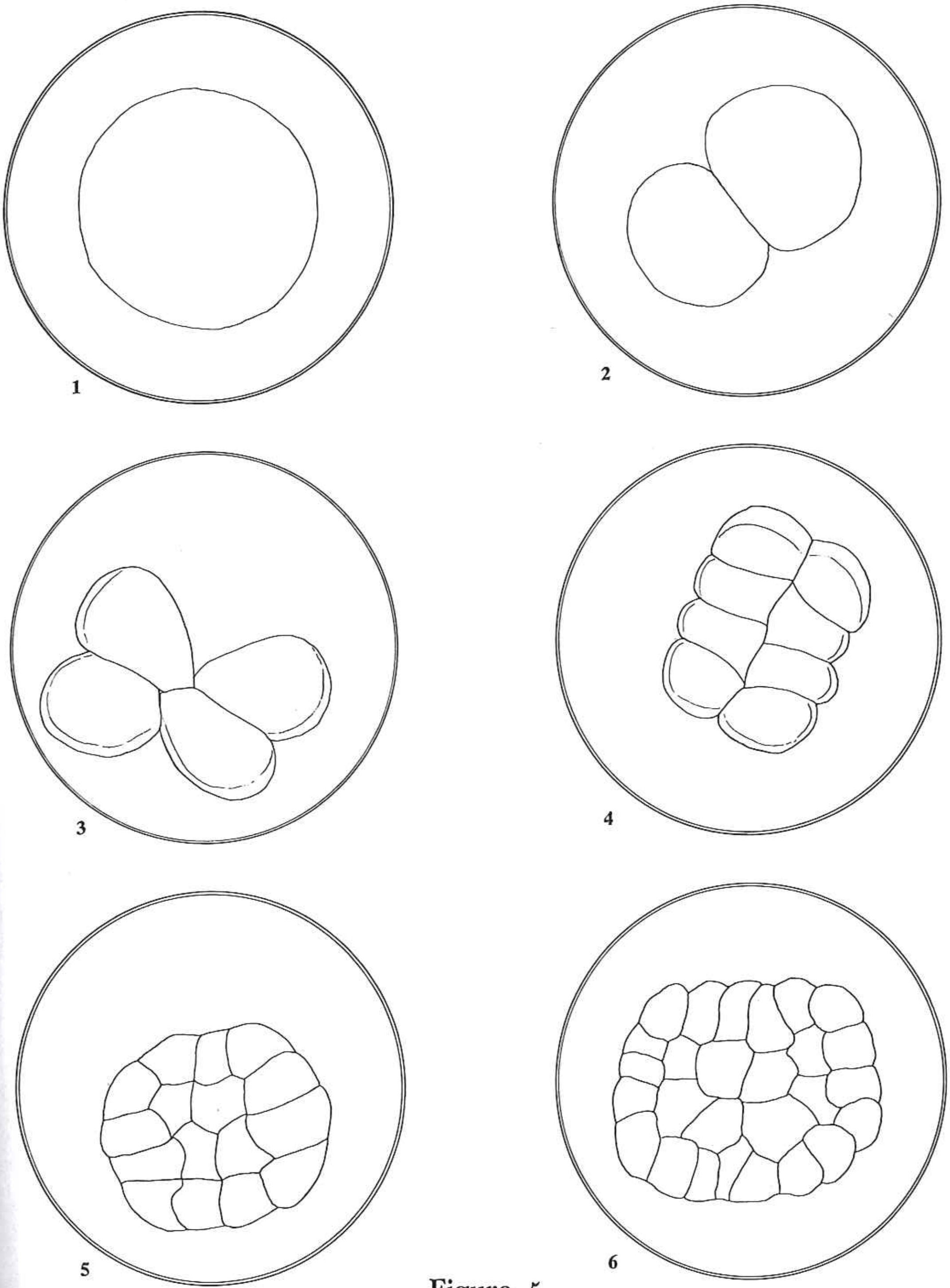


Figure 5

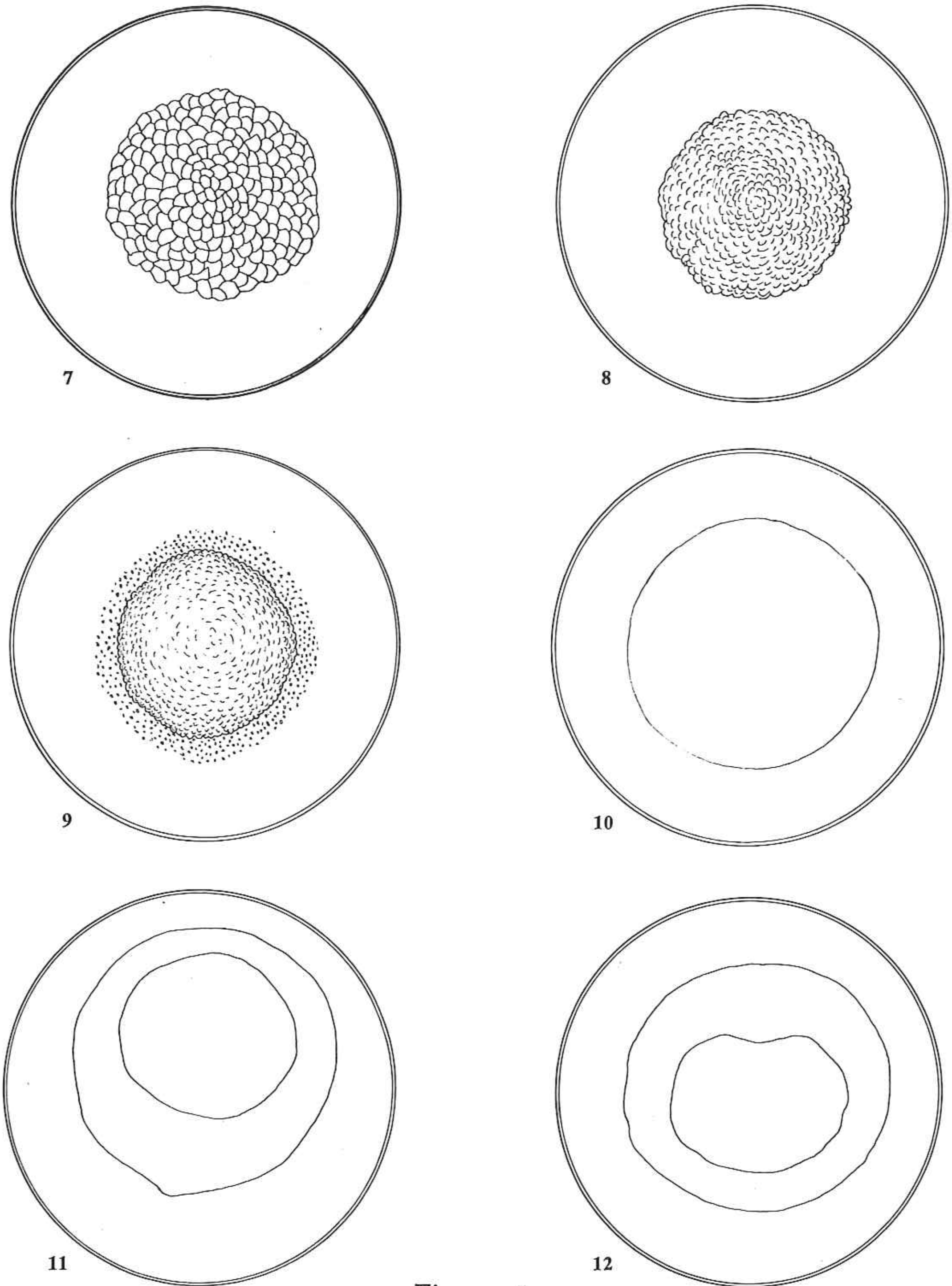


Figure 5

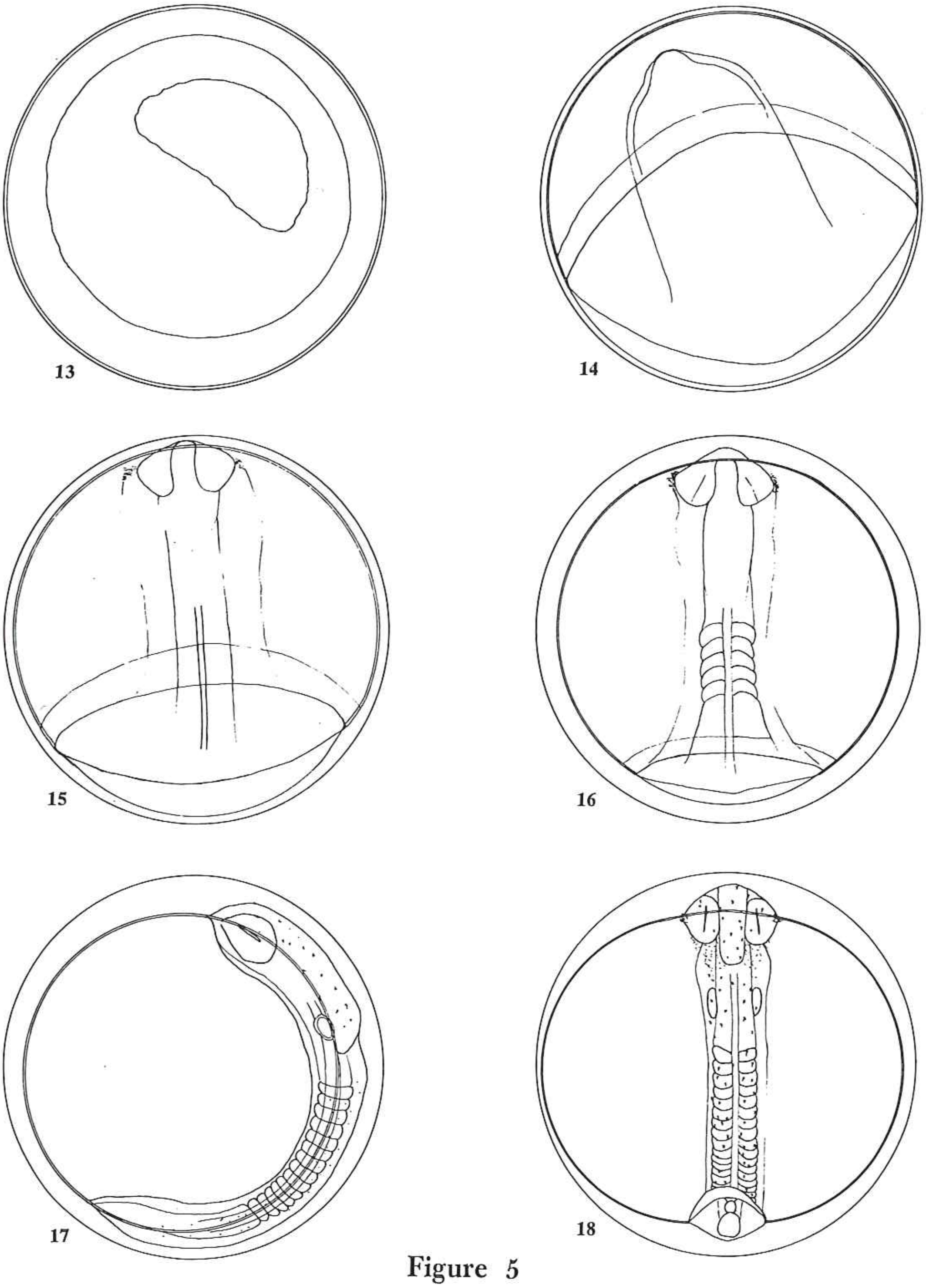


Figure 5

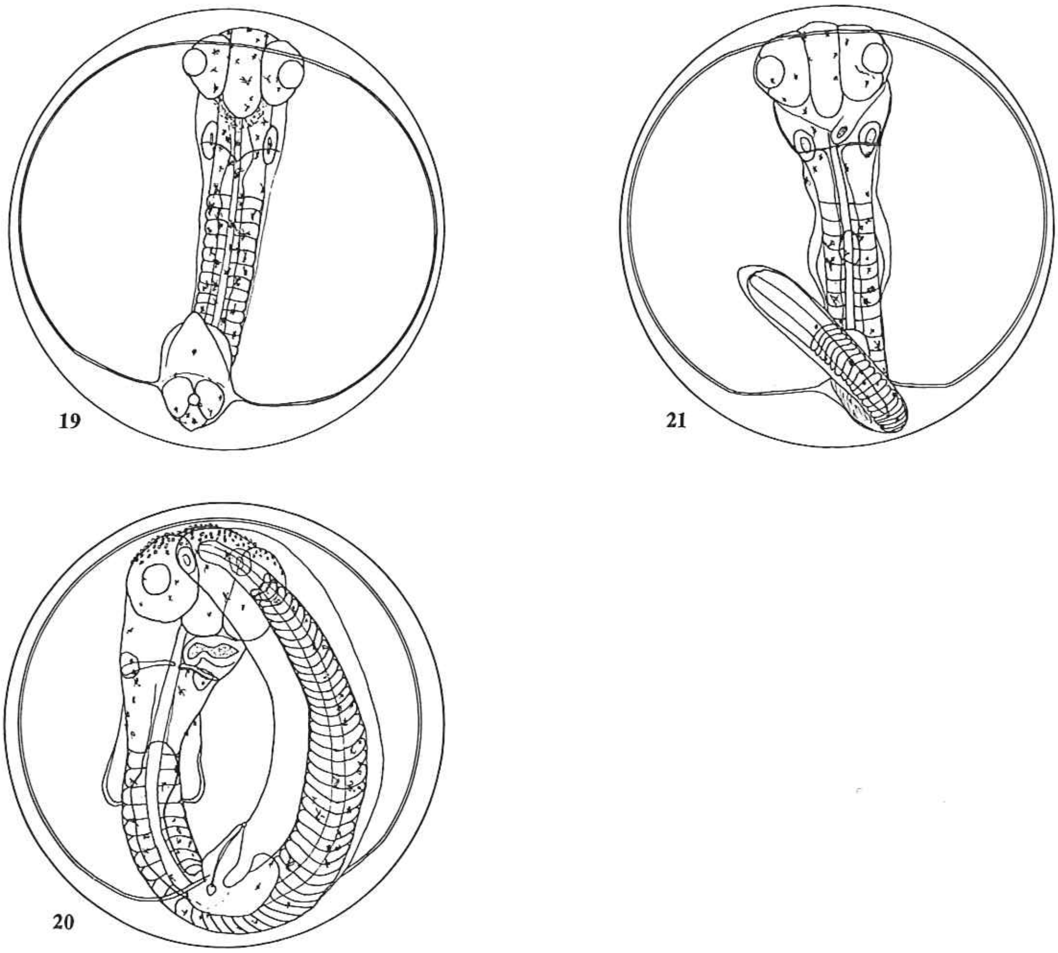


Figure 5

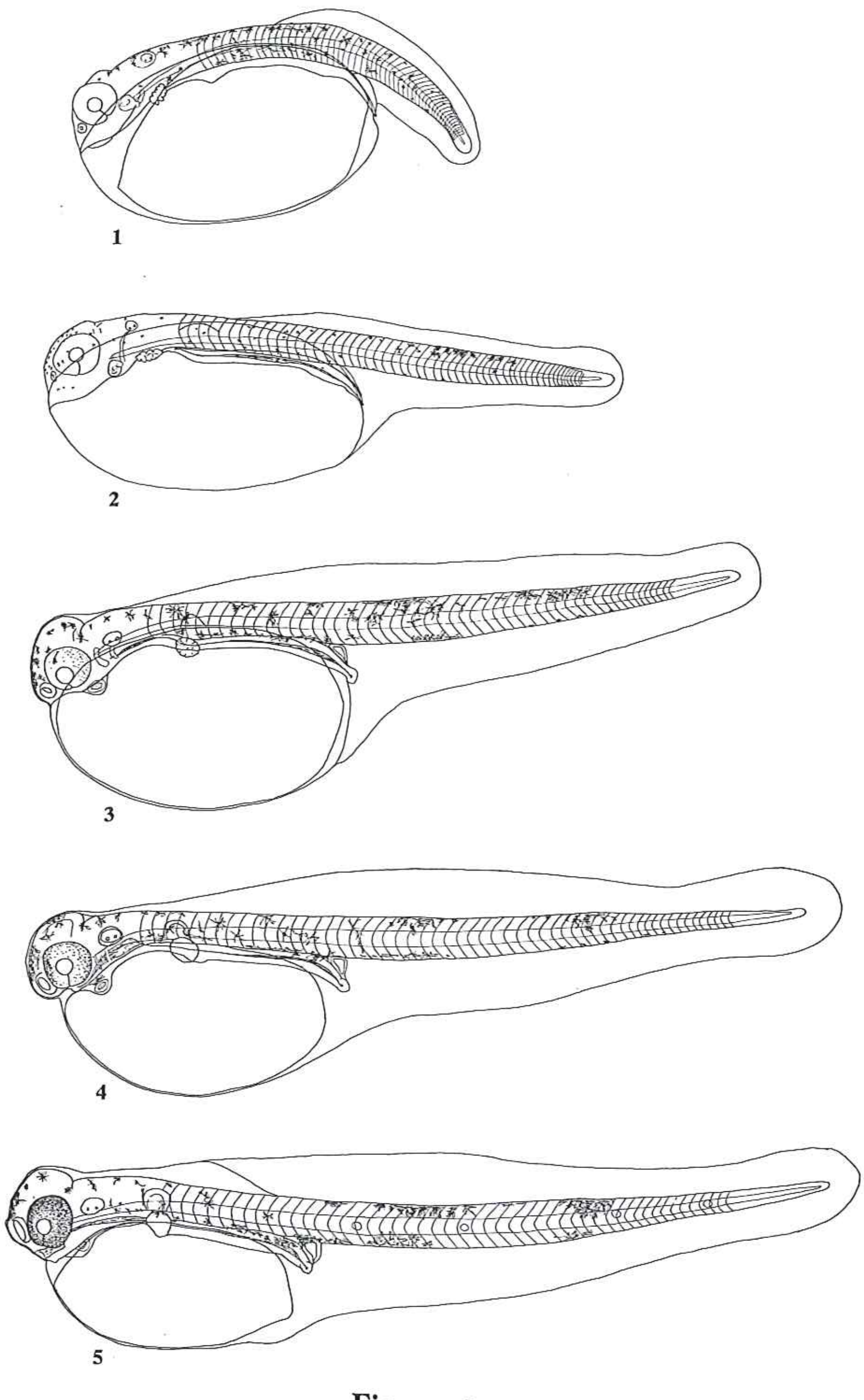


Figure 6

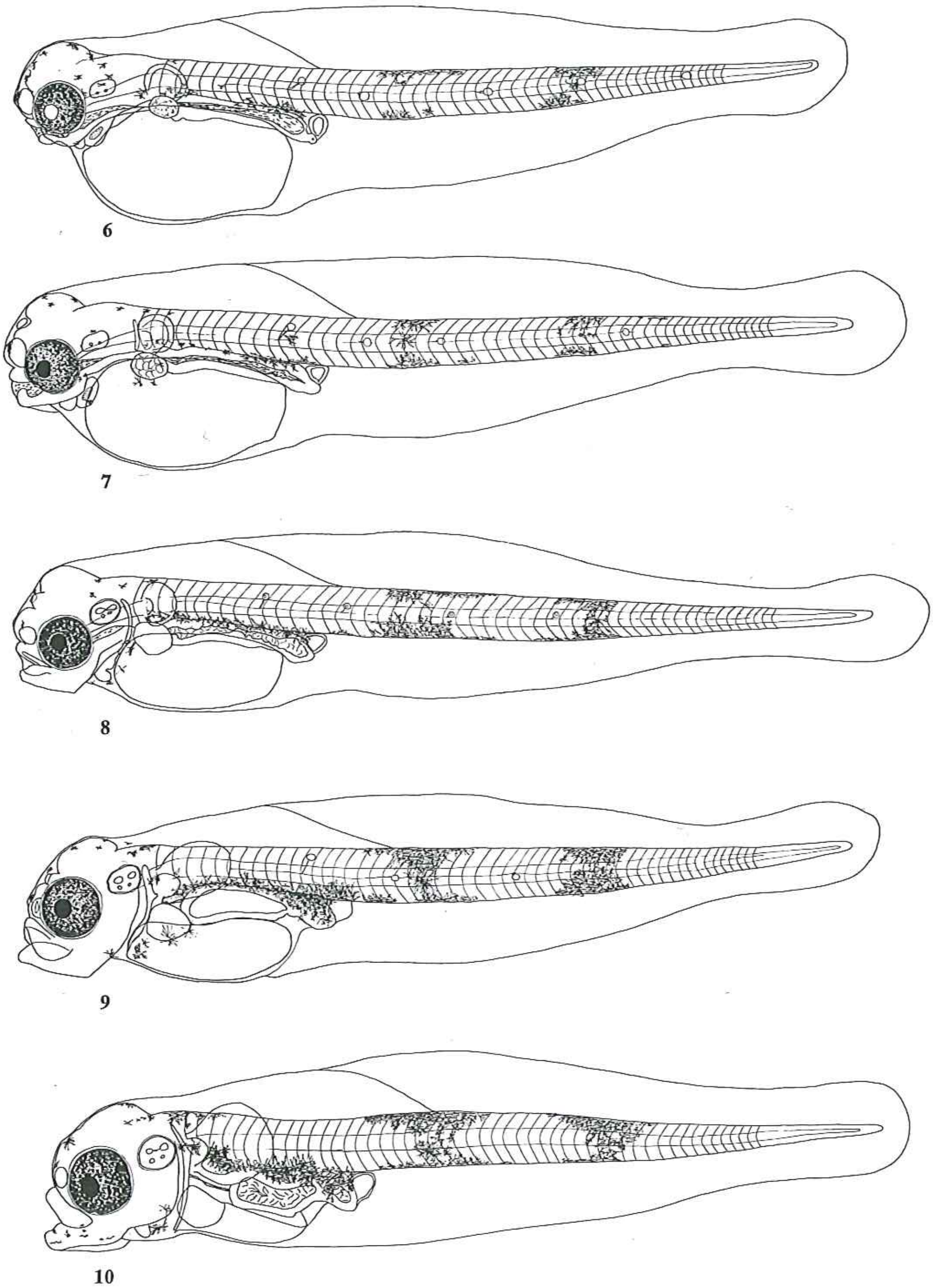


Figure 6

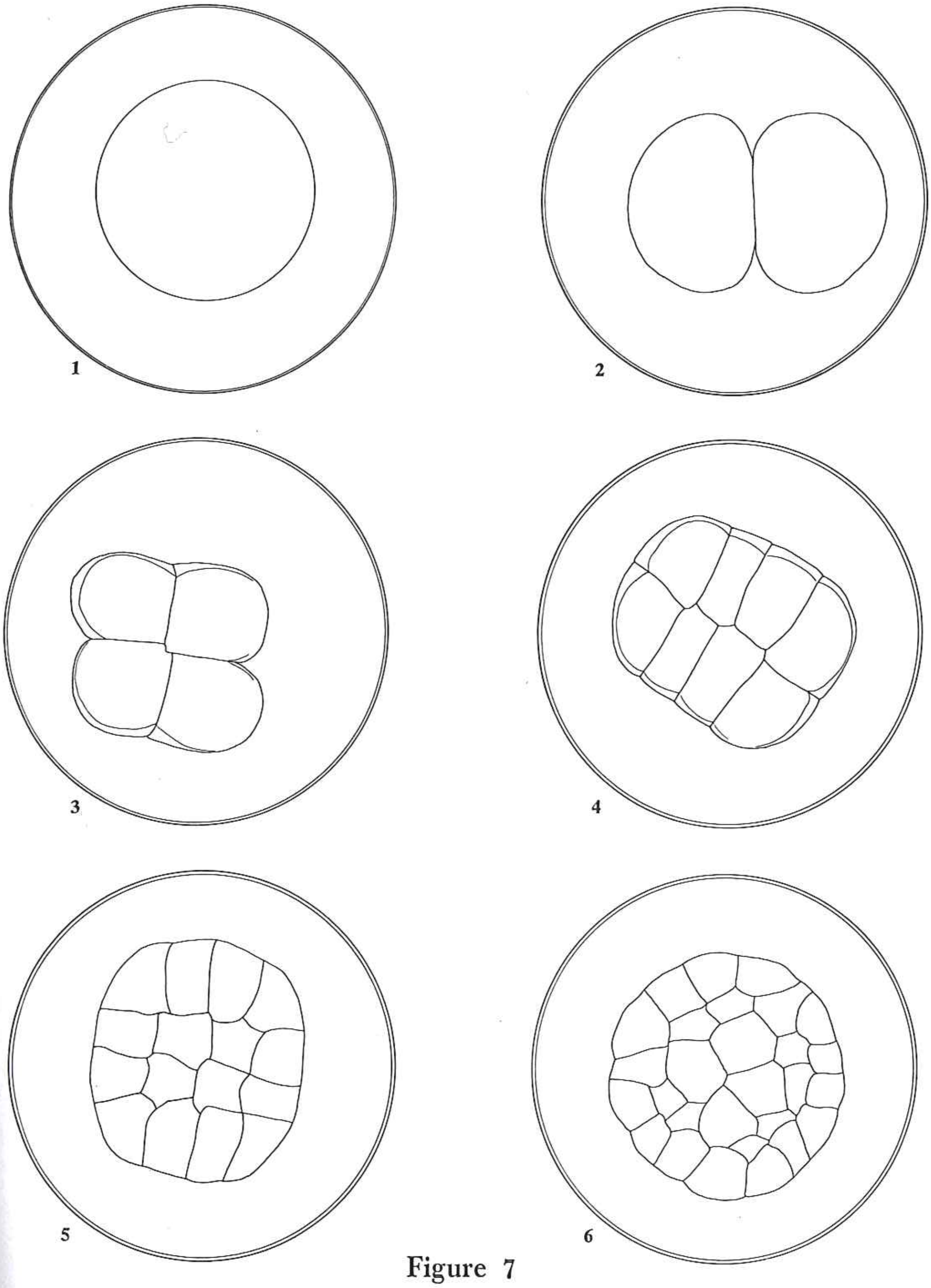


Figure 7

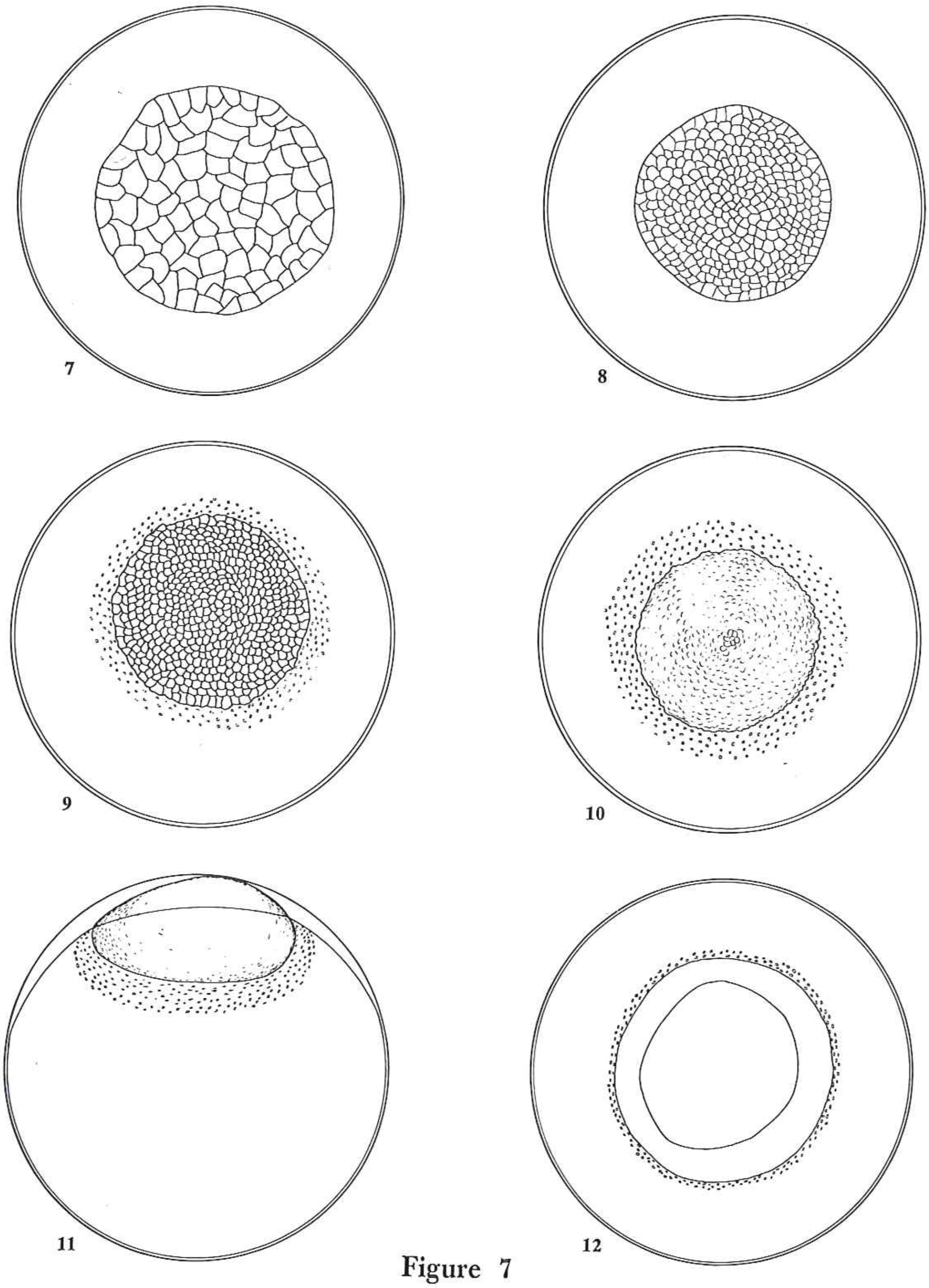


Figure 7

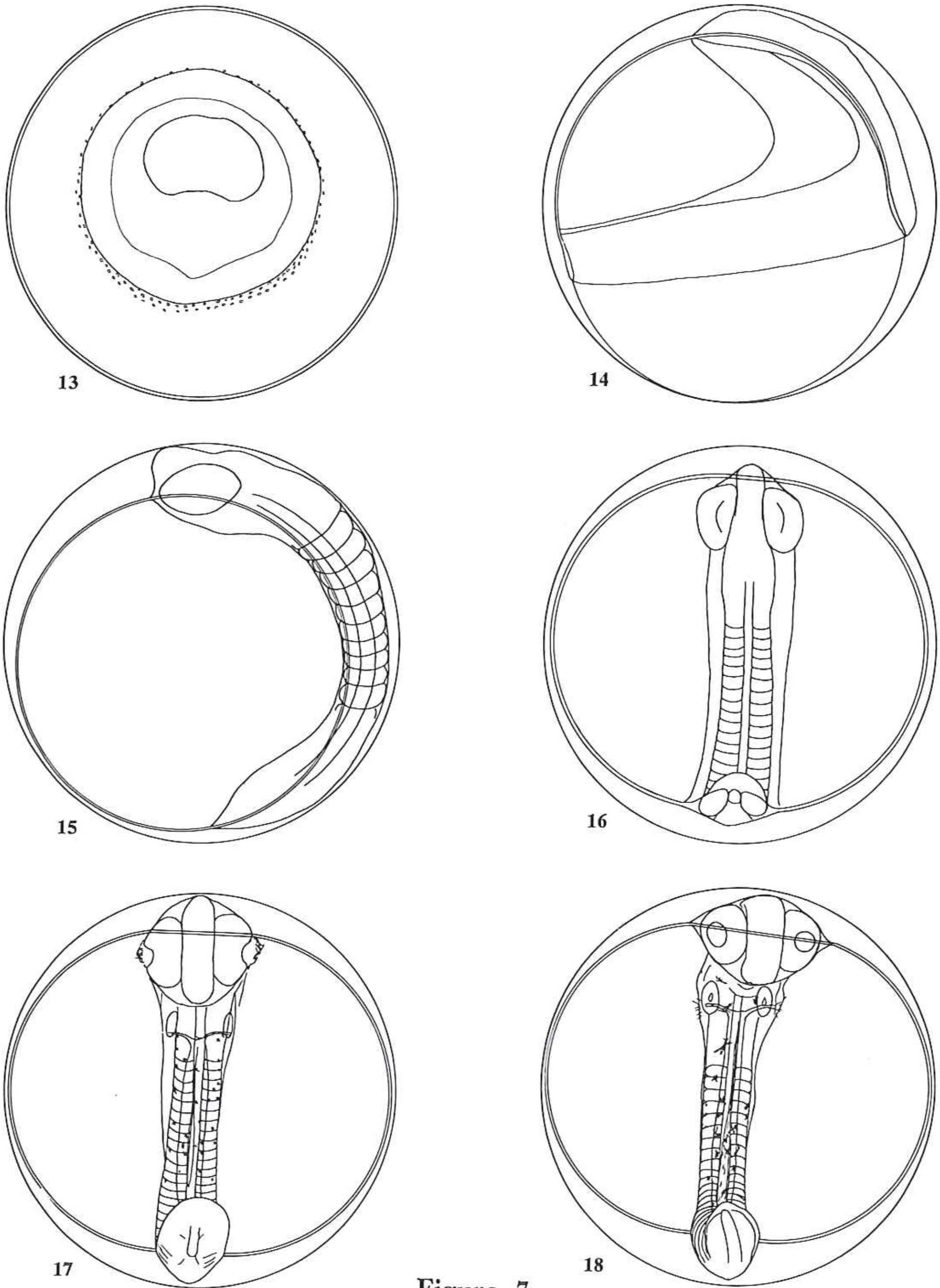
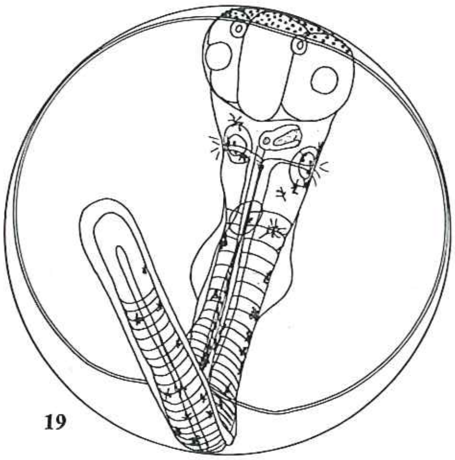


Figure 7



19

Figure 7

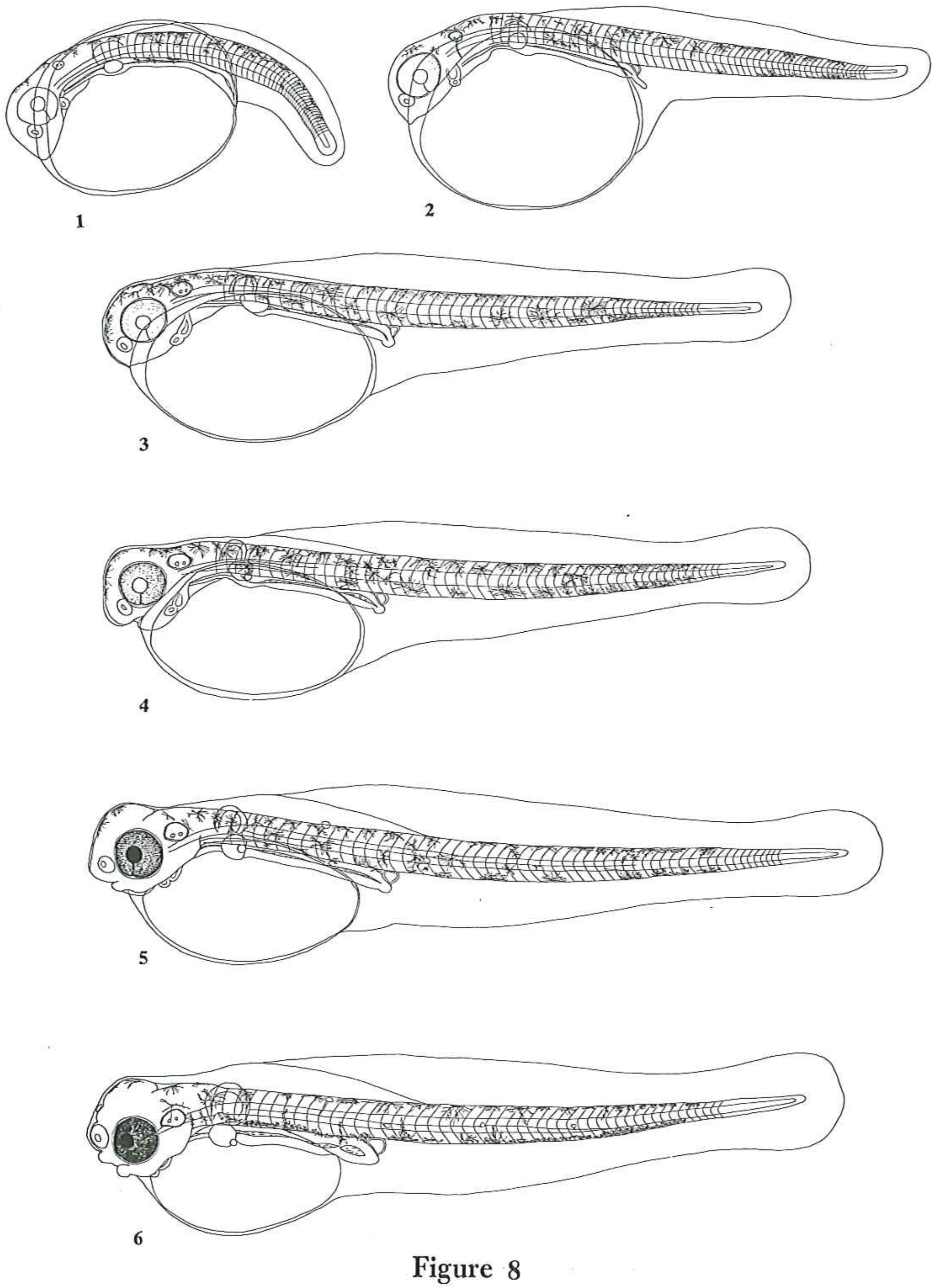
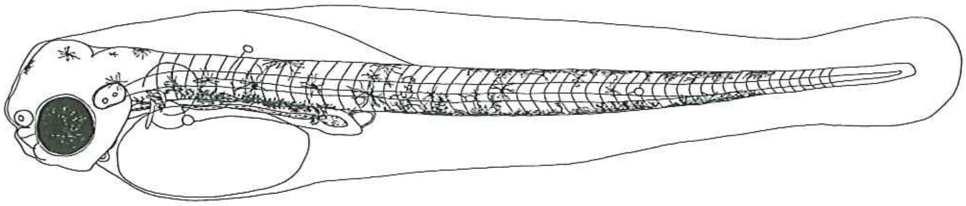
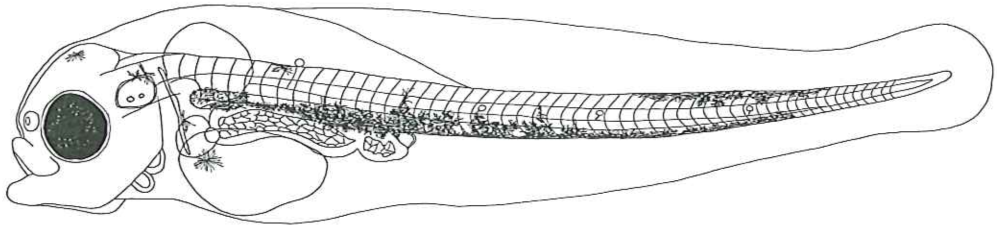


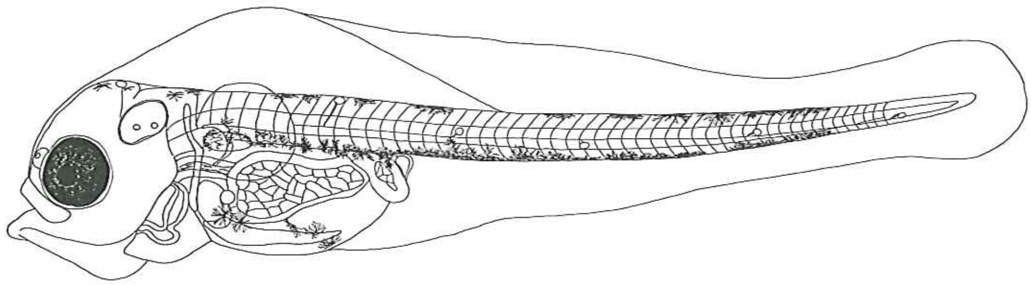
Figure 8



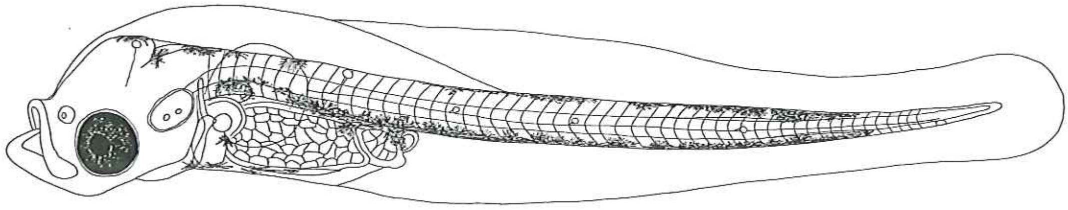
7



8



9



10

Figure 8

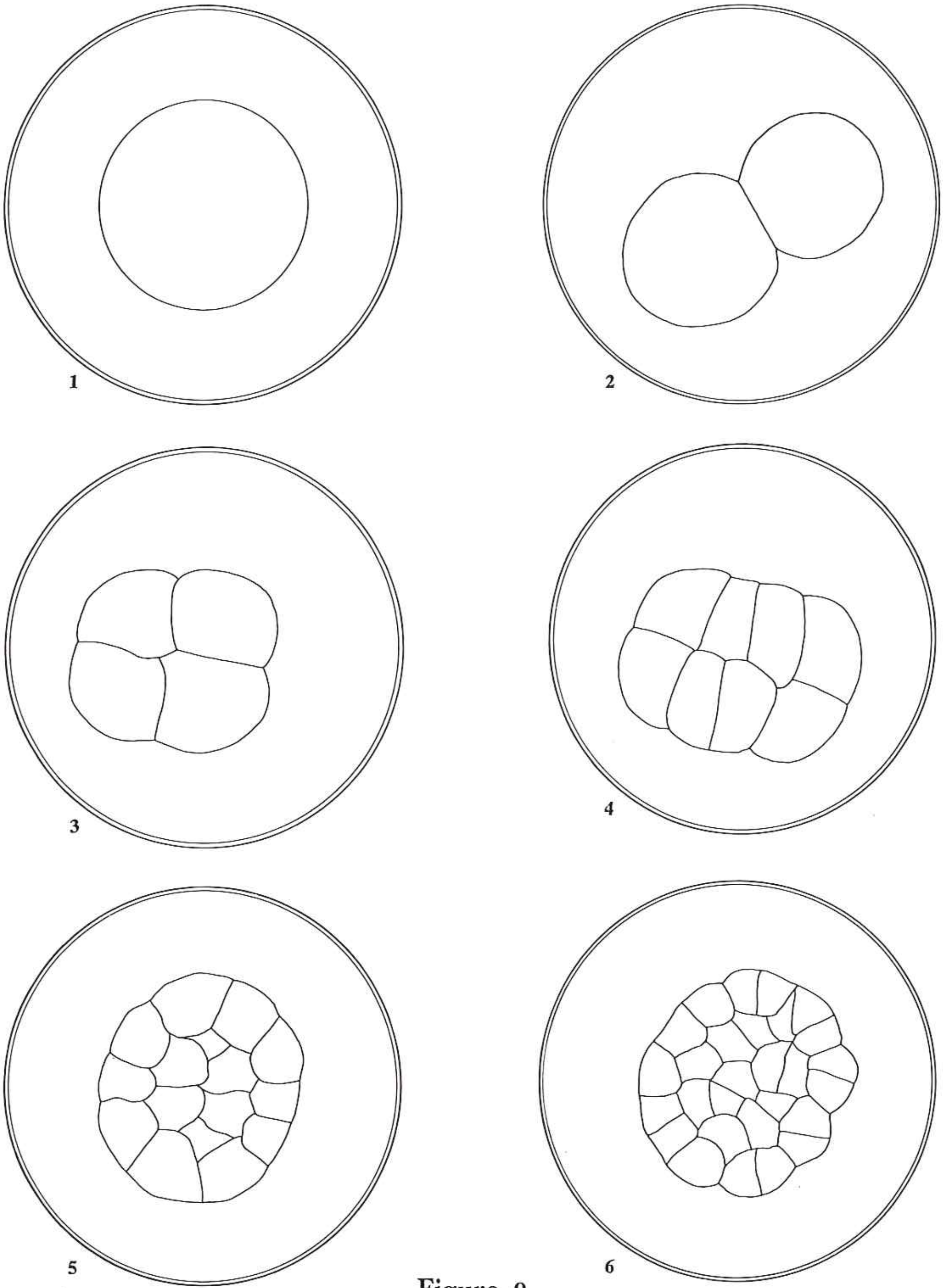


Figure 9

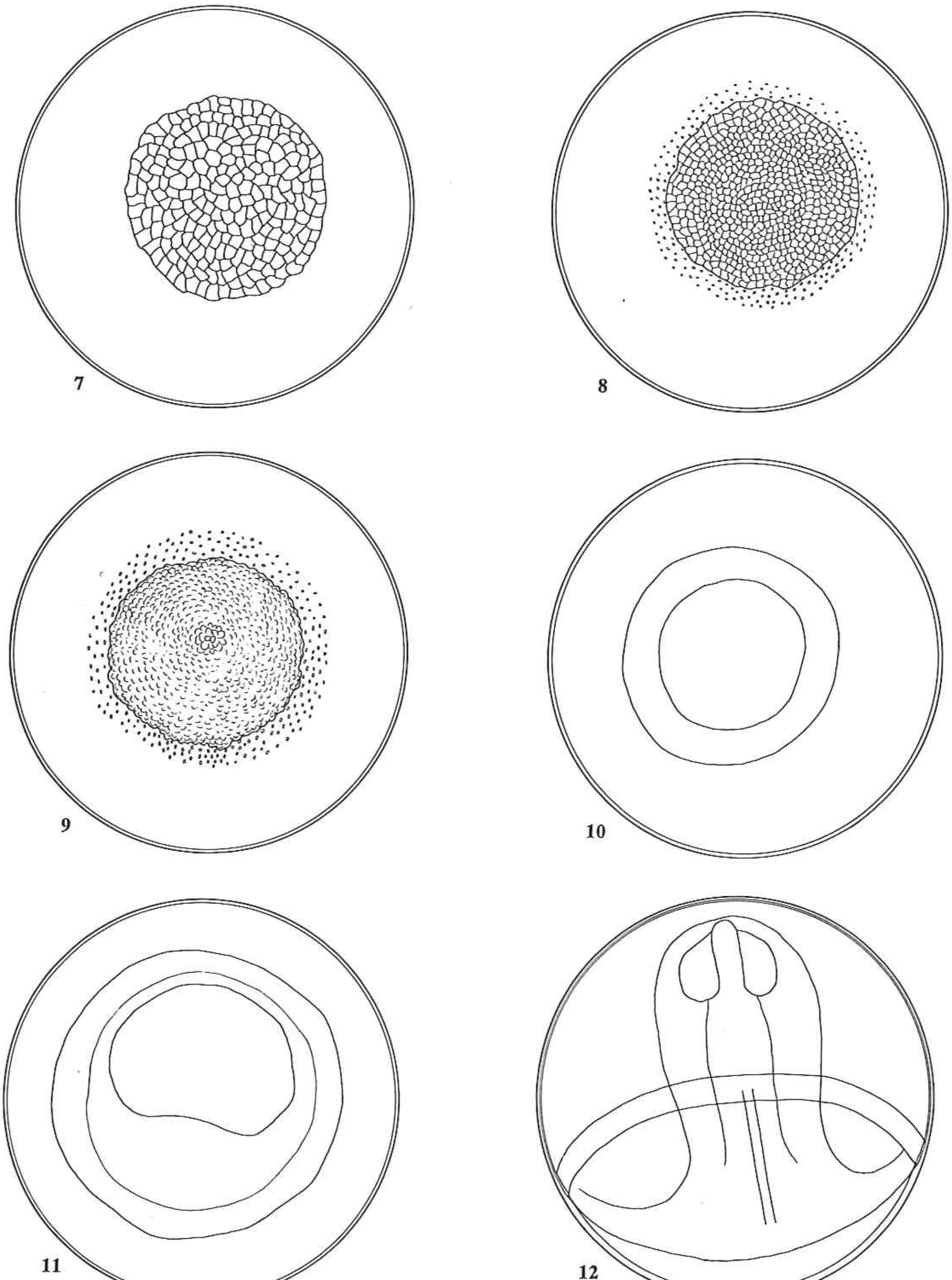


Figure 9

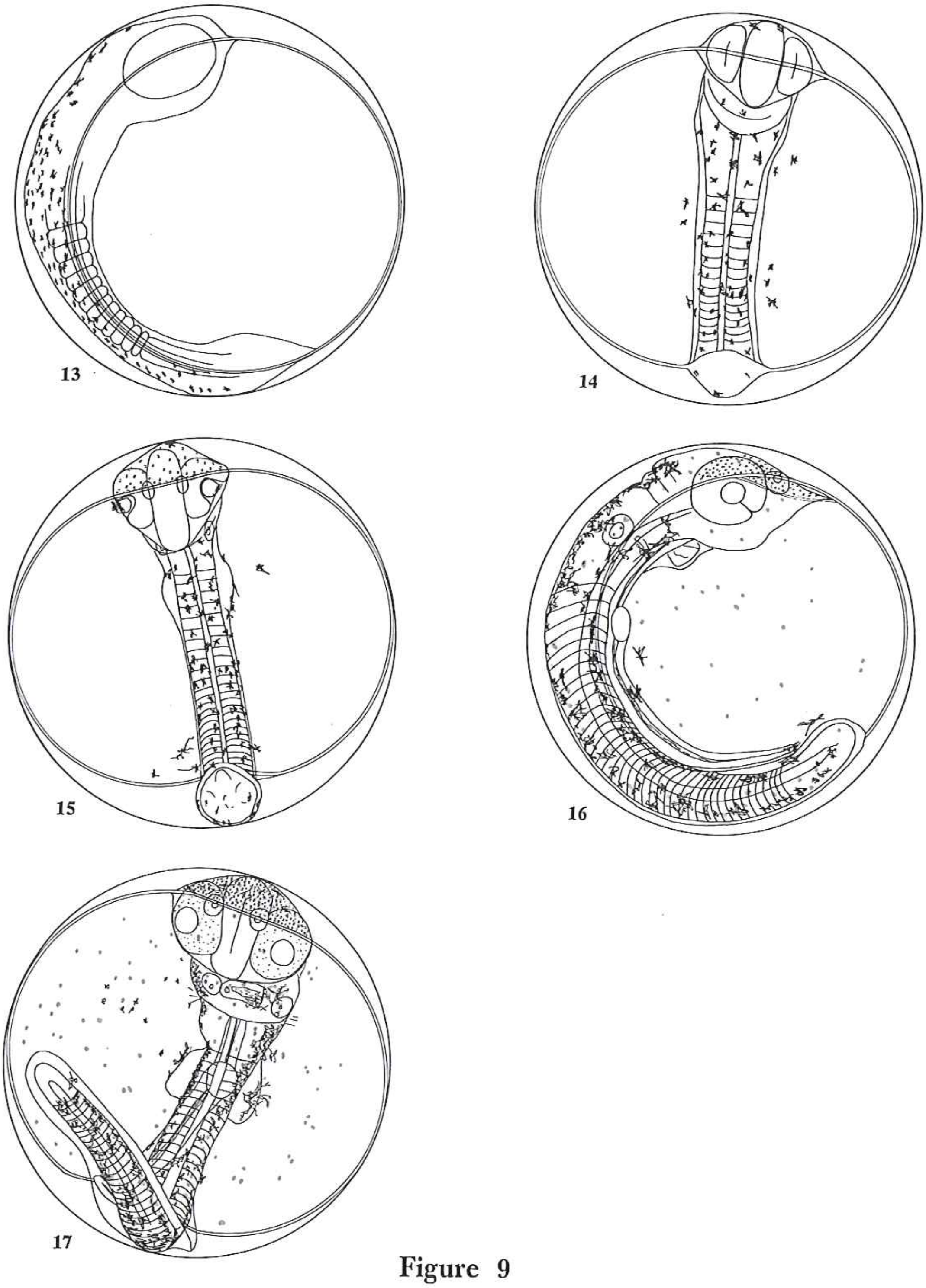


Figure 9

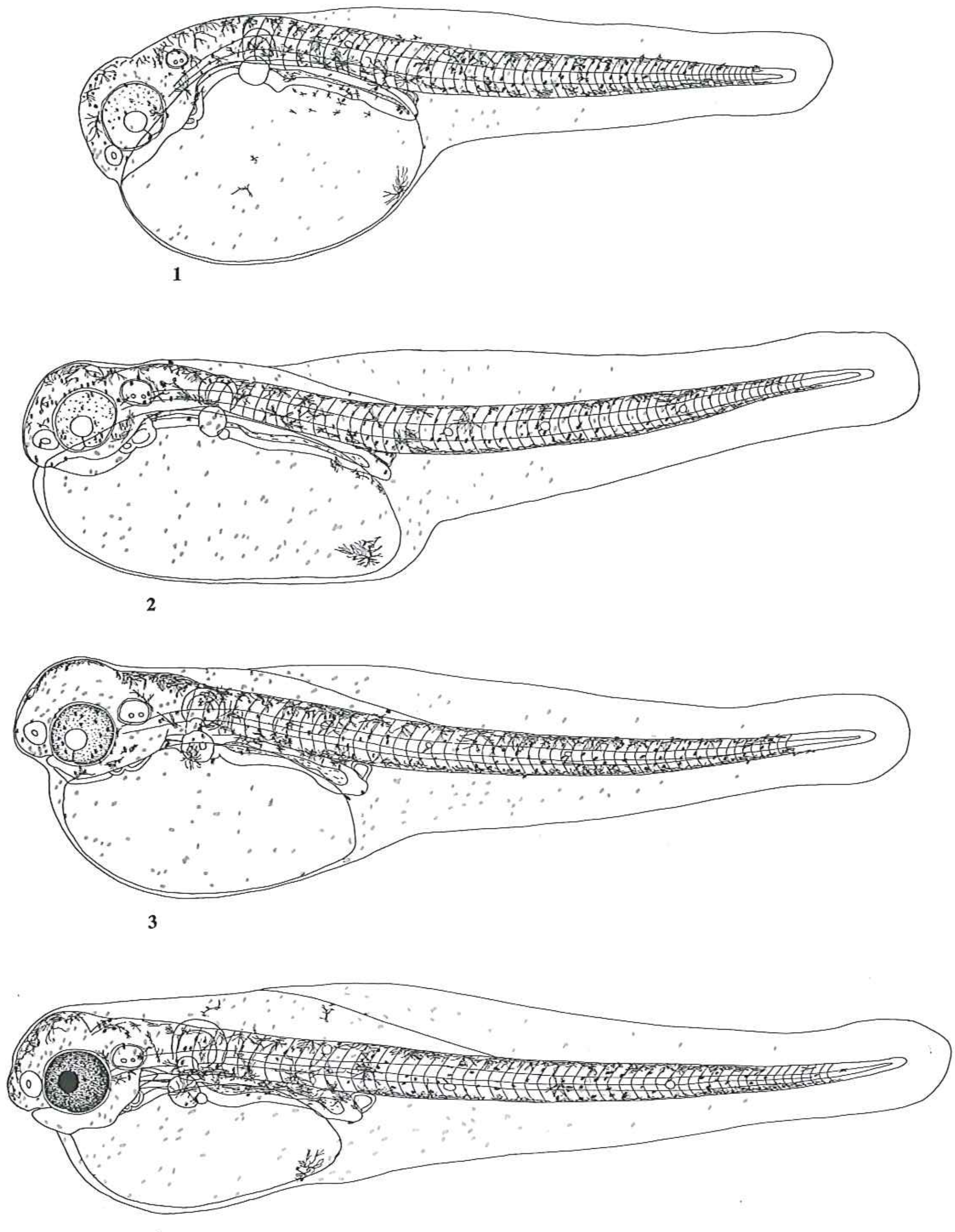


Figure 10

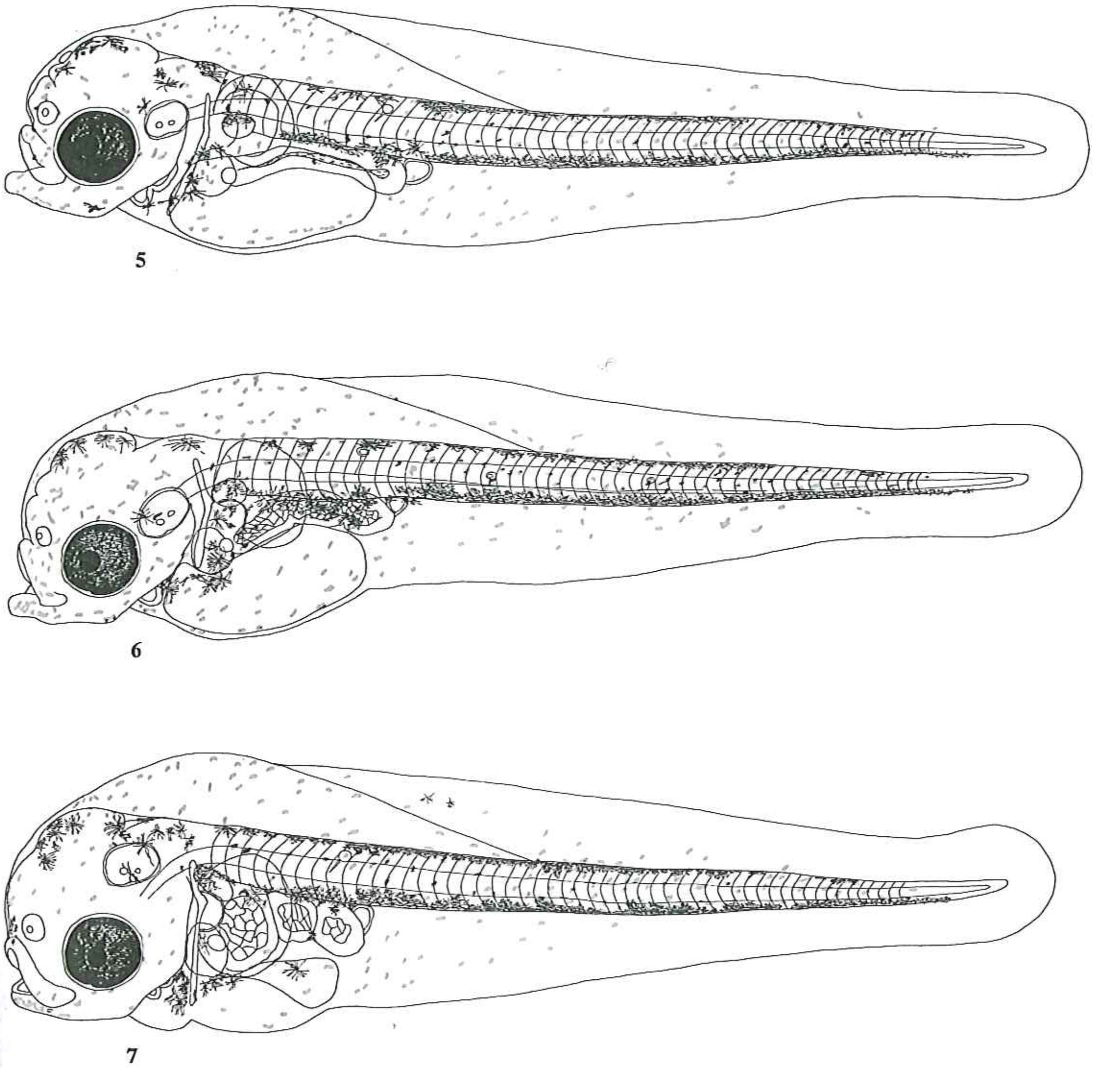


Figure 10

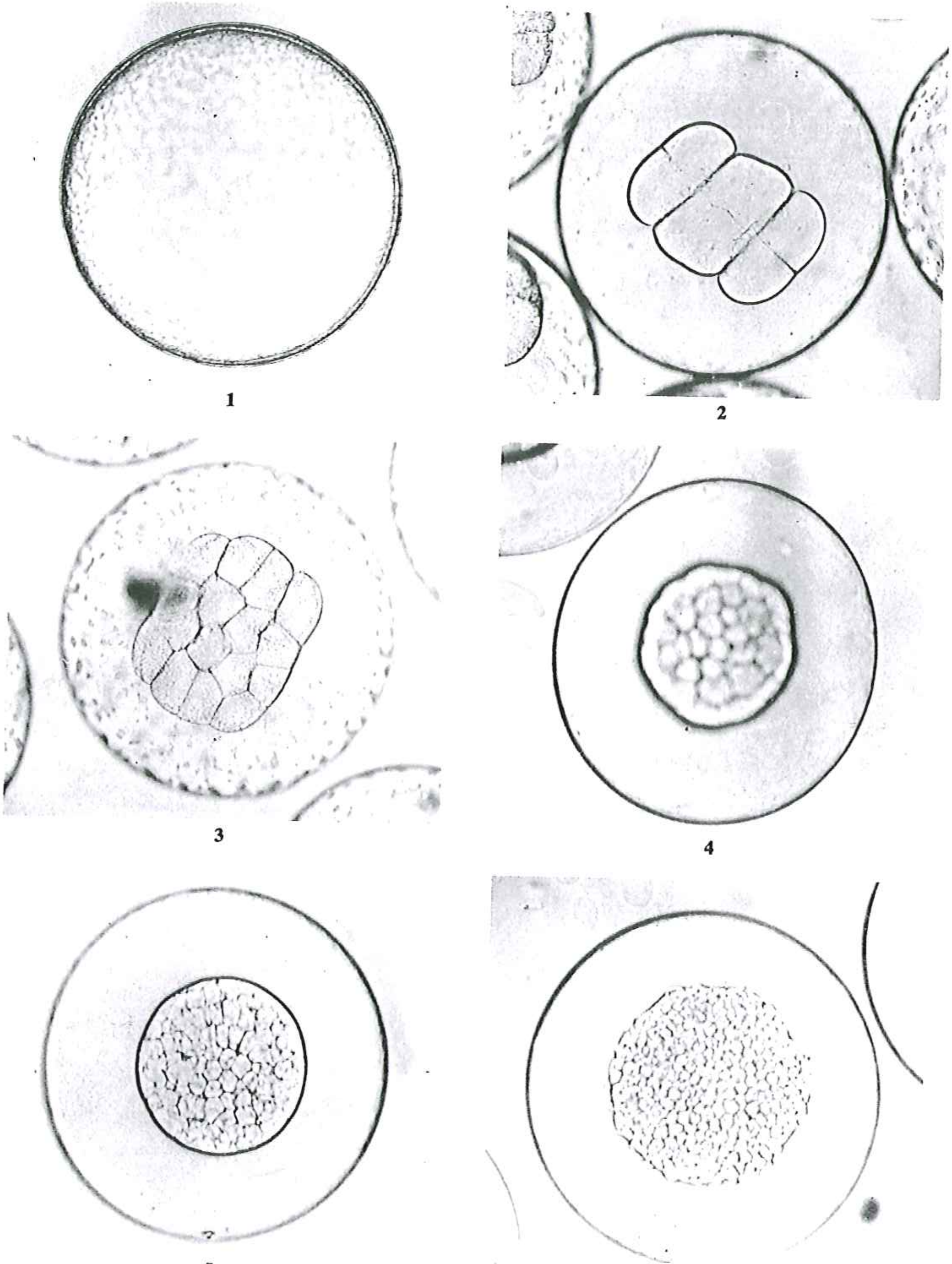
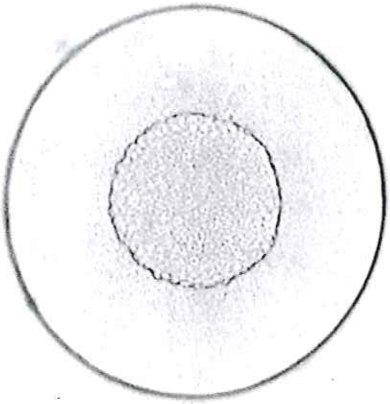
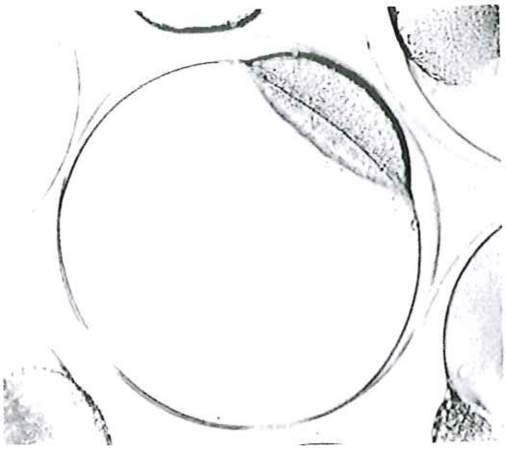


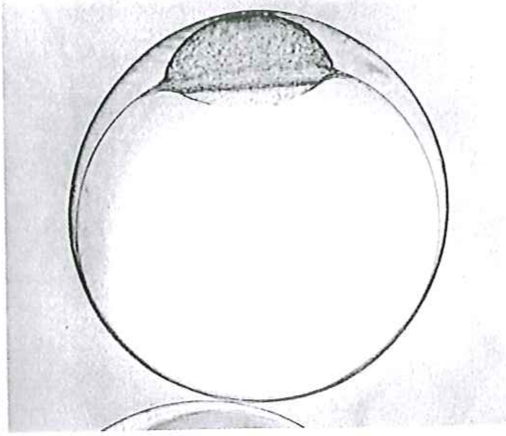
Plate 1



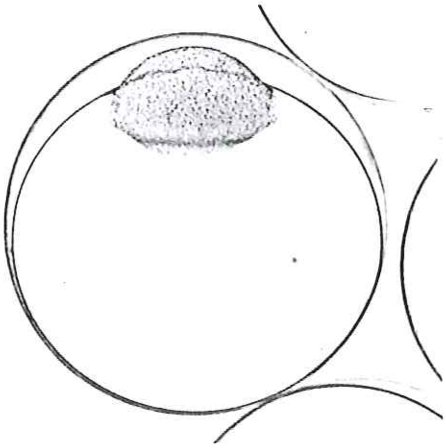
7



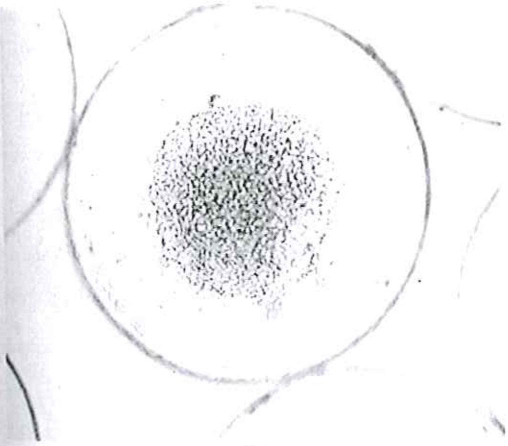
8



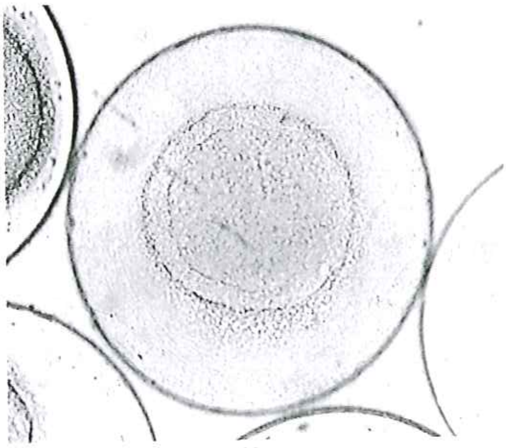
9



10

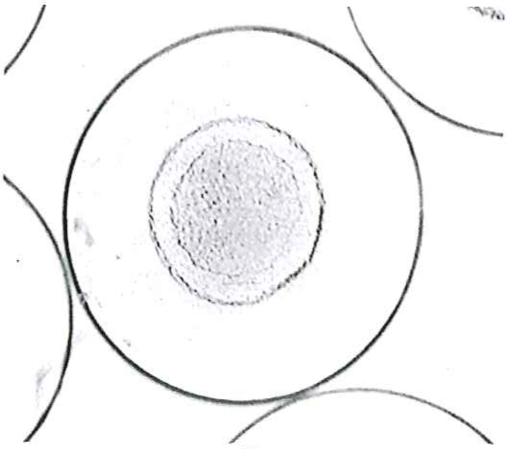


11

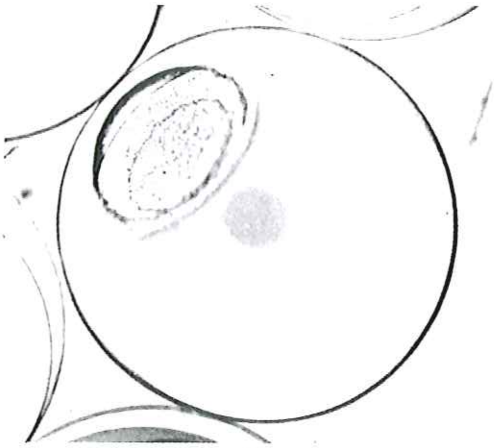


12

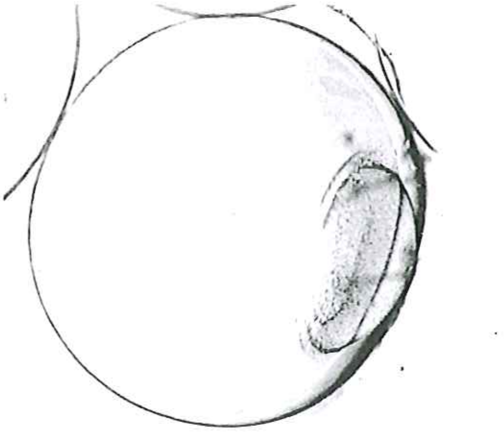
Plate 1



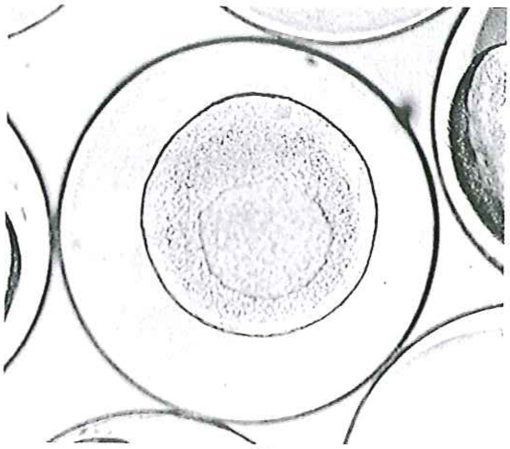
13



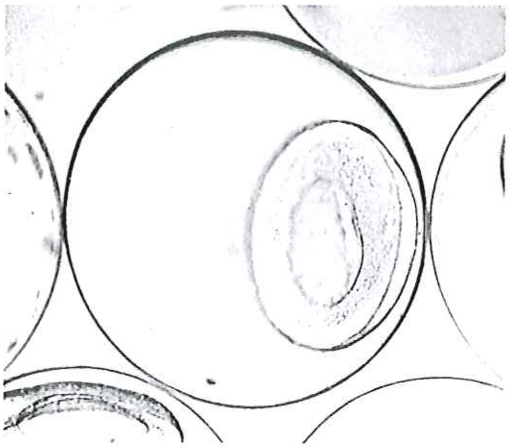
14



15



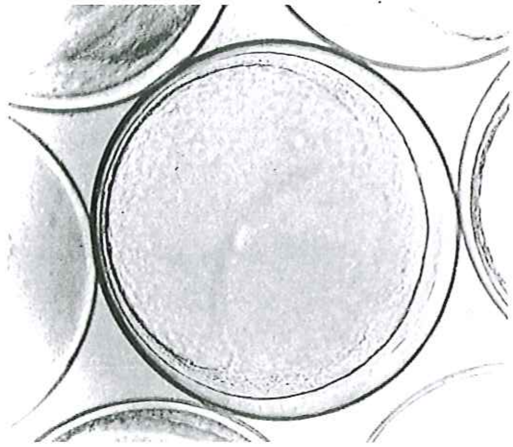
16



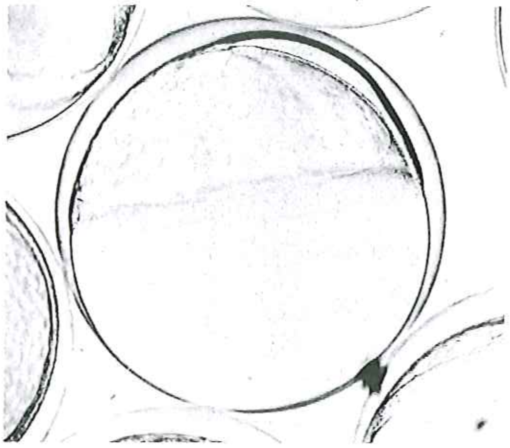
17

18

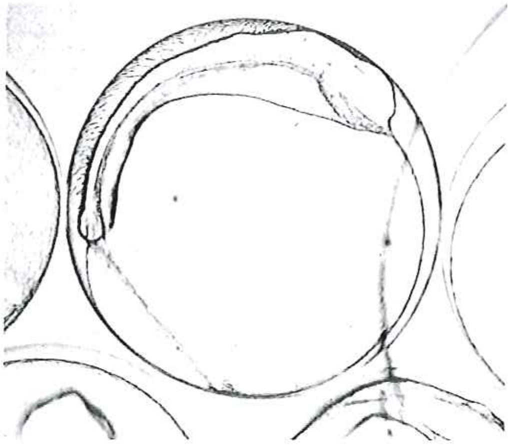
Plate 1



19

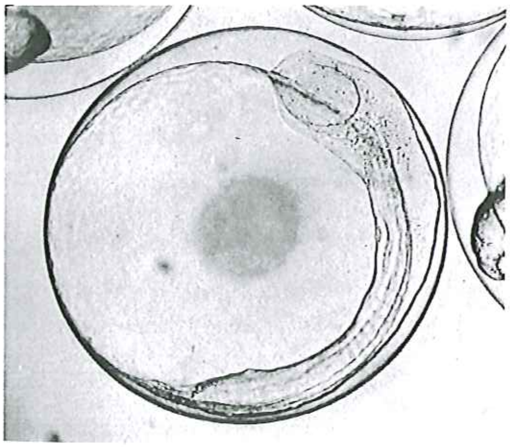


20

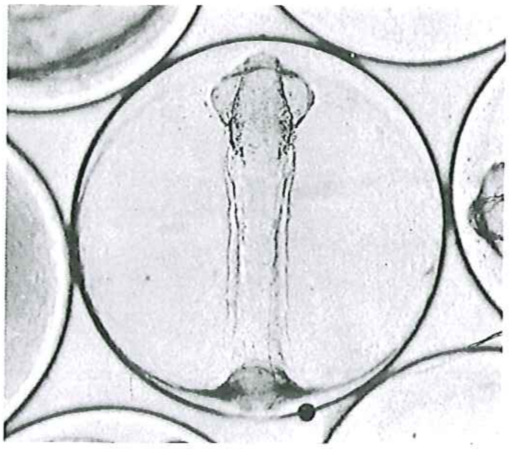


21

22

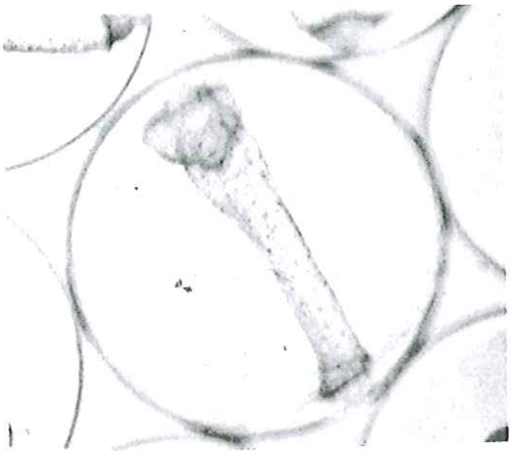


23

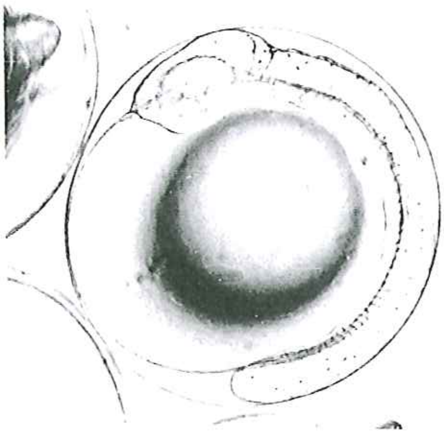


24

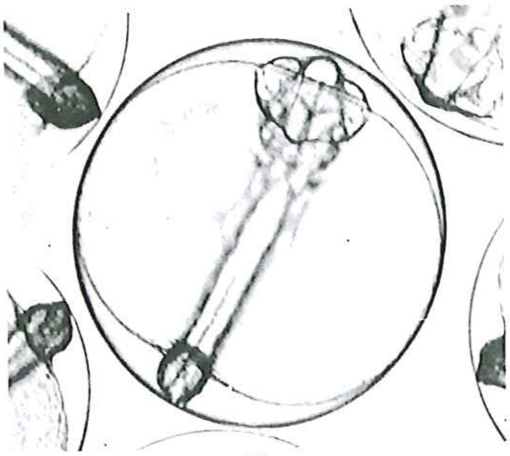
Plate 1



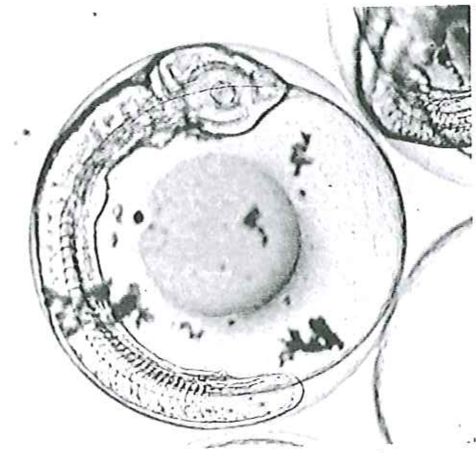
25



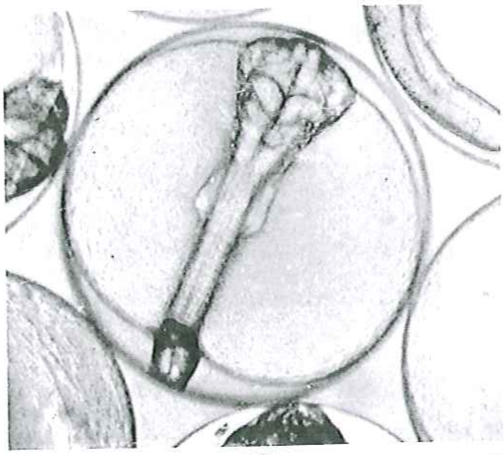
26



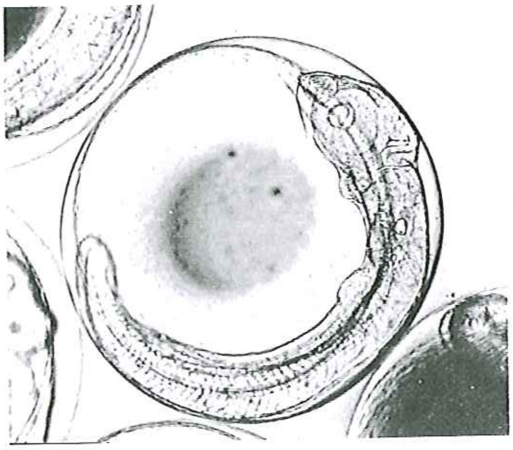
27



28

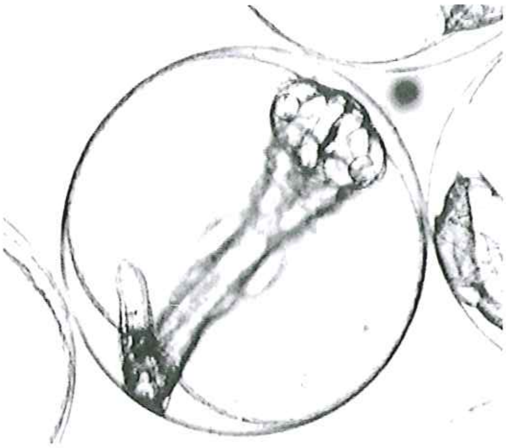


29

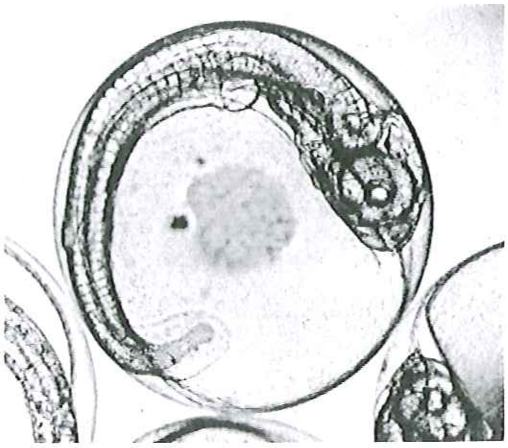


30

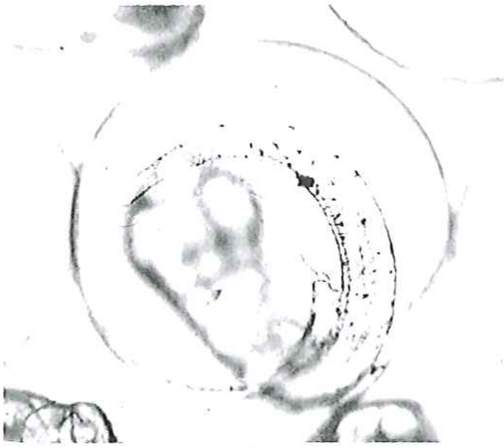
Plate 1



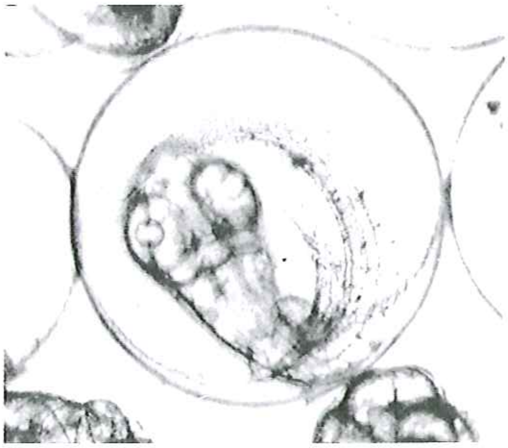
31



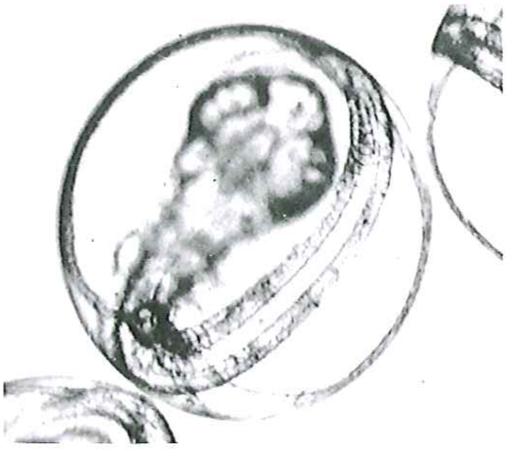
32



33



34



35

Plate 1

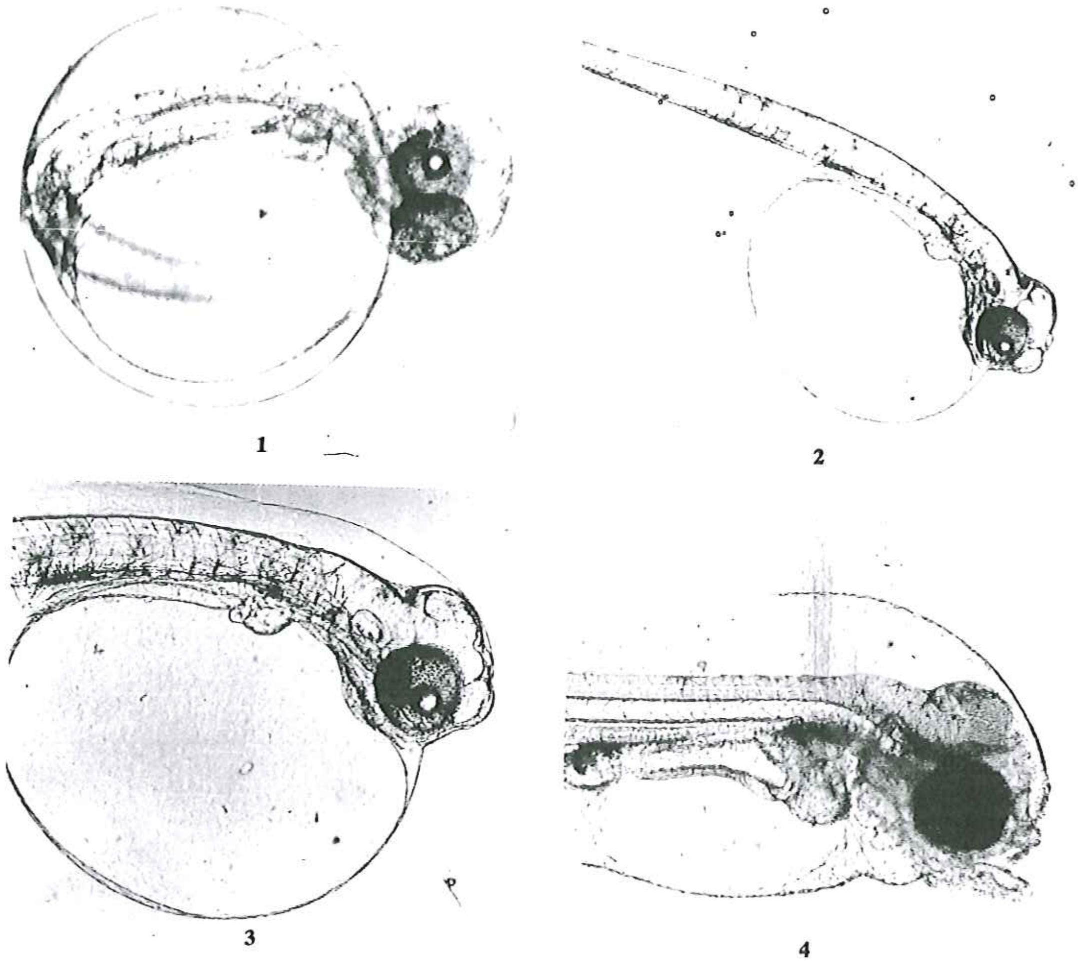
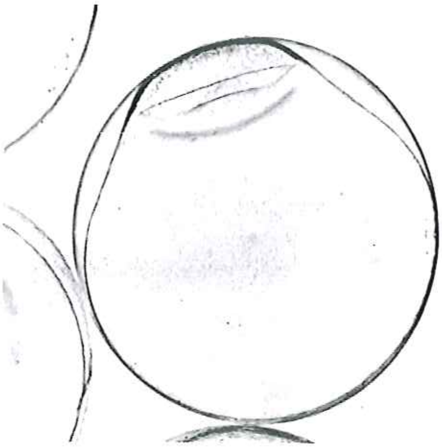
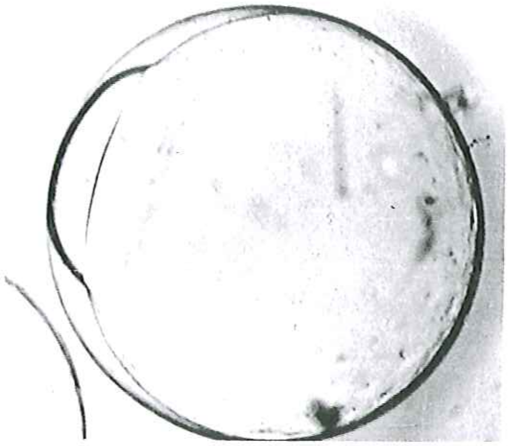
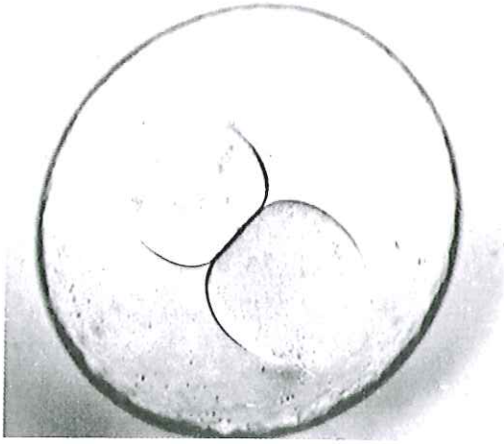
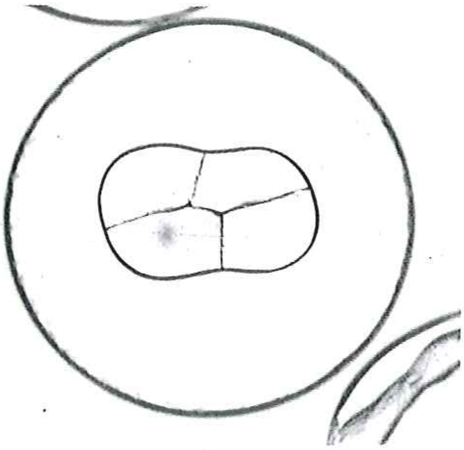


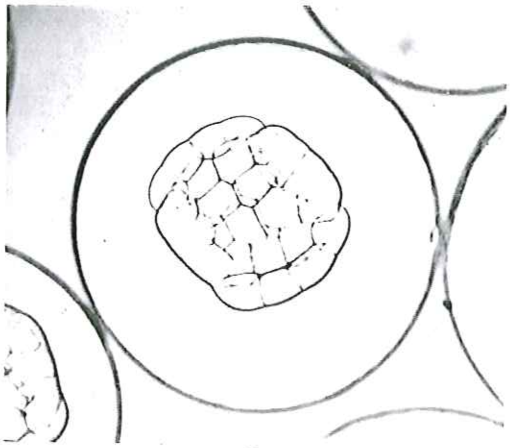
Plate 2


1


2


3


4


5

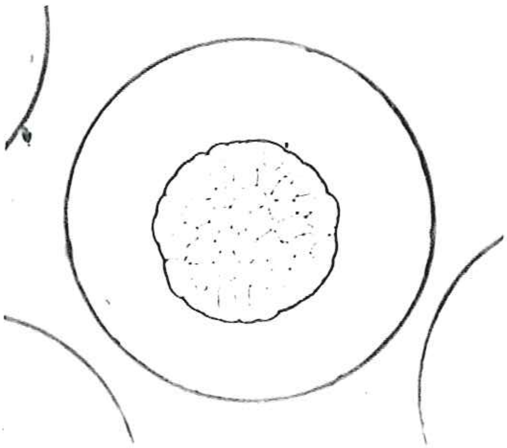
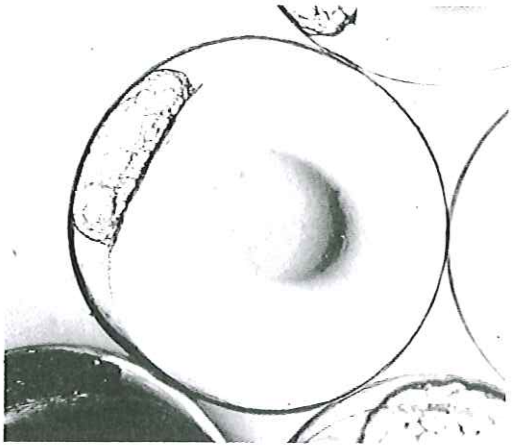
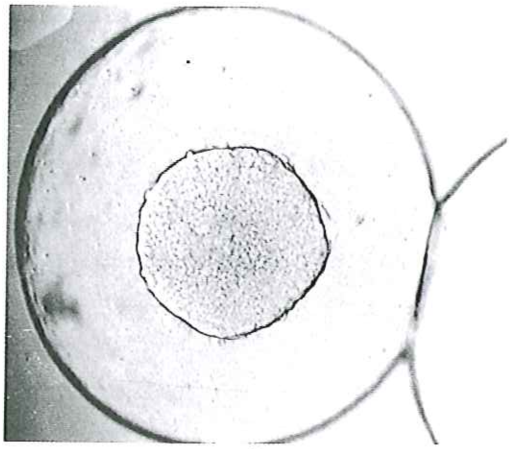

6

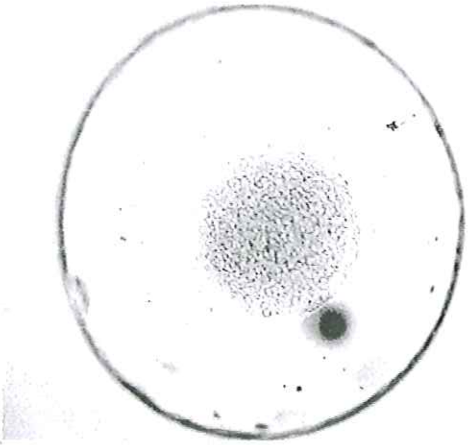
Plate 3



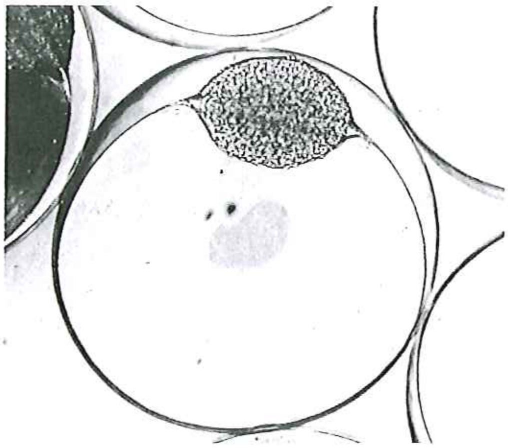
7



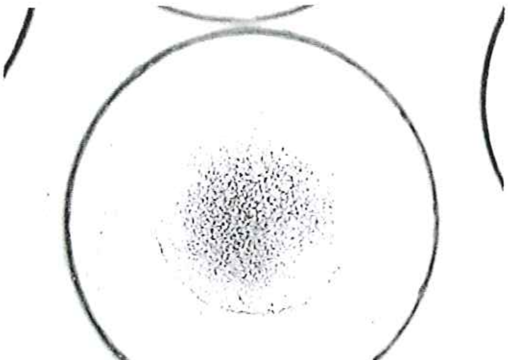
8



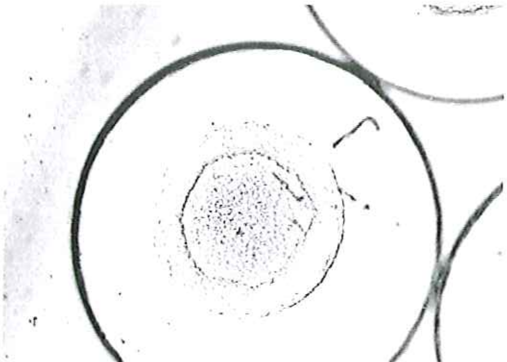
9



10

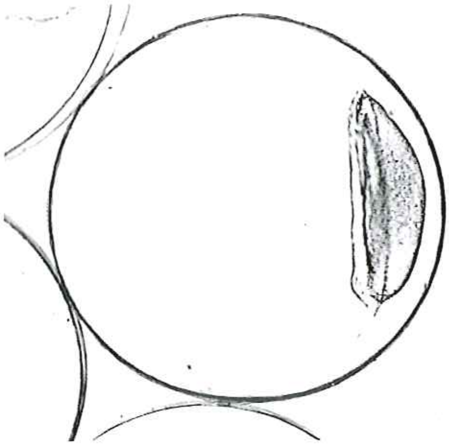


11

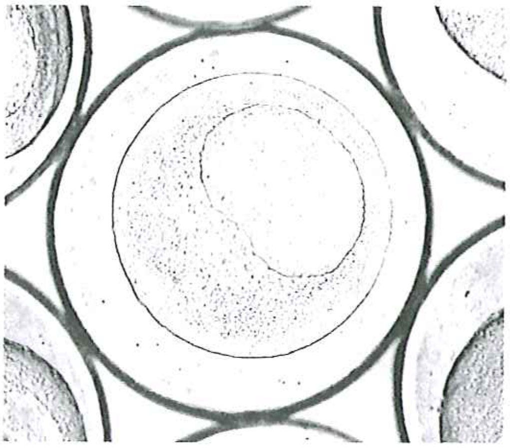


12

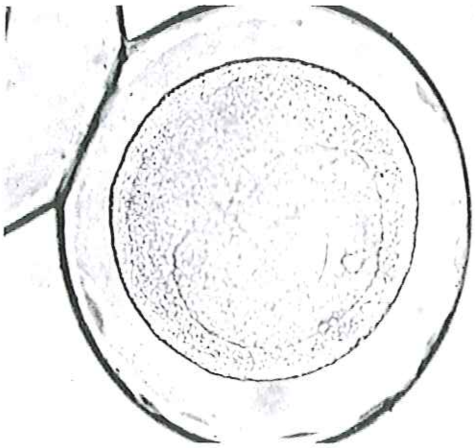
Plate 3



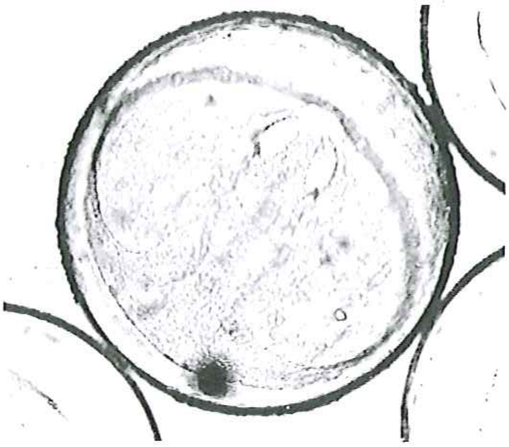
13



14

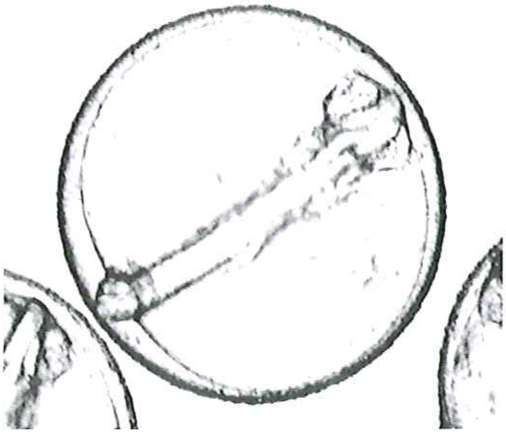


15



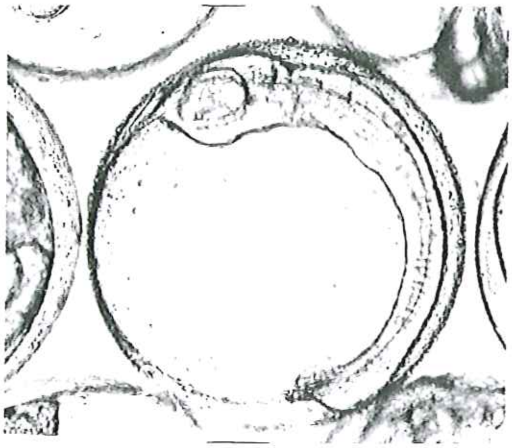
16

17

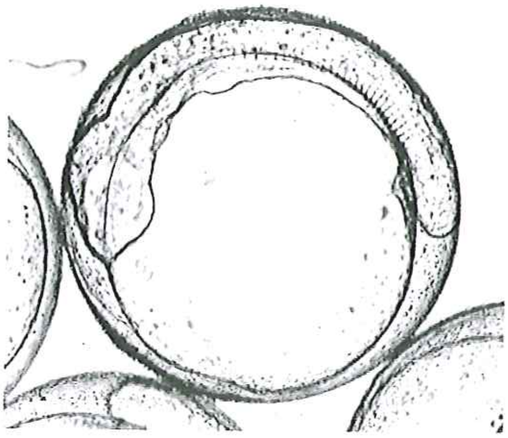


18

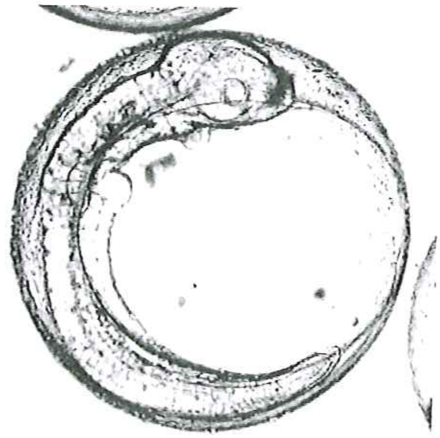
Plate 3



19

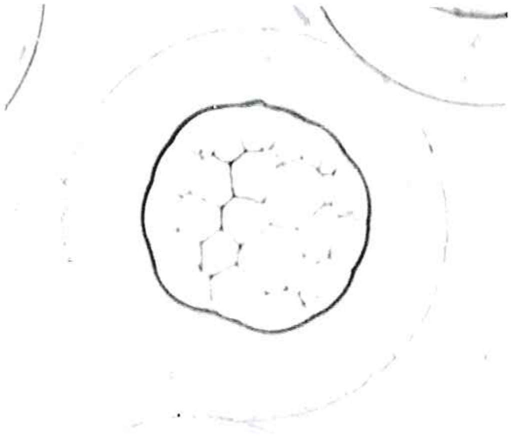


20

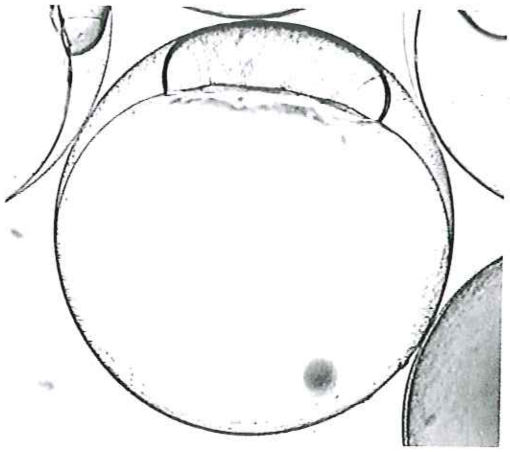


21

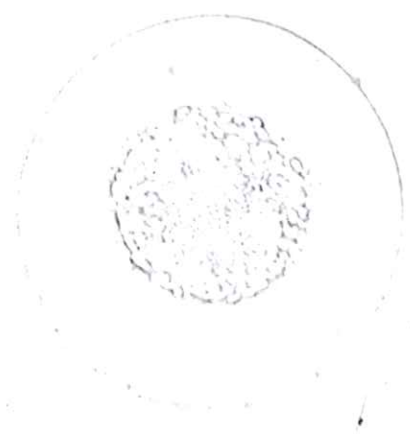
Plate 3



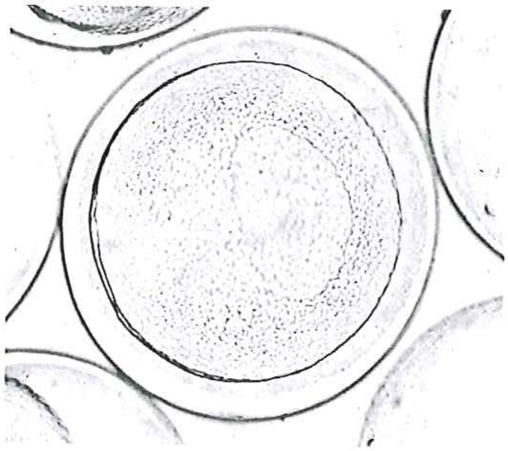
1



2

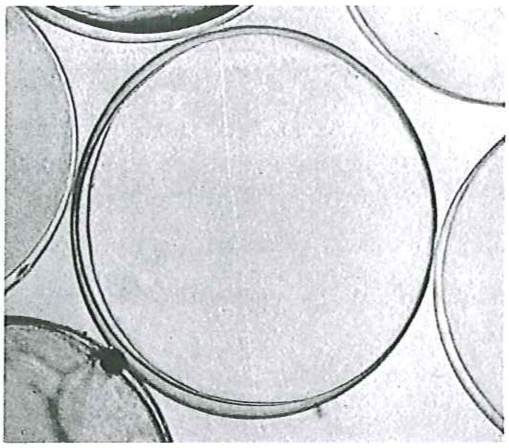


3

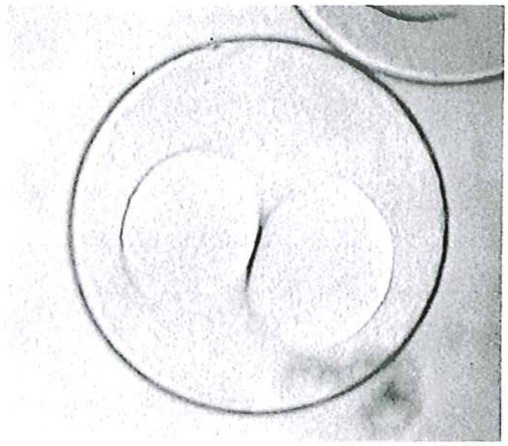


4

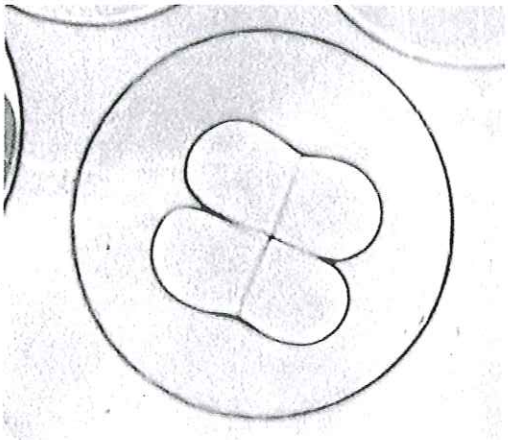
Plate 5



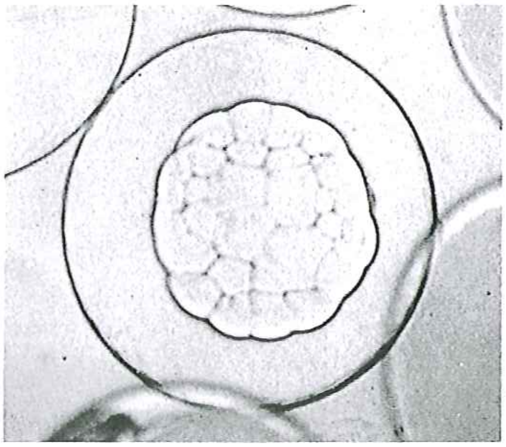
1



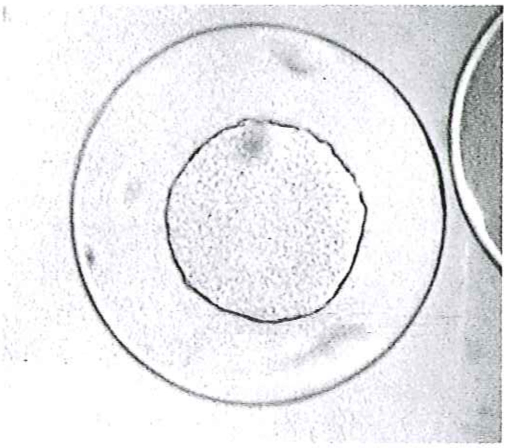
2



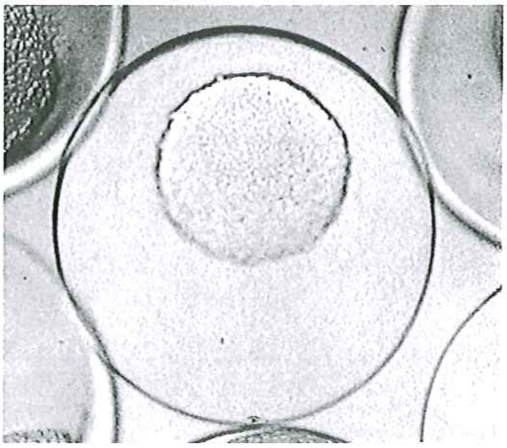
3



4

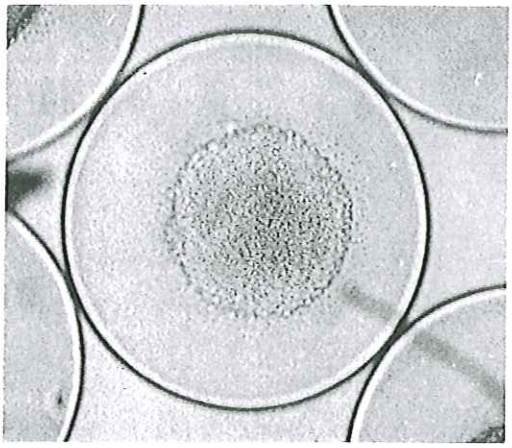


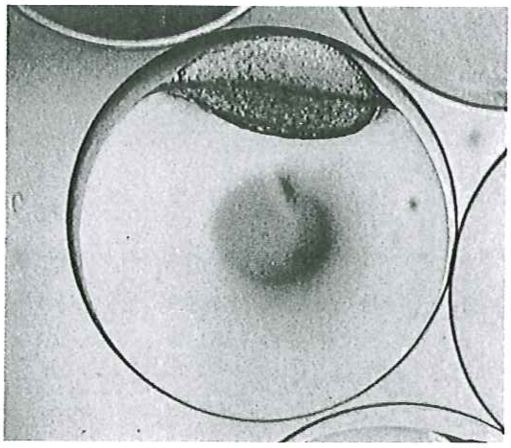
5

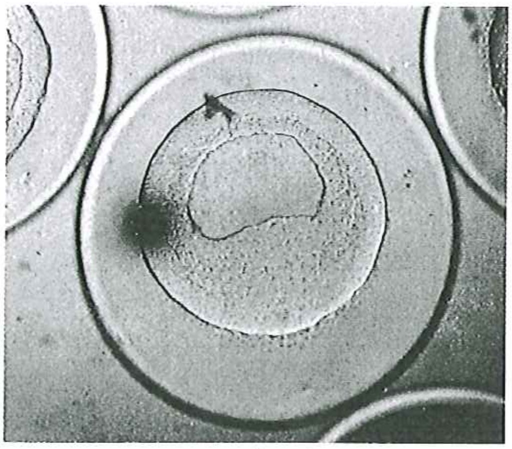


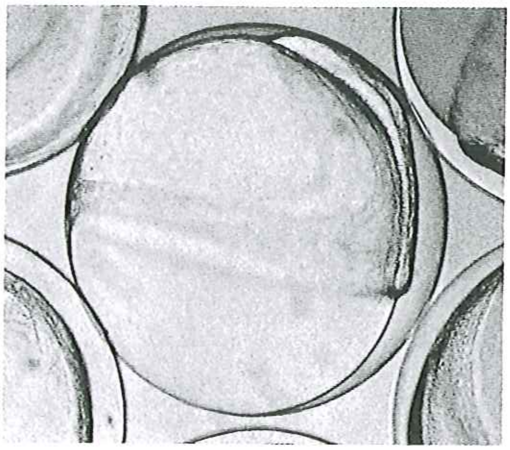
6

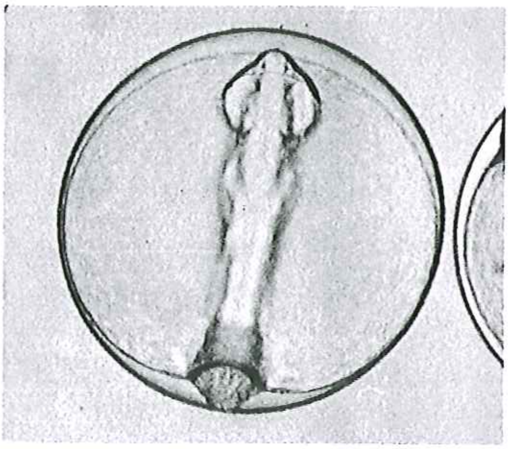
Plate 7


7


8


9


10


11

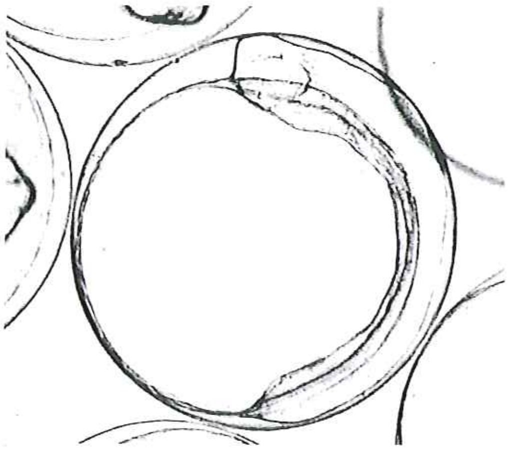
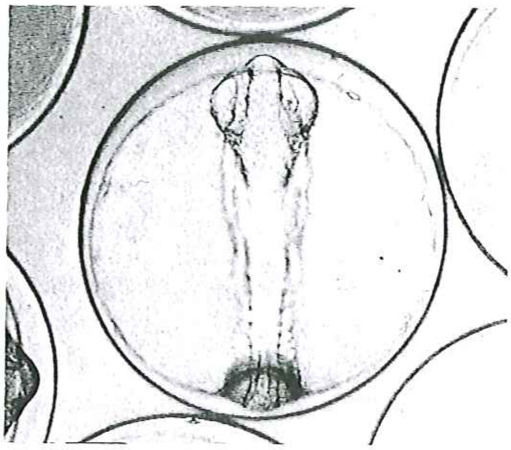
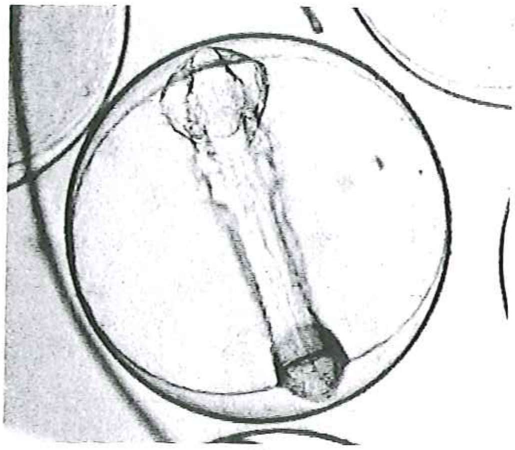

12

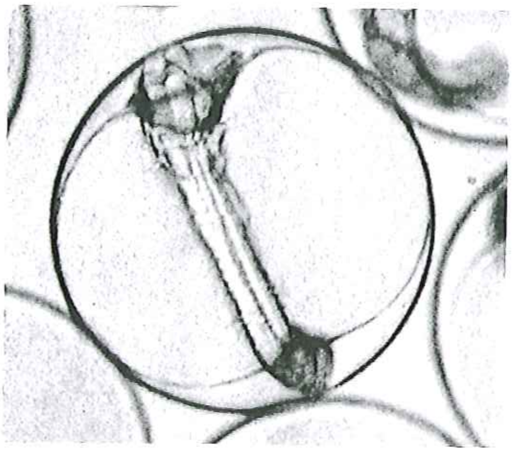
Plate 7



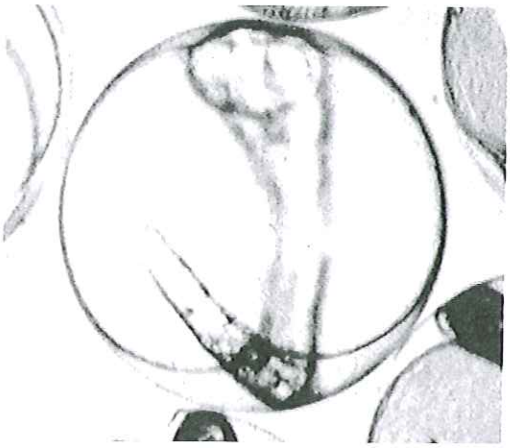
13



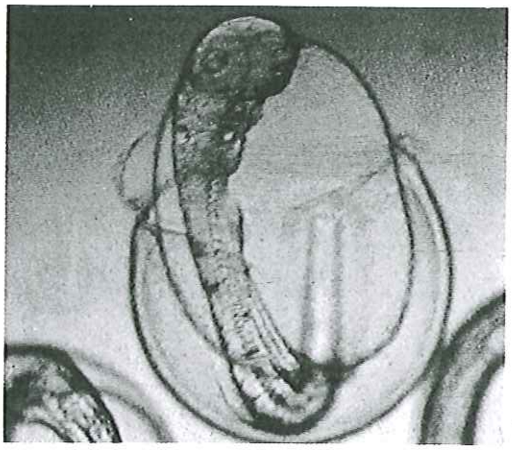
14



15

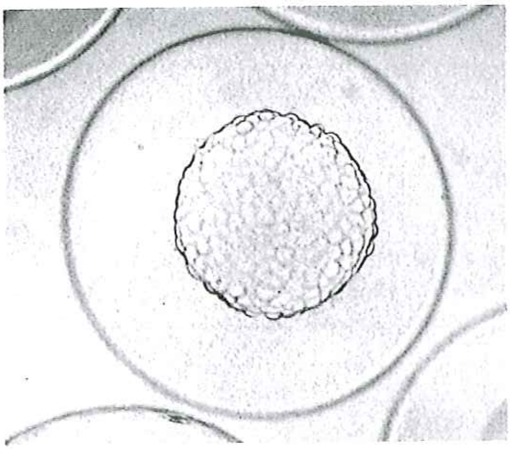


16

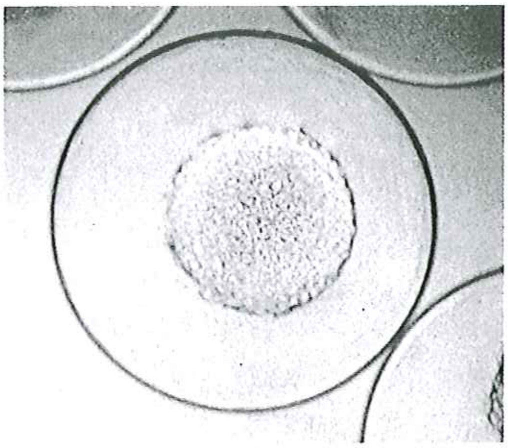


17

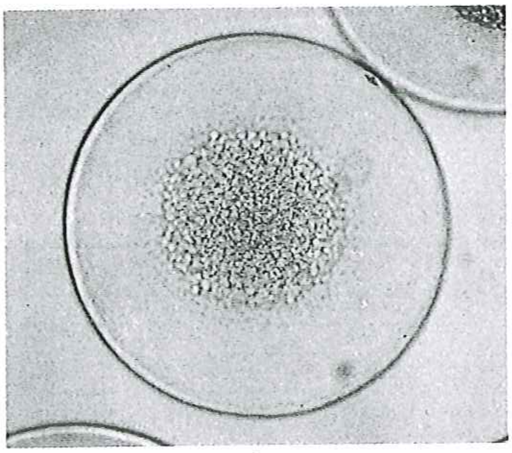
Plate 7



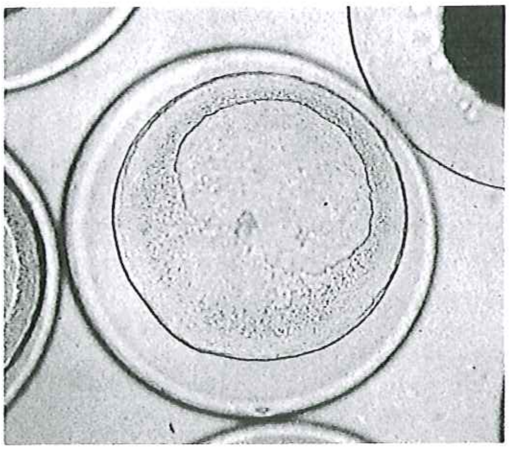
1



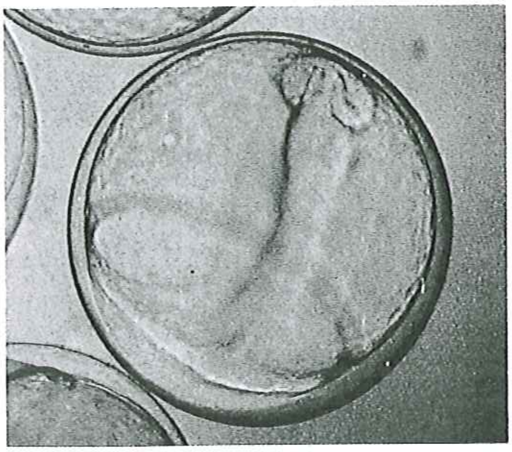
2



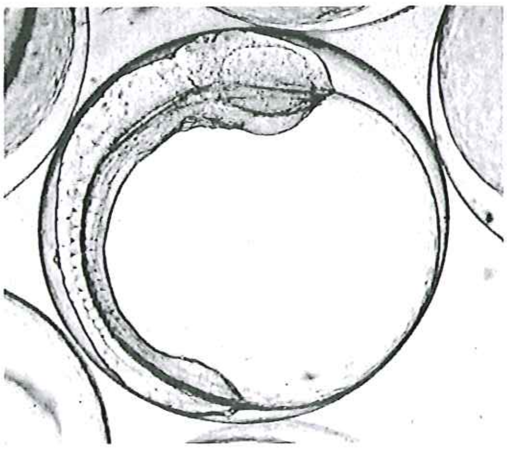
3



4

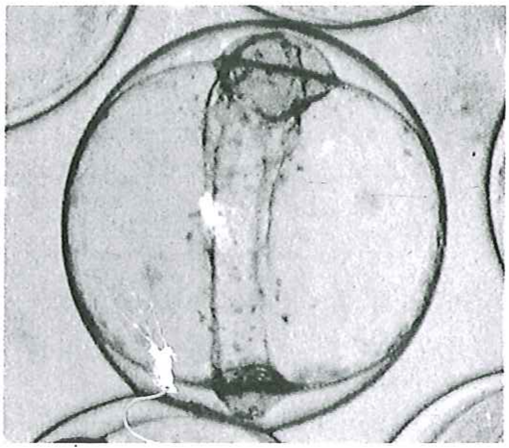


5

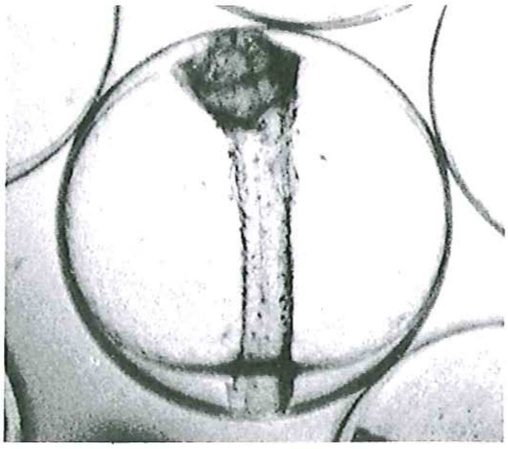


6

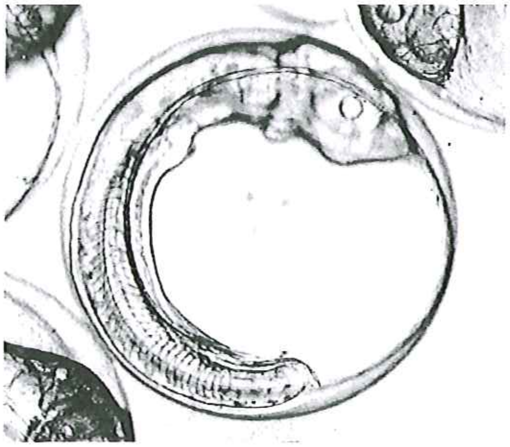
Plate 9



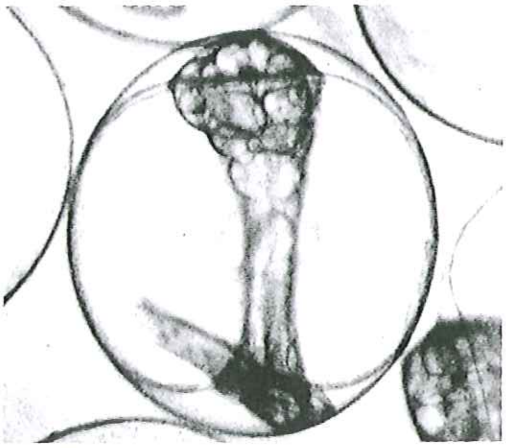
7



8



9



10

Plate 9