Notes on the Habits and Development of *Lepidosiren paradoxa*. By G. S. Carter, M.A., Ph.D., F.L.S., and L. C. Beadle, B.A. (Communicated by Dr. G. P. Bidder.)

(With 1 Text-figure.)

[Read 3rd January, 1929.]

The habits of the American lung-fish, *Lepidosiren paradoxa*, have been described by several authors, and especially by Prof. Graham Kerr (Phil. Trans. R. S. London, B. cxcii, 299) and by Mr. R. J. Hunt (Proc. Zool. Soc. London, 1898, 41) *. The observations on which both these accounts were based were made in the Paraguayan Chaco, where the fish is common in the swamps which cover a large part of the country. During a recent visit to the same district, we were engaged in breeding the young of this fish, and several points in its natural history, which have not previously been recorded, came to our notice.

The burrow, which the fish makes when the swamps dry, has been accurately described by Mr. Hunt (*loc. cit.*). It passes vertically, or sometimes obliquely, downwards into the soil to a depth of two or three feet. The opening is covered with a biscuit- or bun-shaped cake of mud, and the burrow is blocked at intervals by partitions of mud, provided with openings by which air can diffuse into the burrow. In the examples which we saw there was only one of these, but, according to Mr. Hunt, there may be several at intervals down the burrow. The fish lies coiled in an oval expansion of the burrow at its bottom.

The soil below the soft mud at the bottom of the swamp is a pure clay which is very impervious to water. The burrow is made in the bed of the swamp as it dries, and, as the mud is only one, or at most two, feet thick, the burrow passes downwards into the clay. Probably the impervious nature of this clay is of great importance to the fish. The burrow is always damp (as Mr. Hunt remarks), and in the examples which we opened there was a considerable amount of water in it, enough almost to fill the expanded portion in which the fish lies. This water is probably essential to the life of the fish in keeping the skin damp. When a *Lepidosiren* is left in the air without a protective covering of water, the skin quickly dries and the fish lives only a few hours. It is unlikely that it would survive for long in the burrow, if it dried completely. It seemed to us a nice adjustment between the habits of the fish and its environment, that this layer of clay below the

* A bibliography of the subject is given in Prof. Graham Kerr's article on *Lepidosiren* in Keibel's 'Normentafeln zur Entwicklungsgeschichte der Wirbeltiere.'

swamp should be essential for its survival during the periods, sometimes of many months, when the whole country is dry. The cocoon of hardened mucus, with which *Protopterus* surrounds itself in its burrow, is presumably an adaptation to the same end. In the burrow of *Lepidosiren* there is no such cocoon, the clay apparently providing sufficient protection. Whether a similar layer of clay occurs in other localities where *Lepidosiren* is found is not known. The habits of the fish in the valley of the Amazon are described by Goeldi (Trans. Zool. Soc. London, xiv, 1898, 413), but he did not investigate the structure of the burrow.

Except in the expanded part at its bottom, the burrow exactly fits the body of the fish, and it must be made by its forcing its way through the clay by muscular contraction. The clay can be kneaded by the hand, but it is stiff, and the resistance, which the fish meets in forcing its way through it, must be great. It is therefore a striking witness to the great muscular power of the fish that it is able to drive a burrow vertically downwards into this clay to a depth of 3 feet.

The Indians often dig up the fish from its burrow during the dry weather and use it for food. In doing so it is not necessary to dig to the bottom of the burrow. As the part in which the fish lies is approached, it can be heard moving at the bottom of the burrow and often making a peculiar grunt. Their method is then to push a stick into the remaining part of the burrow, until it comes into contact with the mouth of the fish. The stick is caught by the fish in its mouth and seized by the strong palatal teeth. It refuses to let the stick go and is drawn out of the burrow.

This habit would perhaps be hardly worth recording, if it were not that another air-breathing fish of these swamps, *Symbranchus marmoratus*, which is entirely unrelated to *Lepidosiren*, has developed precisely the same habit, and is caught by the Indians in the same way. The parallel adaptation of these two fishes in overcoming the dangers of the dry season is itself remarkable. Their burrows are in similar positions and can be distinguished by the Indians only with difficulty. That they should both have this habit of biting a stick pushed into their holes is even more remarkable.

The lung-fishes leave their burrows as soon as the ground above them is again flooded. The dry season is usually the winter, and the swamps are filled again by the first heavy rain of the summer. *Lepidosiren* breeds early in the summer after rain, and therefore as a rule shortly after leaving the burrow. But in many years the swamps do not dry and the *Lepidosiren* do not hibernate in the burrow. It therefore seems unlikely that a period of hibernation is essential before breeding can take place. The year in which we were in the Chaco (1926–7) was a dry one, and in September 1926 almost all the swamps in which the lung-fishes are found were dry. The swamps were again flooded at the beginning of October, and the first

Lepidosiren, taken in the swamp, were brought to us on October 18th. We first saw the nests on November 20th, after heavy rain on the 5th–7th. The eggs in these nests had only just begun to segment, and the nests had, therefore, only recently been completed.

The breeding-nest, which is entirely distinct from the dry-weather burrow, has been described by Prof. Graham Kerr, and we have little to add to his description. The eggs are laid at the end of an almost horizontal burrow in the mud at the bottom of the swamp. The nest is made of dead leaves and grass collected by the parent and taken into the burrow. Among these leaves the eggs are laid. The male, which guards the nest, is found coiled round the mass of leaves and eggs in an expansion at the end of the burrow, where the nest is made.

At the time at which we were observing the development of the lung-fish, we were also making observations on the physical characteristics of the environment of the swamps, among others observations on the amount of dissolved oxygen in the water. We found that there was hardly ever a measurable amount of oxygen in the water just above the mud at the bottom of the swamp during the summer months, when the climate is tropical. The nests of *Lepidosiren* are made at this time, and the water in them would therefore contain practically no oxygen, unless a supply is somehow secured by the parent fish. While the larvæ are within the egg-capsule and for some time after they hatch, their respiration is aquatic, and the method by which their need for oxygen is satisfied therefore needs explanation. It has been suggested by Mr. J. T. Cunningham ('Animal Life: Reptiles, Amphibians, and Fishes,' Methuen, 1911) that the long vascular filaments on the pelvic fins of the male during the breeding-season serve the purpose of keeping up the oxygen-content of the water of the nest, the parent aerating his blood by breathing at the surface. This, if true, would be a curious reversal of the normal function of the blood of bringing oxygen from the environment for the use of the body. In this case oxygen would be excreted by the blood *into* the surrounding water. We have no observations of our own on the source of oxygen in the nest, and the point needs further work.

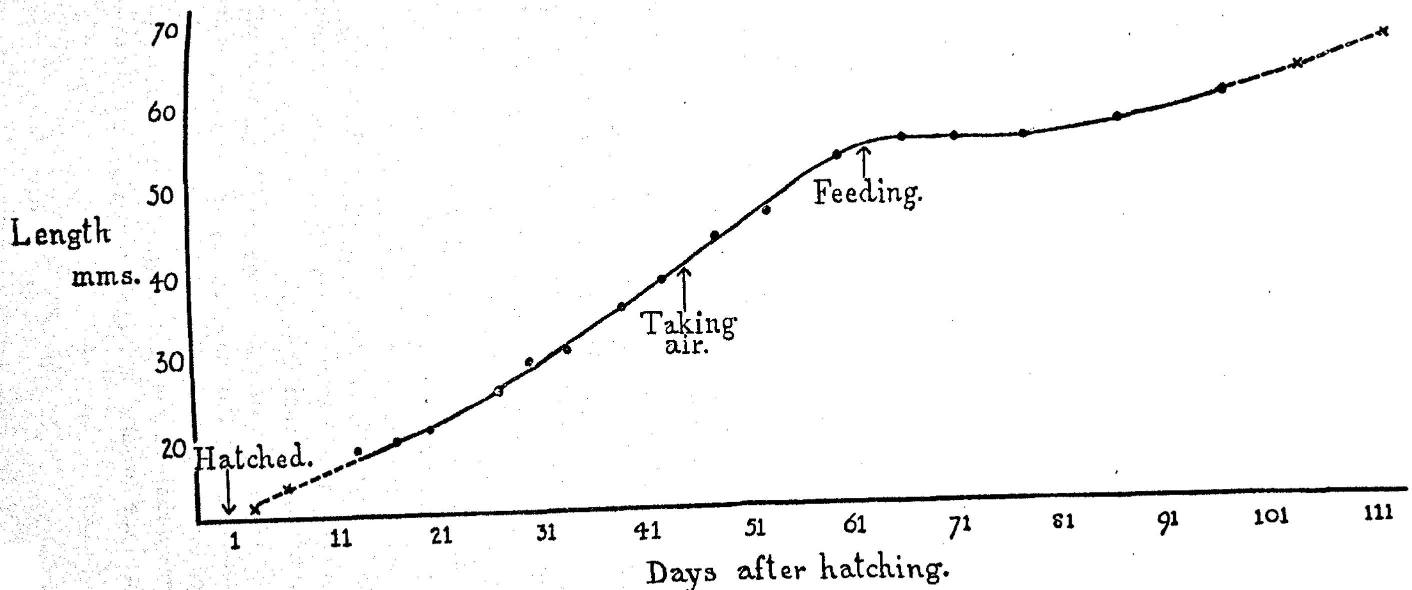
It can, however, be said that the respiratory needs of the eggs and young larvæ are low. We kept the eggs and larvæ of several fishes in our hut in the Chaco, while we were preserving material of the young. We found that the nests could be divided into two categories. The eggs of those which were normally made on the surface of the water, or in other places where the water contained a considerable amount of oxygen, were extremely difficult to keep alive in cultures. On the other hand, the eggs of species whose nest is in the mud, such as *Lepidosiren paradoxa* and *Symbranchus marmoratus*, lived well. That the insufficiency of oxygen in the water of the vessels in which the eggs were placed was the true cause of the death of those of the first category, was shown by the fact that larvæ hatching from these eggs lived well, if they were able to get their oxygen from the surface, either from the air or from the surface-layer of the water. The larvæ of *Hoplosternum* (*Callichthys*) *litorale* and *Ancistrus anisitsi* both do this as soon as they hatch from the egg, and the ease with which they could be kept at these stages compared with those before the egg hatches was very striking.

These observations indicate that the eggs of *Lepidosiren* and *Symbranchus* are able to live in water in which the oxygen-content is comparatively low. Unfortunately, no direct estimations were made of the amount of oxygen in the water of the vessels in which the cultures were kept.

For the eggs of *Lepidosiren* and *Symbranchus* another difference between the conditions in the cultures and in their natural habitat was much more dangerous. The temperature of the mud at the bottom of the swamp is much lower at midday than that of the surface water or of the air. In growing these eggs, precautions had therefore to be taken to keep the vessels cool. This was done by making use of unglazed pottery bowls of Indian manufacture. In them evaporation kept the temperature of the water below 80° F., even when that of the air was as much as 110° F. The temperature so produced was about the same as that of the mud at the bottom of the swamp, and therefore of the nests. In these bowls the eggs were placed on muslin trays in a single layer, and they developed well, whereas in open dishes they died in one or two days. After hatching, the larvæ lose their sensitivity to temperature changes, and it was found unnecessary to use the pottery bowls. By these means we were able to watch the whole course of development in a single batch of eggs up to the time when the larvæ began to feed and were 2 inches long.

It has been previously noted (Graham Kerr, *loc. cit.*) that the egg is sometimes surrounded by a layer of jelly on the outside of the horny capsule, which is always present. This he has compared to the jelly-layer which surrounds the egg of the Amphibian. We found that this layer of jelly was always present in nests in which the eggs were at an early stage of segmentation, but that it disintegrated at the stage at which the descending lip of the blastopore had covered all but one-quarter of the surface of the egg. If this jelly is not needed at the later stages of the development of the egg within its capsule, it is difficult to see what function it can serve at these early stages. Our observations therefore support Prof. Graham Kerr's suggestion that it is a useless and vestigial character.

After the eggs hatch from the capsule, the two most noticeable crises in their development are the change in respiration at the time when the external gills degenerate (about 45 days after hatching at the temperature of our cultures), and the change from the absorption of yolk to the taking



Growth-curve of larva of *Lepidosiren paradoxa.*

of food by the mouth (about 60 days after hatching). Records of growth in length of the developing larvæ were kept, and a curve derived from these records is shown in the text-figure. The solid line of the curve refers to eggs from a single nest, and has been extended in each direction from records of other batches of eggs. In all, twelve batches were measured. The growth in the abnormal conditions of the cultures was probably slower than in the natural habitat, but there seems no reason to suppose that the effects of the conditions were more marked at one time than another. Without sacrificing a large number of larvæ, it did not seem possible to arrive at a better estimate of the growth than the increase in length. While the larvæ still contain yolk, the increase in mass is clearly no guide to the activity of growth.

Accepting, therefore, the results given in the curve as being very rough, it may still be deduced from the curve that the effects of the two physiological changes, mentioned above, on the growth of the larvæ are very different. The change in respiration had no appreciable effect on the rate of growth, whereas that in the method of feeding led, temporarily, to a very marked slowing in the rate. This presumably means that the blood was efficiently aerated by the gills or lungs throughout the period of the absorption of the gills, and the tissues were therefore unaffected by the change in respiration; but it shows clearly that not all important physiological changes in the development of an animal are reflected in changes of the growth-rate—an assumption which is sometimes made.

The larvæ were found to feed well on earthworms and on the liver of the large swamp-snail, *Ampullaria* (Graham Kerr, *loc. cit.*), but in the later stages they seemed to prefer the aquatic stems of the floating weed of the swamp (*Pistia*), eating not only algal growths around the stems, but also the stem itself. Probably this is the chief diet of the fish in its natural habitat. We could only find some small earthworm (*Aulophorus borelii*) in the mud of the part of the swamp where the *Lepidosiren* live, and these worms not commonly. The young fish of 2 or 3 inches in length would be unable to attack a live snail, although they would probably feed upon any dead one which they found by chance. There seemed little small animal life in this part of the swamp for them to feed upon except, perhaps, insects and their larvæ. It is interesting to note that Longman, in a recent article upon the habits of young *Ceratodus* (Mem. Queensland Mus. ix, 1928), records a precisely similar diet.

Until shortly before the time at which they begin to breathe, the young larvæ are colourless, with the exception of the yolk-sac, which is a creamy yellow, and of the bright red gills. At this time the black pigment-cells which are characteristic of the adult begin to appear in the skin, spreading from the tail and the dorsal side. The contraction of these cells at night has been previously described (Graham Kerr, *loc. cit.*), but we have a few experiments upon them to record. We enclosed larvæ of about 2 inches in length for several days in a dark box and observed the behaviour of the pigment-cells. The box was very tightly closed, and there was little chance of sufficient light finding its way into it to affect the behaviour of the cells. We found that the pigment-cells were not, as might have been expected, continuously retracted in the dark. The larvæ varied considerably in their reactions to these conditions, but in some the normal rhythm of expansion at dawn and contraction at dusk was preserved for three days, the cells expanding and contracting at approximately the right time on each day. After this the rhythm became confused, and in other larvæ it was not preserved for so long a time. It seemed, however, that, in some larvæ at least, the rhythm had become impressed upon the animal and continued in the absence of the stimulus. That the stimulus was still effective was shown by the fact that larvæ, taken out of the box when the cells were contracted and placed in the light, immediately began to darken.