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SOME NOTES ON XENOPUS LAEVIS (Daudin).

(AMPHIBIA, PIPIDAE)

By

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Introduction

The Clawed-frog, Xenopus, is commonly found in the streams and other waters around Nairobi. The animal has a distinctive appearance because of its dorso-ventrally flattened body and small eyes; the skin is always very slimy, more so than that of Ranid frogs. Xenopus is an almost fully aquatic animal and the writer has never yet seen one on dry land.

The Adult Frog

Description. Around Nairobi the usual length of a mature specimen is about 6 cm. (nose to cloaca), the females being larger and heavier than the males. The colour is greyish-brown dorsally, appearing sometimes to be almost black; the belly is silver grey but some specimens have this colour as a ground, mottled with mustard yellow. Two individuals coloured this shade of yellow all over are in the writer's possession.

The flattened head bears the eyes on its dorsal surface, each eye being covered by fixed lids with only a very small round aperture. Vision is apparently limited to an area vertically above. Below the eye on each side is a small projection derived from the tentacle of the tadpole. The nostrils are prominent at the front of the upper jaw.

The four digits of the fore-limbs are free but the five digits of the hind-limbs are fully webbed, and digits I, II and III have each a shiny black claw which gives the animal its common name. A metatarsal tubercle is present, and in other species of the genus this carries a small spur.

The skin is smooth and slimy to touch because of the many mucous glands; this feature makes the frog extremely difficult to hold and is doubtless of great survival value. A conspicuous line of white dots is visible on each side from eye to vent along a dorso-lateral line; each dot is a gland or organ, and much discussion has centred around their function. Vertical sections of the skin shew that these structures are epidermal only, and connections from them to the lateralis branch of the vagus indicate that they are lateral line organs, but the lumen of the organ is filled with corneified cell debris and for this reason some authorities doubt whether the organs are functional. (1)

Sexual dimorphism is limited but the cloaca (vent) of the female is closed by three cutaneous flaps and that of the male by two, (Fig. 2). In the mating season, the male develops a black nuptial fringe

along the inner side of the fingers which enables him to obtain a better grip on the female.

Systematic Position and Distribution.

The genus Xenopus is a member of the sub-order Pipidae, order Aglossa, sub-class Anura, class Amphibia.

Xenopus is confined to Africa, and East Africa boasts two species, X. laevis (Daudin) and X. muelleri (Peters). The former is found from the Cape right through to Ethiopia and the latter from Zanzibar to Benguela. In West Africa only, is found X. calcaratus. Some authorities have split off X. laevis victorianus (Ahl.) and X. laevis bunyoniensis (Lov.) and would raise them to the rank of species. (2).

Other genera of the sub-order are Pipa, Protopipa, and Hemipipa, all from the New World, and Hymenochirus and Pseudohymenochirus both found in Africa (3,4).

General Anatomy.

As the name of its order indicates, Xenopus has no tongue; nevertheless, the hyoid is present and easily seen in the floor of the buccal cavity. Like other members of the Aglossa, the Eustachian tubes unite and have a common opening into the pharynx; it lies medially in the rear palate. Teeth are present in the upper jaw only.

The lungs contain little free lumen because of internal projections called trabeculae. Here is a difference from Ranid frogs whose lungs are simply air-sacs with a vascular lining; the lungs of Xenopus are considered to be much advanced functionally over those of the Ranidae. It is interesting to note that Xenopus spends long periods floating vertically in the water with just its nostrils exposed. In correlation with this developed lung is to be noted the so-called diaphragm, a web of muscle stretching from the ilia to the base of the lungs. As in all Amphibia, the skin is highly vascular. (5-7).

The skeletal structure of Xenopus and other Aglossa differs from that of Ranid frogs in a number of features concerning the vertebrae, the sternum and the lower jaw. The vertebrae are opisthocoelus (concave at the rear face) and the 2nd. 3rd. and 4th. carry long ribs which in old individuals are found to be fused with the diapophyses. The sacral diapophyses are broad and the urostyle is fused with the sacrum and not articulated with it as in the Phaneroglossa. The sternum is slender, and there is no presternum. A small prepubic cartilage is present. The lower jaw is noteworthy in so far as no Mento-Meckelian cartilage is present.

Habits.

Xenopus is fully aquatic, and as mentioned in the introduction, the writer has never yet found one out of water, not even in reeds or other vegetation bordering a stream or pond. A record does exist however, of a large number of X. laevis borealis migrating along a front ten yards wide between two ponds fifty yards apart. This occurred in 1934 on a farm near Eldoret, in conditions of heavy dew and soaking

wet grass. (8).

The adults appear to be exclusively carnivorous and in the wild state are very probably scavengers although they are not averse to taking small worms, Dipteran larvae, and tadpoles - including those of their own species.

Ingestion is brought about by the front legs which serve as hands to push food into the mouth. The motion of the hands begins soon after food is located in the vicinity, and the animals begin to swim in random erratic movements until, so it appears, they arrive directly in front of the food; this is then caught by the constantly moving hands and pushed into the mouth. It seems that the hand movements are a reflex response to the presence of food indicated by chemo-reception; the idea is supported by the fact that a few drops of water soluble meat extract elicits the same response. Such behaviour would be of great value in the conditions of poor visibility common in the muddy water where Xenopus is usually found. In the event of a piece of food being found which is too big to swallow, some portion of it is pushed in the mouth and then shredded from the rest by rapid kicks with both front and rear feet, armed as the latter are with claws.

In captivity, Xenopus feeds well and thrives on a diet of chopped raw liver; beef is also taken well, both lean meat and fat; on one occasion when python meat was available, it was taken readily.

Parasites. On two occasions, once in the Coryndon Museum, March 1961, individuals have been seen swollen like balloons; investigation has shown that this is because of excessive quantities of liquid in the lymph sacs. It is thought to be because of a helminth infection, (2, 8).

Respiration. Observations on the animal in the field and in captivity, make it apparent that Xenopus inhales a great deal of atmospheric air. Even in well aerated aquarium water, the animal rises to the surface at regular intervals; these intervals vary with the size of the frog, the water temperature and other factors, but are usually about seven minutes. While lying submerged bubbles are emitted periodically from the lips. Sometimes, Xenopus may adopt a nearly vertical posture in the water, floating with its nostrils just exposed on the surface; during such periods, the nostrils can be seen to be opening and closing rhythmically. In correlation with this behaviour it should be noted that the lung is of an advanced form when compared with other Amphibia.

Despite these facts, the skin is highly vascular and there is little doubt that gaseous exchange occurs through the cutaneous capillaries. Whether buccal respiration occurs as in other frogs, the writer has not been able to determine.(10-12).

Breeding. This occurs in the field with the onset of the rains; in the Nairobi area therefore, breeding occurs twice a year. The mating call of the males is a short, repeated tock-tock-tock-tock- sound, rather like the noise of a stick being run along a fence; this noise is made under water, but is clearly audible if the frogs are in an aquarium. The mating attitude (amplexus) is different from that seen in other frogs, the male Xenopus seizes the female around her thighs and not under the fore-arms.

The eggs are laid singly attached to leaves of water plants, but no local records exist of eggs of Xenopus ever being found and positively identified as such. Nevertheless, the tadpoles of Xenopus are plentiful in the Nairobi area and are easily recognized. (13-16).

It is difficult to measure or to estimate the life span of Xenopus; Nigrelli gives a figure of fifteen years, but it is doubtful whether any individual attains this age in nature. (17).

The Larva.

Description. The young tadpole, up to about 15 mm. in length, is virtually transparent except for two black pigmented areas around the eyes; these give away its presence in the water to an observer in the air above, but it is probable that the tadpole is invisible to other water living animals. The shape is characteristic; the head is flattened dorso-ventrally and the gape is very wide; a long tentacle projects from the corner of the mouth on each side. The tentacles approximate to half the body length, but their function is uncertain; they may act as balancers to assist them to maintain their head-down attitude in the water. The eyes have a key-hole shaped pupil. The abdominal region is pear-shaped in section, and a conspicuous hump is visible; ventrally, the pericardium is visible by its silver colour. Two long slit-like spiracles allow water to be voided from the branchial chamber; they lie to the left and right of the midline on the ventral surface of the abdomen. A little Indian ink or carmine placed in front of the animal's mouth demonstrates that both spiracles function. The tail is long, and in life the last part of it is held up at an angle reminiscent of the heterocercal tail of sharks.

The period of time spent as a tadpole varies, as it is affected by the food supply, water temperature and amount of oxygen present in the water. In the Nairobi area, it is usual however for metamorphosis to begin at about six weeks and be completed by the twelfth. A larva begins to feed in the adult manner once the fore-legs have developed.

Interest in the tadpole, for one person at least, is centered in its breathing and feeding, and these activities are based upon the form of structures associated with the pharynx.

The Pharynx. In any tadpole over 1 cm in length there are six clearly visible visceral arches, (Fig. 3) counting the mandibular arch as the first; this is followed by the hyoidean arch, but the hyomandibular cleft does not break through. The third visceral arch is the first branchial, and is posterior to the first branchial cleft which lies in the pharyngeal floor. The outer corner of this cleft is level with the eye on each side, and the cleft descends almost vertically to open by a narrow slit into the branchial chamber. The three succeeding branchial clefts are all much larger than the first, and each intervening branchial arch supports a large curtain-like gill septum. These septa have an interesting structure; each is roughly semi-circular and is bounded by an afferent branchial artery connected to an efferent branchial artery by a series of vertical commissures. There are a number of lateral vessels too which provide inter-connections between the commissures. The vertical commissures open out into a complex series of sacs which give rise to a visable series of vertical bands on the septa (Fig. 4). These sacs are absent on the anterior face of

the first branchial cleft, and on its posterior face they are simple and unbranched. The sacs reach their maximum development on the sept supported by branchial arches 2, 3, and 4; on the posterior face of the last cleft the sacs are less complex, (Figs. 5 and 6).

Gaseous exchange will occur as water drawn in through the mouth passes downwards through the clefts into the branchial chamber; this water is separated by only an epithelium from the blood rising upwards through the commissures and their sacs, hence conditions are ideal for the diffusion of oxygen into the blood from the water and for the diffusion of carbon dioxide in the reverse direction.

The ventral openings of the branchial clefts into the branchial chamber are not uniform. Branchial clefts I, open by means of a pair of lateral slits level with the posterior edges of the eyes; branchial clefts II, open some distance behind, via lateral slits on each side just anterior to the heart; clefts III & IV, open on each side into a shallow vestibule at the side of the heart, (Fig. 7).

Nutrition. An examination of the gill septa of a fresh specimen, reveals that each septum is covered with a thick layer of mucus in which are embedded vast numbers of algae and other freshwater plankton; the same material is found in the stomach and indicates that the tadpole is a filter feeder. Plankton and other suspended matter is trapped on the surface of each septum as the water flows over it. A current of mucus doubtless conveys the material from each septum to the oesophagus, but it has not yet been possible for the writer to map these currents; it is hoped that they will form the subject of a second paper.

The filtering is carried out while the tadpole lies still in the water, head downwards at an angle of about 60° from the horizontal. This attitude is maintained for long periods of time and the only visible movement is a rapid serial contraction of the tail; the movement of the waves is clearly seen near the tip of the tail where it becomes a rapid flicker. During this activity, the tip of the tail is held almost vertically, and presumably, enough lift is obtained from the tail just to counteract the tadpole's weight, for it neither rises nor sinks. However, when the movement of the tail stops, the tail gradually falls below the level of the head, and the whole animal sinks. From time to time, a tadpole will swim to a new area of water.

The mechanism of the tail action is rather puzzling for if the waves along the tadpole's tail were of the normal form, the machanical effect would be to drive the animal forward along its own longitudinal axis, yet the waves do not start terminally, nor can one imagine them doing so.

So far as the writer has seen, Xenopus has little appeal to the layman but it is a common creature and repays study. The frog is being used for research into cancer at Oxford and for cytogenetic studies at Geneva, but its claim to fame lies in the use of the female for the determination of pregnancy in women; a positive result can be obtained in twenty four hours. In this connection, it is interesting to note that South Africa is the world's supplier of specimens and exports them all over the globe: even Kenya, where Xenopus abounds, imports them from South Africa for this purpose.

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Further Recommended Literature

A useful general introduction to the study of the genus Xenopus is contained in "Amphibia and Reptiles", Cambridge Natural History Series, MacMillan & Co., reprinted 1923. There is an article too in African Wild Life, 9.

A most useful source of information is Nieuwkoop and Faber, "Normal Table of Xenopus laevis". Amsterdam.

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Xenopus laevis tadpoles
x 0.50

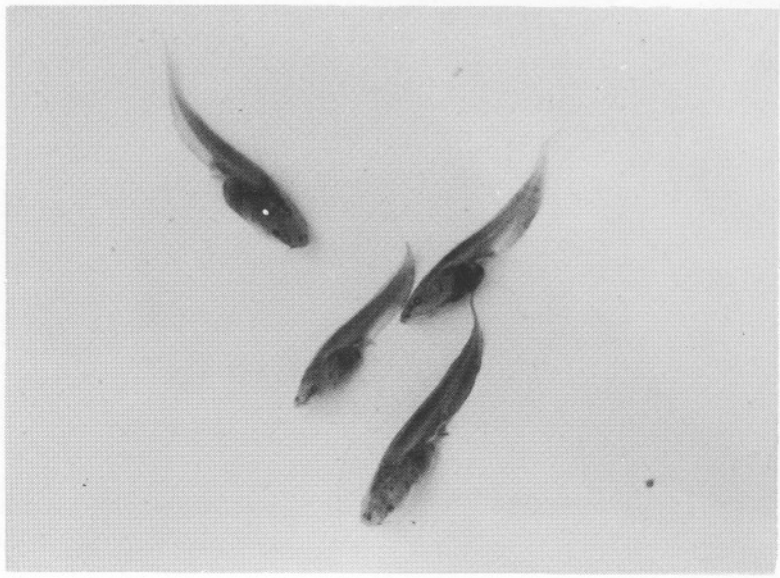
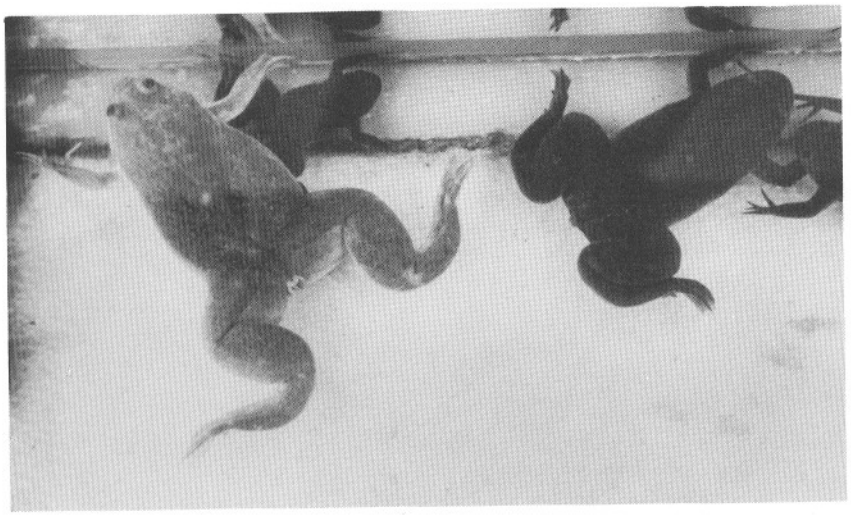


Fig. 1 Tadpoles in feeding attitude x 0.75



Right: Xenopus laevis borealis ♀
Left: Xenopus laevis laevis ♀; on this specimen the line of epidermal glands is clearly visible. x 0.50

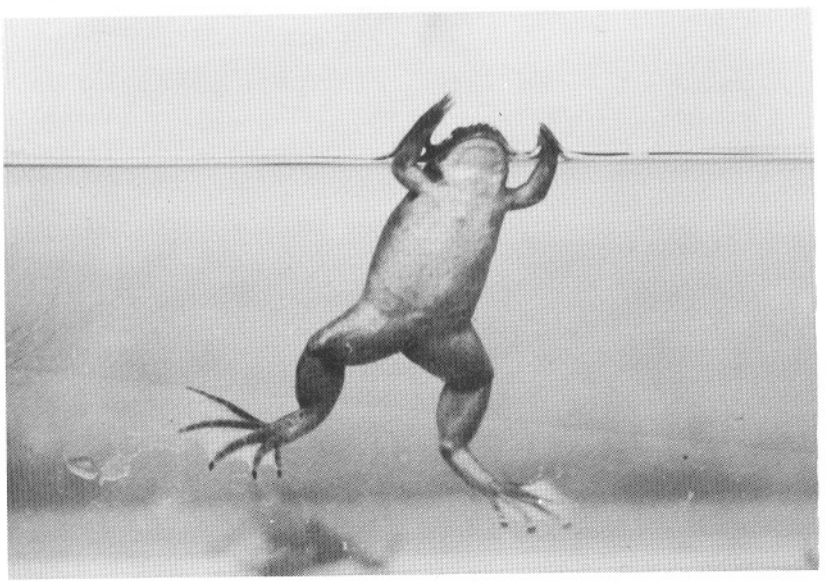


Fig. 2 Xenopus surfacing to breathe atmospheric air x 0.50

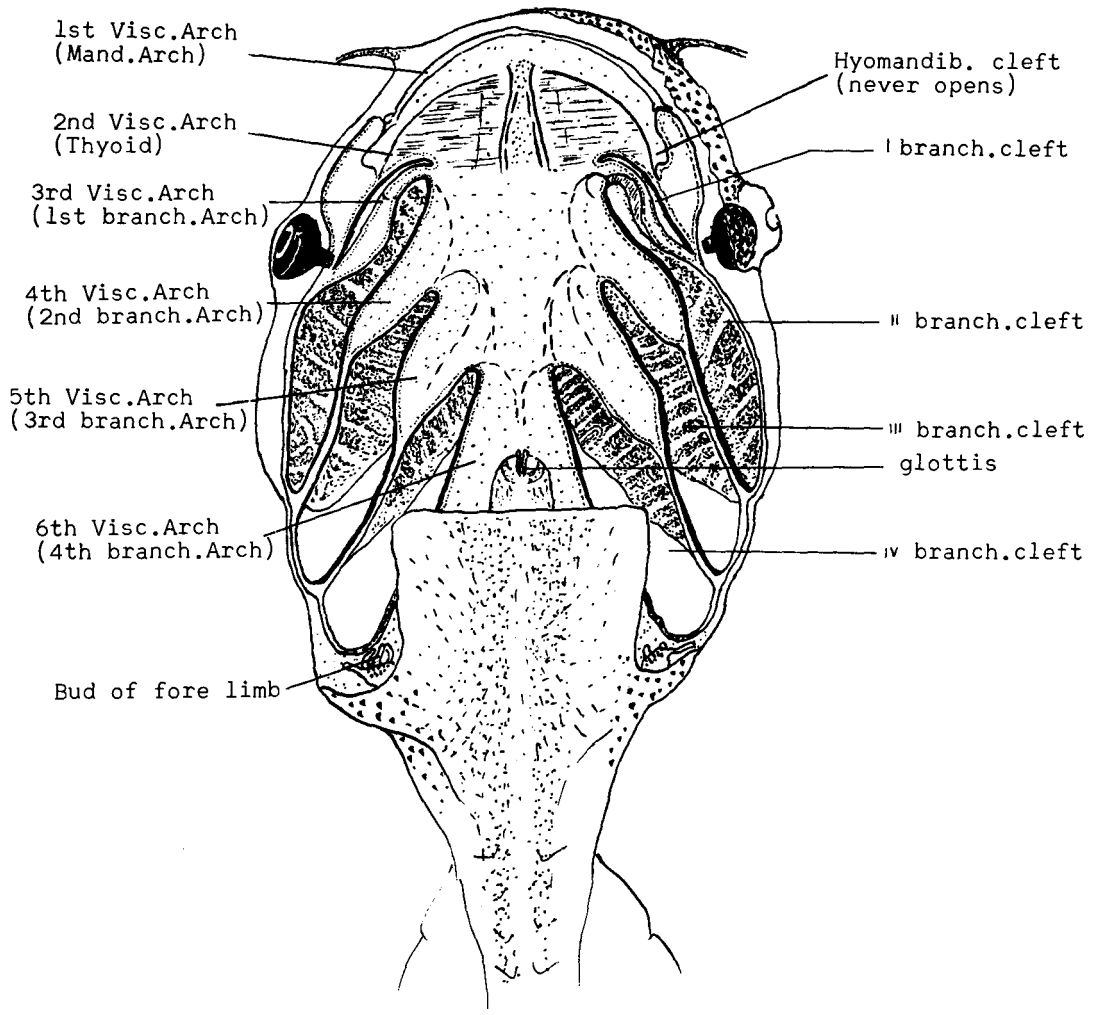


Fig. 3. Xenopus laevis, 7 cm tadpole
pharyngeal floor x 4

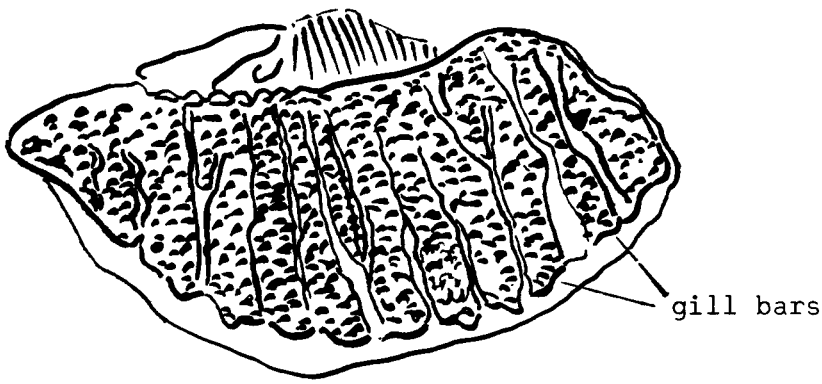


Fig. 4 Xenopus laevis, 7 cm tadpole
The posterior face of the 1st branchial arch septum, right side, shewing the appearance of the bars x 15

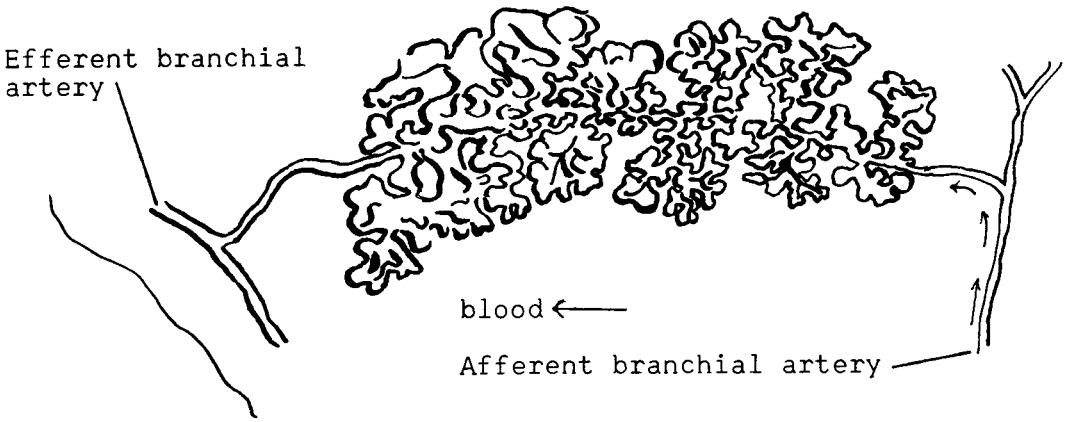


Fig. 5 Xenopus laevis, 7 cm tadpole
A single vertical commissure shewing the development of sacs on the posterior face of the first branchial septum x 70

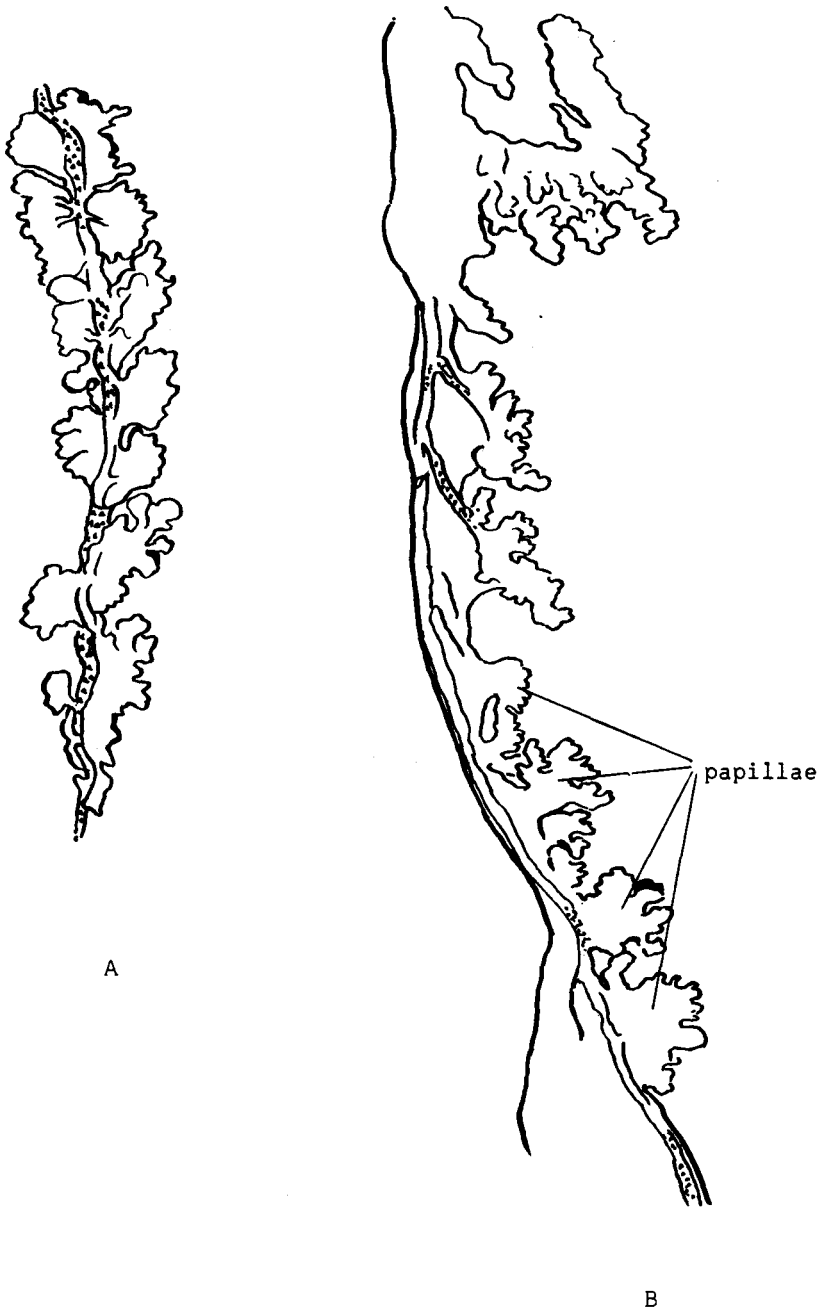


Fig. 6 Xenopus laevis, 7 cm tadpole

A: Horizontal section through fourth branchial septum x 23

B: Horizontal section through hemibranch of last branchial cleft x 23

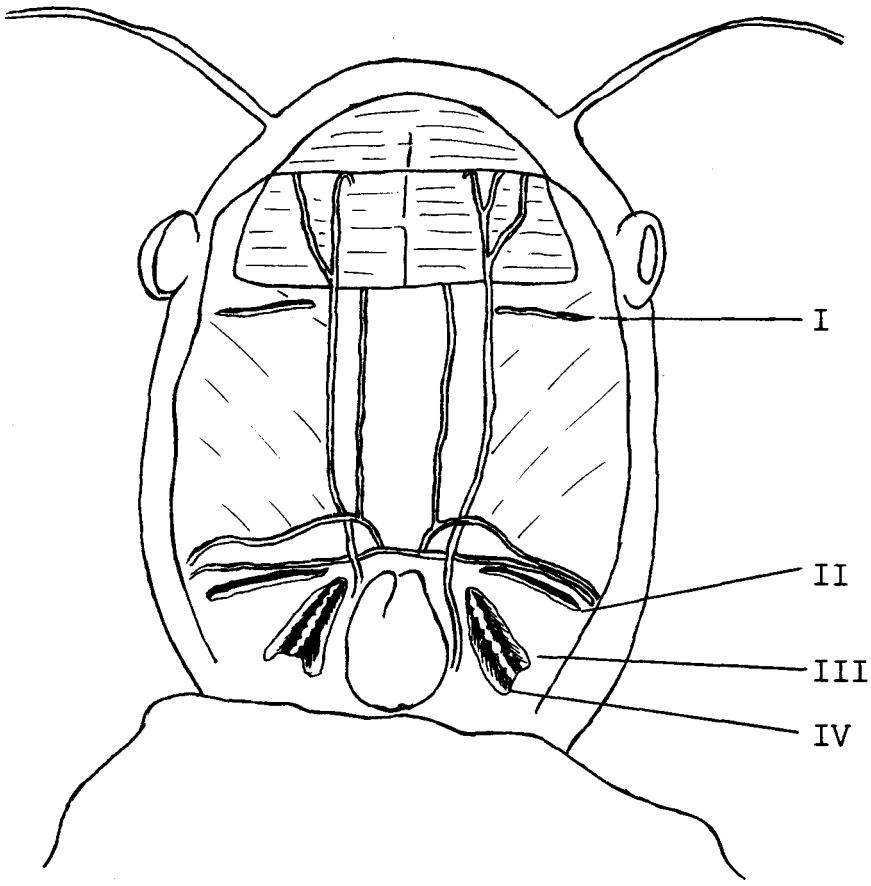


Fig. 7 Xenopus laevis, 7 cm tadpole
Ventral surface of head after removal of operculum, shewing openings into the branchial chamber x 2 1/2