ON THE SPAWNING HABITS AND DEVELOPMENT OF THE SO-CALLED FRESHWATER SHARK, *WALLAGONIA ATTU* (Bloch and Schneider).

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INTRODUCTION.

Wallagonia attu (Bl. and Schn.) belongs to the family of Catfishes (Siluridae) but on account of its fierce and voracious habits is popularly known as a Freshwater Shark. It has a wide distribution, having been recorded from India, Ceylon, Burma, Siam, Java, Sumatra and Western Yunnan. It grows very rapidly, attains a length of six feet and weighs more than a maund. It provides good sport to anglers and a cheap nourishing food to thousands of fish-eating public. But in spite of its importance in more than one way, very little is known about its breeding habits and development. The only literature on the subject appears to be two short notes and five figures by Hamid Khan (1925; 1934) and a few observations by the present author (1943).

In this article a reasonably complete outline of the external changes from the time the egg is laid to the time the fry is able to look after itself is given.

The material of the earlier stages was fixed in Bouin's fluid and dehydration was carried up to 70% alcohol. To remove the last traces of fixative, a drop or two of ammonium hydroxide were added to every tube. The sections were cut by double embedding method. The advanced stages were preserved in formalin and alcohol.

SPAWNING HABITS.

The spawning was observed in the Budha Nala, Ludhiana, on the 28th of July, 1932. The Nala was then a perennial stream running along the old course of the river Sutlej. The actual stream was only a few yards across but during the rainy season the water level sometimes used to rise by a few feet and water would overflow the banks to a great distance. The low grassy banks with their slightly varying levels when inundated to a depth of from six inches to about a couple of feet provided excellent spawning grounds for the fish. The Nala has recently been converted into a regular canal and its water is being used for irrigation purposes. (Plate IV.)

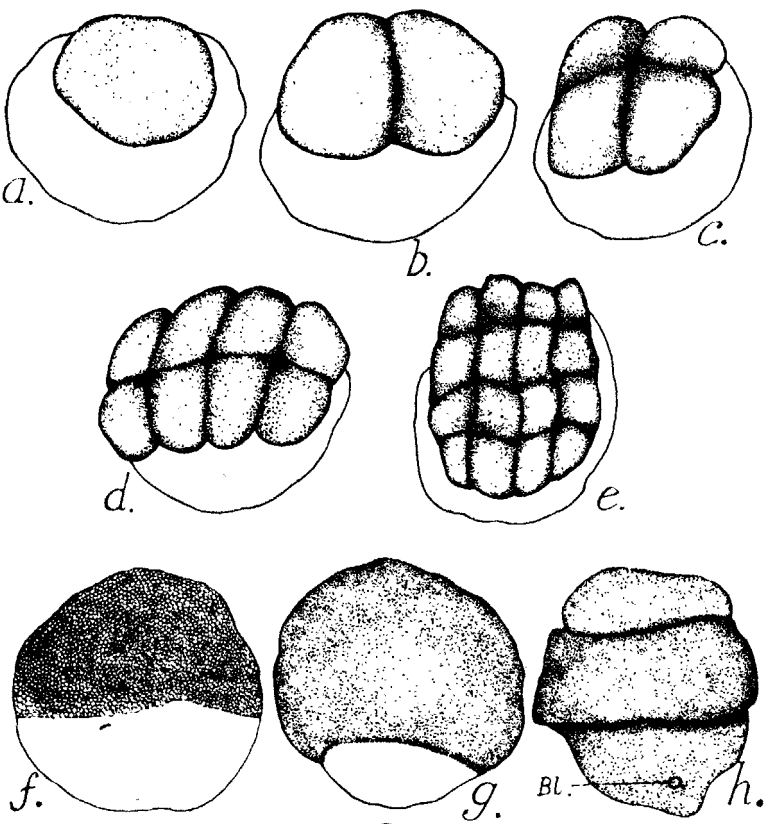
Under natural circumstances two males of *Wallagonia attu* were seen chasing a single female and all the three were playing and splashing water with their fins. It was a lively scene. The temperature of the water and approximately of the atmosphere at the time of spawning was 80°F. and it varied from 80°F. to 86°F. during the period the eggs were collected.

One mature male and one female were netted from the Nala and ripe eggs were gently pressed out from the ovaries and were fertilized by pouring spermatic fluid over them. The ova and spermatozoa were allowed to stand in a clean china dish for about five minutes before adding water to them. As a result of this artificial fertilization about 80 per cent of the eggs were found to have been impregnated. The artificially fertilized eggs were transferred to hatching trays, which were moored in the shallow running water of the Nala.

The eggs were fertilized at 11-30 a.m. The first sixty-one stages were collected after every half an hour, the next eight after intervals of an hour or so, while the more advanced stages were collected from natural spawning grounds during subsequent years. In the account that follows only a few typical stages of development are described.

Egg-membranes and absorption of Water.

The ripe egg is closely surrounded by an inner thin and transparent vitelline membrane and an outer thick zona radiata. The vitelline membrane is quite smooth while the zona shows some sorts of striations. There is no definite space between the egg and its membranes before it is immersed in water. After the fertilized egg is dipped in



Text-fig. 1. Development of the egg of *Wallagonia attu* (Bl. & Schn.). ×24

(*a*) Just after fertilization; (*b*) Fifteen minutes after fertilization; (*c*) Twenty-eight minutes after fertilization; (*d*) Forty-five minutes after fertilization; (*e*) One hour after fertilization; (*f*) Three and one-half hours after fertilization; (*g*) Six hours after fertilization; (*h*) Seven hours after fertilization.

In all cases egg membranes have been removed.

Bl = Blastopore.

water, it swells to about double its original size by the absorption of water. The absorbed water separates the membranes from the egg proper and fills two spaces, one lying between the egg and the vitelline membrane and the second between the latter and the zona radiata. The perivitelline space is found to be much wider than the outer space. The water thus imbibed is probably utilised by the developing embryo as cushion, as well as for respiration before hatching. The absorption of water is complete within ten to fifteen minutes after fertilization.

Structure of the Fertilized Egg.

The fertilized egg (Text-fig. 1*a*) is almost spherical and measures from 1·2 to 1·5 mm. in diameter. The germinal-disc is very small and forms a cap-like mass on the top of the rounded yolk-sac. The yolk is deep yellow in colour while the disc is almost white. There is no oil-globule in the egg, which sinks to the bottom when laid. There is no external difference marking the anterior from the posterior end of the disc. In the sections of the egg, the yolk-sac appears to be devoid of any trace of protoplasm although small yolk-granules are found scattered in the disc itself. The yolk-granules lying immediately below the disc are comparatively smaller.

The healthy eggs neither adhere to each other nor to foreign objects while the unhealthy eggs show opacity in their contents and also wrinkled appearance.

Cleavage.

Segmentation is meroblastic, of extremely discoidal type.

1st stage.—Fifteen minutes after fertilization (Text-fig. 1*b*). As the time of cleavage approaches, one axis of the germinal-disc becomes longer than the other. A depression appears on the surface of the disc which gradually extends inwards. This results in the division of the disc into approximately equal halves. The first plane of cleavage cuts the disc at right angles to the longer axis.

2nd stage.—Twenty-eight minutes after fertilization (Text-fig. 1*c*). As the time for the second cleavage approaches, the shorter axis increases in length and consequently the blastoderm becomes almost square-shaped. The second plane of cleavage intersects the first at right angles, resulting in four almost equal blastomeres.

An egg with three cells has been found in the tube containing the 2nd stage, indicating that the blastomeres after the first stage divide alternately, but this is contrary to the observations, for actually both the blastomeres have been seen dividing simultaneously.

3rd stage.—Forty-five minutes after fertilization (Text-fig. 1*d*). As the time for the third cleavage draws near, one axis of the blastoderm again becomes considerably longer than the other. This plane is parallel to the first and at right angles to the second axis.

4th stage.—One hour after fertilization (Text-fig. 1*e*). The shorter axis now grows and the two axes become almost equal in length. The fourth cleavage plane is parallel to the second and at right angles to the first and third set of furrows. The blastomeres, as seen in surface view, become arranged in four rows of four cells each.

5th stage.—One and one-half hours after fertilization. Externally there does not seem to be any difference between this and the preceding stage but sections show horizontal furrows cutting every blastomere into an upper and a lower half.

6th stage.—Two hours after fertilization. The blastomeres divide actively and form a mulberry-like mass, which stands out clearly at the animal pole. This mass covers only a small portion of the yolk-sac.

7th stage.—Three hours after fertilization. The blastomeres are comparatively smaller than in stage 6 and more of the yolk-sac is invested by them.

8th stage.—Three and one-half hours after fertilization (Text-fig. 1*f*). The blastoderm has extended beyond the equator of the yolk-sac. The blastomeres are smaller than in the last stage and form a single layer several cells in thickness.

9th stage.—Five hours after fertilization. The blastomeres increase in area and cover more of the yolk-sac. The sections of this stage show that unlike the preceding

stage, here the cells are arranged in two layers, each several cells in thickness. Thus the two primary layers, ectoderm and endoderm, are established.

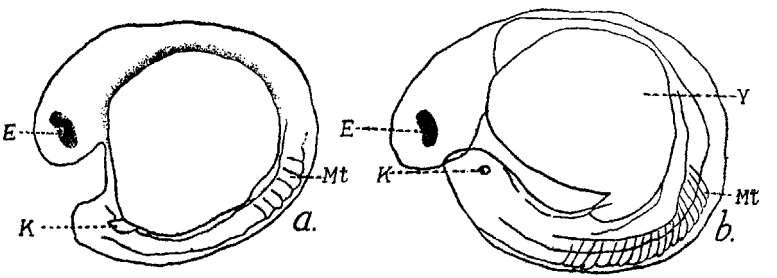
10*th stage*.—Six hours after fertilization (Text-fig. 1*g*). The primary layers cover more than three-fourths of the yolk-sac. Here is found the first indication of the origin of mesoderm.

11*th stage*.—Seven hours after fertilization (Text-fig. 1*h*). Almost the whole of the yolk-sac has been covered over by the cells, except a very small rounded area representing the blastopore. A portion of yolk-sac can still be seen through the blastopore. In the middle of the egg the protoplasm bulges out to form a belt-like structure. In sections of this stage the bulging out portion is thin while towards the poles the protoplasm is sufficiently thick. On either side of the blastopore, lies a sheet of mesoderm, thicker towards the blastopore but thinning out towards the opposite end. The rudiment of the notochord also makes its appearance at this stage.

Formation of Embryo.

12*th stage*.—Eight hours after fertilization. The formation of the embryo is seen in this stage. The anterior and posterior ends of the embryo are not yet fully differentiated though the anterior end is recognisable by its slightly greater width. The embryo extends along the circumference of the yolk-sac. There is no sign of eyes or of otocysts.

13*th stage*.—Eight and one-half hours after fertilization. The embryo has become more prominent. The anterior end has become broader than the posterior. Eyes and otocysts are not yet seen.



Text-fig. 2. Earlier stages in the development of the larva of *Wallagonia attu* (Bl. & Schn.). ×18.
(*a*) Nine and a half hours after fertilization; (*b*) Twelve hours after fertilization.
In both cases egg membranes have been removed.
E = Eye; *K* = Kupffer's vesicle; *Mt* = Myotome; *Y* = Yolk.

14*th stage*.—Nine and one-half hours after fertilization (Text-fig. 2*a*). The anterior and posterior ends of the embryo are rounded, but the former is much broader. Eye is present but is without any pigment. Otocyst has not yet made its appearance. The somites are clearly seen in the middle region of the embryo. At the posterior end of the embryo, a small clear area representing kupffer's vesicle is visible.

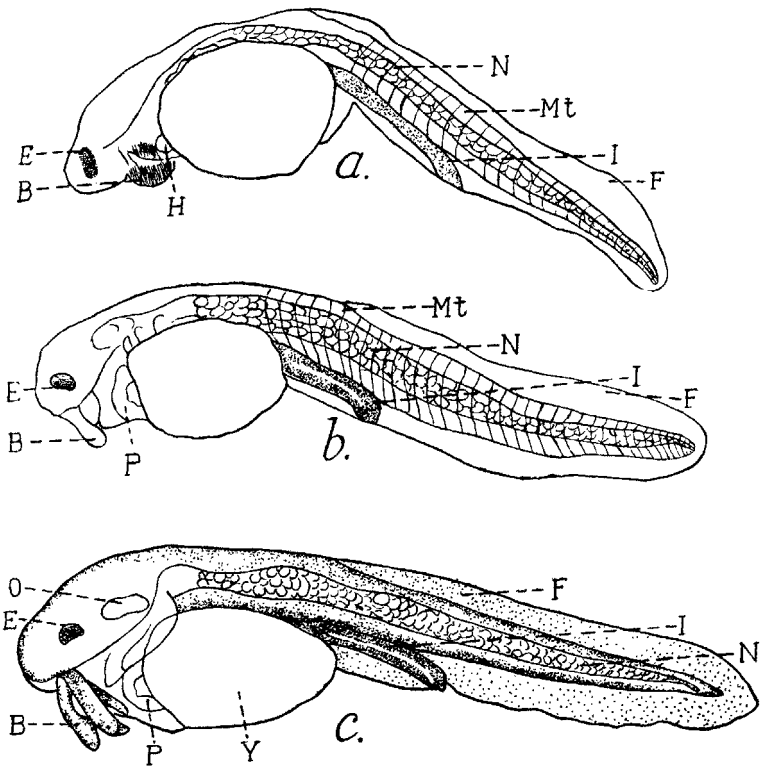
15*th* stage.—Eleven hours after fertilization. The embryo has become elongated, so that its anterior and posterior ends touch each other. Head and tail have slightly separated from yolk-sac but the greater part of the embryo is still attached to it. More somites are visible. Kupffer's vesicle has become enlarged. Eye is without pigments. Yolk-sac is slightly prolonged in its posterior region.

16*th stage*.—Twelve hours after fertilization (Text-fig. 2*b*). Head and tail regions are better formed than in earlier stages. Both the ends have separated from the yolk-sac. The posterior prolonged portion of the yolk-sac can still be seen. Kupffer's vesicle is present, though much smaller than in the preceding stage. Somites are greater in number than in stage 15. Notochord and nerve cord are well developed. A pair of rudimentary gill-slits is present. Eye is without pigments. Otocyst is not present.

17*th stage*.—Fourteen and one-half hours after fertilization. Yolk-sac is almost circular in outline and is not prolonged posteriorly. Kupffer's vesicle is quite small. A narrow embryonic fin-fold makes its appearance; it encircles only the posterior-most region of the body. Somites are seen both in the middle and the posterior region of the body but not extending to the hinder-most end. From the antero-ventral side of the head arise outgrowths, which represent the rudiments of barbels. Nerve cord and notochord are well developed. Otocysts are present. The posterior region of the embryo has deflected from the yolk-sac but still the embryo has not fully straightened out. The embryo wriggles in the perivitelline space and presses against the enclosing membrane, but cannot yet escape.

Hatching.

18*th stage*.—(Newly hatched larva). Fifteen and one-half hours after fertilization (Text-fig. 3*a*). The larva has more or less straightened out and by rupturing the vitelline membrane has come out as a free individual. The intestine appears as a solid structure but for its food supply it depends entirely upon the attached yolk-sac. Nervous tube and notochord are clearly seen and the cells of the latter show vacuolations. Eye does not possess pigments. Embryonic fin-fold is more prominent but as yet there is no sign of the presence of fin-rays; it extends almost to the yolk-sac, both dorsally and ventrally. Kupffer's vesicle has disappeared. Somites are not present in the posterior-most region of the embryo. Heart is seen as a small space, lying dorsal to the rudiments of barbels and touching the yolk-sac.



Text-fig. 3. Later stages in the development of the larva of *Wallagonia attu* (Bl. & Schn.) × 20.

(*a*) Newly hatched larva, fifteen and a half hours after fertilization; (*b*) Seventeen hours after hatching; (*c*) Thirty-one hours after hatching.

B = Barbel; *E* = Eye; *F* = Fin; *H* = Heart; *I* = Intestine; *Mt* = Myotome; *N* = Notochord; *O* = Otocyst; *P* = Pericardium; *Y* = Yolk.

A few larvae hatched at about fourteen hours after fertilization but the last batch came out about six hours later.

19th stage.—Eight hours after hatching. The larva has become quite straight but its length remains the same as in the last stage. Intestine is still solid. Fin-fold is without fin-rays. The anterior region of the nerve tube has developed outgrowths forming the compartments of brain. Eye is without pigments.

20th stage.—Twelve and one-half hours after hatching. Intestine is still a solid structure. Barbels have become longer. Notochordal cells are completely vacuolated. Embryonic fin-fold is wider than in the last stage but is still without fin-rays. Eyes do not possess pigment granules. Somites are well developed and are seen even in the posterior-most region of the body.

21st stage.—Seventeen hours after hatching (Text-fig. 3*b*). Larva becomes more elongated and all the parts become better developed. Barbels are much longer than in early stages. Branchial arches have made their appearance and lie at the antero-dorsal region of the yolk-sac. Rudimentary operculum is visible. Yolk-sac is smaller than in the last stage. Intestine is shorter than in early stages and has acquired a lumen in its middle region only; it does not open to the exterior. Otocyst is seen above the branchial arches. Lower jaw is poorly developed. The pigment granules are seen on the head and the body. The cartilage has not yet appeared.

22nd stage.—Twenty-one and one-half hours after hatching. Larva elongates. Lower jaw is properly developed. The operculum extends from the head region backwards and covers the branchial arches. Notochord is well developed. Eyes develop pigments. Mouth opens to the exterior.

23rd stage.—Thirty-one hours after hatching (Text-fig. 3*c*). Barbels are thin but much more elongated than in early stages. The chondrocranium has developed cartilage. In sections each branchial arch is seen to possess a cartilaginous rod and blood vessels. Heart is enclosed in the pericardium and possesses thick walls. Blood vessels are well developed. Above the yolk-sac is present the stomach. In sections the intestine is seen communicating with the outer world. The pigments are densely scattered on the body and the head. Pectoral fin has the appearance of a bud-like outgrowth. Notochord and nerve cord have bent down at the hind end. The larva now measures 5 mm. in length. Head becomes broad and flattened and resembles that of an adult to some extent. Mouth is wide and tail region very long.

24th stage.—A week's old fry. There is no trace of the yolk-sac and the fry is very active and can hunt for its own food. It closely resembles adult except in weight, size and poor development of sex organs. Head is very much depressed and snout is spatulate. Maxillary pair of barbels is longer than the mandibular pair. All the fins possess definite fin-rays. Caudal fin is deeply forked and its upper lobe is longer than the lower. Lateral line is quite prominent.

SUMMARY.

1. *Wallagonia attu* was observed to spawn in the Budha Nala, Ludhiana, in July, 1932, when it flooded the neighbouring low-lying areas and the temperature of the water was about 80°F. The fish migrate to shallow waters and usually one mature female was found to be chased by two ripe males and all the three showed great excitement and liveliness.

2. Eggs were stripped and artificially fertilized by pouring milt over them in a clean china dish. About 80% of the eggs developed showing thereby that in this fish eggs can be conveniently fertilized artificially.

3. A mature egg measures from 1·2 to 1·5 mm. across and is enclosed in an inner thin and transparent vitelline membrane and an outer thick zona radiata. Yolk-sac is almost circular in outline and deep yellow in colour while the germinal-disc is whitish and forms a small cap-like mass on the top of the former.

4. Fertilized egg, when immersed in water, absorbs it and grows to about double its original size. The imbibed water is probably used as cushion for the developing embryo and also for respiration before hatching.

5. Development is very rapid. In an hour after fertilization the egg possesses sixteen blastomeres. Endoderm appears in 5 hours old egg and mesoderm one hour later. Rudiment of the embryo makes its appearance at about 8 hours after fertilization.

6. Newly hatched larva possesses colourless eyes, rudimentary barbels, solid intestine, vacuolated notochord, embryonic fin-fold, kupffer's vesicle and simple heart.

The first few larvae hatched 14 hours after fertilization and the last batch 6 hours later, at temperature ranging from 80°F. to 86°F.

7. Anterior region of the nervous tube becomes enlarged and complicated to form brain in larva 8 hours old. The 17 hours old larva shows lumen in its intestine. In 21½ hours old larva eyes develop pigments and rudimentary operculum is formed. Chondrocranium develops cartilage, intestine opens to the exterior and buds representing pectoral fins make their appearance, when the larva is 31 hours old. In the same stage operculum covers the branchial arches and notochord and nerve cord bend down posteriorly.

8. In a week's old fry the characteristics of the adult are apparent.

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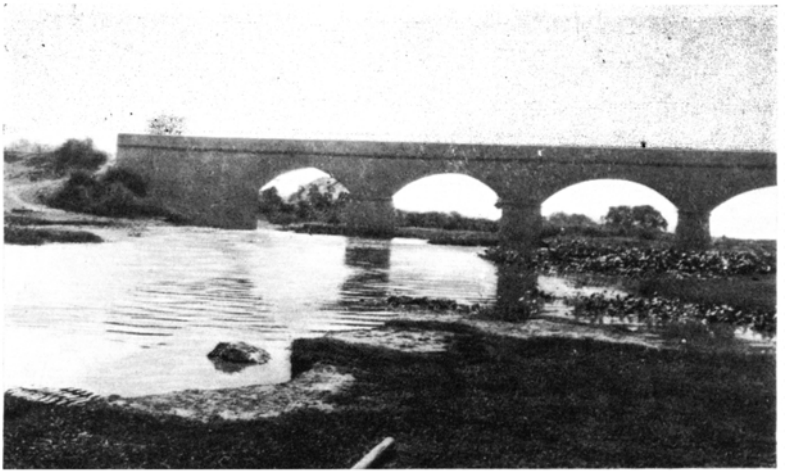
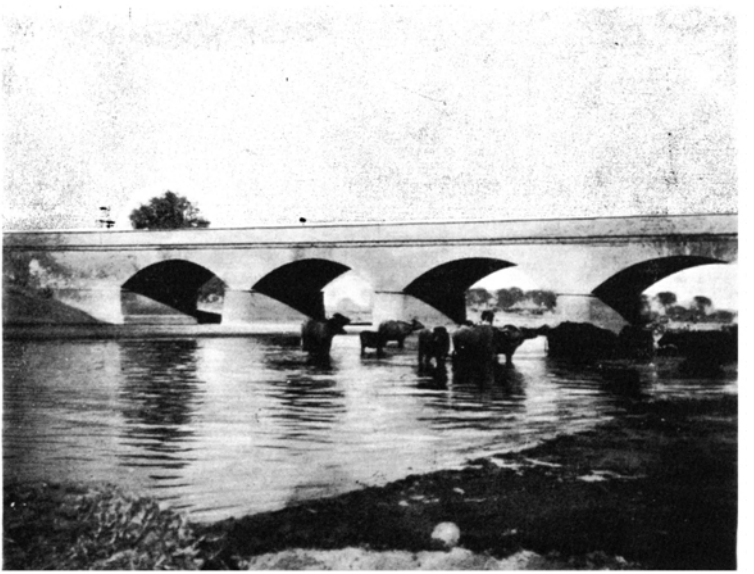


The Budha Nala at Ludhiana, Punjab, as it was in July, 1932. Its low, grassy banks, when flooded during the monsoon months, formed suitable spawning grounds of *Wallagonia attu* (Bloch and Schneider).



The Budha Nala as seen in November, 1943. The Nala has in recent years been converted into a regular irrigation canal.