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MORPHOANATOMICAL SPECIALIZATION  
OF  
THE BUCCOPHARYNGEAL REGION OF THE  
ANURAN LARVAE  
AND ITS BEARING ON THE MODE  
OF LARVAL FEEDING

BY

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*A Thesis Submitted to the University of the Punjab  
in Fulfilment of the Requirements  
for the  
Degree of Doctor of Philosophy  
in Zoology*

Department of Zoology  
University of the Punjab, Lahore

1991

Tadpoles of five species of anuran amphibians, namely *Bufo stomaticus*, *Microhyla ornata*, *Rana cyanophlyctis*, *R. sylvadrensis* and *R. tigerina*, live sympatrically in the waters of Punjab plains. They are a common feature of the pond life and are an important part of the food chain in pond ecosystem. They utilize common pond resources, with no indication of competition among them.

Each species of tadpole differs from its sympatries in its external morphology as well as oropharyngeal anatomy which reflects its habitat adaptability and food preferences. *Bufo* and *Rana* tadpoles are macrophagous and lentic-benthic in habits. They have keratinized mouth parts, each species differs in the details of its beak and dental morphology which is related to its food type. *Bufo stomaticus* and *Rana sylvadrensis* tadpoles graze on the periphytons and other concretions from submerged surfaces. *R. cyanophlyctis* is detritivorous and *R. tigerina* is cannibalistic, larvivorous, preying on tadpoles living sympatrically with it.

*Microhyla ornata* tadpole is unique in having a transparent body. It is microphagous, without hard mouth parts and is nektonic-lentic in habits, swimming at midstream, never resting at the bottom of water. It feeds on plankton suspended in the water column.

The oropharyngeal morphology of each species of tadpoles is typical of its family. Although the oropharyngeal morphology of the three species of *Rana* is typically ranaid, still it shows intraspecific differences in details, reflecting food preferences of each species.

Indo-Gangetic plains took a long time to become ecologically suitable for invasion by different anuran species, during Oligocene-Miocene. Conditions in the upper Indus valley became suitable much earlier, since it received high annual rainfall as compared to the lower Indus valley Punjab and Sindh. Predominantly xeric conditions of the lower Indus valley have recently been made appropriate for wide distribution of anurans due to extensive canalization and urbanization. Human activity has contributed immensely in creation suitable habitat for wider distribution of anurans throughout the lower Indus valley.

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## ACKNOWLEDGEMENT

The work described in this Thesis was undertaken at Zoology Department, University of the Punjab, Lahore, under the supervision of Dr. Shahzad A. Mufti, Ph. D. The author expresses his sincere thanks to Dr. Mufti for his kindness and invaluable guidance throughout the course of this work.

To Dr. Riffat Hussain Jaffery, the Head of the Zoology Department, the author expresses gratitude for his general interest.

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## INTRODUCTION

Temperate riparian waters of Punjab, Pakistan, are inhabited by five sympatric species of anuran tadpoles belonging to three families: Bufonidae, Microhylidae and Ranidae (Khan, 1982; Khan and Tasnim, 1987). Adults of these tadpoles are terrestrial and carnivorous, feeding entirely on living prey. They lay eggs in water, far removed from their usual natural habitat, in order to provide basic requirements to their tadpoles, which are entirely aquatic and feed on vegetative matter. The larval period of frog's life is least understood, despite the fact that it is most crucial period during which selection forces are strong and highly effective. The delicate and defenseless tadpole is at the mercy of changes in environments, which take place from time to time within the confines of a pond. However, despite fragile in structure, tadpoles tolerate all environmental fluctuations due to plasticity in their adaptations (Inger and Collwell, 1997; Wassersug, 1971, 1974, 1984, 1989; Wassersug, et.al., 1981; Wassersug and Heyer, 1983; Dodd and Cupp, 1976; Heyer, et., al., 1975; Nevo and Beiles, 1991).

Early Paleozoic vertebrates were filter feeders, both during adult and larval stages (Jollie, 1982; Nothcutt and Gans, 1983; Mallat, 1985). They fed on water-suspended, microscopic food. Many of the present day vertebrates have evolved this mode of feeding both during adult and larval stages (Mallat, 1981, 1984, a, b). Different groups employ specialized techniques for particulate food acquisition from water current by processing it through its oropharyngeal passage (Rubenstein and Kohl, 1977; Sanderson and Wassersug, 1989; Viertel, 1984 a, b, 1985, 1987, 1989). Amphibian larvae of Type IV (Orton, 1953) have specialized keratinized rows of teeth and sharp, ciliated, strong beaks to scrape and glean nutritive material from submerged surfaces, while Type II larvae (Orton, 1953) lack keratinized mouth parts. The gleaned particulate food is blown into a suspension and sucked in the oropharyngeal cavity, constantly gulping-in the particulate food which is carried in the current (Seale and Wassersug, 1979). This "sucking-in" process involves complex mechanism which Wassersug (1975) and Wassersug and Hoff (1986) called a "buccal pump". The anterior displacement of Meckel's cartilage and its suspensorium allows a forward expansion of the ceratohyal. The articulation of ceratohyal with the platyoquadrate, causes up and downward movements of the floor of the buccal cavity, which serves as a piston of the buccal pump. One way flow of water is ensured by velar valves present in the posterior part of the buccal cavity. The water current carrying particulate

food is processed with the help of an elaborate system of papillae, glandular surfaces and straining plates as it passes through the buccopharyngeal passage. Strained and ultimately trapped particulate matter is pushed into the esophagus of the tadpole through specialized ciliated grooves (Kenney, 1969 a,b; Gradwell, 1970, 1971, 1975; Wassersug, 1972, 1976, 1980; Wassersug and Heyer, 1988; Seale and Beckwar, 1980; Sanderson and Wassersug, 1989; Wassersug and Rosenberg, 1979; Viertel, 1983; Wassersug and Murphy, 1987; Khan and Malik, 1987 a).

Oropharyngeal morphology of sympatric anuran tadpoles shows distinct adaptive radiations. The arrangement and the disposition of various oropharyngeal structures reflect ecological adaptations of the tadpoles (Wassersug, 1980; Inger, 1985; Altig and Johnston, 1989). Tadpoles adapted to the benthic habitat of the shallow pools have small bodies, weaker tails, suctorial oral discs and 2 (2) /3 dental formula. Their beaks are sharp and finely ciliated. They also have wide buccal cavity, having few buccal roof arena (BRA) and buccal floor arena (BFA) papillae. The branchial baskets are shallow and bowl-shaped, while the subvelar secretory surface has ridged as well as pitted pattern. These tadpoles mostly live on scrapped coarse food, and when planktonic food is available they are able to eat that too. In the absence of pond vegetation, which take some time to appear in a newly formed pool, these tadpoles live on planktonic organic matter. This type of tadpole is represented in plains of Punjab by genus *Bufo*. Tadpoles of *Microhyla ornata* are adapted to deep ponds, which are rich in planktonic matter but with little non-planktonic pond vegetation. These tadpoles lack hard mouth parts. Their dorsoventrally flattened head, lateral eyes, transparent body, long, muscular, delicate tail produced posteriorly into a vibratile filament, flattened buccal cavity with few flattened papillae with coalesced bases into membranes, and hypertrophied pharyngeal region as compared with shortened buccal part, make these tadpoles efficient filtering machines, capable of sieving 2  $\mu$  thick food particles from the water current (Wassersug and Rosenberg, 1979). On the other hand, local *Rana* tadpoles are all benthic, living among submerged vegetation in temporary water bodies, where rain water accumulates. Their oral discs are provided with rows of teeth and strong ciliated beaks. They differ from each other in the structure of their teeth and beaks (Khan, 1982a). Apparently morphological differences in their oropharyngeal morphology are reflected in their adaptive radiations to different niches in a sympatric habitat, where they utilize different parts of the common food base. This arrangement is to minimize, intra and interspecific competition among closely allied animals, passing through similar physiological changes (Starrett, 1973; Altig and Johnston, 1989).

Several herpetologists have considered larval morphology very important in determination of higher taxa in amphibian classification (Günther, in Boulenger, 1882; Boulenger and Annandale, 1918; Noble, 1927; Orton, 1953; Lynch, 1973). Recently, feeding morphology of the tadpole larva has also been included in classification criteria (Starrett, 1973; Wassersug, 1980, 1989; Wassersug, and Pyburn, 1987).

Larvae living in a common habitat develop similar oropharyngeal morphology by convergent evolution, which obscures their phylogenetic affinities (Sanderson and Wassersug, 1990), and their basic familial oropharyngeal morphology is drastically modified. Wassersug and Heyer (1988) were not able to correlate oropharyngeal morphologies into a phylogenetic continuum of larvae of Leptodactylid frogs. Despite general acceptance of Orton's (1953) definition of major groups of amphibians on the basis of larval characters, there are certain genera the phylogenetic position of which has jeopardized Orton's conceptions (Wassersug, 1989). For example, South America genus *Otophryne* (Wassersug and Pyburn, 1987) and genus *Pseudohemiscus* from Malagasy (Wassersug, 1984), though, have tadpoles of the type IV by Orton's definition, yet adults and larvae have strong microhylid features (Blommer-Schlosser, 1975; Pyburn, 1980; Donnelly et al., 1990). Moreover, Ueck (1967) found cornified cells present in front of the mouth of the larva of *Hymenochirus*, a representative of Type I of Orton.

Apparently, these modifications in the structure are due to the particular habitat in which these forms of diverse affinities live. Moreover, microhylid frogs belong to suborder Ranoidei (Dubois, 1987), they are phylogenetically related to hard-mouthpart-bearing ranoid tadpoles of genus *Rana* and *Bufo*. Perhaps due to atavism, sometimes phylogenetic characters appear in nature and are selected in particular circumstances of a habitat.

Habitat partitioning in reproductive strategies among adult amphibians has been described by several workers (Goin, 1960; Harvey, 1963; Blair, 1964; Noble, 1931; Orton, 1951; Crump, 1974; Duellman, 1978; Khan and Malik, 1987 b). Sympatric amphibians do not come in direct competition with each other since they differ from each other in their choice of breeding time, breeding sites, croaking sites, egg laying sites and egg laying modes (Nelson, 1973; Crump, 1974; Khan, 1982 b; Khan and Malik, 1987 b; Lamb, 1987; Alcalá, 1962; Blair, 1961). Moreover, sympatric amphibian tadpoles belonging to different genera and families differ in the morphology of their body and oral region (Khan, 1982 a). Obviously, tadpoles, like their adults, especially in temperate regions, have preferences in temporal sympatric habitat to avoid intra and interspecific competition. Even studies on the gut contents reflect interspecific and site differences

... and in general, even in temperate environments, amphibians use common sites for egg laying and their larvae develop sympatrically. The common food base in the temporal sites fluctuates violently from time to time (Parshad, 1916; Ali, 1986 a, 1969). Effort of each species of tadpole, in such unpredictable environments, is mainly centered on gathering as much food energy as possible to hasten completion of its development. At the same time competition for food is avoided with the sympatries. Thus, each species develops a special technology to utilize a particular size range of the available food item (Inger, 1986). Except tropical microhylids, tadpoles of genus *Rana* and *Bufo* are euryphagous, using a wide range of food items available in the temporal habitat. They resort to carnivory when water evaporates and tadpoles come in contact with each other frequently. Bragg (1964) has found that *Scaphiopus bombifrons* tadpoles develop more rapidly in fast evaporating sites to avoid predation by their sympatries.

Amphibian fauna of the plains of Pakistan has achieved its present status as a result of a complex interaction of present and past ecology, geographic accessibility, long term physiographic events and the evolutionary history of its familial units. Genus *Microhyla* is essentially tropical, with primitive, microphagous lotic, Type II tadpole larva. The microhylid frogs and several Himalayan forms invaded Pakistan plains recently, chiefly because of extensive canalization of the area which has contributed significantly to augment the habitat suitability of the amphibians, resulting in their wide distribution in Punjab and Sindh (Khan, 1980, 1990). Genus *Rana* and *Bufo* are most successful modern frogs, with advance microphagous, benthic, generalized grazing Type IV larvae, with hard mouth parts. Thus the frogs of these genera are widely distributed throughout the plains of Pakistan. There is a strong evidence which indicates that bufonid and ranid frogs invaded Eurasia during Cenozoic (Blair, 1972; Savage, 1973; Khan, 1980, 1990). They radiated out to different parts of Eurasian mainland. Present day amphibian fauna contains elements from Oriental as well as Palearctic regions (Khan, 1980, 1990). Toads, being more terrestrial and xerophytic than frogs, are more widely distributed while frogs are restricted to more aquatic regions.

In plains of Punjab, genus *Microhyla* and *Bufo* is represented by a single species each, while genus *Rana* by three forms (Khan, 1982 a). No work exists on the oropharyngeal morphology of the tadpole larvae of these species, and so far no attempt has been made either to study their ecology at adult or larval stages. Savage (1952) reported on oropharyngeal morphology of *Bufo bufo*, *Rana temporaria*, *Calluella guttulata*, *Glyphoglossus molossus* and *Chaperina fusa*.

Though this pioneer work contained lot of ecological information pertaining to these species, but the descriptive part and the diagrams of the oropharyngeal region are very inadequate. Wassersug (1980) has described in detail, oropharyngeal morphology of larvae of eight amphibian families, namely Ascaphidae, Discoglossidae, Rhinophrynidae, Microhylidae, Pelobatidae, Hylidae, Centrolenidae and Dendrobatiidae. He has correlated morphology of these larvae to their ecological adaptations. Inger (1985) has worked on the Borean tadpoles belonging to families Pelobatidae, Bufonidae, Microhylidae, Ranidae and Racophoridae, in a way filling gaps left by Wassersug (1980). Recently, Wassersug and Heyer (1983, 1988) have surveyed oropharyngeal morphology of the leptodactylid tadpoles to find phylogenetic relationships between different genera of this family. Apart from these major works, short reports on the oropharyngeal morphological studies of exotic tadpoles have also appeared in literature. Wassersug (1976) has made a study of the ontogenetic changes which take place in the oropharyngeal morphology of *Hyla regilla* tadpole during its normal development. Wassersug (1984) has described the morphology of the peculiar *Pseudohemisus* larva, while in 1989 he worked on its affinities. Inger (1983) worked on larvae of *Leptobatrachium* and *Leptobatrachilla*. Racophorid tadpoles (*Wassersug et al.*, 1981), *Otopryne robusta* (Wassersug and Pyburn, 1987), *Phyllomedusa trinitatis* (Kenny, 1969) and *Osteopilus brunneus* (Lannoo et al., 1987) have also been described. However, except for short note on the oropharyngeal morphology *Microhyla ornata* tadpole by Wassersug (1980), there is no information on the oropharyngeal morphology of anuran tadpoles found in the plains of Punjab, Pakistan. Recently, Khan and Malik (1987a) have described the oropharyngeal region of the mountain frog *Rana hazarensis* and correlated its torrenticole ecology.

External morphology of the amphibian tadpoles of Indo-Pakistan subcontinent is fairly well known (Anderson, 1895; Annandale, 1905, 1906, 1918; Rao, 1914, 1915, 1917; Smith, 1916 a, b). Annandale and Rao (1918) devised a key for identification of ranid and bufonid tadpoles inhabiting the Indian plains, with short descriptions of various species. Kirtisinghe (1957) has done considerable work on Sri Lankan tadpoles. Khan (1965) worked in the ontogenetic development of *Bufo stomaticus* and later on *Rana tigerina* (1969). Identification of Pakistani amphibian larvae has been the subject of Khan's (1982 a) study. However, upto now oropharyngeal morphology of Pakistani anuran tadpoles has not been described.

The main aim of the present work is to describe the external as well as internal oropharyngeal morphology of the species of tadpoles found in the plains of Punjab, Pakistan, and

the oropharyngeal morphology of the tadpoles belonging to different species but to the same genus, and to find how they live in a sympatric habitat.

Tadpole of *Microhyla ornata* described by Wassersug ( 1980 ) was collected from Bangkok, Thailand, which lies in tropics. This frog also occurs in the plains of Punjab, in temperate habitat. Do the tadpoles of this widely distributed species differ in their oropharyngeal morphology, and how far these differences can be accounted for in terms of differences in their ecologies ?

Ranid tadpoles inhabiting waters of the plains belong to three species. Another objective was to find interspecific differences in their oropharyngeal morphology and to correlate it to the niche they occupy in a sympatric habitat. Answers to these questions, it is hoped, will help us better understand the organization of pond ecological system and the role played by the anuran amphibians both at adult and larval stages. It will also help us understand how far a biological form can tolerate strains and stresses in a temporary, unpredictable habitat.

## MATERIALS AND METHODS

Tadpoles for the present study, were collected from various ponds and puddles lying along the western suburbs of Rabwah city, falling within a radius of approximately three kilometers of the northwestern boundary of the city (Khan and Malik, 1987 b). The area presents a typical country habitat of Punjab plains.

During summer, temperature of the pond water varied from 27-28.5 C, while pH fluctuated from 6.8 to 7.5, apparently due to changes in the volume of the pond water from periodic rains. Tadpoles do not appear to be affected by temperature and pH variations. *Microhyla ornata* tadpoles were collected from deep, calm, semipermanent ponds with lot of planktonic bloom, after mid-monsoons. Ranid tadpoles prefer shallow seepage pools with considerable vegetation, while larvae of *Bufo stomaticus* were collected from all situations.

### Collection, Preservation and Storage of the tadpoles:

Tadpoles were collected from nature with the help of fine meshed handnet. Microhylid tadpoles were netted at midstream, while those of *Bufo* were scooped from marginal water of the pond. Ranid tadpoles were difficult to collect, since they retreat to the bottom of the pond when disturbed, and were collected by dredging with the help of a handnet. A lot of mud comes along with the tadpoles, the net was kept dipped in water and the swimming tadpoles in the net were scooped up with the help of a teapot sieve. The tadpoles were kept for half an hour in clear water to wash their body and buccopharyngeal region. Some of these tadpoles were preserved in Bouin's fixative following suggestion by Khan (1965, 1982 a) and stored in diluted Bouin's with water (1: 1).

The shape as well as the dark pigment of the tadpole is ideally preserved by Bouin's fixative. The iridiocytes on the belly of *Microhyla ornata* tadpoles, however, are gradually lost within one or two months. Moreover, Bouin's yellow colouration accentuates the location and shape of various structures present on the oropharyngeal surfaces, thus making their study a lot easier.

For the study of cartilaginous support of the ventral velum, the tadpole was stained following Wassersug (1976) and Henken and Wassersug (1989):

Absolute alcohol = 60 ml

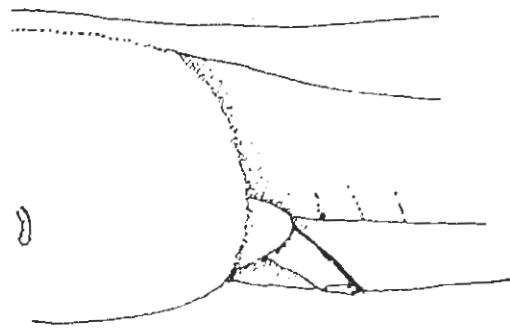
Glacial Acetic acid = 40 ml

The cartilage was stained deep blue, while rest of the tissue light blue. The tadpoles so stained were rendered soft and elastic, allowing free manipulation without damage. The dull blue dye accentuated visibility of various morphological structures.

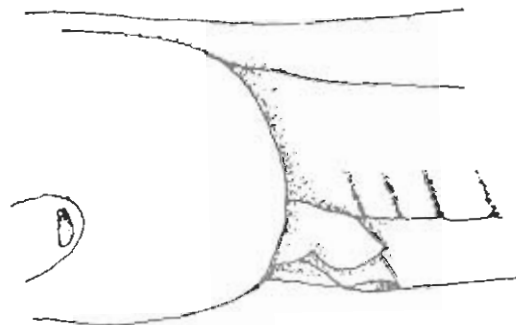
*Study of the living tadpoles:* Living tadpoles of *Bufo* and *Rana* were kept in glass aquaria (45 x 30 x 45 cm). Water plants like *Elodea* and *Hydrilla* were kept in water for aeration. The tadpoles were fed on boiled lettuce. The feeding behaviour of these tadpoles was studied. In spite of the fact that the tadpoles fed voraciously, still they remained weaker, as compared to those collected from nature (Khan, 1965). Apparently some important nutritive element may be missing from the aquarium water. When the tadpoles were provided with meat in their feed, they showed improvement. Rearing of *Microhyla ornata* tadpoles was a problem. It was difficult to maintain enough planktonic growth in the laboratory to support them. Mixing of corn or wheat flour in aquarium water did not help, it actually polluted the water.

*Identification key for tadpoles from the plains of Punjab:* The tadpoles collected from nature and preserved were identified and allotted to their respective species by using following key (Khan, 1982 b):

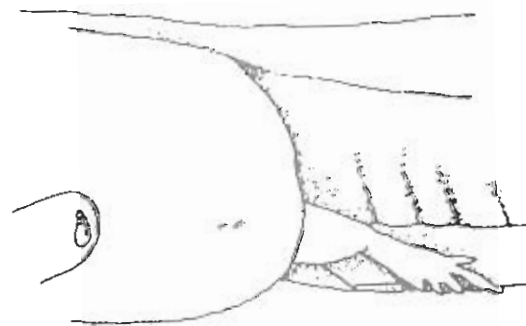
1. Oral disc with keratinized beak and rows of teeth present .....2  
No oral disc with keratinized parts.....*Microhyla ornata*
2. Cloacal opening median; dental formula 2(2) /3.....*Bufo stomaticus*  
Cloacal opening dextral .....3
3. Anterior labium of oral disc with five rows of teeth .....*Rana trigerina*  
Anterior labium of oral disc with one to two rows of teeth..... 4
4. Two rows of teeth on posterior labium of oral disc.....*Rana cyanophlyctis*



Stage 26



Stage 30



Stage 35

Fig. 1. Criteria used for identification of developmental stage of anuran tadpoles in present study. Stages from Khan (1965). Diagramatic, for abbreviations see page 11.

Posterior labium of oral disc  
with three rows of teeth,  
third very small.....*Rana syhadrensis*

*Choice of study material* : Following developmental stages of the anuran amphibian tadpoles represent critical periods in their ontogeny ( Khan, 1965 ). These stages were studied surgically so as to decide at what stage the oropharyngeal morphology is typical for each species of tadpole:

Stage 26: Hind-limb bud stage: The larva has a typical "tadpole" form, with oral disc and spiracle. Feeding has started. At this stage the tadpole is very small so proper surgery is not possible.

Stage 30: Hind-limb stump stage: Though the tadpole is larger, but it is still small for surgery.

Stage 35: Full tail-piece stage: The tadpole is large enough to allow accurate surgery. The oropharyngeal morphology is maintained during ontogenetic development from stage 26 to 40, after which metamorphic changes start taking place. Morphology, external as well internal, of stage 35 was taken as typical for all species (Fig. 1).

*Study of the preserved material*: For each species, at least 10 specimens were studied surgically. For difficult species more specimens were sacrificed until a satisfactory dissection was obtained. Tadpoles of each species were described per following parameters.

External morphology: Shape and location of various morphological characters were noted. Measurements, in mm, were taken with the help of a dial-meter to the nearest millimeter. At least 10 tadpoles pertaining to each species were studied. Camera lucida drawings were made to illustrate various morphological characters.

Internal morphology: The buccopharyngeal region was exposed by special surgical procedures (Wassersug, 1976). Devacker's angular special surgical iridectomy scissors were preferred over straight blades, because these made it easier to proceed with the operation on a tadpole which comes up to about 2 mm above the surface of the Petri dish. The surgical dish was prepared as follows:

Four angular pieces of plastic were glued in a large Petri dish (6 mm), at opposite sides, so as to prevent hardened wax from becoming loose. The dish was then filled with melted black paraffin (two parts of black paint to six parts of melted white wax). The black paint is used to provide dark background to enhance visibility of structures on the semitransparent body of the tadpole. On the other hand, if the tadpole has been stained by Alcian Blue there is no need for dark

Preparation for surgery: The tadpoles were prepared for surgery as follows:

The tadpoles were washed in running water for about 10-15 minutes so as to remove as much of the preservative as possible.

Surgical procedure: A groove, large and wide enough to contain the tadpole, was excavated in the centre of the dissection dish. The tadpole was fixed, belly upward, in the groove with the help of entomological needles. The Petri dish was filled with enough water to cover the tadpole. The ventral body wall was cut so as to expose the intestinal coil, which was lifted and removed, taking care not to remove the stomach, lungs and closely associated branchial region. The tadpole now was ready for buccopharyngeal surgery.

Often, mouth of the preserved tadpoles is closed. It can be opened by gently pressing the floor of the buccal cavity just behind the lower beak. The tip of one blade of the scissor<sup>s</sup> was gently inserted into the corner of the mouth in view, and the wall of the buccal cavity was cut back along the lateral, side of the buccopharyngeal cavity<sup>to</sup> its posterior most end. Then the tadpole is pinned left side up and a similar cut was made on the other side. These cuts pass through ceratohyal, dorsal and ventral vela, buccopharyngeal muscles, thus separating pressure cushions and ciliary grooves from ventral pharynx. A third cut was made through the posterior ends of the earlier two cuts, thus freeing buccopharyngeal floor from its roof.

At the time when tadpoles are put into fixative, their pharyngeal cavities get compressed due to avoiding reflex. Thus, the tadpoles are preserved with tightly closed mouth and compressed buccopharyngeal cavity. During surgery<sup>y</sup> therefore, the blade of the scissor may peel off the wall of the tightly compressed buccopharyngeal cavity, resulting into an un<sup>a</sup>satisfactory dissection. It is thus, quite difficult to obtain a suitable dissection. This difficulty has also been experienced by other workers (Wassersug, 1976 and personal communication, 1988).

During present work, it has been found that better results are obtained, if the tadpole is held in hand instead of pinning it in the dish. The tadpole in this way can easily be orientated at desired angle during surgical procedure described above. *Microhyla ornata* tadpole has dorsally disposed mouth. The dissection cuts must therefore pass through mideye backwards. The upper beak<sup>k</sup> of *Bufo* and *Rana*, except *Rana tigerina*, tadpoles overbite the lower beak, so here the cut must first run obliquely dorsoid, smoothly becoming<sup>ing</sup> lateral. *Rana tigerina* tadpoles were easiest to dissect, since their anteriorly displaced mouth requires straight cuts on each side so as to separate<sup>dorsal</sup> buccal from ventral.

For description of the buccopharyngeal morphology of the tadpoles in this work, terminology by Wassersug (1976) and Khan and Malik (1987 a) has been followed. For description of external morphology of the tadpoles, Altig (1970), Khan (1982 b) and Johnston and Altig (1986) have been followed.

Description of the external morphology and that of the buccopharyngeal region of *Bufo stomaticus* may be taken as an introduction to understand morphology of other amphibian tadpoles studied in this work.

### ABBREVIATIONS USED

AL	Anterior labium	LRP	Lateral ridge papillae
AT	Anal tube	M	Mouth opening
B	Body	MR	Median ridge
BFPA	Buccal floor arena	N	Naris
BFAP	Papillae of Buccal floor arena	NS	Narial slit
BC	Buccal canal	NV	Narial valve
BP	Buccal pocket	OD	Oral disc
BRA	Buccal <del>floor</del> <sup>roof</sup> arena	PA	Prenarial arena
BRP	Buccal roof papillae	PC	Pressure cushions
CG	CILLIARY GROOVE	PL	Posterior labium
DF	Dorsal fin	PNA	Postnarial arena
DV	Dorsal velum	PP	Prepocket papillae
E	Eye	PVM	Posterior velar margin
EAP	Extra arena papillae	RR	Rostral region
EF	Esophageal funnel	S	Spiracle
FC	Filter cavities	SC	Secretory cells
FR	Filter rows	SR	Secretory <sup>e</sup> ridges <sub>1</sub>
FT	Food traps	T	Tail
G	Glottis	TO	Torus
HLB	Hind limb bud	TR	Tooth row
ILP	Infralabial papillae	TRA	Trachea
INP	Internarial papillae	UB	Upper beak
L	Lingual analage	VF	Ventral fin
LB	Lower beak	VV	Ventral velum
LP	Lingual papillae		
LBA	Labial papillae		
LG	Lung		

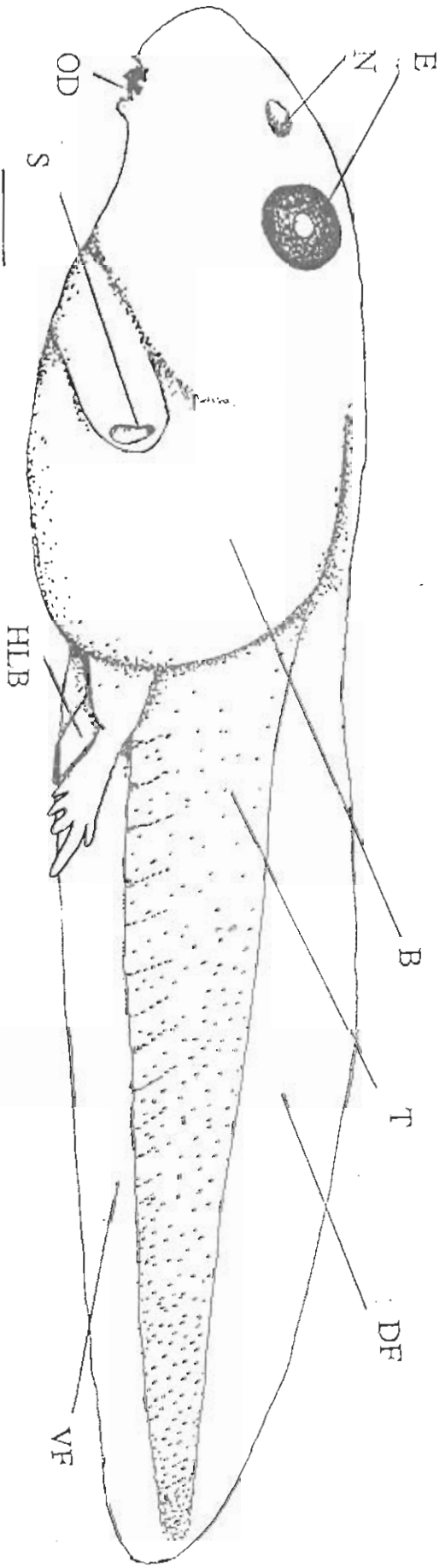


Fig. 2. *Bufo stomaticus* tadpole, lateral view. Scale 1 mm. For abbreviations see page 11.

It is the commonest toad found in Pakistan (Khan, 1972; Khan and Tasnim, 1987), and is most frequent chordate animal encountered during summer evenings. It is seen swarming under light-posts, even in most busy streets feeding on photophilic insects. It is the only thoroughly terrestrial amphibian and the only representative of its genus in the plains of Punjab. It invades water bodies only during summer monsoons, for breeding. It is an opportunistic breeder, calling males are very vocal, their guttural call could be heard from miles around (Khan and Malik, 1987 b). Amplexus is axillary, eggs are strung in a double gelatinous string which is wound round the submerged vegetation (Khan, 1965, 1982 b).

Dark brown larvae of *Bufo stomaticus* aggregate along water margin, feeding on vegetation etc., not venturing into deep water. Summer heat dries <sup>up</sup> off majority of the ephemeral shallow puddles destroying lot of tadpoles (Khan and Malik, 1987b, Khan, 1990).

### Morphological Description of the Tadpole

*Material:* Bulk of the tadpoles of *Bufo stomaticus*, for present study, was collected during 1986-87, from different localities along northwestern suburb of Rabwah City.

*References:* Khan (1965) has described stages in the normal development of *Bufo stomaticus*. Its egg and larva is distinguished from those of other local amphibians (Annandale and Rao, 1920; Kirtisinghe, 1957; Khan, 1982 a,b). Khan and Malik (1987 b) recorded breeding and larval ecology of this toad. Khan (1969) has described morphogenesis of its digestive tract.

*Description of tadpole:* Measurements of the tadpole (in mm), (Fig. 2). Following description is based on 10 tadpoles at Stage 35 (Khan, 1965):

The total length of the tadpole ranges from 17.4 - 17.9. The body is ovoid, tail about twice the length of body, and gradually tapers to posterior obtuse end. The snout is semicircular in dorsal profile. The eyes are dorsolateral, their vertical <sup>a</sup> diameter being 0.64, horizontal 0.92 and are separated by a distance of 1.32. The nostrils are closer to eye than to the tip of snout, are dorsolateral in position, internarial distance is 0.62-0.64. The spiracle is sinistral, near to posterior end of the body than to the tip of snout. Anal tube is mesoid. Caudal muscles are widest at base, gradually tapering posteriorly. The caudal fins are extending to the base of the tail as well as on body dorsum and are broadest approximately at midtail.

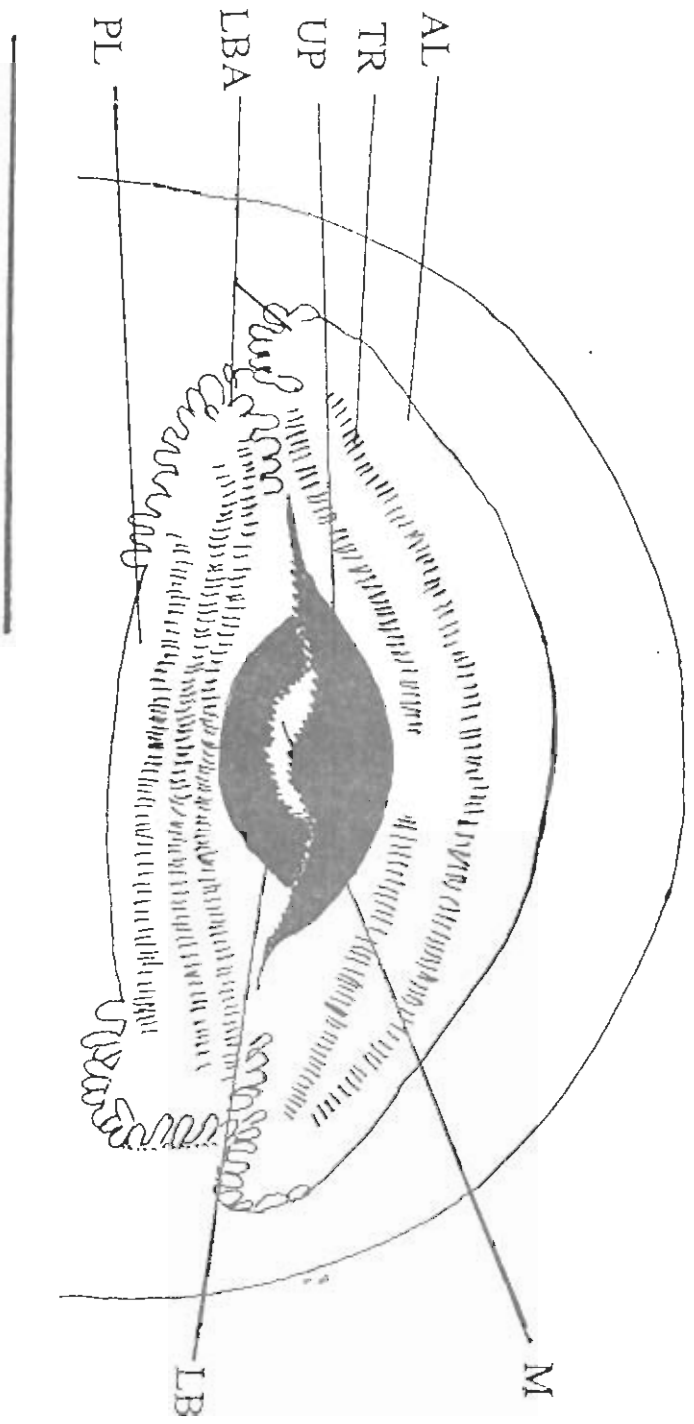


Fig. 3. *Bufo stomaticus* tadpole, oral disc. Scale 1 mm. For abbreviations see page 11.

*Oral disc:* (Fig. 3). The mouth is surrounded by keratinized and papillated structures collectively called the oral disc. Major elements of the oral disc are preoral and postoral labia with rows of keratinized spine like tiny teeth and a preoral and postoral, sharp ciliated edged broad blades called as beak. There are rows of delicate filiform processes along the rim of the oral disc called oral papillae. Lateral sides of the rim of the oral disc is sometimes free and is called labial palp or flap. There is a pair of tooth rows on preoral labium, outer most extend from side to side, across the oral disc while second is interrupted in the middle. The dental formula is indicated as 2 (2), /3 [total number of tooth rows (number of interrupted row in order of its arrangement on the labium)]. Posterior labium is with three complete rows of teeth.

The teeth range from 0.04 - 0.06 mm in length, each has a cylindrical thick base which is fixed in a pad of tissue. Its distal half is flattened, orally concave produced into five to six sharp cusps (Fig. 4), three on each lateral side. The labia of the oral disc are capable of free movements. The teeth are used to rasp the surface of the submerged vegetation, shredding it into small pieces, while the sharp beak is used to cut large chunks from animal matter as well as vegetative matter and to cut it into smaller pieces.

*Description of the oropharyngeal region:* Surgically exposed surfaces of the dorsal buccal (roof of the buccopharyngeal cavity) and ventral buccal (the floor of the buccopharyngeal cavity) were pinned exposed side up in the wax-dish and studied in order of ventral, anterior to posterior; then dorsal, anterior to posterior. Relative positions of various features were noted and their outlines were recorded by camera lucida drawings.

*Ventral buccal:* (Fig. 5). The shape of the buccal floor is squarish, with sides slightly bowed out and angles rounded off. The ratio of total width to total length of the oral cavity is 1:1.2

A single "palm" like anteroposteriorly compressed infralabial papilla arises on each side of the infralabial cartilage. The "palm" is produced along its free margin into four well attenuated fingers projecting forwards. The papilla ranges from being as high as wide to twice as long as wide. Narrow prelingual arena has two to several small papillae arising from its lateral wall, anterior to the infralabial papilla on each side. The lingual anlage is a prominent median transverse protruded area lying in the anterior half of the ventral buccal. Its surface is slightly trilobed, a transverse row of four attenuated filiform lingual papillae arise from its middle lobe.

The buccal floor arena (BFA) is roughly trough-shaped, with mouth of the trough directed anteriorly, where it is more open and its limits are ill defined. The BFA narrows down posteriorly, mesially it is deep, gradually rising towards lateral and posterolateral sides of the buccal floor.

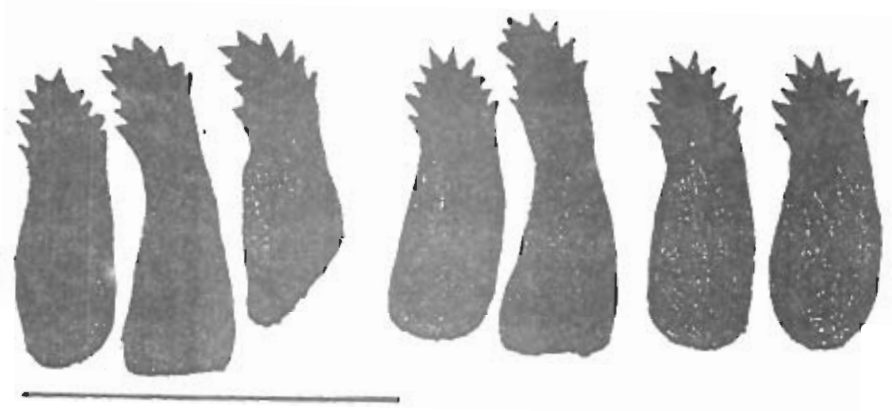


Fig. 4. *Bufo stomaticus* tadpole, teeth. Scale 0.25 mm.

The BFA papillae are arranged in two groups on each side. Outer group of 4-5 large attenuated papillae are arranged in a semicircle laterally, the anterior most papilla is curved mesoid while rest are orally directed. Second group of the papillae are pustular, about half of the size of the papillae of the first group. They occupy centre of BFA and extend on sides to continue with 5-7 similar prepocket papillae, anterior most of which is very small, almost a pustule. None of the BFA papillae show blunts or irregularities.

The buccal pockets are relatively large and prominent feature of the midventral buccal, they extend mesially to the middle of the BFA, and are disposed transversely. The ventral velum is distinct as a posterolateral arch. its posterior margin is irregular and jagged, with three prominent peaks on each side mark the position of the underlying filter plates. The glottis is poorly differentiated and completely under the velum.

The subvelar surface of the *Bufo stomaticus* tadpole is peculiar. Mesially it is covered with fine pits of glandular openings, while laterally it is finely ridged. The ridges run transverse to the lateral margin of the subvelar surface (Fig. 6).

**Ventral pharynx:** Branchial baskets are prominent posterolateral structures of the ventral buccal. Each lies at an angle of 45 degree to 50 degree to the longitudinal axis of the ventral buccal. The first branchial cavity is distinct, while second and third are indistinct (Fig. 5). First filter plate is the longest, vertical and is supported by the first ceratobranchial. It has 10-12 filter rows and is about 1/4 under the velum (see Table I). Second filter plate is oblique, crescentic, longer than deep, it is slightly under the velum and is attached to it. The III and IV filter plates are deeper than long and both are horizontal.

The velum is supported by delicate spicules arising from the hypobranchial plate on each side.

The filter mesh of *Bufo stomaticus* larva is rather loose. The full filter rows alternate with partial filter rows, 3 degree filter ruffle is present. the filter rows are widely spaced with deeper than wide noncanopied filter canals. The œsophagus is wide.

**Dorsal buccal:** (Fig. 7). The buccal cavity of *Bufo stomaticus* tadpole is narrow and dorsoventrally depressed. Features on the buccal roof correspond to the complimentary structures on its floor.

**Anteroventral disposition of the oral orifice of *Bufo stomaticus*** tadpole causes a strong overbite of the upper beak, so that the prenarial (rostral) region is narrow and strongly curved ventrad. Its anterior border is a broad arch while posteriorly it continues with the narial region.

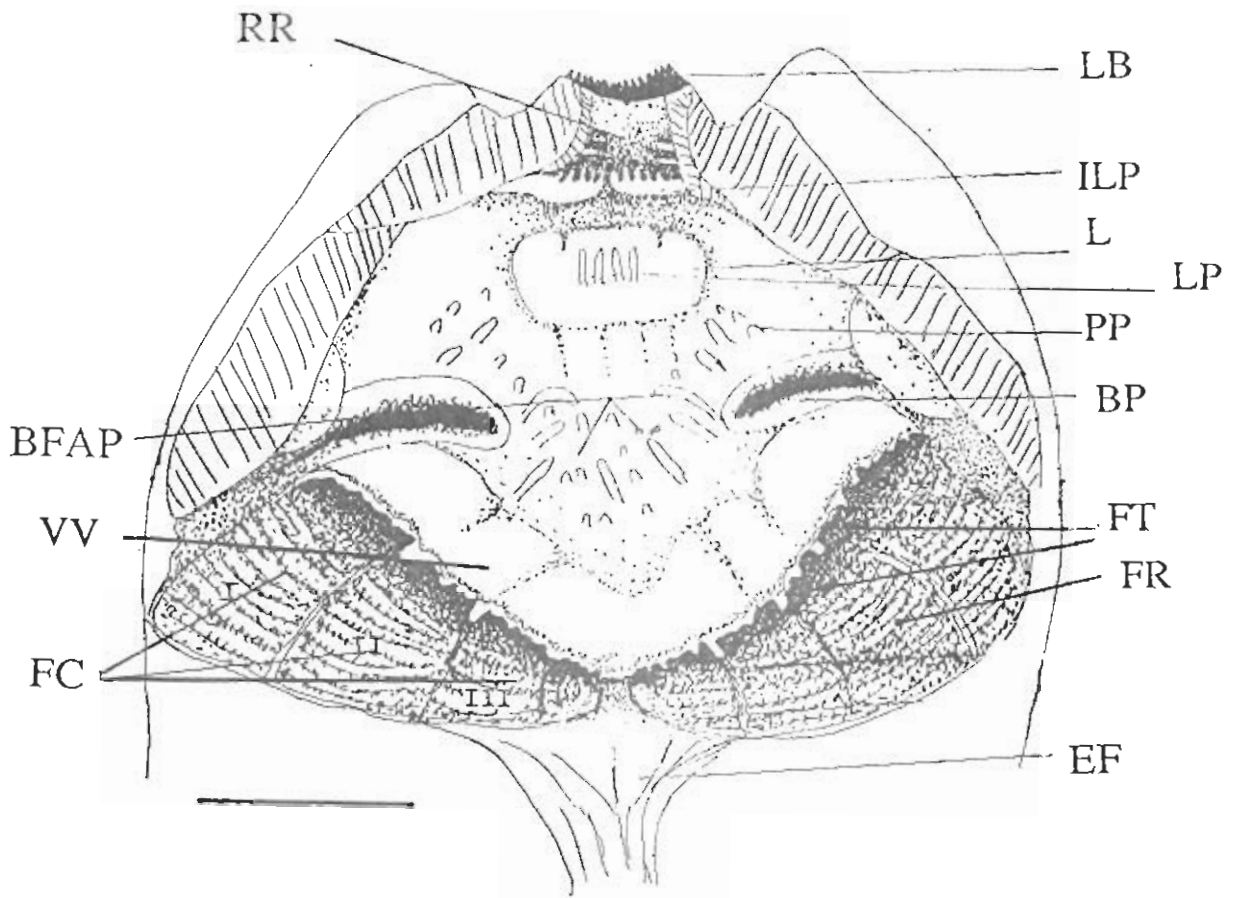


Fig. 5. *Bufo stomaticus* tadpole, buccopharyngeal floor. scale 1 mm. For abbreviations see page 11.

**Table I. Branchial region of *Bufo stomaticus* tadpole at Stage 35 (data from 10 specimens)**

Ceratobranchial (cb) supporting filter plate	Length of filter plate	Breadth of filter plate	Number of filter rows on filter plate
cb I	1.2-1.3	0.9-1	10-12
cb II	1.8-2	1-1.5	9-10
cb III	0.9-1.4	1.5-1.7	7-9
cb IV	0.5-0.6	1.2-1.9	6-8

Internal nares are prominent oblique slits, running anteromesoid to posterolateral, at an angle of 30 degree to the transverse plane of the dorsal buccal. Outer narrower, and inner broader narial valve guards the narial opening. A slight postnarial ridge with thick four pustules curves mesially in the internarial region to meet an internarial pustule. the ridge-papillae are small with tuberculated tops, postnarial arena is narrow, without any special morphology.

The median ridge is broader than high, with sloping sides and narrower jagged top, which is about half the length of its base. At the level of the median ridge, a single large lateral ridge papilla arises from lateral wall of the dorsal buccal, which is laterally compressed and its palm is produced into three fingers.

Buccal roof arena (BRA) is well marked, wide and trough-shaped, narrowing posteriorly, with posterolateral comers rounded off. The BRA papillae are large and arranged in two groups: outer of four long papillae arranged in a row along laterum of BRA, the middle pair is bifurcated at the tip. All the papillae are mesoid directed. The second group consists of 15 to 20 smaller pustular papillae which are scattered all over BRA. Two to three lateral roof pustular papillae lie on each side of penultimate pair of larger papillae.

A distinct glandular strip extends along posterolateral side of BRA. The secretory pits are distributed evenly all over it. The dorsal velum is thin, delicate, bilaterally symmetrical flap of epithelium, a slight transverse median ridge connects right and left halves of it. Laterally it is continuous with the ventral velum. Its free margin is smooth.

*Dorsal pharynx:* The posterodorsal pharyngeal epithelium, on each side, is loose,

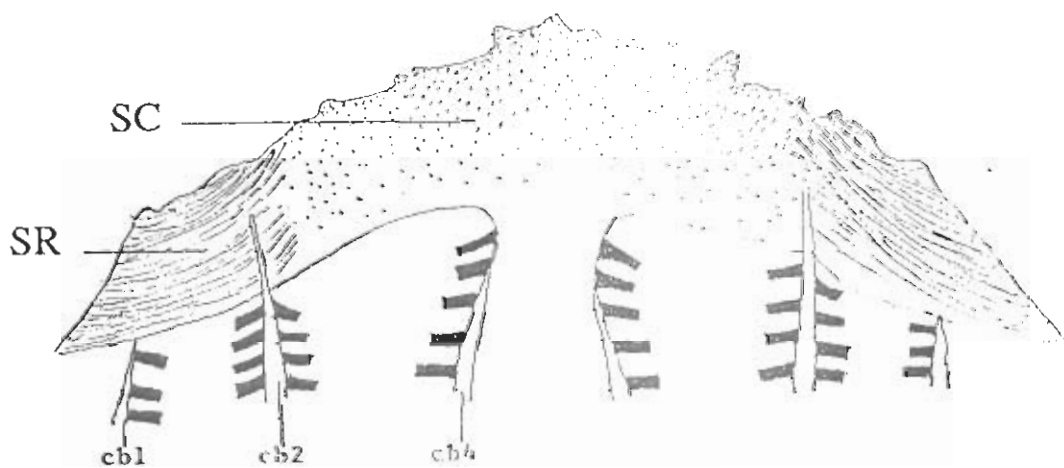


Fig. 6. *Bufo stomaticus* tadpole, subvelar secretory tissue and attachment of filter plates, diagrammatic. For abbreviations see page 11.

forming extensive folds known as pressure cushions. It is difficult to assess their shape and proportion, however, they almost conform to the shape and extent of the underlying branchial baskets. Ciliary grooves are difficult to resolve in *Bufo stomaticus* tadpole.

*Lungs*: (Fig. 32, A). At stage 35, the glottis and lungs of *Bufo stomaticus* larva are poorly differentiated. The glottis is completely blanketed by the ventral velum. The lungs are like crumpled small sacs, completely nonfunctional.

### General Morphology of *Bufo* Tadpole larva e

Cosmopolitan genus *Bufo* includes more than 200 species of toads (Blair, 1972). Terrestrial mode of life and a generalized type of short larval stage are the characters which have contributed for the success of toads and their wide distribution throughout the world. There are few reports on the description of oropharyngeal morphology of the toad larva: *Bufo bufo* (Savage, 1952; Viertel, 1982), *Bufo asper* and *Bufo divergens* (Inger, 1985). Following generalizations could be made from the present and the published work about the oropharyngeal morphology of *Bufo* larva (Table II):

The *Bufo* larva ranges ~~from~~ <sup>from</sup> 18 mm to 25 mm in total size. Its body is oval to round, moderately depressed, little shorter than the tail, which is weak with low fins. The larva is laevogyrid with medioventral cloacal opening; the eyes and nostrils are dorsal.

The oral disc is anteroventral with a pair of emarginated lateral palps, fringed with filiform labial papillae. The tadpole has typical universal bufonid dental formula 2 (2) /3. The beaks are thin, with fine ciliated cutting edges.

The oropharyngeal region of ~~the~~ *Bufo* larva is triangular in outline. The prelingual arena is distinct, squarish with 1-2 palmate infralabial papillae which are produced into several filiform processes and 2-4 additional infralabial simple papillae. The prenarial arena is broader than long, with a low prenarial ridge which has dentated to jagged outline. Tongue and glange is distinct or indistinct, with 2-4 simple lingual papillae. the nares are perforate, simple, obliquely elongated, posterior narial valve three times thicker than anterior. Distinct median ridge; a single lateral ridge palmate papilla, produced mesially into 3-4 short filiform processes. BFA and BRA wide, trough-shaped, posteriorly concave with three types of papillae: 1-6 large filiform papillae which are simple, may be curved or bifurcated at tips, medium sized papillae and pustular papillae scattered at mid BFA and BRA. Few papillae and pustulations are in the prepocket region.

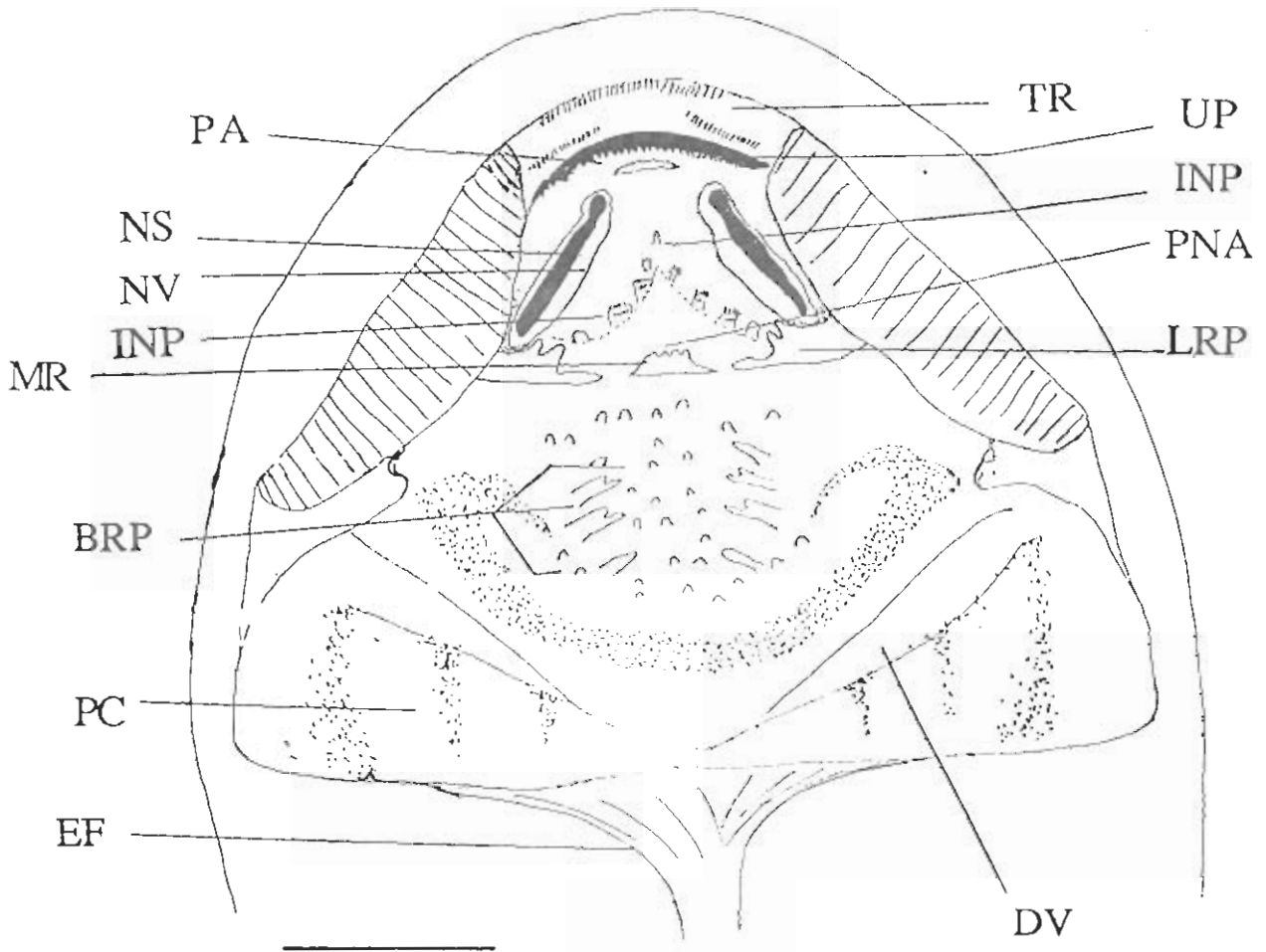


Fig. 7. *Bufo stomaticus* tadpole, buccopharyngeal roof. Scale 1 mm. For abbreviations see page 11.

Table II. Comparison of external and oropharyngeal morphology of *Bufo* larvae. Data for *Bufo asper* and *B. divergens* from Inger (1985) and *Bufo bufo* from Viertel (1982).

Character	<i>B. stomaticus</i>	<i>B. asper</i>	<i>B. divergens</i>	<i>B. bufo</i>
Body length	6.3-6.8	6.5-7.5	5.8-7.3	?
Tail length	10.8-10.9	13-14	14-15	?
Lateral emargination of				
oral disc	palp + papillae	palp + papillae	palp + papillae	?
No. of dental cusps	8-10	8-16	18-20	?
Dental formula	2 (2) / 3	2 (2) / 3	2 (2) / 3	2 (2) / 3
Infralabial papillae/side	1 palp + 2 papillae	1 palp	1 palp	1 palp
Tongue analage	distinct	indistinct	indistinct	indistinct
Tongue papillae	4	4	2	3
Postmarial papilla	+ 4-5 pustules	-	+ 2 pustules	+ 4 pustules
BFA Papillae/side	Large 4-6+ pustules	large 5-6+ pustules	large 4+ pustules	large 4+ pustules
Filter ruffle	3°	3°	3°	3°
Median ridge	broader than deep	deeper than broad	deeper than broad	deeper than broad
Lateral ridge papillae/side	1	1	1	1
Spicular support of velum	+	-	-	?

Transverse buccal pockets are characteristic of the *Bufo* larva. Ventral velum has spicular support, posteriorly it is distinctly jagged with 3-5 distinct peaks. A distinct glandular strip lies along posterolateral border of BRA.

The branchial region is posterolateral-triangular, bowl-shaped. There is a single shallow branchial cavity. The filter plates are horizontally placed, and line the base of the branchial cavity. There are 10-12 filter rows on the second filter plate. The filter ruffle has 3 filter mesh, which is moderately loose, primary filter rows alternate with secondary rows. The filter canals are open, pressure cushion are indistinct. The glottis is obscure and lungs are weakly developed.

### Diagnosis of the *Bufo stomaticus* tadpole

*Bufo stomaticus* tadpole is medium sized as compared to that of *B. asper* and *B. divergens* (Table II), with shorter tail. The teeth are with 8-10 sharp cusps. There are two distinct additional infralabial papillae, the tongue and flange is distinct, with four papillae. There is a postnarial papilla, 4-6 BFA papillae, second curved mesoid; 4 BRA papillae, median two bifurcated at tips. Prenarial ridge with ciliated edge and a row of internarial pustules.

### Ecological adaptations of the *Bufo stomaticus* tadpole

Dorsolateral eyes, depressed round globular body and short tail with low fins of *B. stomaticus* tadpole are adaptations to shallow pond habitat. Delicate fine ciliated beak and rows of sharp keratinized teeth with fine cusps, suggest its grazing habits on periphytons, microphytes and detritus material. The wide and trough-shaped buccal cavity indicates its dependence on water suspended food particles. presence of both pitted and ridged pattern of glandular tissue and well developed filter ruffle indicate that this tadpole has an efficient filtering mechanism.

### Behavioural adaptations of *Bufo stomaticus* tadpole

*Bufo stomaticus* tadpoles form loose aggregates, fringing the marginal waters of ponds. This behaviour appears to be universal among bufonid tadpoles (Allee, 1931; Bragg, 1965; Beiswenger, 1972, 1975). Wassersug (1973) recognizes this habit of *Bufo* tadpoles as “*Bufo* mode”. Aggregation behaviour has also been observed in tadpoles of other amphibians <sup>e.g.</sup> *Bufo marinus*.

(Wassersug, 1971), *B. americanus* (Beiswenger, 1975), *Rana calconota* (Liem, 1959), *R. alticola* (Annandale, quoted in Boulenger, 1920), *R. <sup>a</sup>aurora* (Calef, 1973), *Leptodactylus melanonotus* (Wassersug, 1973), *Aubria subsigillata* (Schlotz, 1963), *Hyla geographica* (Kennedy, 1969), *Hyla pseudopuma* (Crump, 1984), *Philautus gherrapunjiaae* (Roonwal and Kirpalani, 1961), and *Rana heckscheri* (Altig, and Christensen, 1981).

These aggregates make the tadpoles conspicuous and prone to attack by their potential predators. However, it has been argued that the unpalatability of *Bufo* tadpoles not only protects them, it also gives protection to the other palatable tadpoles mimicking *Bufo* tadpoles by forming aggregates, since predators come to associate tadpole aggregations to unpalatability (Licht, 1968; Voris and Bacon, 1966; Wassersug, 1971, 1973; Heyer et al., 1975; Walter, 1975; Grubb, 1972).

Aggregation behaviour is short lived in *Bufo stomaticus* larvae. An ontogenetic change takes place after Stage 33 (Khan, 1965). The tadpole becomes solitary, its dark colouration is changed to grey spotty. It becomes bulky and very agile. When disturbed it quickly retreats under the roots of the water plants, or buries itself under the gravel along pond bottom. Heyer et al., (1975) reported ontogenetic changes in the palatability of *Bufo marinus* tadpoles, which is palatable at Stage 20-26, becoming unpalatable at Stages 30-32. Similar ontogenetic changes have also been reported in other amphibians (Crump, 1984; Brodie et al., 1978; Liem, 1961). The behavioural change from aggregate to nonaggregate in *Bufo stomaticus* may reflect unpalatability changing to palatability.

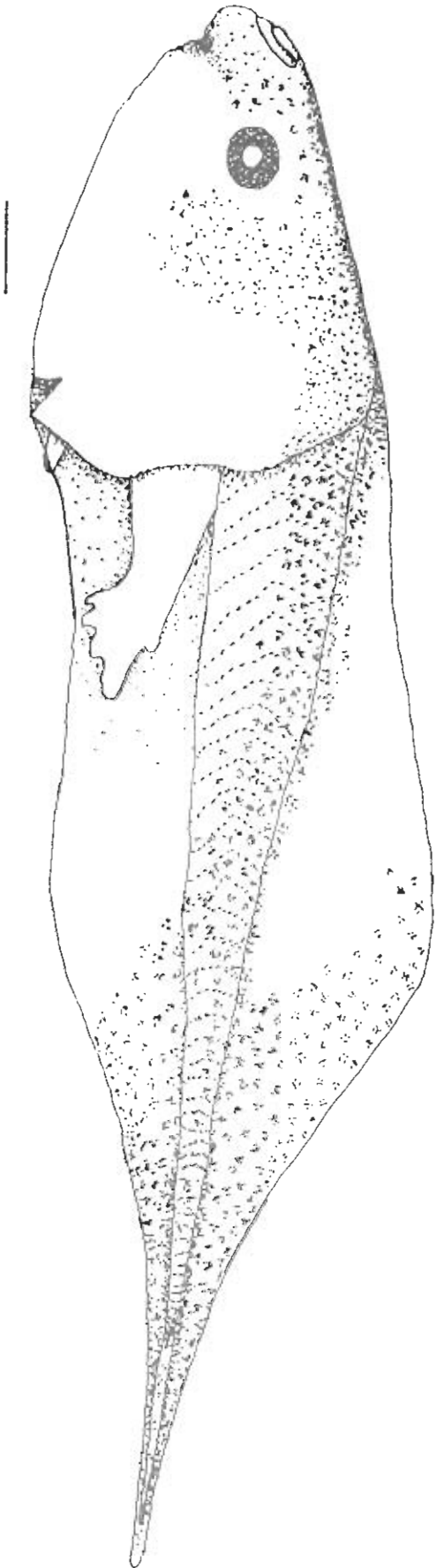


Fig. 8. *Microhylia ornata* radpole, lateral view. Scale 1 mm.

*Microhyla ornata* was first recorded from Pakistan by Khan (1974). Later it was found to be widespread throughout Punjab, Sindh, N. W. F. P. and Azad Kashmir (Khan, 1979, 1980 and Khan and Tasnim, 1987). Its rasping call is easily distinguished from that of rest of the local amphibians (Khan and Malik, 1987 b). It is the tinnest of the local amphibians. Taking advantage of its small size, it hides under vegetation, leaf litter, stones, holes and fissures in the ground. At midmonsoon it invades large water bodies, which by this time are filled with water and have sufficient growth of planktons. It chooses a perch well away from water and calls in its characteristic rasping call, solitarily.

*Microhyla ornata* is not<sup>an</sup> opportunistic breeder like its sympatrics, it waits till temperature, vegetation, water level and planktonic growth has reached certain level in semi or permanent ponds, by the midmonsoon (Khan and Malik, 1987 b). The amplexic pair stays in water close to the water margin, among emergent vegetation. Eggs are laid in groups enclosed in a jelly like material, which floats at the surface of water as an "egg raft" (Khan, 1982 b).

Transparent delicate tadpole of *Microhyla ornata* is micro-phagus<sup>o</sup>, lacking an oral disc with hard mouth parts; instead the mouth is anterodorsal, with a U-shaped permanent mouth opening. It swims at midstream in schools with its kins. The school of the tadpoles is difficult to be made out due to the transparency of the tadpoles.

#### *Morphological Description of the tadpole*

*Material:* Tadpoles of *Microhyla ornata*, for the present study, were collected during 1986-87 from different localities along northwestern border of Rabwah City (Khan and Malik, 1987 b). Tadpoles collected from Ghakkhar, District Gujranwala (Khan, 1974). and Azad Kashmir (Khan, 1979), were used as comparative material.

*References:* Flower (1899), Liu (1950) and Khan (1982 a) have given accounts of the *Microhyla ornata* tadpole. Wessersug (1980) has given brief description of larval oropharyngeal region and has illustrated it. Khan and Malik (1987 b) have studied breeding habits and larval ecology of this frog. Parker (1935) and Khan (1979) have discussed taxonomy of this species.

*Tadpole:* (Fig. 8). *Microhyla ornata* tadpole is semitransparent with streamlined body. The head is dorsoventrally depressed while body laterally compressed. The body is ovoid in dorsal

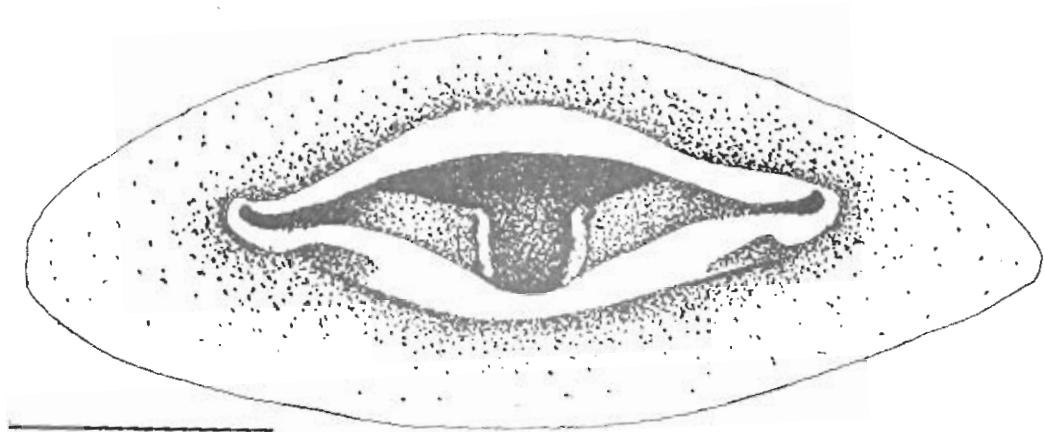


Fig. 9. *Microhyla ornata* tadpole, oral disc. Scale 1 mm.

profile. The snout is countersunk displacing mouth opening anterodorsally. The tail is long, more than twice the length of the body and is produced posteriorly into a long vibratile flagellum. The caudal fins are broad, narrowing abruptly in the posterior half of the tail.

The body is widest at a point at the level of eyes. The snout is narrower, eyes are lateral and smaller as compared to the size of the body. Position of imperforate nostrils is marked by anterolateral pits which are heavily pigmented. The spiracle is median ventral, lying at the posterior ventral end of the abdomen. There is a prespiracular flap which may fit over the spiracular opening. A typical oral disc with hard mouthparts is absent. The mouth opening is a horizontal slit with a median U-shaped cleft in the lower (anterior) jaw, which remains open even if the mouth is closed. The belly wall of this larva has a silver shine due to the presence of iridiocytes. A median band of melanophores covers the brain extending onto the base of eyes and the nasal pit.

*Measurements* (in mm): Body length 5.2-5.8; tail length (including flagellum) 12.6-13.7; total length 17.8-18.9; greatest breadth of body (at the level of eyes) 2.7-2.9; greatest depth of body (at level of spiracle) 3.2-3.4; interorbital space 2.3-2.4; internarial space 1.5-1.95; tail muscle height (at base) 1.7-2.0; tail fin height (at midtail) 4-4.4; length of tail flagellum 2.0-2.3.

### Description of the oropharyngeal region

Dorsoventral compression of the head has correspondingly affected the form and shape of the buccopharyngeal cavity. The buccal cavity is widened sideways with flattened floor and roof. The buccal part is much reduced and the pharyngeal region is exaggerated and about twice the length of the buccal cavity.

*Ventral buccal* (Fig. 10): the buccal floor of *Microhyla ornata* tadpole is produced anteriorly into a narrow U-shaped prelingual chamber. A series of three small infralabial papillae line it on each side; first two are small while posterior most is longer with tip bent forward. Their tips almost touch each other in the centre of the prelingual chamber. The buccal floor is anterolaterally rounded, its cavity widens posterolaterally.

The lingual anlage lies just posterior to the prelingual chamber as a conical structure. Its anterior end is broad while posteriorly pointed. There is no lingual papilla.

The buccal floor arena (BFA) is rectangular with several melanophores, it is raised

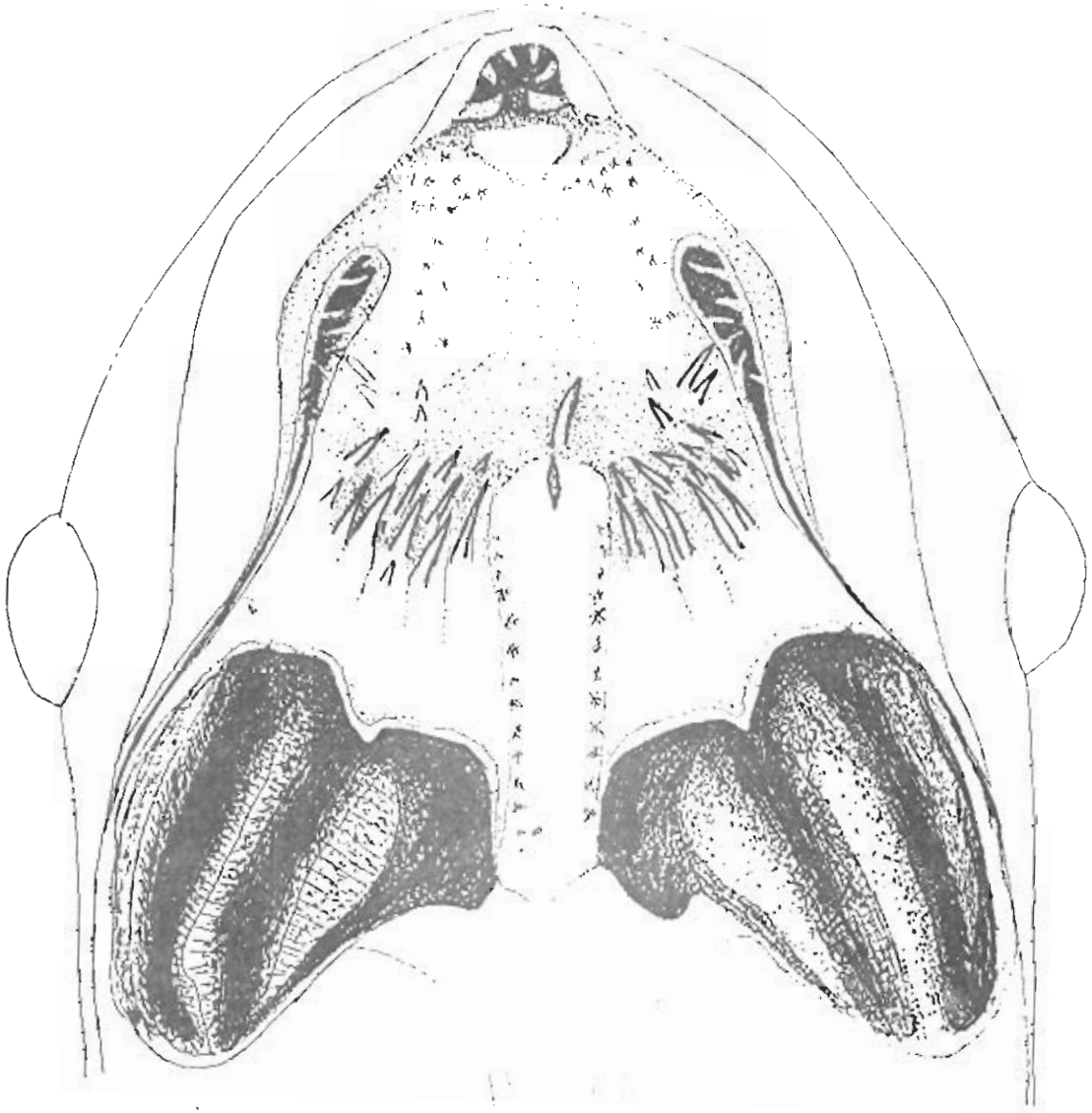


Fig. 10. *Microhyla ornata* tadpole, buccopharyngeal floor. scale 1 mm.

Table IV. Comparison of external morphology and oropharyngeal features of *Microhyla* tadpoles, data for *M. berdmorei*, *M. heymonsi* from Wassersug (1980), for *M. borneensis*, *M. perrigena* and *M. perparva* from Inger (1985); for *M. ornata* present study

Character	<i>ornata</i>	<i>berdmorei</i>	<i>heymonsi</i>	<i>borneensis</i>	<i>perrigena</i>	<i>perparva</i>
Body length	6-6.5	?	?	5.9-6.8	4.0-5.8	2.3-4.1
Total length	18-20	?	?	22.4	16.2	10.3
Infralabial papillae/side	3	3	3	2	?	?
Prepocket papillae	3-8	?	?	?	?	?
Velar peaks/side	?	1	0	?	2	?
Filter rows/filter plate/side						
cb. 1	15-18	22	?	?	?	?
cb. 2	13-16/20-23	20	?	20 to	?	?
cb. 3	16-17/13	18	?	25	?	?
cb. 4	8-9	10	?	?	?	?
Filter mesh density	very dense	very dense	medium	very dense	medium	?
Folding of filter ruffle	3°	3°	2°	3°	3°	3°
BRA Papillae/side (Pustules)	4-5 (12-18)	4 (0)	?	2 (7)	4 (7)	?

laterally allowing a median narrow passage. There are 12-14 large flat BFA papillae on each side, these are fine tipped and arranged in two posterolateral rows, six papillae of the outer most row being longest. A pair of medium sized papillae lies at the level of midpocket. The buccal pocket is long and narrow, running anteroposteriorly on the sides of BFA. Each pocket is a longitudinal slit, its anterior end is wider with 3-6 pre and 5-8 postpocket small conical papillae extending across the pocket cavity touching opposite lip of it. Posteriorly the buccal pockets narrow down into a long passage and continue with the outer branchial pressure cushion (Fig. 10).

The trachea of *Microhyla ornata* tadpole is long cylindrical. It extends mesially through the ventral buccal carrying the glottis far anterior to the posterior margin of the velum, dividing it in lateral halves. A row of melanophores is present along the sides of the trachea. The laryngeal disc is bulbous while the glottis is a sharp slit with thin lips. There is a single, long, attenuated fine tipped preglottal papilla, tipped left, lies just anterior to the glottal opening.

The ventral velum is broad and covers considerable part of the branchial basket. Posterior velar margin is smooth, not jagged and is regular. There is a single broad projection above third filter plate. The velum has spicular support. Small secretory pits line the posterior velar edge.

*Ventral pharynx.* It is most prominent part of the ventral buccopharyngeal region of *Microhyla ornata* tadpole. It is more than twice the length of the buccal cavity. The branchial baskets are posterolaterally disposed, are triangular in shape, with broad side forward. The filter plates are longer than broad, vertical, enclosing deep filter cavities, the third filter plate is tilted mesoid and is partially blanketing the fourth filter cavity. Three filter chambers are visible in dorsal view. A considerable part of the filter plates is under the velum, almost 1/2 to 1/3, making the study of that part difficult, and necessitating cutting off of the ventral velum. In this operation the branchial food traps are also exposed. The shape of the branchial food traps of *Microhyla ornata* is round to oval forming distinct tori, well distinguished from the surrounding tissue. Each torus is concave with raised rim, covered with very fine ridges. the branchial food traps are present in first to third filter cavity (Fig. 11).

A tight filter ruffle covers the surface of the filter plates. The 3 degree dense filter ruffle abuts across the filter canals which are fully canopied and are broader than high. The filter ruffle covers both sides of the second and third filter plates (see table III).

The subvelar surface is covered with fine ridges running parallel to its transverse axis. They are in line with the ridges of tori of the food traps.

*Dorsal buccal* (Fig. 12): The buccal roof is flatish and square like its floor. The prenarial

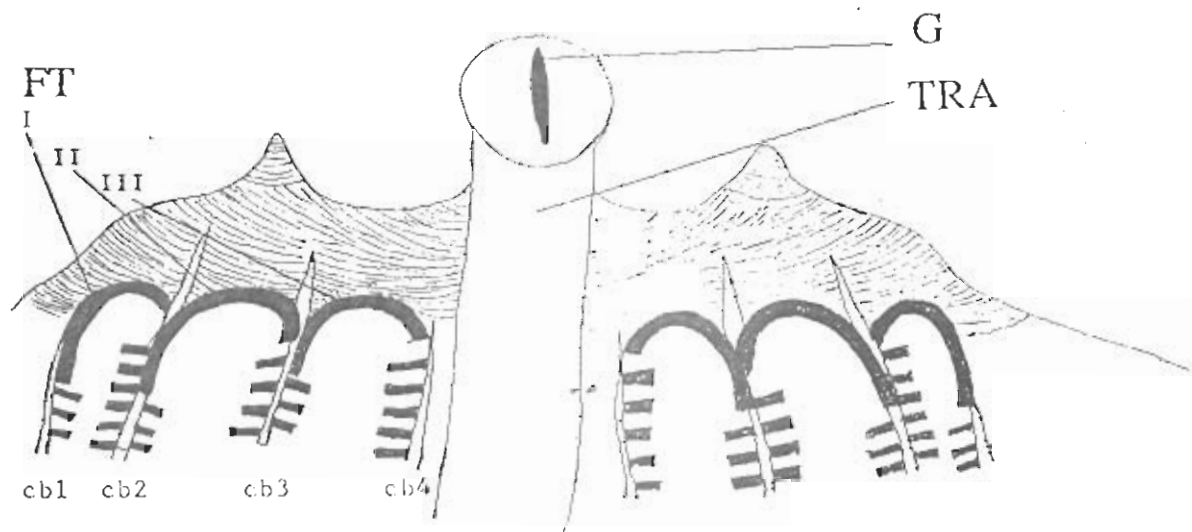


Fig. 11. *Microhyla ornata* tadpole, subvelar secretory tissue and attachment of filter plates, diagrammatic. For abbreviations see page 11.

**Table III. Branchial region of *Microhyla ornata* tadpole at Stage 35 (data from 10 specimens)**

Ceratobranchial (cb) supporting filter plate	Filter plate		Food-trap		Filter rows on filter plate/side	
	length	breadth	length	breadth	anterior	posterior
cb. 1	3.5	1.8	1.2	1.0	0	15-18
cb. 2	3.7	1.5	1.0	1.1	13-16	20-23
cb. 3	2.5	1.4	0.8	0.3	16-17	13
cb. 4	1.9	1.2	0.8	1.2	8-9	0

arena is flat and rectangular also, with a small V-shaped anteriorly directed shallow depression, just posterior to which there is a small prenarial papilla. The internal naris is a small shallow depression, side of which is drawn into a foliaceous flat vertical process. At its base it curves clockwise, hanging down into the buccal cavity. There are 3-4 slight indentations along its inner margin. A delicate low postnarial ridge extends obliquely mesoid from side. Its free margin is produced into 4-5 distinct papillae. There are 6-7 pustules in the internarial area. A postnarial papilla, median ridge and lateral ridge papilla is absent.

The buccal roof arena (BRA) is broader than long and much spacious as compared to that of the other tadpoles studied. A delicate membrane extends mesoid on each side of BRA. Its free margin is produced into flat papilla-like structures of various sizes. The membrane appears to be formed by their flattened coalaced bases. The third of the inner most papilla-like structure is largest with four low bluntings on its inner side, while first and fourth papillae are simple with sharp tips. However, second and third BRA papillae are bifurcated at tips. The BRA membrane gradually narrows down laterally into a wavy margin.

Few pustules are present in the posterior mid BRA, while several lie in the anterior half of it, gradually increasing from inside to outside of this part of BRA, outer most almost the size of a small papilla.

The buccal roof glandular zone is broad and divided into rectangular halves which lie in the posterior half of the BRA. The anterior and posterior margin of each half are straight. The areas ~~are~~ covered by dense pits all over.



Fig. 12. *Microhyla ornata* tadpole, buccopharyngeal roof. Scale 1 mm.

The dorsal velum is broad narrowing mesoid gradually, at mid BRA it staggers narrowly to continue with that of the other side.

Three pressure cushions are distinct. They have an elaborate morphology (Fig. 13). First (the outer most) and the second pressure cushions are four times longer than broad. The first is continuous anteriorly with buccal pockets on each side, while the third (inner most) is broadest and has a median hook-like accessory appendage. Along the posterior border of the pressure cushions, a deep ciliary groove runs on each side.

*Lungs* (Fig 32., B): At Stage 35, *Microhyla ornata* tadpole has well developed long lungs lying on the dorsal side of the abdominal cavity. The anterior half of each lung is broad, with well developed air sacs, it gradually narrows down caudally where it is darkly pigmented.

### *General morphology of Microhyla tadpole*

Following characterization of *Microhyla* tadpoles is based on the descriptions given by Wessersug (1980), *Microhyla berdmorei* and *M. heymonsi* and Inger (1985), *M. borneensis*, *M. petrigena* and *M. perparva*. Data for *Microhyla ornata* pertaining to the present study is given in Table IV.

The *Microhyla* tadpole has depressed head and compressed body; its tail long, with broad fins produced posteriorly into a long tail filament. The mouth is anterodorsal, without hard mouthparts; the spiracle is medioventral with a distinct spiracular flap. The nares are imperforate; the ventral body wall may have silver shine due to the iridiophores.

The pharyngeal region is characteristically exaggerated, it is about more than twice the length of buccal area. The infralabial cartilages are much reduced, with a corresponding reduction in the prelingual arena. There are 0-3 peg-like infralabial papillae on each side; generally the tongue analage is distinct, without lingual papillae. Buccal pockets are lateral, narrow, long and more anteriorly placed in the oral cavity, posteriorly they are connected with the pressure cushions. The trachea is exceptionally long, extending forward through the middle of the buccal cavity, dividing the velum into lateral halves. Laryngeal cartilage is bulbus, with distinct glottis, 1-4 pregiottal papillae. The BRA papillae are long, with broad bases and fine tips, their bases coalace into a fine membrane. Velum is deep, smooth. The branchial basket is long and broad, with three deep filter cavities. The filter plates are deep and long, with 9-23 filter rows. Tight filter mesh, 3 degree filter ruffle abuts over deep and narrow filter canals. There are three

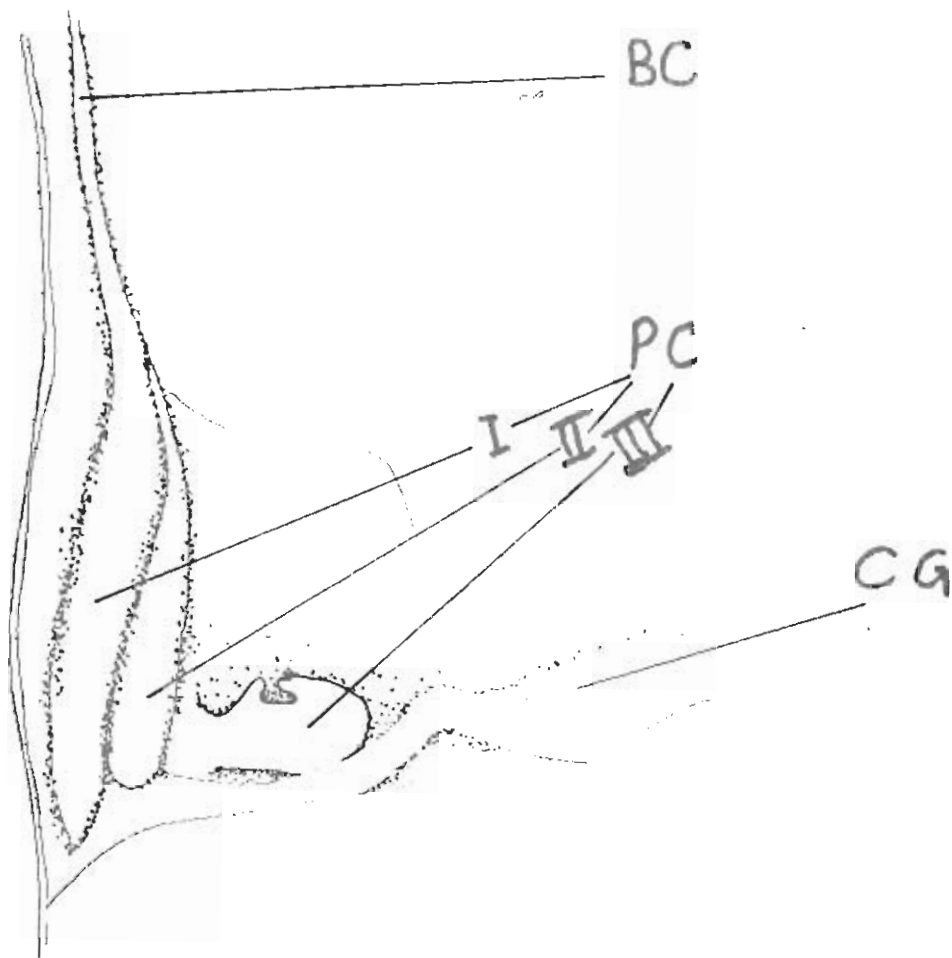


Fig. 13. *Microhyla ornata* tadpole, right pressure cushion, diagrammatic.

food traps, on<sup>e</sup> in each filter cavity in the form of distinct tori, with parallel ridges, running parallel to their longitudinal axis. The velum has spicular support. Buccal glandular zone may or may not be mesially divided.

Nares are imperforate, produced into a free app<sup>e</sup>andage extending vertically down into the buccal cavity. There is no postnarial arena. A prenarial papilla is always present. BFA and BRA are broad with 0-18 pustules scattered at anterior as well as posterior half, 4-7 BRA papillae with or without bluntings, bases of these papillae may or may not coalesce to form a fine membrane.

### Diagnosis of *Microhyla ornata* tadpole

The *Microhyla ornata* tadpole is longer in total length as compared with larvae described by Wassersug (1980) and Inger (1985). It has silver shine on its abdomen. Distinct tongue analage is without lingual papillae; 4-7 BRA and BFA papillae with bases coalased into membranes; three filter cavities; 9-23 filter rows on filter plates; no lingual, lateral ridge papillae and a median ridge; rows of melanophores along tracheal sides and lateral sides of BFA are present.

*M. ornata* and *M. berdmorei* are similar in their oropharyngeal morphology (Wassersug, 1990). Both species of tadpoles were collected from pooled water in Thailand. Oropharyngeal morphology of *M. ornata* tadpoles collected form Rabwah, and Ghakkhar, District Gujranwala, differ from those reported from Thailand by Wassersug (1980), in important respects: the infralabial papillae are longer; filter plates are with more filter rows; BRA and BFA papillae are indistinct since their bases are coalaced into membrane; postnarial papillae are represented by a membrane; glandular zone mesially divided; single preglottal papilla. No silver shine is reported on the belly of the tadpoles from Thailand. Flower (1899) reported differences in the adult and larval morphology of *Microhyla ornata* from Malay peninsula and Siam. Liu (1950) reports dextral anal tube in *M. ornata* tadpole, which is straight<sup>e</sup> in the tadpoles collected from Pakistan.

### Ecological and Behavioural Adaptations of *Microhyla ornata* tadpole

*Microhyla ornata* tadpoles were collected at midmonsoon rains from deep ponds with heavy planktonic load. The environmental conditions at that time are favourable to allow rich growth of zoo and phytoplanktons, making the pond water light green in colour.

*M. ornata* tadpole is well adapted to lentic habitat. Its transparent body, with broad tail

fins and long filament, lateral eyes, median ventral spiracle and abdominal silvershine, are adaptations to nektic habits. A school of *M. ornata* tadpoles swimming at midstream, is almost invisible from outside, while abdominal silvershine make them invisible from inside water since the water surface when viewed from inside water, appears shiny due to the reflection of sunlight from it. The vibrant tail filament and median ventral spiracle help to support the midstream position of the tadpole. The broad caudal fins help the tadpoles to react almost instantaneously to any stimulus. Laterally placed eyes are efficient receptors for a tadpole swimming at midstream.

*M. ornata* tadpole constantly gulps-in water through its anterodorsal mouth opening. It is never seen nibbling at the submerged surfaces or resting at the bottom like *Bufo* and *Rana* tadpoles.

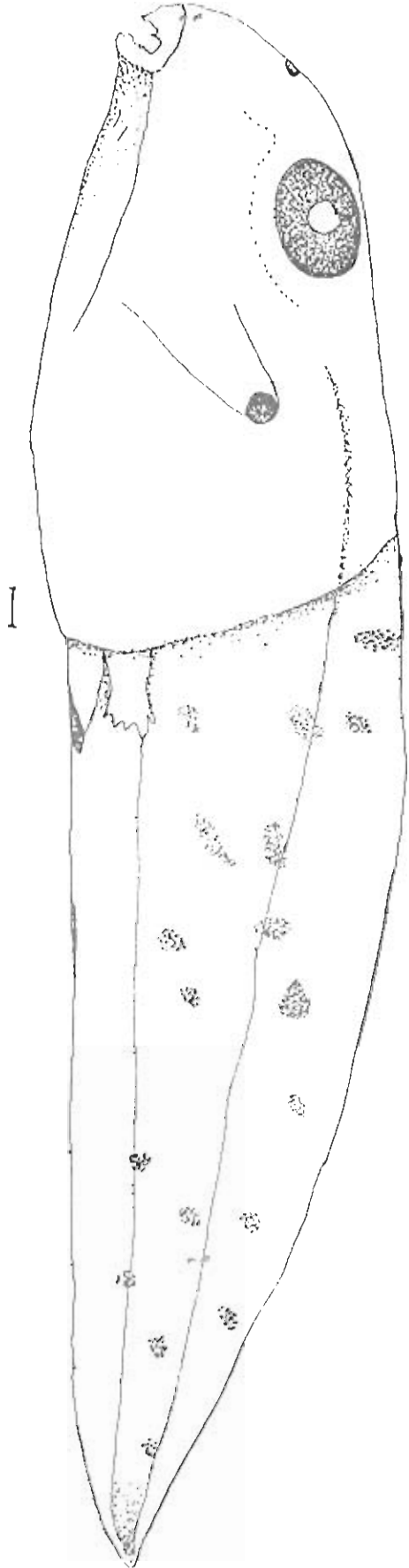


Fig. 14. *Rana cyanophlyctis* tadpole, lateral view. scale 1 mm.

## RANA CYANOPHYCTIS Schneider

*Rana cyanophlyctis* is most frequent frog to be found around water bodies throughout most of the southeast Asia and also extends into Middle East (Khan, 1968, 1980). Its unique habit of skittering on the water surface for considerable distances, fascinates equally an amphibiologist and a casual observer (Khan and Tasnim, 1987). It is thoroughly aquatic, littoral and resident frog, very rarely ventures out of water for foraging or to migrate from one drying pond to another (McCaan, 1932; Khan, 1979).

Its characteristic call heralds summer season in the plains of Punjab, and its cessation after monsoons indicates the onset of winter. The male calls while afloat in water. Axillary amplexus results in small batches of fertilized eggs, which soon sink or adhere to the submerged plants (Khan, 1982 b). Pruthi (1933) reports *R. cyanophlyctis* from ponds where salinity varied from 0.12 to 9.5 along salt mines of Khewra, District Jhelum, Punjab, Pakistan. However, in the localities from where present collection was made, pH varies from 0.6 to 0.7.

Large robust tadpoles with drab spotty colouration, of *Rana cyanophlyctis*, are difficult to be detected in the muddy pondwater, since they are solitary and confine to the roots of the pond vegetation. These tadpoles feed on debris and occasionally on vegetable matter or carcasses of water animals which have sunk down. Tadpoles kept in aquaria are seen attacking each other and those of other species, often larvivory results. However, this phenomenon in nature appears to be rare, since escape chances for each species of tadpoles are greater, mainly this tadpoles is detritivorous.

**Material:** Tadpoles for present study were collected during 1986-1987 from different localities along northwestern border of Rabwah City. The tadpoles were collected mostly in premonsoonal period from March to May. Tadpoles from Ghakkhar District Gujranwala, collected during 1967, and Manshera and Datta, District Manshera (Khan, 1979) were used for comparison.

**References:** Anderson (1985) described tadpole of *Rana cyanophlyctis ehrenbergi* from Arabia. Annandale and Rao (1918, McCaan (1932), Kirtisinghe (1957) and Mohanty-Hejmadi and Dutta (1975) have given brief description of the tadpoles of *R. cyanophlyctis*. Daniel (1975), Mohanty-Hejmadi and Dutta (1979) have commented on the breeding and the larval habits of this frog. There is no work on the anatomy of the oropharyngeal region of the tadpole of this frog.

**Tadpole** (Fig. 14): The tadpole is large, with broad muscular body and tail, which is one

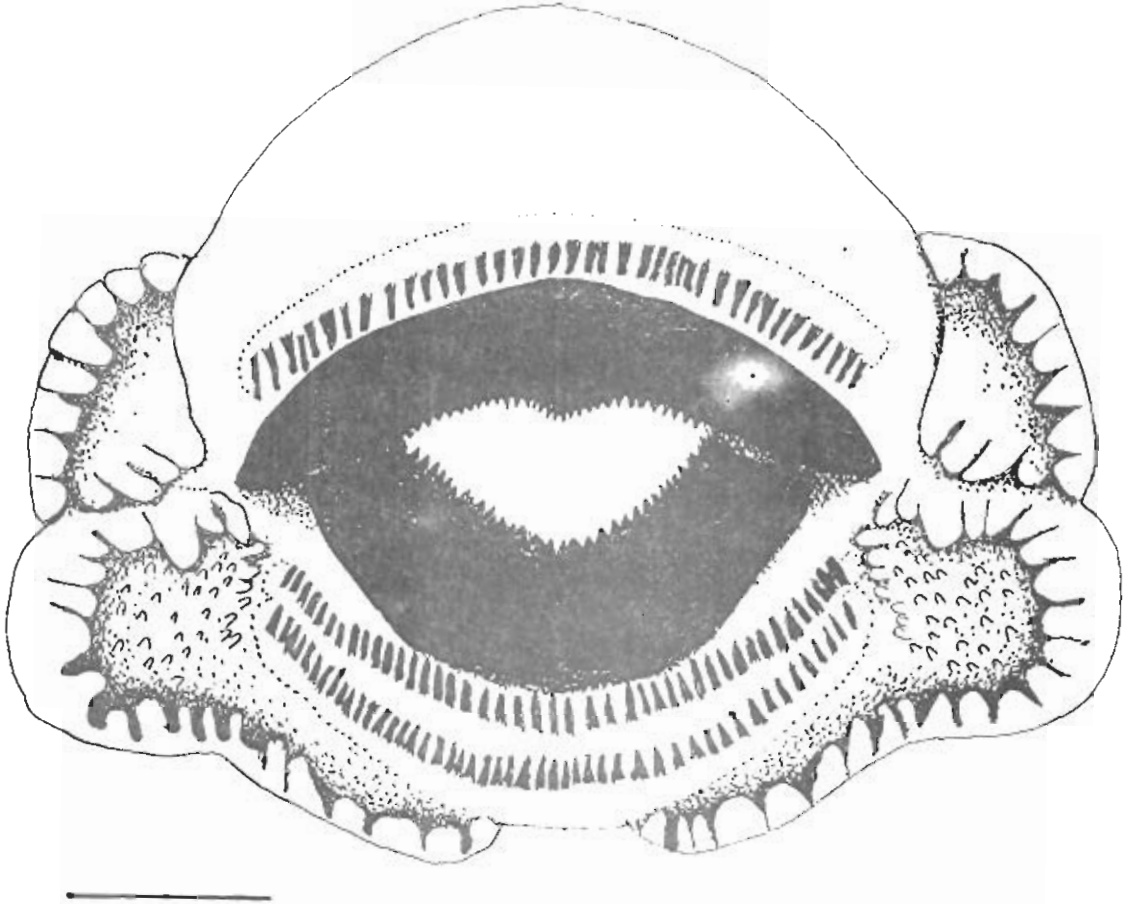


Fig. 15. *Rana cyanophlyctis* tadpole, oral disc. Scale 1 mm.

and a half to twice the length of the body. The body is broadest at midpoint, its venter is flat. The tail has a gradual taper, its pointed tip is turned upward. Tail muscle is broader than fins, dorsal fin is broader than ventral, both are parallel to the tail.

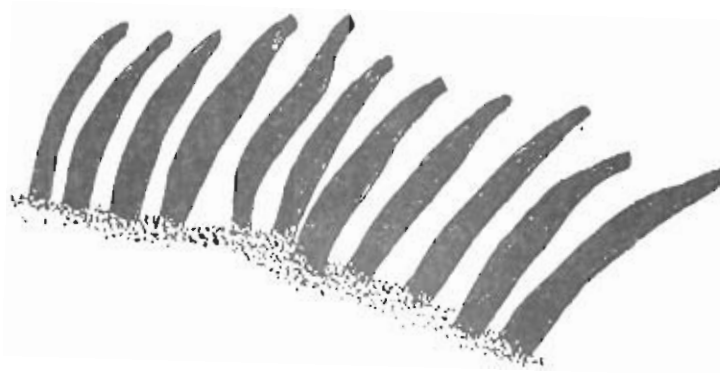
The eyes are large, and are a part of the lateral profile of the body. Full eye is not visible from dorsum, it is nearer to snout tip than to posterior end of body. The nostrils are small and are anterolateral, are a little closer to eyes than to snout. The spiracular opening is round, located on the left side of the mid-body, it is nearer to the posterior end of body than to the tip of snout. The spiracle tube is long, fused with lateral body wall at an angle of 30° to the longitudinal axis of body. The anal tube is wide, depressed, its dextral or sinistral position unclear. The oral disc is well developed and antero-ventral in position.

The body dorsum is drab coloured, with distinct melanophores all over, tail and fins are with dark blotches.

*Measurements:* (in mm) Body length 17.2-18.4; tail length 22.98-23.8; total length 40.18-42.2; greatest breadth of the body 9.9-9.3; greatest depth of body 29.2-31.6; interorbital space 2.98-3.1; internarial space 1.99-2.3; tail muscle height at base 4.4-4.9; greatest breadth of the dorsal fin 2.8-3.2 and of ventral fin 1.6-1.8.

*Oral disc* (Fig. 15): The oral disc is a prominent feature of the ventral profile of the body of the tadpole. It is roundish, broader than long, with broad anterior and narrower posterior labium. The anterior labium is arched and non papillated. A single row of keratinized dark brown teeth line its outer border. There are two rows of teeth on the posterior labium. Dental formula of *Rana cyanophlyctis* tadpoles is 1/2. Each tooth is a long structure, almost squarish in transverse section and mesially curved, with blunt tip. The teeth are arranged in a single row. The size of the tooth varies from 0.13 to 0.34 mm (Fig. 16).

Beak is prominent part of the oral disc, anterior part of it is broadly arched dark brown keratinized plate, with sharp fine ciliated cutting edge, mesially it is produced into a ciliated low tooth. Posterior part of the beak is similarly broad and V-shaped. There is a pair of distinct labial palps on each side of the oral disc. Posterior palp on each side is narrowly separated from its fellow along posterior border of the oral disc. The free margin of the palps is cut into thick papillae which are bent orally. A group of small pustulations is enclosed by the posterior labial palp on each side of the oral disc (Fig. 15).



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Fig. 16. *Rana cyanophlyctis* tadpole, teeth. Scale 0.5 mm.

### Description of the oropharyngeal region

The roof of the buccal cavity extends far forwards over its floor due to the overbite of the anterior beak, since the oral disc is anteroventral in position.

*Ventral buccal* (Fig. 17): Ventral buccal is longer than broad, with a distinct lateral bulge at middle. A pair of palmate infralabial papillae <sup>arise</sup> from lateral side of the prelingual chamber, <sup>lie</sup> one behind the other. Each infralabial papilla is produced into 5-8 filiform processes, which extends across the prelingual chamber, their tips do not touch each other. In addition, there are many pustules in the prelingual arena at the base of the lower jaw. The lingual analage is transversely oval, with a median notch, a pair of lingual papillae with bifurcated tips arise from its middle, a similar pair of papillae lie at the anterior side of the tongue analage, just at the orifice of the preoral chamber into BFA. The lingual analage lies between prelingual and buccal floor arena, the narrow passage goes round it to enter BFA.

The BFA (buccal floor arena) is longer than broad, mesially it bulges out. The postlingual part of it is raised from its general floor. The BFA has many papillae of varying sizes which could be sorted out as long, medium sized pustulations. The pustulations lie at the center of BFA and extend mesially well to the anterior half of the BFA, while larger papillae lie on the sides of it arranged in two to three rows. Most of these papillae are bifurcated at tips. Largest papillae form the inner-most row along BFA latrum <sup>and</sup> mostly have bifurcated tips. The bifurcated tips are mostly unequal, usually outer branch is smaller than the inner. Four to six larger papillae lie in the prepocket region which also have bifurcated tips.

The buccal pockets are conspicuous transverse structures, lying on the lateral side of the buccal floor, extending almost to 1/4th of the breadth of the BFA. Their lips are thin, the anterior lip almost flushed with the general surface of BFA, while posterior is little shallower, enclosing a thin slit. The buccal pockets are imperforate.

Broad lateral part of ventral velum gradually narrows down mesially. It is supported with moderately soft spicules. Its posterior border is jagged, with three equally placed peaks, a distinct median cleft is present. The glottis is distinct and exposed, slightly under the velum. Glottal lips are thin and the laryngeal disc is oval in shape.

The buccal glandular zone is distinct, it is spread all along the length of ventral velum, and it is 5-6 pit thick mesially and 2-3 rows thick laterally.

*Ventral pharynx*; The branchial region of *Rana cyanophlyctis* tadpole is triangular and

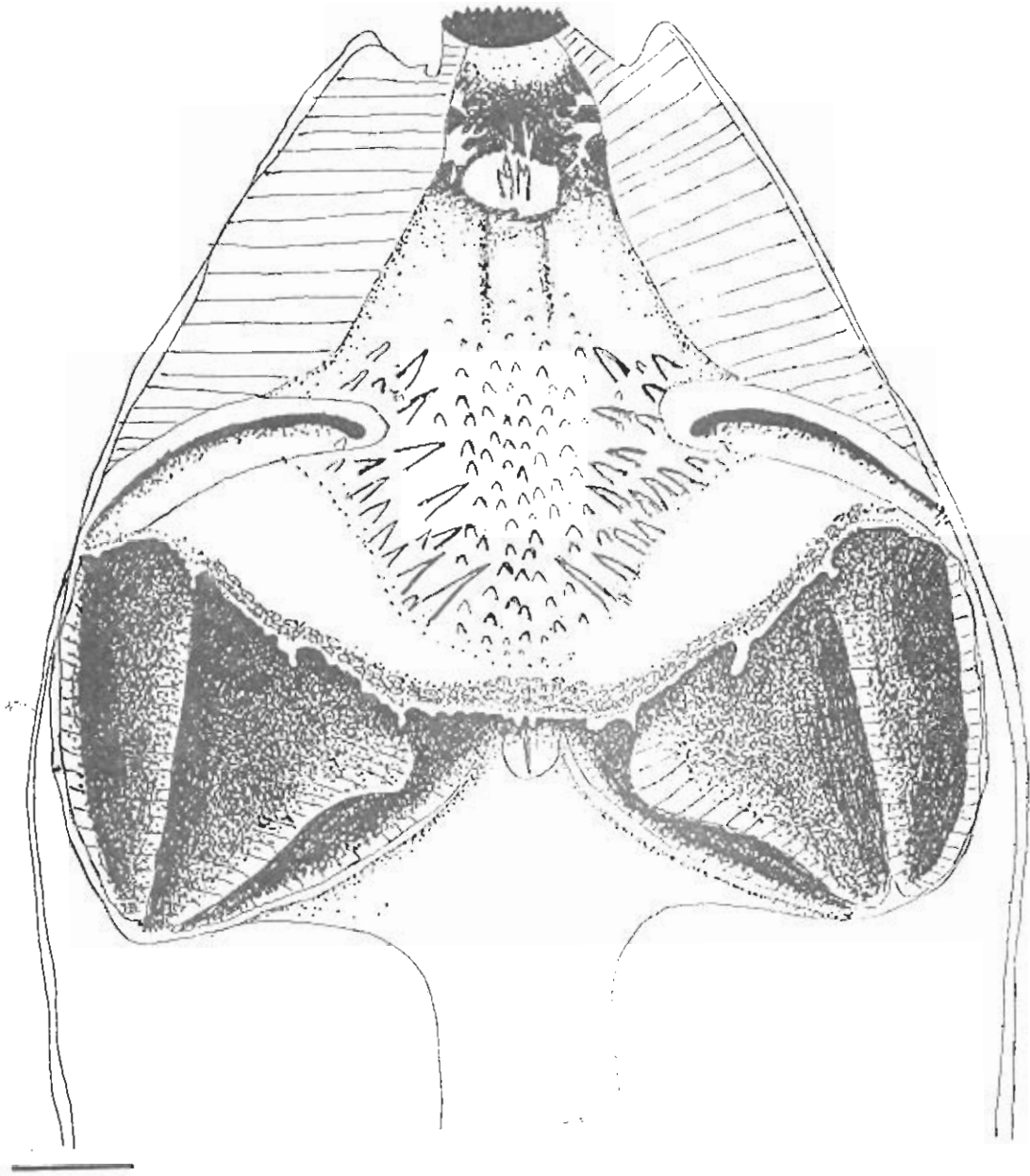


Fig. 17. *Rana cyanophlyctis* tadpole, buccopharyngeal floor. Scale 1 mm.

is more lateral than median. There are distinct three deep filter cavities, first is longest and deepest and broadened mesially, anterior one third is under velum. The second filter cavity is shallower, mesially broad and about 1/4th under velum. The third filter cavity is narrowest, squeezed mesially due to mesial deflection of the third filter plate, which partially blankets it. The third filter cavity is slightly under velum. The first filter plate forms the outermost border of the branchial basket while the fourth plate the inner most. The first filter plate is longest and slightly concave, not attached to the velum, while second is straight and attached, the third is broadest and almost horizontally disposed and is attached, mesially it is broadened and blankets the third filter cavity. The filter plates bear 6-16 filter rows (see Table V). The filter rows of the second filter plate continue with those of the third plate along the floor of the second filter cavity.

Filter rows are quite separated from each other, the filter ruffle shows 3 degree foldings. The filter canals are open, and the adjacent filter rows do not abut over them. The filter canals are deeper than broad. There are no branchial food traps. Subvelar surface is covered with fine parallel transverse secretory ridges, all over.

The esophageal funnel is broad anteriorly, narrowing abruptly posteriorly.

*Dorsal buccal* (Fig. 19): Dorsal buccal of *Rana cyanophlyctis* tadpole is longer and spacious than ventral buccal. It is longer than wide. The prenarial arena is considerably enlarged anteriorly and has a deep roof, due to the overbite of this part of the dorsal buccal over ventral buccal. A series of 4-5 hard pustules, on each side of the prenarial arena, extend forwards to

**Table V. Branchial region of *Rana cyanophlyctis* tadpole at Stage 35 (data from 10 specimens)**

Ceratobranchial (cb) supporting filter plate	Length of filter plate	Breadth of the filter plate	Filter rows on the filter plates
cb. 1	2.2-2.3	1.1-1.15	14-16
cb. 2	2.6-2.65	0.85-0.9	12-14/10-11
cb. 3	2.3-2.5	1.0-1.12	13-14/10-12
cb. 4	1.4-1.9	0.7-0.8	6-7

become continuous with each other in the roof of prenarial arena through a transversely placed

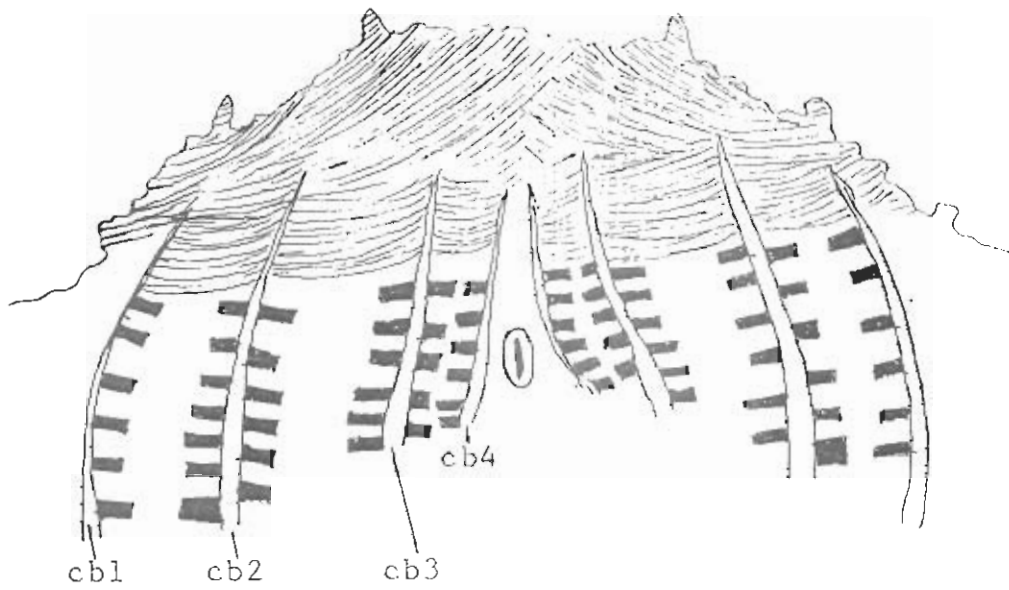


Fig. 18. *Rana cyanophlyctis* tadpole, subvelar secretory tissue and attachment of filter plates, diagrammatic.

larger rostral pustule.

Internal nares are conspicuous structures of the anterior buccal, each is an oblique slit, lying at an angle of  $30^\circ$  to the longitudinal axis of the dorsal buccal. The nares are twice as long as broad, with equally developed narial valves. There arises a fine tipped long prenarial papilla from the middle of the prenarial valve. The Prenarial papilla is covered all over with bluntings. There are 15-20 pustules in the internarial region. The postnarial arena is large, much broader than long. A series of five postnarial papillae arise from just posterior to the inner nares, which can be distinguished into an inner group of three larger fine tipped papillae with bluntings on sides and a group of two outer smaller similar papillae. Tips of the papillae of either side narrowly miss each other mesially. The bases of all postnarial papillae are broad and have a gradual taper.

The median ridge is thrice as broad as deep, with gradually inclining <sup>in</sup> sides and tipped by a long papillary process, some times a pair of such processes are present. The median ridge is covered with bluntings all over it. There is a large lateral ridge papilla extending mesially from each side. It is fine tipped, with bluntings on sides, its tip narrowly misses the sides of the median ridge on each side.

The BRA in *Rana cyanophlyctis* tadpoles is wide bowl-shaped, wider than long. BRA papillae are few, three on each side arranged in a row on the lateral sides of BRA. Each papilla is long, almost of the size of the lateral ridge papilla, with fine tip and bluntings on sides. A row of 4-8 smaller fine tipped extra BRA papillae lie on their outside. Moreover, There are numerous pustules scattered all over BRA, extending onto the extra BRA. The glandular area is distinct dark strip due to concentration of melanophores, lining the base of velum. The melanophores are scattered among the secretory pits. The glandular strip is 5-6 pit deep all along dorsal velum. Dorsal velum is broad on sides, it gradually narrows mesially where it continues with that of other side through a low staggering ridge with papillated broken border. The pressure cushion are distinguishable, the outer most is large and thick, while the inner one is inconspicuous. The ciliary groove is not resolveable.

*Lungs* (Fig. 32, D). Lungs of *Rana cyanophlyctis* tadpole at Stage 35 are large, they extend along the abdominal dorsum to the end of the abdominal cavity. The laryngeotracheal chamber is swollen on lateral sides into balloon-shaped chambers, to which lung is attached on its caudal end. Each lung is narrow, much narrower than the laryngeotracheal chamber. It gradually tapers posteriorly. Each lung is dark, with distinct air chambers, which are well marked on its surface.

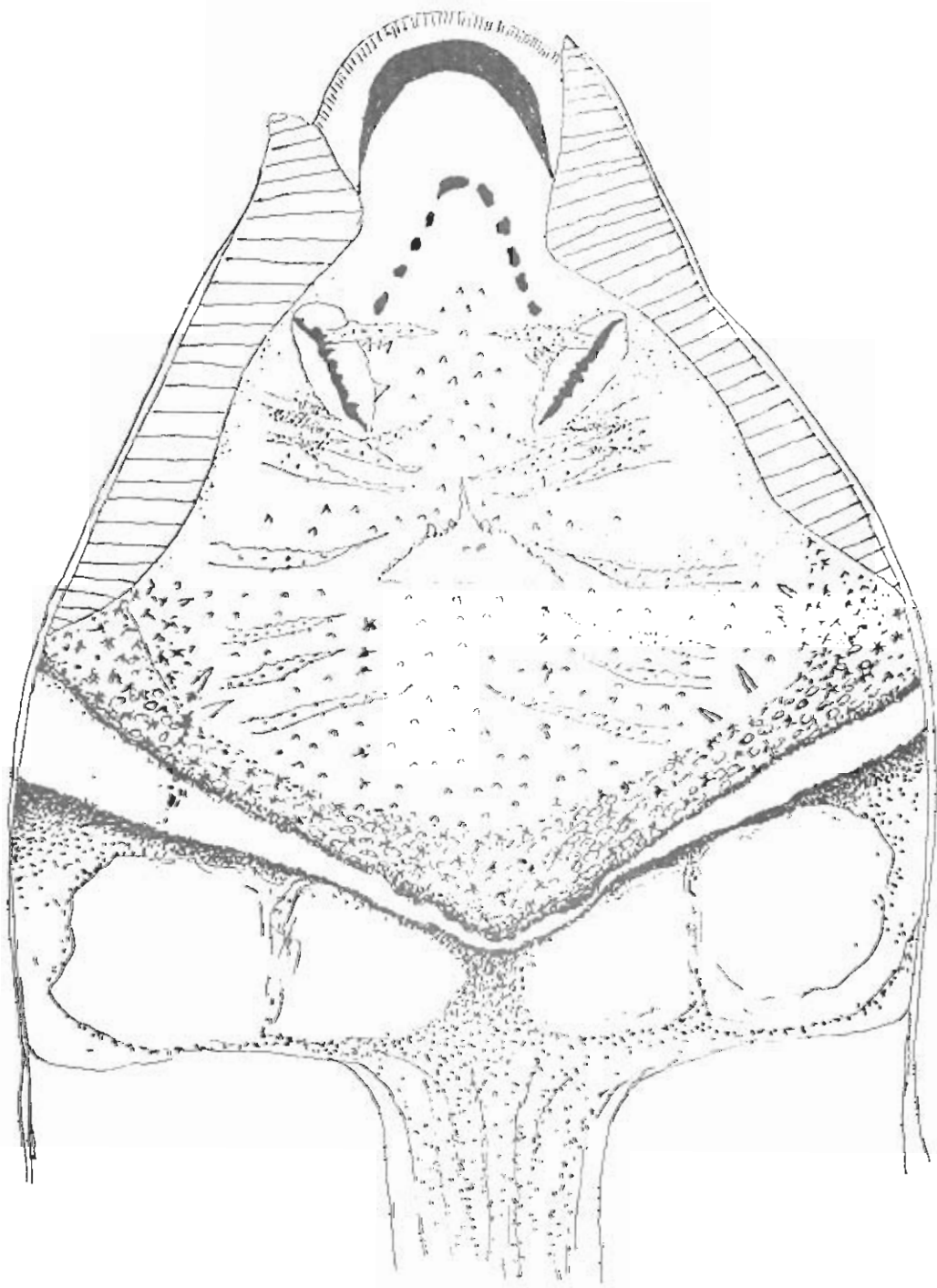


Fig. 19. *Rana cyanophlyctis* tadpole, buccopharyngeal roof. Scale 1 mm.

## Diagnosis of *Rana cyanophlycits* tadpole

*R. cyanophlycits* tadpole is distinguished, from those of its congener *ranid* and of other anuran species, by the following features:

1. The oral disc is anteroventral in position, with dental formula 1/2. A pair of well developed lateral palps fringed with papillae are present.
2. The teeth are long curved rods, squarish in transverse section with blunt tips. There are no cusps.
3. The beaks are broad, with sharp ciliated edge.
4. The internal nares are oblique, with irregular orifice and swollen lips.
5. There is a single prenarial and five postnarial long fine tipped papillae, with bluntings all over.
6. The prenarial and narial arenas are large and spacious.
7. A row of hard pustules extends from internarial region to prenarial arena.
8. Two pairs of lingual papillae with bifurcated tips are present at the midlingual angle, while other lies anterior to it.
9. There are 15-20 simple BFA papillae on each side, longest, 8-10 papillae form the innermost row, while smaller ones the outermost.
10. BRA papillae are three in number, longest in the buccal cavity. They have bluntings on sides, and are arranged in a continuous row with a similar lateral ridge papilla on each side.
11. The median ridge is broader than deep, produced in one or two median papilla like long process.
12. There are pustules scattered primarily in the posterior half of the prenarial arena, all over the narial, postnarial and BRA, extra BRA and BFA area.
13. The branchial basket is 45% of the oropharyngeal cavity. There are three filter cavities visible in dorsal view, second is blanketing the third.
14. Full filter and partial filter rows form the filter mesh, which is moderately thick on the filter plates. These filter rows alternate with each other. There are filter rows on both sides of second and third filter plate.
15. Secretory region is quite extensive in the buccal cavity, running along dorsal and ventral velum. It is 3-6 pit deep. The subvelar surface is covered with parallel transverse fine secretory ridges.

There is considerable confusion in literature regarding the morphology of the oral disc of *Rana cyanophlyctis* tadpole. McCaan (1932) illustrates a typical *R. tigerina* tadpole as that of *R. cyanophlyctis* in Fig. 1, A,b; while in Fig. 1, c the shown oral disc in neither of the two species. However, morphology of the beak and the palatine plate is typical of *R. tigerina* tadpole. Daniel (1975) largely dwells on McCaan's work, inheriting its misleading informations concerning these tadpoles. Annandale and Rao (1918) have shown anterior labial tooth row largely interrupted mesially, while Altig and Johnston (1986) have quoted Kirtisinghe (1957) for dental formula  $1/2 (2)$  for *R. cyanophlyctis* tadpole from Sri Lanka. Perhaps these differences in the morphology of this tadpole are due to geographical races of this widely distributed southeast Asian littoral frog.

### Ecological adaptations of *Rana cyanophlyctis* tadpole

Benthic thigmotactic tadpole of *Rana cyanophlyctis* has been collected from a variety of habitats. However, this tadpole prefers shallow pond habitat, with vegetation and detritus accumulating at the bottom in the form of decaying plant and animal material, bacteria, infusoria etc. This tadpole avoids main water stream by retiring to the ephemeral pools and puddles along the course of water channels. The oropharyngeal morphology of this tadpole combines characters of a pond as well as stream adapted tadpole. Benthic thigmotactic habits enable *R. cyanophlyctis* tadpole to invade wide range of different types of water bodies. Its well developed lungs which develop early in life, enable it to live in oxygen deficient benthic environs of deep pool habitat. For respiration, the tadpole rises periodically to the surface of water. The ascending and descending movements of the tadpole are very quick, since during these movements it is exposed to attack by its enemies. In the ephemeral shallow pond habitat which is rich in Oxygen and is not rich in detritus, this tadpole lives on phytoplanktonic bloom seldom going to surface for respiration.

*Rana cyanophlyctis* tadpole remains solitary throughout its life. When concentrated, in drying ponds, they are aggressive to each other, a habit primarily developed to avoid sharing the potential grazing area at the bottom. Crowding tadpole lose pieces of their tails to siblings. On disturbance they quickly hide themselves under the debris accumulated at the bottom of pond, producing a dense suspension of particles which cloud the water to deter the enemy.

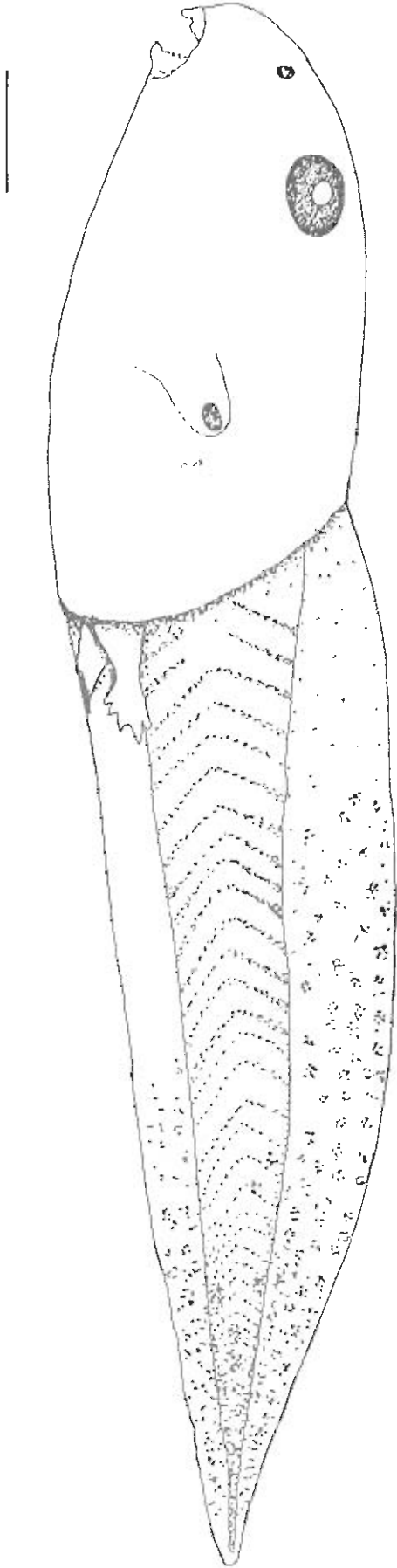


Fig. 20. *Rana sylvatica* tadpole, lateral view. Scale 1 mm.

*RANA SYHADRENSIS* Annandale

*Rana syhadrensis* is a small inconspicuous frog. It frequents marshy grassland, vegetation around irrigation channels, torrents, and permanent ponds (Khan, 1979; Khan and Tasnim, 1987). It is rarely seen away from its aquatic habitat. It readily jumps in water to escape from its enemies, but comes out quickly and hides in the vegetation around. Its small size (40 mm) makes it inconspicuous and difficult to detect in the grass. However, during breeding season, at midmonsoon, its characteristic call indicates its abundance in an area. The call is a repeated note, giving an impression of clatter produced during typing or telegraphy. The calling male perches well away from water (Khan and Malik, 1987 b). The spawn floats for some time then sinks in the deep water (Khan, 1982 b).

The tadpole of *Rana syhadrensis* is delicate, thin, light brown creature, with spotted tail. It keeps well away from the marginal water, it does not go into the deep water. It feeds primarily on vegetation, occasionally takes animal diet when available. This tadpole is quite active and agile, making for the submerged vegetation when disturbed.

*Material:* Tadpole of *Rana syhadrensis* for the present study, were collected during 1986-1987 from different localities along northwestern border of Rabwah City. Tadpoles of this frog which were collected in 1976 from Datta and Manshera, N. W. F. P. were used for comparison.

*References:* Short notes on the description and habits of this species in literature (Van Kampen, 1909; Annandale and Rao, 1918; Liu, 1950; Khan, 1982 a). Khan and Malik (1987 b) have reported on the breeding ecology and larval habits of the frog. So far no study has been made on the oropharyngeal morphology of *Rana syhadrensis* tadpole.

*Tadpole* (Fig. 20): The tadpole is delicate, with long oval body which is broadest and deepest at the middle. Its ventrum is convex and anterior half of the body is flexed forwards and upwards. The eyes are dorsolateral and are nearer to the snout than posterior border of the body, are visible from dorsal and lateral sides, but not from ventral side. The nostrils are small and are nearer to the tip of snout than to eye. They are dorsolateral, visible from dorsal and lateral sides. The snout is broadly obtuse, slightly projecting over the oral disc which is moved ventroanteriorly.

The spiracle tube is distinct, short and fused with lateral body wall. The spiracle opening is oval lying at midleft of body. The tail is long, about one and half to twice the length of the body, it is broadest at the base, has a gradual taper with an acute pointed tip. The dorsal fin is broader

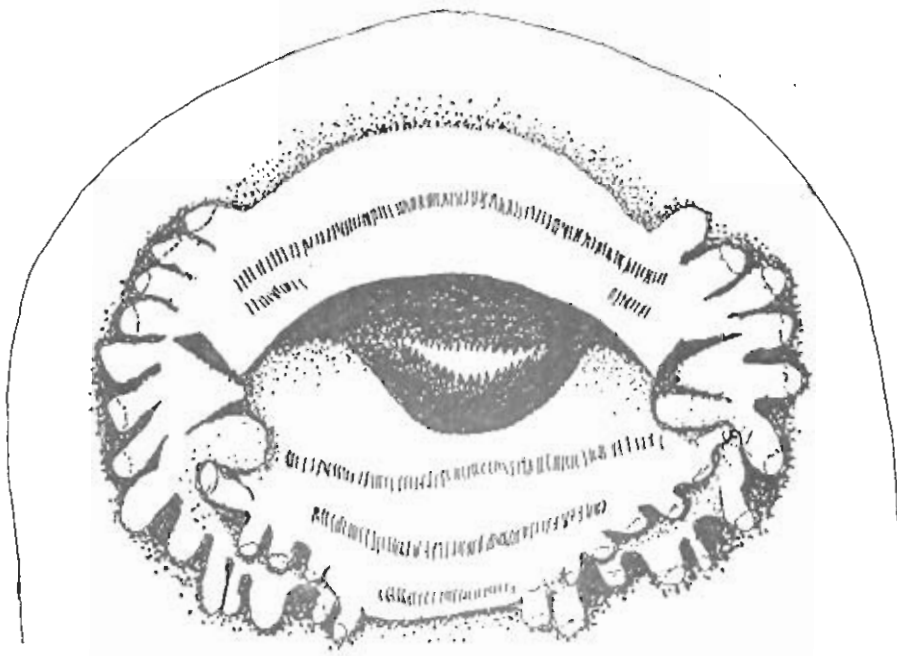


Fig. 21. *Rana syhadrensis* tadpole, oral disc. scale 1 mm.

with wavy outline, is broadest at middle. The ventral fin is less broad with a constant breadth throughout its length. The anal tube is distinct, with a slight leftward flex.

*Colouration*: Specks of melanophores adorn the outer margin of the fins, are more concentrated on the posterior half of it. The body is light brown on dorsum, white along ventrum.

*Measurements* (in mm): Body length 7.2-7.6; tail length 11.0-11.2; interorbital space 1.6-1.8; internarial space 1.0-1.1; greatest breadth of body 4.6-4.8; depth of body 3.8-3.9; tail muscle height 2.4-2.5; dorsal fin height 1.3; ventral fin height 0.8-0.9.

*Oral disc* (Fig. 21): The ventro-anterior flexure of the buccal floor has pushed the oral disc, so that it is more anterior than anteroventral. The oral disc is wider than long. Anterior labium is narrower than the posterior. There are well developed papillated oral palps on the lateral sides, without a distinct emargination. papillae on the posterior side of the posterior labium are narrowly interrupted mesially. The papillae do not extend in the anterior of the anterior labium. The papillae are thick, cylindrical with blunt tips.

The anterior labium is with a continuous row of keratinized dark brown teeth, while the second row is small on each side as it is broadly interrupted mesially. The posterior labium is with three complete rows, the third, which is the outermost, is very small, about  $\frac{1}{3}$  of the size of the first two. The teeth are uniserial in arrangement. Each tooth consists of three tiers of similar pieces, one lying on the other, one at the top is in use. Each piece (the functional tooth) is less than 0.5 mm in length, with free flattened tip, which is orally curved and produced into three sharp cusps on each lateral side. The base of the tooth is cylindrical and embedded in a muscular pad (Fig. 22). The dental formula for *Rana syhadrensis* tadpole is  $2(2)/3$

The beak blades are thin and delicate. The anterior beak is broadly arched with fine ciliated edge, while lower is V-shaped and has a ciliated sharp edge. The lateral flaps of the oral disc are thick with no apparent emargination and are produced into thick filiform papillae. the papillae along the posterior flap are arranged in a double row on each side of the oral disc. At the commissure of the beaks, on each side, there are thick lobulations of this part of the oral disc, alternating with deep furrows.

### Description of the Oropharyngeal region

*Ventral buccal* (Fig. 23): The ventral buccal of *Rana syhadrensis* tadpole at Stage 35, is triangular. It is narrower anteriorly and broader posteriorly with base bowed out. The prelingual



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Fig. 22. *Rana syhadrensis* tadpole, teeth. Scale 1 mm.



arena is small and narrow, with a pair of short infralabial papillae on each side, of which the anterior papilla is a narrow palm produced into short cirrations on its free margin. The posterior infralabial papilla is also palmate with 4-5 longer cirrations.

The tongue analage is indistinct, is in the form of a slight thickening located at the anterior, mesial part of the BFA. There are four attenuated simple lingual papillae arising from the center of the analage and are arranged in a transverse row.

The buccal floor arena (BFA) is bowl-shaped, it is wider anteriorly narrower posteriorly with a deep floor. Its middle part is quite spacious in the middle. Overall it is wider than long. There are four BFA papillae arranged in a staggering row on each side of the BFA, and are all mesially directed. The middle pair consists of longest papillae, each with one blunting at the middle and a bifurcated tip, while first, third and fourth pairs are simple, smaller with fine tips. The BFA papillae of *Rana syhadrensis* tadpole are fine, unlike those of other tadpoles studied. About 30-35 pustules are scattered at the center of BFA and few extend on to the bases of BFA papillae. There are about 8-10 prepocket pustules on each side of BFA. A pair of mole like tubercle lies at the midanterior region of BFA. The buccal pockets are oblique, narrow and form an angle of 75 with the longitudinal axis of ventral buccal. The anterior lip of buccal pocket is thick and its inner tip curved inwards like a strong hook. The posterior lip is indistinct and flushed with the general surface of the BFA. The perforation of the buccal pockets is difficult to ascertain.

The ventral velum is a distinct, uniformly broad strip. Its anterior border is indented at the level of second filter plate, while posterior border is considerably irregular. There is a distinct median notch over the glottis, which is half exposed.

Velar buccal surface is covered over with secretory pits. The subvelar surface on the other hand is covered with fine, parallel transverse ridges, spreading across it. A distinct torus is present between second and third filter plate under the ventral velum (Fig. 24).

*Ventral pharynx:* The pharyngeal basket is about half the size of the ventral buccal. It is more lateral than mesoid in disposition. Each branchial basket has a distinct lateral bulge which gradually narrows down mesoid. The basket are broader than long.

Two branchial cavities are visible in dorsal view, first lying between first and second filter plates, is the longest and deeper, about 1/4th of it is under the velum, while second is transversally enlarged, formed by the coalesce of the second and third filter cavities. It is shallower than the first. Its about one third part is under the velum. The filter plates vary in length from 1.3-1.5 mm. the first filter plate is vertically and longest, not attached to the velum, while second is narrower

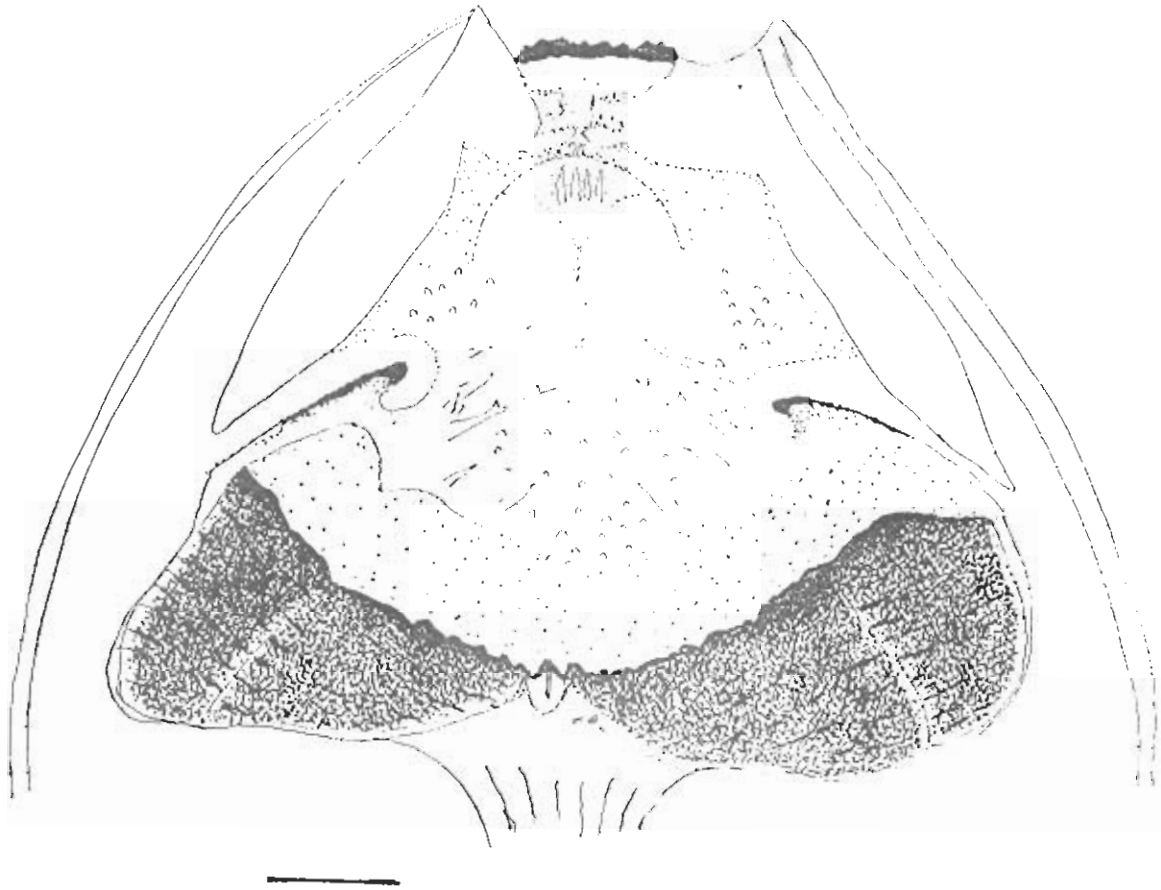


Fig. 23. *Rana syhadrensis* tadpole, buccopharyngeal floor. Scale 1 mm.

and vertical, slightly attached with the velum (Fig. 24). The third and fourth filter plates are horizontal, they abut along their bases. Number of filter rows in the filter plates vary from 5-14 and are widely spaced (see Table VI). The filter rows are on one side of all the filter plates.

The filter ruffle is moderately developed with 2 degree foldings. The filter canals are open and are as wide as deep or deeper than wide. Generally the filter mesh is loose due to small number of filter rows on the filter plates.

The esophageal canal is moderately broad. The lungs at Stage 35 are well developed, with

**Table VI. Branchial region of *Rana syhadrensis* tadpole at Stage 35 (data from 10 specimens)**

Ceratobranchial (cb) supporting the filter plate	Filter plate length	Filter plate breadth	Filter rows on filter plates
cb. 1	1.4-1.5	0.4-0.42	13-14
cb. 2	1.25	0.5-0.53	7-8
cb. 3	1.0	0.6-0.63	7-8
cb. 4	0.8	0.7-0.7	4-5

alveolar chambers, filled with air and have papery thin walls.

*Dorsal buccal* (Fig. 25): The dorsal buccal of *Rana syhadrensis*, at Stage 35, is pear shaped. it is anteriorly narrow and widens posteriorly, and is longer than <sup>a</sup> wide. The prenarial arena of this tadpole is dome-shaped, and is as broad as long, due to the overbite of the upper beak. On each side, a lateral row of 4-6 small tubercles converge mesially in the midprenarial arena and become continuous with each other.

The internal nares are prominent feature of the narial arena. Each nare is a distinct transverse slit. The anterior narial valve is narrower than posterior. The anterior valve is produced into a distinct process with ciliated tip, in the middle, representing the prenarial papilla. The postnarial papilla is longer, mesially directed, lying between postnarial valve and the lateral ridge papilla. It is all over tuberculated. The midinternarial side of the narial valves is produced into 4-5 ciliated processes. The postnarial arena is much broader than long. The lateral ridge papilla is longest, with ciliated anterior face and three ciliated bluntings. There are 8-10 pustules in the

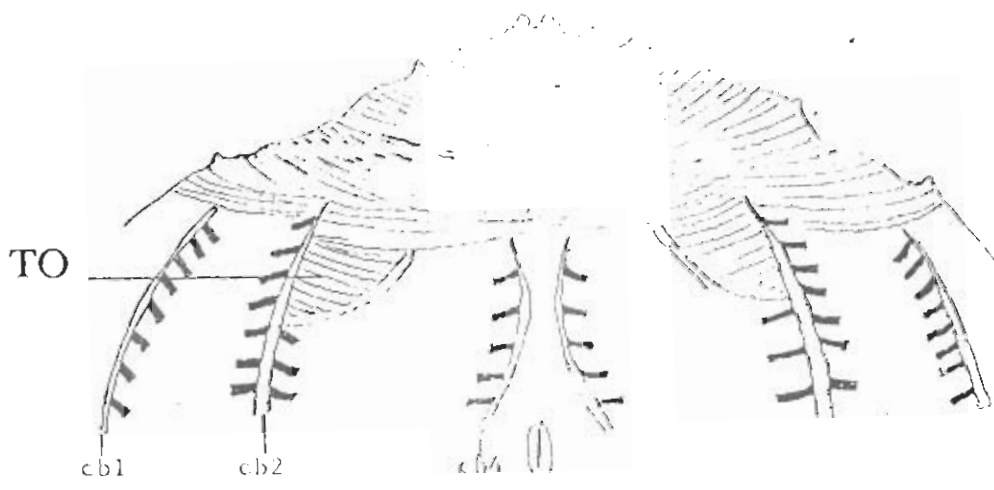


Fig. 24 *Rana syhadrensis* tadpole, subvelar secretory tissue and attachment of filter plates, diagrammatic. For abbreviations see page 11.

midpostnarial arena. The median ridge is low, thrice as broad as deep, with ciliated free edge.

The buccal roof arena (BFA) is spacious, and gradually broadens posteriorly. There are three long attenuated BRA papillae, with fine tips arranged in a lateral staggering row. The anterior two pairs of BRA papillae are longer than last pair, about twice their size. At mid BRA there are 40-45 pustules, uniformly scattered, concentrated in the posterior buccal. The dorsal buccal glandular zone is a thick broad band, with many scattered melanophores, especially along its lateral sides. The glandular strip bounds BRA along posterolateral sides. The dorsal velum is wavy and gradually narrows mesially, where it is separated from that of the other side by a wide gap equalling the breadth of the median ridge. The outer pressure cushion is thick and broad, indistinct from second and third which are coalaced and transversely disposed. The ciliary grooves are not resolveable.

### Diagnosis of *Rana syhadrensis* tadpole

Characteristic features of oropharyngeal region of tadpole of *R. syhadrensis* are as follows:

1. The oral disc is ventro-anterior, with lateral palp and a fringe of characteristically thick blunt papillae along lateral sides.
2. The dental formula for this tadpole is 2 (2) /3. A tooth consists of three tiers of similar tooth-pieces, the one at the top is functional.
3. The tooth piece has a cylindrical base, with spatulated free part produced on sides into three sharp cusps.
4. The beaks are narrow plates with sharp ciliated edges.
5. There are two pairs of flat infralabial papillae with free sides finely ciliated.
6. The nares are small and transverse with well developed valves. The prenarial valve has a short flat papilla with ciliated edge. The mesial border of the narial valves is produced into fine ciliations.
7. There is a single postnarial papilla posterior to the postnarial valve, with bluntings all over it.
8. There are four BFA papillae, on each side, which are long and simple, the second papilla is longest and fine with a pair of sharp bluntings on its anterior side.
9. There are three pairs of BRA papillae, which are simple and attenuated, and have fine tips.
10. A single lateral ridge papilla, on each side, is longest with three bluntings on its anterior side,

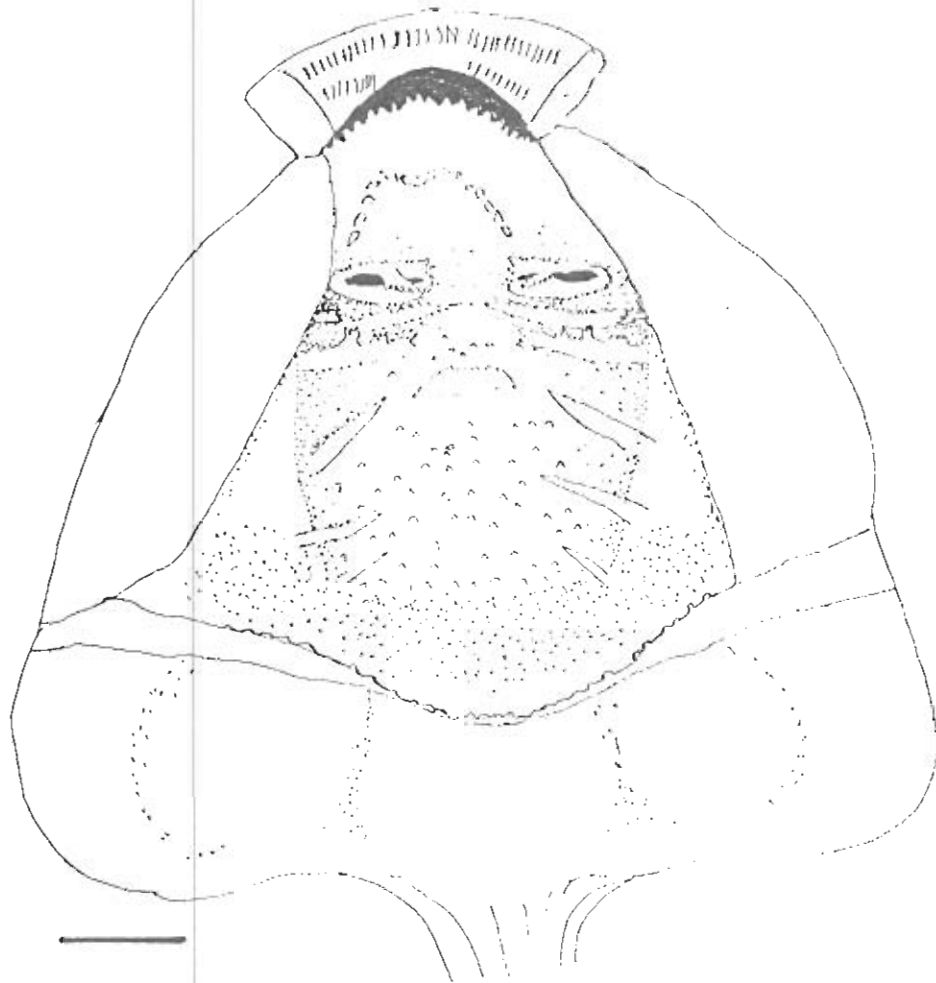


Fig. 25 *Rana syhadrensis* tadpole, buccopharyngeal roof. roof. Scale 1 mm.

The bluntings are ciliated, similar to the tip of the papilla.

11. The median ridge is low, about four times as broad as deep, with ciliated free margin.
12. The branchial basket is 25% of the length of the oropharyngeal region, with two filter cavities.
13. There are only primary filter rows, 4-14 on a filter plate. The filter ruffle has low density.
14. The buccal glandular zone extends along ventral and dorsal velum in the buccal cavity. It consists of fine pits. The subvelar tissue consists of fine parallel secretory ridges, which in second filter cavity, form<sup>s</sup> a distinct torus.
15. The buccal pockets are hook-shaped at inner end, and are feeble. Posteriorly they are flushed with the floor of BFA.
16. The lingual analage is with four simple papillae.
17. The BFA and BRA are broader than long and are wide trough-shaped.

Annandale and Rao (1918) gave dental formula for *Rana syhadrensis* tadpole as 2 (2) / 13, apparently 13 is a misprint. Boulenger (1920) mentioned one pre and two postoral tooth rows, while in another specimen he records five tooth rows.

The Fig. 78, in Liu (1950) shows tadpole of *Rana limnocharis* in lateral view, it closely resembles that of *R. syhadrensis*.

### Ecological adaptations of *Rana syhadrensis* tadpole

*Rana syhadrensis* tadpoles were collected from shallow seepage pools and water channels with standing water and rarely from large pools and ponds. The tadpole is seen making up and downward movements periodically in the water, as if trying to stay for long period in the water column. Moreover, the tadpole gulps-in water constantly as *Microhyla ornata* tadpoles do. It also feeds on the submerged vegetation. Apparently this tadpole is capable of feeding on fine planktonic particles which are suspended in water column, as well as coarse vegetative material which it scrapes from the submerged surfaces with the help of its keratinized mouthparts.

The buccopharyngeal processing of coarse as well as fine planktonic particles, is clearly depicted by the oropharyngeal morphology of *R. syhadrensis* tadpole. There is reduction in BFA and BRA papillation, fine ciliations on buccal papillae, low filter mesh on filter plates depicts that the coarse food particles on which this tadpole feeds is of moderate size. On the other hand efficiency of mucous entrapment system is depicted by the fine porosity of buccal glandular surfaces, fine ridged pattern of subvelar secretory tissue and specialization of subvelar ridges into

a distinct food trap in the form of a distinct torus, which indicates specialization of this tadpoles to feed on ultra fine particles.

*Rana syhadrensis* tadpole is mainly adopted<sup>a</sup> to stream habitat, where a constant washout of the planktonic nutrient takes place, and for some time the tadpole had to live on scrappings from submerged surfaces. Monsoon period is unpredictable in the temperate environs of the plains of Punjab, Pakistan. Some time rain comes in the form of continuous showers almost daily, while at times it is intermittent, there being several days between two showers. Small pools and puddles get dried before the next spell comes, killing all the tadpoles at the site. *Rana syhadrensis* breeds in the paddy<sup>a</sup> fields, where a constant level of water is ensured, and it is rich in planktons (Khan and Malik, 1987 b).

*Rana syhadrensis* and its congeners (Dubois, 1984, recognizes 12 species) are widely distributed in the paddy producing areas throughout southeast Asia.

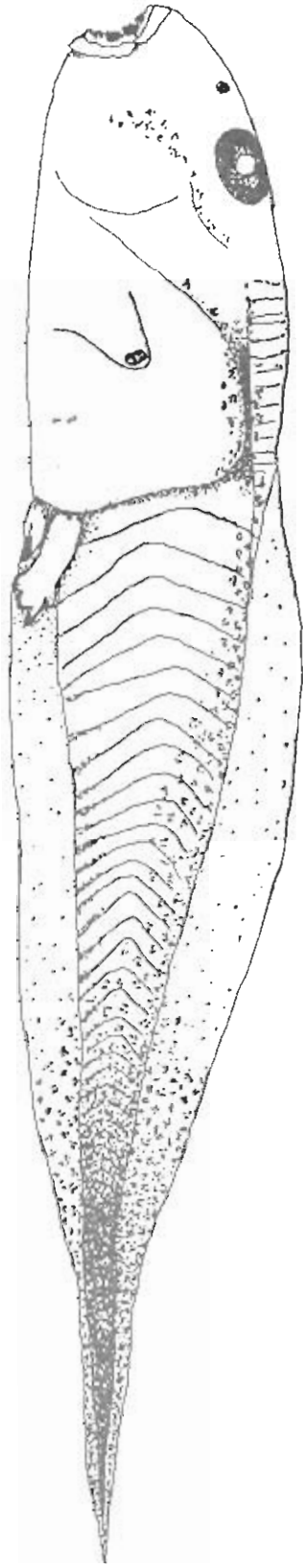


Fig. 26. *Rana tigerina* tadpole, lateral view. Scale 1 mm.

*RANA TIGERINA* Daudin

The "tiger frog" is the largest amphibian in the plains of Punjab. It frequents the marshy areas, grass around ponds and puddles (Khan and Tasnim, 1987). It is reported from throughout Pakistan and Azad Kashmir, except highland of Balochistan (Khan, 1976, 1979, 1980). Its usual habitat is marshy land with occasional puddles and thick to moderate vegetation, supporting various types of arthropod fauna, which forms its primary food. On slightest provocation, the frog jumps into the deep water and burries itself in the debris at the bottom. This frog is voracious feeder, feeding on a variety of food items (Khan, 1973).

*Rana tigerina* is a sporadic breeder. Breeding starts with first monsoon shower and lasts till midmonsoon (Khan and Malik 1987 b). Breeding males develop characteristic yellow body colouration. They gather in low lying areas to which the rain water is fast receding, and croak in chorus. Its characteristic nasal voluminous "cronk, cronk," is a common noise around marshy areas in Punjab, during monsoon rains. The eggs are laid in small loose patches, which float for some time, soon to sink in the deep water (Khan, 1982 b).

The tadpole of *Rana tigerina* has an elongated muscular nonbulging body. Its tail is very muscular, almost round in cross section, with narrow weak fins. The tadpoles are solitary, primarily carnivorous and are voracious feeder. Their primary food consists of tadpoles which may be of their own kind or of other amphibians, plus other creatures living in water (Mohnaty-Hejmadi and Dutta, 1981). It is never observed feeding on vegetation. Breeding time of *Rana tigerina* coincides with that of *Bufo stomaticus*, the larvae of which form the main food item of its tadpoles.

*Material:* The tadpoles of *Rana tigerina* were collected from different localities along northwestern border of Rabwah City, during early monsoon rains. comparative material was available from Ghakkhar, District Gujranwala and Datta and Manshera, N. W. F. P., collected during 1976.

*References:* Flower (1899) described and illustrated tadpole and its mouthparts, while Ferguson (1940) gave an account of the mouth parts supplementing that given by Flower. Several short notes on eggs and larvae of this amphibian have been appearing in literature (Annandale and Rao, 1917; McCaan, 1932; Minton, 1966; Daniel, 1975; Dutta and Mohnaty-Hejmadi, 1976; Mohnaty-Hejmadi and Dutta, 1981; Khan, 1982 b). Khan (1969) has arranged early development of *Rana tigerina* into stages. Khan and Malik (1987 b) have described the breeding habits and

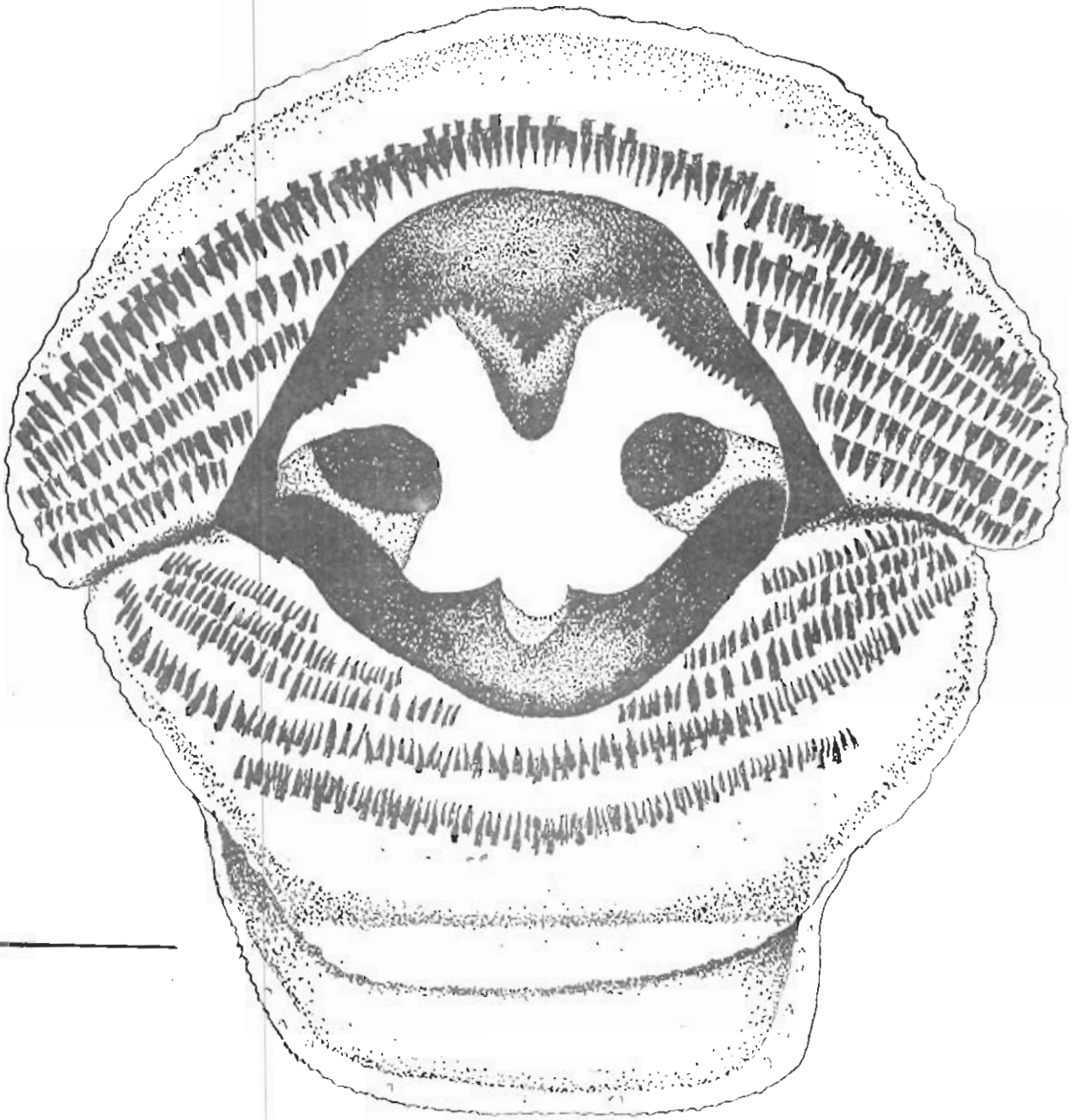


Fig. 27. *Rana tigerina* tadpole, oral disc. Scale 1 mm.

larval developmental ecology of this frog. Chako (1965) has reported in the metamorphosis of the hyolaryngeal apparatus of this tadpole, so far no work has been done on the oropharyngeal morphology of *Rana tigerina* tadpole.

*Tadpole* (Fig. 26): The tadpole of *Rana tigerina* at Stage 35 is a muscular creature, with an almost cylindrical body and tail. The body is oblong, almost as broad as high, without lateral abdominal bulge. the lateral abdominal walls of the sides are almost parallel to each other, while the belly ventrum is flat. The infraocular region, on each side, is distinctly bulging out, due to enormous development of the jaw musculature. At this point the body is widest. The snout is nearly semicircular, occupied by the oral disc, which is well developed, without a fringe of papillae. The teeth are biserial in arrangement, and the beak is quite strong. There are extra keratinized structures in the buccal cavity, keratinized tipped lateral spurs lie at the angles of the mouth, while there is a broad keratinized plate in the roof of the buccal cavity.

The eyes are large, dorsal in position, lying in the anterior half of the body. Small external nares are dorsolateral and are nearer to eyes than to the tip of snout. The spiracle opening is round, lying at the midleft of the body, nearer to the end of the body than to the oral disc. The spiracle tube is small, its base about three times as broad as the diameter of the spiracle opening. It is posterolaterally directed at an angle of  $45^\circ$  with the median axis of the body. The anal tube is mesial and collapsed, its dextral or sinistral position is not clear.

Tail is long, about two and half times longer than the body. The base of tail is almost as high as the body, subcylindrical and has an even taper. the posterior one fourth of the tail is much narrower, and is heavily pigmented. The tail is acutely pointed at the tip.

*Colouration*: The body is grey, melanophores are concentrated below eye and along body latrum. Dark specks are present on tail and tail fins, while the narrower posterior  $\frac{1}{4}$  part of the tail is heavily pigmented.

*Measurements* (in mm): Body length 12.5-13; tail length 24.5-25.9; total length 38.9-40; greatest breadth of body (at the level of eyes) 7-7.13; interorbital space 2.2, internarial space 1.6-1.8; tail muscle height (at base) 4.8-4.95; tail height (at midtail) 6.5; body depth 6.1.

*Oral disc* (Fig. 27): The oral disc of *Rana tigerina* lies at the anterior end of the body. It encloses a large, distinct circular area. The oral papillae are absent, the disc is emarginated on the sides. The anterior labium is broadly arched and has an outer complete and four inner broadly interrupted rows of keratinized biserial teeth. The inner most, fourth row is irregular, and it is about half the size of the outermost interrupted row. The posterior labium is with two outer most

continuous rows while inner three are broadly interrupted mesially. The second complete row is longest extending on to the full length of the labium. The dental formula for *Rana tigerina* tadpole is  $5(4+4)/(3+3)5$ . a typical tooth is 0.4 mm long. Its basal part is cylindrical, gradually tapering to the pointed tip.

The beak is prominent feature of the oral disc. It consists of anterior strongly arched keratinized half which is mesially produced on the anterior side into a large ciliated tooth, and posteriorly it encloses the anterior part of the prenarial arena. It is laterally produced into flattish flanks which enclose the lateral processes of posterior half of the beak. The free edge of the anterior beak is strongly ciliated. The posterior beak is thicker than anterior, it is mesially excavated into a U-shaped concavity. Its outer edge is sharp nonciliated, when beak is closed the median ciliated tooth of the anterior beak fits into concavity of the posterior part of the beak.

Extra keratinized surfaces are present in the buccal cavity of *Rana tigerina* tadpole. A pair of cylindrical long papillae lie on sides of the mouth opening. They are tipped with keratinized plates. A keratinized shield is present in the centre of prenarial arena (Fig. 31)

The oral disc is without papillae. The rim of the disc is indistinct. The posterior labium is broad and it is widened, when necessary, into a sucker (Fig. 27). In preserved material it is not distinctly observable.

### Description of Oropharyngeal region

*Ventral buccal* (Fig. 29): The ventral buccal of *Rana tigerina* tadpole at Stage 35, is longer than broad. The lateral walls of the buccal region are hypertrophied due to buccal musculature. The anterior half of the ventral buccal is narrower than posterior, which is much broader. The prelingual arena is elongate, separated from rest of the ventral buccal by a distinct lateral constriction. a series of three infralabial papillae are present on its sides, in its anterior half: the anterior most papilla is a broad flat palm, it is orally produced into 2-4 long, thick, blunt fingers, covered all over with tuberosities. The second and third papillae are long attenuated with pointed tips and overlap each other.

The tongue analage is distinct, transversely ovoid, with a pair of medium sized lingual papillae arising from its middle. The surface of these papillae is covered with tuberosities.

The buccal floor arena (BFA) is broader than long. There is a median longitudinal shallow groove in BFA, it dilates sideways in its posterior half. The BFA papillae are few and

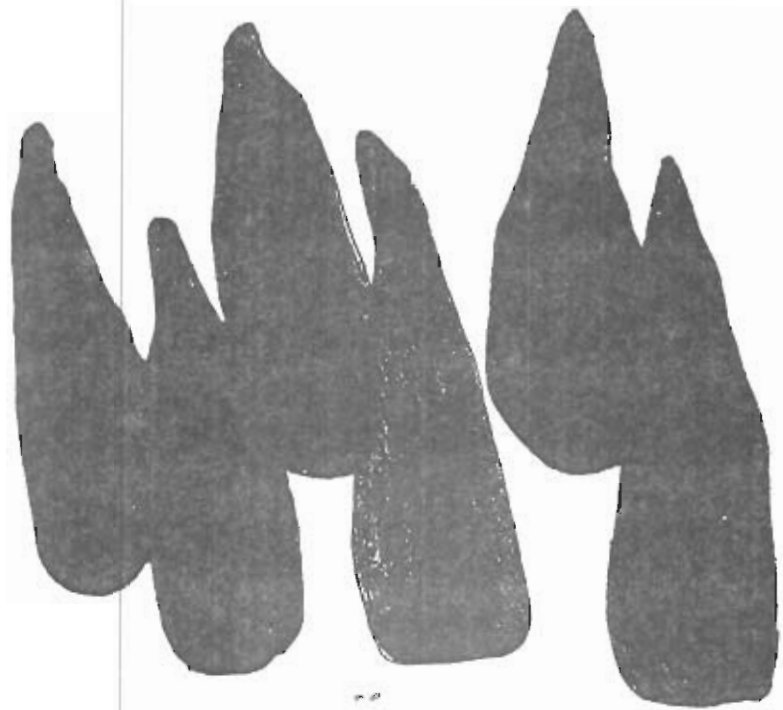


Fig. 28. *Rana tigerina* tadpole, teeth. Scale 0.25 mm.

inconspicuous. Each papilla is small, much thicker and columnar. BFA papillae are arranged in a staggering lateral row on the sides of the median groove. Their tips are blunt, flat, sides and tips covered with tuberosities. The first BFA papilla is smallest, the second and fourth are slightly bifurcated at the tips. There are 18-30 pustules scattered along lateral sides of BFA, few are present in the prepocket region. Similarly pustules are scattered all over the extra BFA and the posterior border of BFA.

The buccal pockets are quite small as compared to the rest of the ventral buccal. Each buccal pocket is transversely disposed in the buccal cavity, with equally developed thick lips, and is imperforate.

The ventral velum is indistinct, with indistinct anterior and straight posterior border, showing no jagging or peaks. Its posterior border is thick, a mesial notch over glottis is absent, instead, the mesial part of the velum is folded forwards to expose the glottis completely. The velum has a strong spicular support.

*Ventral pharynx:* The branchial baskets of *Rana tigrina* tadpole is much abbreviated, as compared with the buccal region, it is almost one third of it. The branchial baskets, on both sides, lie posterior to the buccal region. Each branchial basket is triangular, broader than long, enclosing a bowl-shaped cavity. The filter plates are loose, ranging in size from 0.8-1.15 mm, and are narrow, ranging in breadth from 0.17-0.33 mm. The filter ruffle is loose, poorly developed, 2 degree foldings are present, mostly with swollen tips. Number of filter rows on filter plates vary from 8-10 (see Table VII).

The filter canals are wide and open. The filter plates are free on their velar side, only feebly covered by it. First and fourth plates are vertical while second and third are horizontal, and they abut with each other at the base of the filter chamber. The secretory pits are large, scattered all over velar dorsum, are confined to velar margin along subvelar surface. The esophagus is broad, gradually narrowing posteriorly.

*Dorsal buccal (Fig. 31):* Dorsal buccal conforms to the shape and size of the ventral buccal, however there are some obvious differences: the prenarial arena is about twice as long as broad, and it is not dome shaped, rather it is flat, unlike that of other ranid tadpoles. The anterior beak is straight and does not overbite. A keratinized shield lies at the roof of midprenarial arena. The peculiar lateral columnar narial papilla is tipped with a keratinized plate and lies at each angle of the mouth. Internal nares are distinct and transverse with thick lips, they are much smaller as compared to the width of dorsal buccal. The anterior narial valve is narrower than the posterior

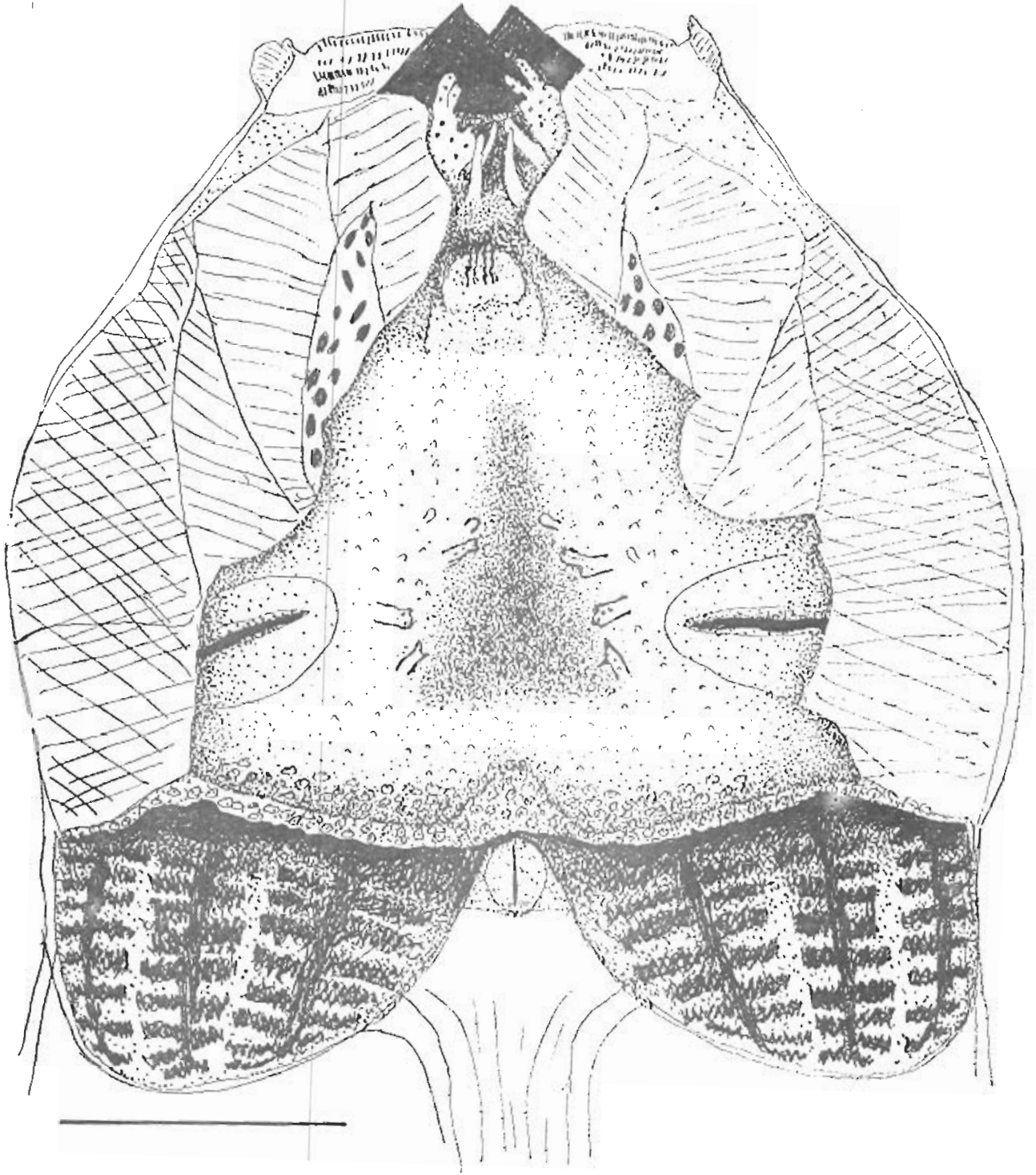


Fig. 29. *Rana tigerina* tadpole, buccopharyngeal floor. Scale 1 mm.

Table VIII. Oropharyngeal region of ranid larvae. Data for *R. blythi* (bly), *R. finchi* (fin), *R. ibanorum* (iba), *R. ingeri* (ing), *R. kuhli* (kuh), *R. laticeps* (lat), *R. lucuasa* (luc), *R. palawanensis* (pal), *R. chalconota* (cha), *R. signata* (sig) from Inger (1985), and for *R. hazarensis* (haz) from Khan and Malik (1987 a). Explanation: abbreviations in parenthesis denote name as used in the table. d=deep, p=pustule, s=shallow, vs=very shallow.

Character state	Taxa													
	cya	syh	tig	bly	fin	iba	ing	kuh	lat	luc	pal	cha	sig	haz
Body length (average)	18	6	7	11	8	10	10	9	8	6	8	18	14	25
Head length (average)	42	19	40	36	23	26	28	26	?	47	24	48	41	71
Dental formula														
Anterior labium	1	1	5(4-5)	1	2(2)	2(2)	2(2)	2(2)	2(2)	(1)	?	4(2-4)	3(2-3)	8(2+8)
Posterior labium	2	3	5(1-3)	2(1)	2(1)	3(1)	2(1)	2(1)	2(1)	3	?	2(1)	2(1)	2(1)
Number of papillae/side														
Infralabial	2	2	3	2	1	?	4	4	4	4	4	2	2	2
Lingual	2	4	2	4	4	4	4	4	4	4	4	2	4	2
BFA	17-20	7	3-4	6-7	7-8	10-14	7	15-20	4-5	7-8	4-5	5-7	6-8	5-8+p
BRA	6	3	0	6	5	6-8	5	10-11	?	10	5	4-7	4-5	9-10+p
Prepocket	4-6	1-10	0	12p	8p	6	p	6p	?	?	?	25p	p	8-10
Postnasal	5	1	1	1	1	1	1	1	?	1	?	?	?	2
Palatal ridge	1	1	0	3	1	1	?	1	?	0	?	0	0	5
Rostral peaks	3	0	0	2	0	6	4-6	6-8	1	5	1	5	4	8-10
Rostral cavities	3	2	1	3	3	3	3	3	3	3	3	3	3	3
Number of branchial basket	d	s	vs	?	?	?	?	?	?	?	?	?	?	?
Number of teeth	0	6	1	5	?	9	5	4	?	?	?	12-15	12-15	9-10

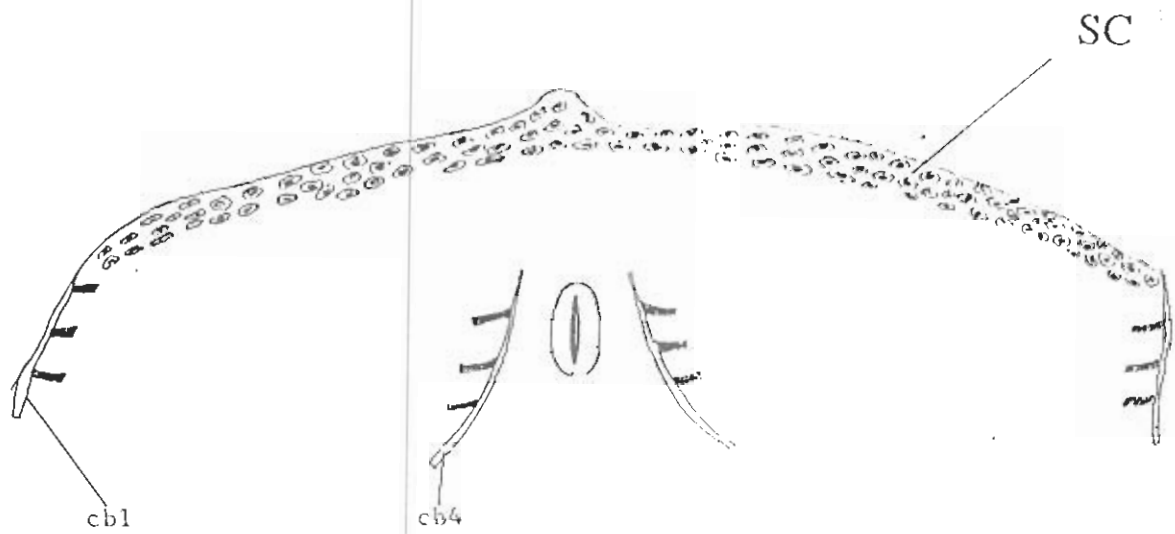


Fig. 30. *Rana tigerina* tadpole, subvelar secretory tissue and attachment of filter plates, diagrammatic. For abbreviations see page 11.

**Table VII. Branchial region of *Rana tigerina* tadpole at Stage 35 (data from 10 specimens)**

Ceratobranchial (cb) supporting the filter plate	Filter plate		Filter rows on filter plates
	length	breadth	
cb. 1	1.0	0.2	6-7
cb. 2	1.15	0.4	9-10
cb. 3	0.8	0.4	9-10
cb. 4	0.8	0.6	8

which is about four times its breadth. There is a medium sized prenarial papilla, with tuberosities all over, arising from the middle of the prenarial valve, while the postnarial papilla is similar but longer in size, arising well posterior to the posterior border of narial valve. The postnarial arena is distinct, broader than long, without any special topography.

The median ridge is distinct, almost rectangular in shape. It delimits postnarial arena from buccal roof arena. The ridge is about twice as broad as high, with slightly sloping sides, without jagging or any irregularity at its surface. A lateral ridge papilla is absent.

The buccal floor arena (BFA) is flat. It suddenly widens just posterior of the median ridge. It is about twice as broad as long, BFA papillae are absent. Pustulations are scattered in groups at special parts of BFA. First group of 30-50 pustulations lie at the centre of BFA, running mesially, from anterior to the posterior extent of BFA. The second group of 12-20 pustules is arranged in staggering double row on each side of BRA. A transverse row, 2-3 pustules thick, lines the posterior border of BRA, continuing with the other groups of pustulations. The dorsal velum is a narrow strip, broader on sides, gradually narrowing mesially, where continuing as a very low staggering ridge. The pressure cushions are not distinct from each other. The sides of the pressure cushions are thick becoming narrower towards mesial axis of the body. The ciliary grooves are broad and shallow.

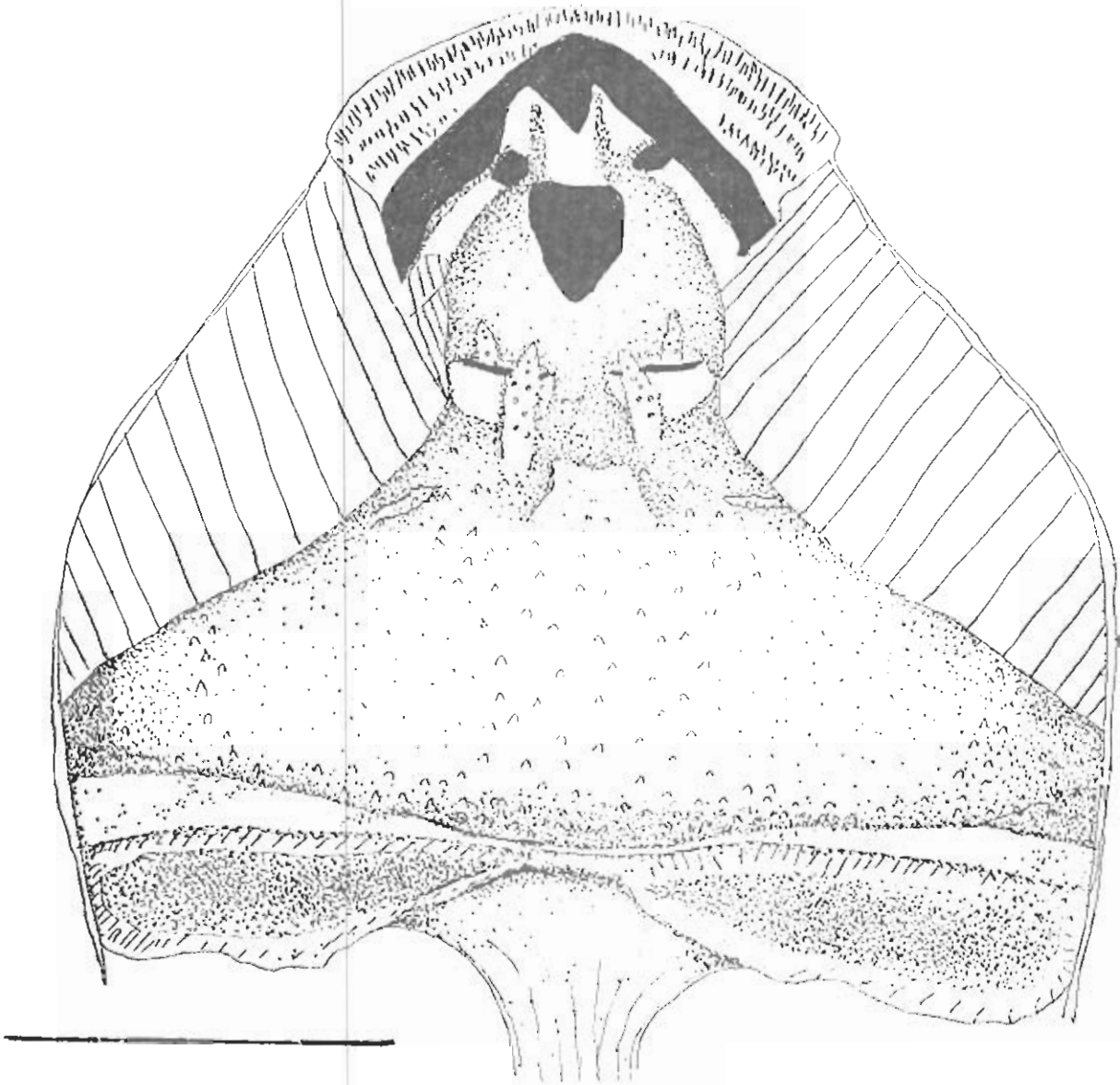


Fig. 31. *Rana tigerina* tadpole, buccopharyngeal roof. Scale 1 mm.

### Diagnosis of *Rana tigerina* tadpole

Comparative oropharyngeal features of the *Rana tigerina* tadpole are as follows:

1. Tooth rows are hypertrophied on both labia, and the dental formula is 5 (2-5) / (1-3) 5.
2. the oral disc is without palps and papillae.
3. A typical tooth is cylindrical, tapering at a pointed tip. Teeth are arranged in double rows (biserial).
4. The beak is thick and broad frontally. Its anterior half has ciliated edge with a median tooth, while the posterior half is sharp, with a median concavity into which the tooth of the anterior part of the beak fits when the beak is closed.
5. There are additional keratinized structures in the buccal cavity.
6. There are three infralabial papillae, first is palmate, produced into strong three fingers. All papillae are covered with bluntings.
7. The internal nares are small as compared to the breadth of buccal roof. They are transverse, with thick valves and pre and postnarial papillae.
8. Buccal pockets are small, transverse, with thick lips. There are no prepocket papillae.
9. Lingual analage is with a pair of lingual papillae, which are tuberculated all over.
10. Both BFA and BRA are spacious, flatish and broader than long.
11. There is general reduction in the number of buccal papillation. BFA papillae are 4-6, are as short stumpy structures with flat tuberculated tips.
12. The BRA is with pustules all over, papillae being absent.
13. Buccal musculature is hypertrophied.
14. The branchial basket is about 15% of the oropharyngeal region. There is a single filter cavity on each side.
15. Buccal as well subvclar secretory tissue is pitted. The pits are large and distinct. There are no secretory ridges.
16. Filter plates are loose, with 6-10 filter rows. The filter ruffle is with 2 degree foldings. The filter canals are wide and open. There is no food trap.
17. The lungs are large and functional.

In literature there is considerable confusion regarding the number and arrangement of the tooth rows on the oral disc of *Rana tigerina* tadpole. Annandale and Rao (1918) recorded five tooth rows on each labium in the tadpoles collected from eastern Himalayas. Boulenger (1920)

Table IX. Comparison of the buccal morphology of amphibian tadpoles from plains of I Pakistan (bi=bifurcated; ex=exposed; im=imperforate; kp=keratinized; lo=longitudinal; me=membrane; nx=not exposed; pe=perforate, pu=pustule, si=simple, sm=strongly muscular; sp=series of pustules; pm=papillary membrane; tr=transverse; wm=weakly muscular; en=entire; or=*Microhyla ornata*; st=*Bufo stomaticus*; cy=*Cyanophlyctic*; sy=*R. syhadrensis*; ti=*R. tigrina*; +=present, -=absent).

Character	or	st	cy	sy	ti
Sucker	-	+	+	+	+
preoral tooth rows	0	2 (2)	1	2 (2)	5 (2-5)
Post oral tooth rows	0	3	2	3	5 (3-5)
Number of cusps on a tooth	-	10	0	6	0
Anterior beak ciliated	-	+	+	+	+
Posterior beak ciliated	-	+	+	+	-
Buccal wall	wm	wm	sm	wm	sm
Length of buccal cavity percentage of buccopharyngeal length	27-30	64-65	61-62	72-73	80-82
Labial palps	-	+	+	+	-
Labial papillae	-	+	+	+	-
Lingual papillae	0	4 si	2, 2 bi	2, 4 si	2, si
Prenarial papillae	im	pe	pe	pe	pe
Postnarial papillae	2	0	i	1	1
Median ridge	3 me	0	5	1	1
Lateral ridge papillae	-	+	+	+	+
Buccal pockets	0	1	1	1	0
BRA papillae	lo	tr	tr	tr	tr
BFA papillae	6 me	4, 2 bi	3	3	pu
Ventral velum	6 me	4	25-30, 15 bi	4	4
Glottis	d	en	en	en	en
Lung function	ex	nx	ex	ex	ex
	+	-	+	+	+

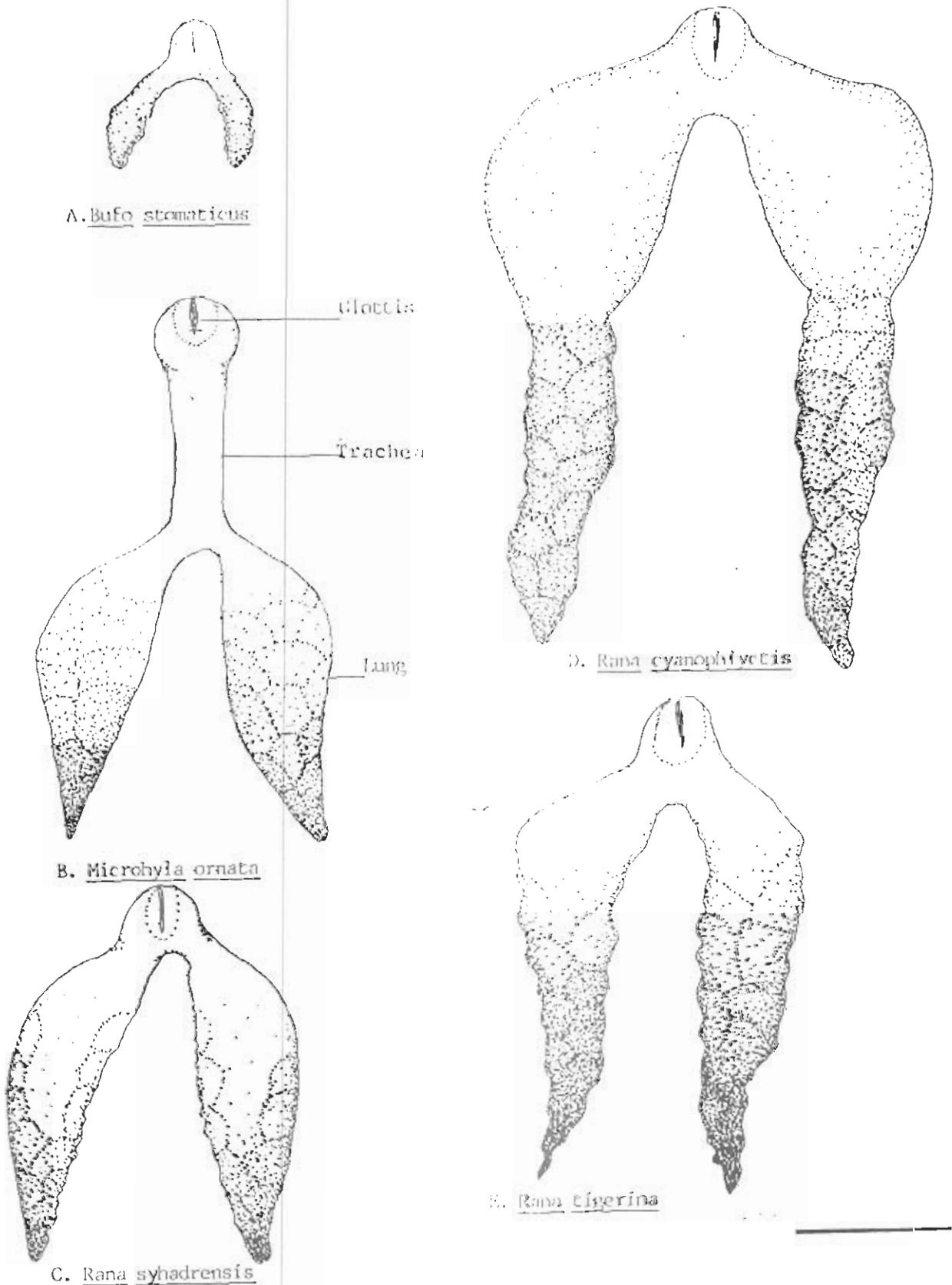


Fig. 32. Lungs of anuran tadpoles at Stage 35(Khan, 1965). Scale 1 mm.

and Boulenger and Annandale (1920) recorded dental formula for this tadpole as 3-4/4-5 rows, and an entirely papillated oral disc. Liu (1961) recorded 4 (1-4)/4(1-3) in the tadpole of this frog from China. While Fig. 1 and 2 in McCaan (1932) are sufficient to show that this author has confused tadpoles of *Rana cyanophlyctis* with that of *R. tigerina*, and had produced a tadpole which is like neither of the species. Minton (1966) has recorded the edges of the both halves of the beak smooth, three long and two short rows of teeth on the anterior lip, while the posterior labium is with two long and one short rows and has a lobulated margin.

### Ecological adaptation of *Rana tigerina* tadpole

*Rana tigerina* breeds in ephemeral puddles and shallow parts of large water bodies in the low lying areas. Later the tadpoles migrate to the deep water, where they confine to the bottom. Dorsally placed eyes of this tadpole enable it to see the animal activity taking place in the water column. As prey comes in its striking range, it at once darts and grabs it in its powerful jaws and drags it to the bottom. The powerful muscular tail with low fins enables quick and agile movements of this tadpole. Carnivorous water creatures like predatory fishes, niads, turtles etc., are avoided by the tadpole by confining <sup>itself</sup> to the <sup>shallow</sup> low water among the roots of the submerged grasses.

In situations where larvae of both *R. cyanophlyctis* and *R. tigerina* are present, they avoid each other due to their peculiar <sup>a</sup> ecological adaptations. Tadpoles of *R. cyanophlyctis* take refuge under the debris accumulated at the bottom. Moreover, breeding time differs in both species (Khan and Malik, (1987 b), so confrontation between the two larvae <sup>is</sup> quite rare.

*Rana tigerina* tadpole rises up to the water surface, periodically, since its benthic habits is low in Oxygen. Its ascending and descending movements are very quick, almost darting type, since at midstream it is highly exposed to the attack of its enemies. In ephemeral shallow pools, because of high <sup>O</sup>xygen, these movements are off and on.

*Rana tigerina* tadpoles is obligate macrophagous <sup>o</sup> carnivore, feeding on tadpoles of its own kind and those of other amphibians. Usually, tadpoles of *Bufo stomaticus* fall prey to it. Tadpoles of *R. syhadrensis*, *R. cyanophlyctis* and *Microhyla ornata* form its rare food item. The food of this tadpole also includes water beetles, bugs, niads, larvae of fishes, *Cyclops* and *Daphnia*. The latter two forms are drawn in with the current of water, and are retained by the filter ruffle in the filter cavity. It is the only planktonic food on which *R. tigerina* tadpole can feed.

**Table x.** Comparison of morphology of pharyngeal region of anuran tadpoles studied. (Figures in parenthesis represent number of filter cavities which have fused together) ridged pattern = ——— ; pitted pattern=.....; or=*Microhyla ornata*; st=*Bufo stomatics*; cy=*Rana cyanophlycits*; sy=*R. syhadrensis*; ti=*R. tigerina*; all measurements in mm.)

Character	or	st	cy	sy	ti
length of branchial basket in percentage of buccopharyngeal length	70-73	34-36	38-40	28-30	18-20
Largest branchial plate	II	I	III	I	III
Length of largest branchial plate	3.7	1.3	2.5	1.5	0.15
Breadth of largest branchial plate	1.5	1.0	1.12	0.4	0.4
No. of filter rows on largest branchial plate	20-23	10-12	12-14	13-14	9-10
Nc. of filter cavities in branchial basket	3	1(2+3)=2	3	1(2+3)=2	1(?)
Composition of subvelar secretory tissue	———	.....	———	———	.....
Branchial food trap tori per side	3	0	0	1	0

## Interspecific Comparison of the Oropharyngeal Morphology of genus *Rana*

Taxonomy of the frogs belonging to the cosmopolitan genus *Rana*, has always posed a problem for the herpetologists (Boulenger, 1920; Pacc, 1974; Afzal et al., 1988). Dubois (1984, 1986) has partitioned genus *Rana* into several genera and subgenera, rearranging various ranid taxa. According to him present taxonomic position of the frogs from the plains of Punjab is as follow:

*Rana cyanophlyctis*=*Occidozyga (Euphlyctis) cyanophlyctis*

*Rana syhadrensis*=*Rana (Fejrvarya) syhadrensis*

*Rana tigerina*=*Limnonectis (Holobatrachus) tigerina*

Tadpoles of frogs of closely allied species are difficult to be identified from each other. Species of *Rana pipiens* complex have almost similar tadpoles (Wassersug, 1976) ~~1976~~. The three frogs found in the plains of Punjab are quite different in their adult as well as in tadpole morphology and are easily distinguishable from each other (Khan, 1976; Khan and Tasnim, 1987; Khan, 1982 a).

So far few works are known concerning the oropharyngeal morphology of ranid tadpoles. Savage's (1952) account of *Rana temporaria* does not contain details of the oropharyngeal structures. However, Inger (1985) has described and illustrated in details the oropharyngeal anatomy of *Rana blythi*, *R. finchi*, *R. ibanorum*, *R. ingeri*, *R. kuhli*, *R. laticeps*, *R. luctuosa*, *R. palavanensis*, *R. chalconota* and *R. signata*, tadpoles from Borneo. Recently, Khan and Malik (1987 a) have described the oropharyngeal morphology of *R. hazarensis*, a torrenticole tadpole from western Himalayas.

In the following section a comparison is made of these known oropharyngeal morphologies with those described in the present work, and general characters of a ranid tadpole are described.

### Oropharyngeal Morphology of a ranid tadpole

Table VIII compares the known morphologies of ranid tadpoles. The ranid tadpoles are large, ranging in size from 13-71 mm, while tailless body measures from 8-25 mm. The tail fins are narrow to broad. The tail muscles are very thick. The oral disc is well developed, anterior or anteroventral in position. The anterior labium is with 1-8 and posterior with 2-5 rows of

keratinized teeth, most of the inner rows are mesially broadly interrupted. The teeth are cusped, rarely simple. The beak is strong, sharp edged, ciliated. Morphology of oral disc and its components reflects adaptive radiations of the tadpoles, and the nature of tadpole's food. In carnivorous tadpoles there are additional keratinized surfaces in the buccal cavity.

The infralabial papillae are usually palmate, 1-4 in number; lingual analage is distinct with 2-4 papillae; BFA papillae are 3-20, while BRA papillae are 0-11 per side. The buccal arenae are with several pustules. The prepocket papillae vary from 0-10 plus several pustules. Postnarial papillae are 1-5, the median ridge is well developed and broader than long. There is a single to several lateral ridge papillae which are simple or ornamented. The ventral velum is well developed, always supported by strong spicules, the posterior border of the velum has 0-10 peaks. The branchial basket is distinctly reduced in size as compared to the buccal region. The filter cavities are 1-3, shallow, with a tendency of murgence of ~~the~~ filter cavities <sup>into</sup> with each other. The secretory tissue is composed of secretory pits and secretory ridges, even branchial food traps are present in the form of distinct tori, according to the feeding habits of the tadpoles, which vary from periphyton grazing type to specialized macrophagus carnivorous. Several species are specialized microphagus and some are detritus feeders. *Rana* tadpoles are primarily benthic in habits.

### Intergeneric Differences in the Oropharyngeal Morphology of the Tadpoles.

Tables VIII and IX summarise the intergeneric differences in the oropharyngeal morphology of tadpoles belonging to genera *Bufo*, *Microhyla* and *Rana*. *Bufo* and *Rana* tadpoles share certain characters; however, there are several features in their morphology which distinguish them from each other, <sup>w</sup> While *Microhyla* tadpole is typical, it differs distinctly from *Bufo* and *Rana* tadpoles. Important intergeneric oropharyngeal differences are as follows:-

**Oral disc:** *Microhyla* tadpole lacks a typical oral disc with keratinized tooth rows, beaks and palps, while a typical oral disc is present in both *Bufo* and *Rana* tadpoles.

**Buccal region:** Buccal region of *Microhyla* is less than 30% of the oropharyngeal cavity, while it is more than 50% in *Bufo* and *Rana* tadpoles.

**Lingual papillae:** There is no lingual papilla in *Microhyla* tadpole while 2-4 lingual papillae are present in *Bufo* and *Rana*.

**Buccal pockets:** The buccal pockets are longitudinal and without lips in *Microhyla*, while they are transverse and lipped in *Bufo* and *Rana* tadpole.

**Internal nares:** The nares are imperforate in *Microhyla*, While these are perforate and valvular in *Bufo* and *Rana* tadpoles. *Bufo* does not have narial papillae, which are present in *Rana*.

**Median ridge:** There is no median ridge and lateral ridge papilla in *Microhyla*, while both are present in *Bufo* and *Rana*.

**BRA papillae:** Bases of BRA papillae are coalesced to form a fine membrane in *Microhyla*, while in *Bufo* and *Rana* these papillae are distinct and lie on the lateral sides of the buccal roof arena.

**Ventral velum:** The ventral velum in *Microhyla* is mesially divided by the anterior extension of prolonged trachea, while in *Bufo* and *Rana* tadpoles it is entire, since these tadpoles do not have a trachea.

**Glottis:** The glottis in *Microhyla* tadpole lies in the buccal cavity, well anterior to the ventral velum. The glottis of this tadpole is large, with a large glottal disc. In *Bufo* and *Rana* tadpoles, glottis is small with smaller glottal cartilage and it lies ventral to the ventral velum, between the branchial baskets. In *Microhyla* there is a preglottal papilla, while this is absent in *Bufo* and *Rana*.

**Lungs:** The lungs in *Bufo* tadpoles are poorly developed and are non functional at Stage 35 (Khan, 1965). In *Microhyla* and *Rana*, these are well developed and functional.

**Subvelar secretory tissue:** The subvelar surface in *Bufo* tadpole is covered mesially with pitted secretory surface, while on lateral sides the secretory tissue is ridged. The fine ridges are transversely parallel to each other. while whole of the subvelar surface of *Microhyla* tadpole is ridged, the ridges are finest. In macrophagus *Rana* tadpoles (*R. tigrina*) pitted tissue is present,

the pits are largest, scattered along the velar margin, while in *Rana* tadpoles feeding on smaller food particles (*R. syhadrensis*, *R. cyanophlyctis*) ridged pattern is present.

**Buccal musculature:** The buccal musculature of *Rana* tadpoles tend<sup>to</sup> be hypertrophied, extreme conditions are seen in carnivorous tadpoles, while *Microhyla* and *Bufo* have normal buccal musculature.

**Branchial baskets:** Branchial baskets are more extensive in *Microhyla*, and are more than 70% of the buccopharyngeal region, while they are less than 50% in *Bufo* and *Rana* tadpoles.

**Filter cavities:** The tadpole of *Microhyla* has most extensive three filter cavities, while *Bufo* tadpole has predominantly one cavity formed due to coalescence of three filter cavities. Number of filter cavities in *Rana* tadpoles vary according to the feeding habits of the tadpole.

**Filter plates:** *Microhyla* tadpole has largest filter plates, while in *Bufo* and *Rana* they tend to be smaller with loose filter ruffle.

**Filter mesh:** *Microhyla* has tight filter mesh, while it is loose and simplified in *Bufo* and *Rana* tadpoles.

The above stated points pertaining to the tadpole's oropharyngeal morphology well differentiate the tadpoles of genus *Microhyla*, *Bufo* and *Rana* from each other.

## DISCUSSION

In the following section, morphology of the five amphibian tadpoles described in the first part of the present study, is correlated to its functional role. Though considerable work exists on the external as well as internal morphology of the amphibian tadpoles, however, little work is available on its functional aspect.

Wassersug (1973) defined an anuran tadpole, as an independent, free living, nonbreeding vertebrate, facing all environmental processes confronting any aquatic animal. Tadpoles differ from each other in body shape, tail morphology, buccopharyngeal region, locomotion, feeding habits, disposition of eyes and spiracle, and in general habits and ecology. Most of these tadpoles are sympatric, the morphological differences among syntopic larvae can be explained on the basis of larval habitat and dietary preferences (Hills, 1982). Mostly the interpretation of functional autecology of the amphibian tadpole is speculative and hypothetical (Wassersug, 1980). However, the functional correlates presented here are mostly based on my observations on tadpoles in nature and in laboratory.

### Functional Correlates of the External Morphology of the Amphibian Tadpoles

*Body shape and form:* Body shape and form is correlated with the micro and macrohabitat of a tadpole. The body of *Bufo* and most of the *Rana* tadpoles bulges sideways. This indicates their benthic type of habitat. The heavy globose body of the tadpole does not allow it to swim for long distances. After a sprint, the tadpole <sup>e</sup>spittles down, due to strong drag forces on this type of body form (Wassersug, 1989). On the other hand, *Microhyla ornata* tadpole has a streamlined body, with dorsoventrally depressed head and laterally compressed abdomen, like the common dogfish *Scoliodon sorrakowah*. This tadpole is lentic-nektic in habits; it never rests at the bottom of water while constantly swims at midwater (Khan, 1982 a). Body of *R. tigerina*, unlike its sympatric ranid tadpoles, is cylindrical, almost round in cross section, a form suited to stream adapted tadpoles (Wassersug and Heyer, 1983). Cylindrical muscular body of this tadpole, is an adaptation for fast swimming. This tadpole typically darts from one place to another, resting for short periods only. Such a swimming behaviour is <sup>correlated</sup> due to its carnivorous habits. It can out swim all its sympatric tadpoles.

Position of eye: Eye is an important photoreceptor organ. A tadpole is able to detect its prey or enemy from a considerable distance in clear water. *Microhyla ornata* larva has laterally directed eyes, situated at the lateral most margins of the depressed head, as in *Scoliodon sorrokowah*. Their peculiar lateral position on the head enables this tadpole a constant surveillance of its surrounding water during its constant lentic midstream swimming. On the other hand, the eye of *R. syhadrensis*, *R. tigerina* and *B. stomaticus* are dorsally placed, while those of *R. cyanophlyctis* are dorsolaterally disposed. Variations in the disposition of eyes in these tadpoles indicate their normal resting position in natural environments. The sloping sides of a pond presents a variety of niches (Loschenkohl, 1986). When a tadpole is lying at the bottom of a pond, its dorsally located eyes enable it to survey the animal activity taking place above in the water column. This is the case with *R. tigerina* tadpole, which is benthic and lolls at the bottom most of the times. The detritivorous tadpole of *R. cyanophlyctis* has dorsolateral eyes. It rests at higher level at the pond bottom, so as to be able to look out for its predacious enemies, and surveys other grazing sites.

*Bufo stomaticus* tadpole is mostly littoral, usually confining itself to the shallow marginal waters. Its dorsal eyes move to dorsolateral side as it advances in age and moves to more deeper water, feeding on submerged vegetation. On the other hand, eyes of *Rana syhadrensis* tadpole are more dorsal than lateral. It swims up and down along the sloping sides of pond, feeding on the vegetation as well as planktonic bloom. Its dorsal eyes enable it to locate plankton rich strata in the water column.

Dorsal and dorsolateral position of eyes does not allow a tadpole to see what it is eating. In these tadpoles, detection of the position of the food takes place by the circum-oral structures, like nares, oral papillae and oral palps (Altig and Brodie, 1972). Eyes, in the detritus eating and herbivorous tadpoles, do not play important role in feeding. In carnivorous tadpole of *Rana tigerina*, eyes play important role. The tadpole detects its prey with the help of sight, and while it is feeding, the jaws work according to the cues received from brain guided by the sense of sight.

Position of oral disc: Employment of similar food gathering system by the amphibian tadpoles, may reflect morphological constraints imposed by phylogeny or it may indicate specializations of tadpole mouth parts to exploit the same food resource in different ways (Lynch, 1973). Same morphological structures of the oral region are modified in different ways in different species of tadpoles, so that each morphotype represents a particular niche (Thibaudeau and Altig, 1988).

Even the orientation of the oral disc of a tadpole reflects its ecological preferences (Altig and Johnston, 1989).

*Microhyla ornata* tadpole lacks a typical oral disc and its associated organs. Its anterodorsal mouth constantly remains open, and gulps-in pond water. This tadpole has to cycle enormous amount of water to get its dietary requirements. On the other hand, *Bufo* and *Rana* tadpoles have typical oral disc surrounding oral orifice. The oral discs are armed with keratinized ciliated sharp beaks and rows of teeth. The orientation of the oral disc in *Bufo stomaticus*, *R. cyanophlyctis* and *R. syhadrensis* is anteroventral, not visible to the tadpole, since the eyes in these tadpoles are dorsal or dorsolateral. These tadpoles depend on the labial palps and papillae in orientation of the oral disc during feeding process, sense of sight playing no role in it. *Rana tigerina* tadpole is unique in having anteriorly orientated disc, which is visible to the tadpole when it is feeding. The tadpole is able to keep in view its prey while feeding. The struggling prey necessitates vigilance on the part of the predator to orient its oral armature to subdue its prey as quickly as possible.

The oral papillae are important character which <sup>are</sup> usually used in the identification of tadpoles. Various functions are assigned to the oral papillae as chemosensory, tactile, flow and water content monitors, substrate manipulation and modification of mouth shape during feeding. Khan (1982 a) reports two pairs of pustular oral papillae, a pair on each later side and two pairs in the anterior middle part of the lower (anterior) lip of *M. ornata* tadpole at Stage 25. These papillae are lost by Stage 30. During earlier stages, this tadpole stays close to the marginal vegetation where these oral papillae perhaps help in anchorage of the tadpole.

*Rana tigerina* tadpole totally lacks oral papillae, however its infralabial papillae are long, columnar and help in orientation of the food material. The anteroventral mouth of *B. stomaticus*, *R. cyanophlyctis* and *R. syhadrensis* is positioned according to the sensory cues received through oral papillae; sense of sight dose not play a role in food detection. The oral papillae also help in the anchorage of the tadpole to the substratum in flowing water (Altig and Johnston, 1989), for which *R. tigerina* has a postoral sucker.

Absence of oral disc (*Microhyla*) is regard as primitive by several workers (Orton, 1953; Hecht, 1963; Starrett, 1973), while other workers (Tihen, 1965; Kluge and Farris, 1969) regard it as a derived state. Savage (1973) thinks that microhylid tadpoles were first to invade southeast Asian waters during Miocene, followed much later by the ranoid tadpoles.

**Morphology of the oral disc:** The circumoral structures of amphibian tadpole differ in the morphology and arrangement, from species to species and from genera to genera. They have extensively been used in the taxonomy of the tadpoles (Altig, 1970; Khan, 1982 a; Altig and Johnston, 1986, 1989).

*B. stomaticus* and *R. cyanophlyctis* have a pair of oral palps on each side, with papillated margin, while in *R. syhadrensis* the palps are not distinguishable, still the papillae are larger and thicker than those of other tadpoles studied. *R. tigerina* tadpole does not have palps as well as papillae. The posterior lip of oral disc dilates to form a cup like sucker when needed.

The palps and the labia of the oral disc are capable of free movements. The anterior and posterior movements (oral hitching of Altig and Brodies, 1972) of the labia, which take place while the oral disc is closely applied to a surface, allow the tooth rows to scratch the substratum repeatedly, shredding it in pieces. At the same time the beak is also working, cutting the vegetative material into pieces. In flowing water, together with the labia, the oral disc acts as an effective sucker, giving a firm hold to the tadpole against considerable force of flowing water.

**Morphology of teeth:** Larval teeth are arranged in definite rows on anterior and posterior labia of the oral disc. The tooth rows arise from thick tooth pads. A typical tooth has a cylindrical base and a spatulated crown which is laterally cusped on both sides. However, in *R. tigerina* the cylindrical base gradually tapers to the pointed tip, while the teeth of *R. cyanophlyctis* are peculiar. They are longest observed in the tadpoles studied and are, in the form of quadrangular rods with blunt tips. They have a slight bend in the middle towards mouth. In *R. tigerina* the teeth are biserially arranged, while in other species they are uniserial.

The outermost row of teeth on the anterior labium is complete in all tadpoles. It extends from one side of the labium to the other across the oral disc. It is followed by one (*B. stomaticus*, *R. syhadrensis*) or four (*R. tigerina*) broadly interrupted tooth rows. On the other hand *R. cyanophlyctis* tadpole has only one complete row on the anterior labium. On the posterior labium, there are three uninterrupted rows in *B. stomaticus*, and *R. syhadrensis*, two in *R. cyanophlyctis*, while one entire and four broadly mesially interrupted rows are present in *R. tigerina*. The dental formula of *R. tigerina* with five rows on each labium, is balanced, while 1/2 of *R. cyanophlyctis*, 2/3 of *B. stomaticus* and *R. syhadrensis* are negatively imbalanced (Altig and Johnston, 1989). Cuspidate teeth are recorded in *Bufo*, *Scaphiopus*, *Pelobates*, *Hyla* and several other genera, and they are mostly uniserial in arrangement (Gosner, 1959). In genus *Rana* extreme tooth forms have

been reported within a single genus, as has been observed during present study (Altig and Johnston, 1989).

Cusped teeth of *B. stomaticus* and *R. syhadrensis* are adapted for rasping and scratching the organic concretions from the submerged surfaces, while peculiar teeth of *R. cyanophlyctis* shovel detritus into the mouth of the tadpole. The fine tipped pike-like teeth of *R. tigerina* hold the body of the prey by piercing it, while the strong jaws of the tadpole are working on it. Similar cusplless teeth have been reported in larvivorous leptodactylid tadpoles (Starrett, 1973) and tadpoles of *Scaphiopus* (*halbrooki*, *hammodi*, *hrteri*) and *Ascaphus* (Gosner, 1959).

Typical Bufonidae tooth formula  $2(2)/3$  is most common in anuran larvae and is regarded primitive, while increase or reduction in tooth rows as shown by *Rana* tadpoles is an advanced state (Altig and Johnston, 1989). The alterations from normal typical oral disc morphology, usually reported during ontogenetic studies represent teratological aberrations with no ecological significance (Khan, 1965; Grillitsch and Grillitsch, 1989).

**Morphology of Tail:** Tail is an important part of the body of a tadpole, and it is characteristically and universally present in all the amphibian tadpoles. It is the organ of the body which helps in swimming, moving the tadpole from place to place in search of food, or flee from its enemies. The movements are brought about by the sinusoidal movements of the tail. Tadpole's tail differs from that of fishes in having no skeleton, less musculature and has simpler myotomes (Nishikawa and Wassersug, 1988, 1989; Wassersug, 1989). Presence of notochord, as the only skeletal element, gives tadpole's tail high flexibility. This helps in the propulsion and great maneuverability during swimming. However, amphibian tadpoles cannot swim at a constant speed for long times (Wassersug, 1989, Dudley et al., 1991).

The tadpoles studied so far, differ from species to species in detail morphology of tails. Weak muscled short tail, with moderate fins, is characteristic of pond inhabiting tadpole of *B. stomaticus*. It swims sluggishly with sideways lashing movements of its tail. The globose body is pushed forward in water by tail movements. *Rana* tadpoles on the other hand are fast swimmers.

tadpole can swim faster than all its congeners.

*M. ornata* tadpole is unique among the tadpoles studied. The tail of this tadpole is much longer as compared to its body. Moreover, the tail tip is prolonged into a long flagellum. Dorsal and ventral fins are exceptionally broad. Similar tail has been reported in other midstream swimmers (Wassersug, 1980, 1989; Wassersug and Sperry, 1977; Nishikawa and Wassersug, 1988, 1989; Hoff, 1986). Midstream swimming and its maintenance is made possible by independent movements of the tail flagellum (Khan, 1982 a; Altig and Johnston, 1989). Microhylid and ranoid tadpoles differ in their tail morphologies, as well as that of their notochords, caudal spinal nerves and mechanism of swimming. Like *Xenopus*, *M. ornata* larvae swim by rapid vibrations of the tail filament, while ranoid tadpole generates propulsive waves from the base of the tail (Hoff, 1986).

Tail tip functions as a steer during swimming. Tail tip morphology differs in different tadpoles, reflecting their swimming ability and ecology of their habitat (Diaz-Paniagua, 1985; Altig and Johnston, 1989). Lotic tadpole of *B. stomaticus*, lives in smaller water pools and had rounded tail tips, while midstream *M. ornata* tadpole has long slender tail with broad fins and a very gradual taper merging into the tail flagellum. Benthic tadpoles of *R. cyanoplyctis*, *R. syhadrensis* and *R. tigerina* have gradually tapering long tails with parallel fins and pointed tips. These tadpoles live in deep ponds. They ascend and descend periodically in the water column for air, during which they are quite exposed to the attack of enemies. These vertical movements are made with great agility, and are made possible by the strong caudal muscles and pointed tail tips steering the tadpole in a rectilinear passage.

**Disposition of spiracle:** Position of spiracle, on the body of a tadpole, is an important character in the taxonomy of amphibian tadpoles (Orton, 1949; Kluge and Farris, 1969; Starrett, 1973; Lynch, 1973). Orton (1953) described and classified the anuran tadpoles in four morphotypes according to the position of the spiracle, which are now regarded to be in a phylogenetic order (Orton, 1957; Hecht, 1963; Starrett, 1973). *Microhyla* tadpole is Type II of Orton (1953) with a median ventral single spiracle, a symmetrical arrangement necessary for continuous midstream swimming (Wassersug, 1973; Khan, 1982 a) while *Bufo* and *Rana* tadpoles are Type IV, with a single, asymmetrical posterodorsally directed sinistral spiracle. These tadpoles are benthic. Obviously, they do not need balanced buoyancy, since they keep resting most of the time at the substratum.

The jet of water, issuing from the spiracular opening, might affect the drag on swimming tadpole (Starrett, 1973). The median position of the spiracle in *Microhyla* is of an important adaptive value. The tail filament together with the inflated lungs keeps the tadpole afloat. The jet of water from the median ventral spiracle, gives the body of tadpole the necessary upward push. Altig and Johnston (1989) have reported similar observations in the *Gastrophryne* tadpole. *Bufo* and *Rana* tadpoles, when disturbed, rush to the deep water. The posterodorsal jet of water from the spiracle help the tadpole in such spontaneous movements. In squids, the phenomenon of jet propulsion is quite well understood. The jet of water from mantle cavity issues through the funnel. It helps the animal to move in water. When it is following a prey, it can move very fast. The squid can changes its direction by twisting the funnel (Gosline and De Mont, 1985). Though the push, from the sinistrally located spiracle, is asymmetrical in *Bufo* and *Rana* tadpoles, it is compensated by corresponding movements of the tail, so as to move the tadpole straight in water as desired. The route of the tadpole, during ascent and descent in the water column, is oblique, as expected from the dorso-ventral push from the posterodorsal jet of water from the spiracular opening. Starrett (1973) believes that jet of water from *Bufo* and *Rana* tadpoles helps to disturb the food particles which are later sucked in by the tadpole. This does not seem plausible, because the jet is directed posterodorsally, well above the tadpole, and does not strike the substratum.

**Body size of the tadpole:** Extreme variability in the body size of the anuran tadpoles is exhibited, during ontogeny as well among genera. Predator avoidance and escape ability are correlated to the body size and developmental stage of the tadpole (Heyer et al., 1957; Caldwell et al., 1980; Huey, 1980; Smith, 1983; Formanowicz, 1986; Semitsch and Gibbons, 1988; Richards and Bull, 1990)

*Bufo stomaticus* tadpole is smallest of the tadpoles studied, and it is most preyed upon by the sympatric *Rana* tadpoles and other aquatic predators (niads, fishes, turtles etc.). However, *Rana* tadpoles are large and agile, so are able to avoid predators easily. Midstream *Microhyla* tadpole is seldom preyed upon, due to its peculiar<sup>a</sup> position in water and agility. Its transparent body is hardly visible to the potential predators.

In temperate Punjab plains, tadpoles interact closely with each other and with their potential predators. Usually in such situations, *B. stomaticus* and *R. tigerina* larvae are found together. Soon the *Bufo* larvae succumb to the *R. tigerina* larvae, which are last to die off as a result of drying of the site or fall prey to the water birds. It is rare that tadpoles of all the five species

of amphibians occur sympatrically, except in large ponds, which can hold water throughout or most of the summer. Even here, despite the fact that hiding places are available, *B. stomaticus* are largely preyed upon, so are *R. syhadrensis*. The large sized tadpoles of *R. cyanophlyctis* and *R. tigerina* rarely fall prey to the potential predators.

Altig and Brodie (1972) and Wassersug and Heyer (1983), have shown that body profile of a tadpole reduces the drag force in the flowing water. Long body of a the tadpole is flexed according to the currents and eddies produced in water, and it reduces chances of being swept downstream. *Bufo* and *Rana* tadpoles, have depressed head and body. They adhere closely to supports at the sides and bottom of the water current, with the help of the oral sucker, and often are successful in holding on against moderately fast flow of water.

**Colouration of tadpole:** Lactate and pyruvate level in the amphibian tadpole's tail vary little during intense swimming (Gatten et al., 1984). The energy deficit is an important constraint on the swimming ability of the tadpole. They cannot out swim their predators as fishes do. So the amphibian tadpoles rely on reduced conspicuousness to their predators (Feder, 1983). Drab inconspicuous colouration of a tadpole reflect open type of pond habitat with little vegetation, where tadpole's colour blends against background, spotty pattern is found in tadpoles living in ponds with much vegetation, where light and shade pattern blends with pattern of the tadpole. Darker tails may serve to deflect attack of predator from vitally important part, the body (Caldwell, 1982, 1986; Kehr and Basso, 1990).

*Microhyla ornata* tadpole is almost transparent, with silvery abdominal colouration. The transparency of the tadpole reduces shadow and makes it invisible from outside, while the silvershine of the abdomen, blends it against shiny surface, as it appears to the predators from inside pond. Neither a predator from outside nor from inside water can detect *Microhyla* tadpole easily.

Melanistic tadpoles of *Bufo* are distasteful during early ontogeny, becoming palatable only later. During early life this tadpole is dark and forms schools which are conspicuous. Later, during ontogeny, the tadpole becomes solitary, agile and light coloured, matching well with the debris accumulated at the bottom of the shallow pond. Those *Bufo* tadpoles living in ponds with vegetation, develop spots on their tail and fins. *R. syhadrensis* tadpole is more melanistic than its congeners. It has conspicuous dark spots on its body and tail. This tadpole inhabits ponds and puddles along the side of water courses, where light and shade pattern during day camouflages

the tadpole effectively. However, *R. cyanophlyctis* tadpole is more melanistic than that of *R. tigerina*. The former confines itself to the roots of the pond vegetation, while the latter changes its place constantly along the pond bottom in search of prey.

From the above discussion it becomes clear that the variations in shape, location and morphology of different parts of the body of the tadpoles reflect variations in the functions of these parts. Each species of tadpole thus occupies a unique niche in a sympatric habitat so as to avoid competition. Present study of the autecology of anuran tadpoles has shown that convergence and divergence in adaptations has produced lot of variations in the morphology of its body, so that each species fits in its microhabitat for which its morphology is designed.

### Functional Correlates of Larval Oropharyngeal Morphology

In the descriptive part of the present work, the buccal and pharyngeal structures are described from the surgically exposed surfaces, in order of their arrangement, from anterior to posterior and mesial to lateral. For discussion of ecological correlates of the oropharyngeal organs, they are being considered according to their natural position in the oropharyngeal passage, and their relation to each other.

Oropharyngeal region of the anuran tadpole is functionally distinguished in oral and pharyngeal cavities. These parts are morphologically as well as functionally different from each other. For this reason they are being discussed separately in this part of the discussion.

#### Oral Cavity

Table IX, compares the buccal morphology of the five anuran tadpoles described in the first part of this study. Relative length of the buccal cavity to branchial cavity varies in different species of tadpoles. This buccopharyngeal relationship is correlated to the mode of feeding of the tadpole. In microphagous *M. ornata* tadpole, buccal cavity is smallest (27-30% of the total buccopharyngeal length) of the five tadpoles, while it is largest (72-82%) in carnivorous *R. tigerina* and detritivorous *R. cyanophlyctis* tadpoles. Coarse particle eating tadpoles of *B. stomaticus* has a buccal length which is intermediate between the two extremes. The buccal musculature is hypertrophied in *R. tigerina*, less so in *R. cyanophlyctis*, due to which the buccal cavity of these

tadpoles in much narrower ventrally as compared to its breadth. The buccal cavity of *B. stomaticus* and *R. syhadrensis* is broad and trough-shaped, since these tadpoles have normal buccal musculature. Flattest and broadest buccal cavity is observed in *M. ornata*, it has weakest buccal musculature. Wassersug and Hoff (1979) have shown that macrophagus (here *R. tigrina* and *R. cyanophlyctis*) and microphagus (*M. ornata*) have large buccal volumes, while coarse particulate food eating tadpoles (*R. syhadrensis* and *B. stomaticus*) have an intermediate buccal volume.

Functionally, buccal cavity is divisible in two parts, anterior food gleaning and posterior food processing part. To understand the functional correlates of these parts they are being taken one by one in the following discussion.

1. Food gleaning part of the buccal cavity: It is the anterior most part of the buccal cavity, overhanging the prelingual and lingual arena of the ventral buccal. Its size and shape depends on the rostral curvature, size of the internal nares and the breadth of the upper beak. It is dorsally enlarged in suctorial mouthed tadpoles of genus *Bufo* and *Rana*, but its floor is much reduced. *M. ornata* lacks an oral disc and has a dorsal mouth. The floor of the buccal cavity, of this tadpole, is produced anterodorsally, reducing its roof. Here it is deep and ventrodorsally enlarged. Wassersug (1980) has treated this part together with buccal arena, but these two parts are morphologically and functionally different from each other. Prebuccal arena part of buccal cavity is food gathering while buccal arena part is concerned with food retrieval from the water current.

In *Bufo* and *Rana* tadpoles, the food gleaning part is morphologically composed of prenarial, narial and postnarial arenae. Its floor consists of prelingual and lingual arenae. Anteriorly it opens to outside through mouth, dorsally through internal nares and posteriorly it opens into the buccal cavity through a narrow opening. *Microhyla* tadpole has imperforate nares, so here food gleaning part of the buccal opens anteroposteriorly only. The food gleaning part of the *Bufo and Rana* tadpoles is anterodorsally enlarged and ventrally reduced, while in *Microhyla ornata* it is reverse, dorsally reduced and anteroventrally enlarged.

The prenarial ridges, pustules and keratinized plates and other irregularities help in handling and cutting the food to appropriate size which can pass through the infralabial sieve. *R. tigrina* tadpole has a pair of strong spurs which are tipped with keratinized plates, which help in conjunction with the jaws of the tadpole, in tearing and shearing of the fleshy food of the tadpole. The palmate structure of the infralabial papillae in *Bufo* and *Rana* tadpoles, produced into long filiform processes extending across the opening between food gleaning cavity and the food retrieving cavity, regulates food particle size entering the main buccal cavity. Reduced

fingers of infralabial papillae in *R. syhadrensis* and of *M. ornata* reflect the microscopic size of the food particles of these tadpoles. From time to time these tadpoles are seen coughing out large food particles which are not allowed to enter the buccal cavity by the infralabial sieve.

The tongue analage, lingual, circumnarial papillae and pustules are obviously sensory in function. Primarily they are chemoreceptors and thigmotectic organs, sensitive to the pressure in the oral cavity and chemistry of food and water entering the buccal cavity. Respiratory sole of these organs is not supported by evidence (Gradwell, 1972 a). During feeding of *Bufo* and *Rana* tadpoles, the food particles accumulate in this part of the buccal cavity for some time, the respiratory current moves through the narial passage. Periodically, the accumulated food is released in the current entering the main buccal cavity, at this time the narial valves close the nares, preventing the loss of food particles through them. The palmate prenarial papilla of *R. syhadrensis* indicates its role in preventing the food particles through the nares. *Bufo* larva does not have circumnarial papillae, instead, its nares are long with a small anterior recess, which indicates that nares can partially be closed, while the food is passing into the buccal cavity.

Microphagus *M. ornata* larva lacks an oral disc, has imperforate nares and feeds on planktonic particles. The food current passes into the buccal cavity without hindrance except the infralabial sieve.

A median ridge is a universal phenomenon of *Bufo* and *Rana* oral region, while it is absent in *Microhyla* tadpoles (Wassersug, 1980; Inger, 1985; Viertel, 1982). The median ridge of *B. stomaticus* and *R. syhadrensis* is a narrow ridge with dentated free edge, while that of *R. cyanophlyctis* is produced into one or rarely two long fine papillae. *R. tigrina* has a rectangular ridge with smooth edges. Apparently, this posterior most feature of the anterior buccal is sensory as well as mechanical in function. Its peculiar median dorsal hanging position in the buccal cavity indicates that together with the lateral ridge papilla, it may sense the concentration of food particles in the water current. Moreover, it deflects the water current to sides towards the buccal papillary mesh and over the secretory surfaces.

In food gleaning part of the buccal cavity, the food is broken, cut, torn and sheared to appropriate size, by the action of teeth, jaws, prenarial ridges and keratinized surfaces. Moreover, quality of food relative to its chemical nature, food value, palatability and particle size is assessed by various papillae and ridges in this part of the buccal cavity.

2. Food processing part of the buccal cavity: It is the main and posterior part of the buccal passage. Its shape and ornamentation differs in different species, depicting their feeding habits and ecology. In pond tadpoles, *B. stomaticus* and *R. syhadrensis*, it is wide and trough-shaped, while in benthic carnivorous tadpole of *R. tigerina* it is squarish, whereas in detritivorous *R. cyanophlyctis* it is oval in shape. In microphagus *M. ornata* this part of the buccal cavity is strongly dorsoventrally depressed. Posteriorly, it is bounded by the velum, which separates it from the branchial cavity. Laterally, BFA and BRA are lined by papillae, which are arranged in rows, except in carnivorous and pipid tadpoles, where they are either absent or reduced in size (Wassersug, 1980; Inger, 1985; Wassersug and Heyer, 1988). The buccal papillae are numerous in stream adapted tadpoles as in *R. hazarensis* (Khan and Malik, 1987 a), and fewer in pond tadpoles, while they are rudimentary and almost none in carnivorous tadpoles as in *R. tigerina*. Detritivorous *R. cyanophlyctis* has thick papillary meshwork, like stream adapted tadpoles; it strictly confines itself to larger water bodies where water is calm most of the time. Here thick papillae form a fine meshwork to intercept heterogeneous particles contained in the detritus. However, fewer BRA and BFA papillae of *B. stomaticus* and *R. syhadrensis* are typical of a pond adapted tadpole. Wide spaces between these papillae allow coarser particulate food to pass freely over the secretory tissue, which play leading role in food entrapment. The membranous papillation BRA and BFA of *M. ornata* is characteristic of microphagus tadpoles, they act as food guiding organs rather than food sieving structures. Rudimentary and few BFA papillae and totally absent BRA papillae in *R. tigerina* are typical of a carnivorous tadpole, where papillae are not appropriate organs to handle large chunks of flesh.

Apart from BRA and BFA papillae, there are other important structures in food retrieving part of the buccal cavity, like buccal pockets, secretory tissue and velum. These are functionally important features which necessitate separate treatment, one by one.

### Buccal pockets

Buccal pockets are almost universally present in the anuran tadpoles (Wassersug, 1980; Inger, 1985; Viertel, 1982; Wassersug and Heyer, 1988; Khan and Malik, 1987 a). The buccal pockets differ in shape, disposition and ornamentation from species to species. microphagus *M. ornata* tadpole the buccal pockets are longitudinal, open and with few papillae. They are lipless. Posteriorly, they are continuous with the pressure cushion. In *Bufo* and *Rana* tadpoles they are

transverse and closed due to thick lips. Those of *B. stomaticus*, *R. cyanophlyctis* and *R. syhadrensis* are transverse, longer and mesially orally curved, while *R. tigerina* has smallest transverse pockets with thickest lips. Wassersug (1980) does not assign any function to these universally present structures, however, Gradwell and Paztor (1968) regard these structures as pharyngeal bypass, opening into pharyngeal cavity on the ventral side, while Khan and Malik (1987 a) have suggested that they act as pressure releasers during pumping action of the buccal cavity. Volume of water, filling the buccal cavity, is much larger than the capacity of the branchial basket. Excessive water escapes through the buccal pockets, ensuring moderate pressure on delicate velum and the filter ruffle, preventing damage to these important structures. The buccal pockets in *M. ornata* are connected to the pressure cushion posteriorly, indicating important role it plays to ensure turgidity in the pressure cushions. The water, which is pumped in the pressure cushions, ensures required turgidity due to which they fit on the branchial baskets. There are three distinct pressure cushions in *M. ornata* corresponding to the three filter cavities. In *R. cyanophlyctis* the first cushion is distinct, while second and third are confluent with each other. *B. stomaticus* and *R. syhadrensis* have first two distinct, while in *R. tigerina* there is a single transversely enlarged inconspicuous pressure cushion.

Number of filter cavities and their distinctiveness from each other, number, shape distinctiveness of pressure cushions and the branchial basket, reflect efficiency of the filtering system of a tadpole.

### Buccal Secretory tissue

Tadpoles differ in the position, configuration, extent and pit size of the buccal secretory tissue, from species to species. Contrary to the view of Wassersug (1980), the morphology of the secretory tissue reflects the type of food a tadpole normally takes. In most cases food particle size also is depicted from morphology of secretory tissue. In *Microhyla ornata* the secretory tissue is composed of broad lateral strips, extending on the posterior lateral sides of BRA, and are mesially narrowly interrupted and is covered with finest pits. Fine planktonic food particles are efficiently entangled by the fine sheet of mucous secreted by these glands. The secretory glandular strip of *B. stomaticus* and *R. syhadrensis* is narrow, continuous across the roof of the buccal cavity as well as the floor of it. The pore size is larger than recorded for *M. ornata*, where the tissue is confined to the roof of the buccal cavity only. The pore size of the secretory tissue

of *R. syhadrensis* and *Bufo* is intermediate, while largest is recorded in *R. cyanophlyctis* and *R. tigerina*, where the secretory tissue is mainly confined to the margins of the dorsal and ventral vela. The secretory tissue in *R. cyanophlyctis* is much thicker than that of *R. tigerina*. The pore size of the secretory tissue is clearly correlated to the food particle size. The secretory pits are largest in *R. tigerina*, since the fleshy food of this tadpole consists of large chunks. The secretory tissue is broader in *R. cyanophlyctis*, since the detritus food of this tadpole consists of particles of various sizes, needing broader mucous surface and copious secretion of mucous for entanglement.

### Ventral Velum

It is the delicate curtain-like membrane hanging from the posterior border of the buccal cavity, separating the buccal from the branchial cavity. Ventrally it covers the anterior part of the pharyngeal cavities. The ventral velum is supported by cartilaginous spicules and forms stiffer part of posterior buccal, playing important role in regulating the passage of water through the buccopharyngeal region. Dorsal velum is more or less similar in all the tadpoles. It is mesially interrupted, except in *R. cyanophlyctis* where it continues staggeringly with that of the other side.

Tadpoles differ in form and structure of their ventral velum. *M. ornata* has mesially divided velum in lateral halves, while *Bufo* and *Rana* tadpoles have an entire ventral velum, that of *R. tigerina* is peculiar in being narrower and folded forwards. Posterior margin of ventral velum in *M. ornata* is smooth, while it is crenulated in *Bufo* and *Rana* tadpoles, with several peaks and irregularities. strong ventral velum is present in *M. ornata*, while it is weakest in *B. stomaticus*. It is broadest in *M. ornata* and narrowest is recorded for *R. tigerina*.

Dorsal and ventral vela differ in function. Herpetologists have two views about the function of dorsal velum. Kratochwill (1933) and Kenny (1969 a) believe that dorsal velum together with pressure cushions seal off the branchial chamber from the buccal cavity, preventing regurgitation, while Gradwell (1974), Savage (1961) and Wassersug (1980) suggest that it helps in deflecting the current of water to the filter cavities on sides. De Jongh (1968) believes that it prevents the flow of water from displacing the mucous cords laden with entrapped food particles from the ciliary grooves, where they are on their way to esophagus.

Valvular action of ventral velum, on the other hand, is universally acknowledged by the herpetologists (Kenny, 1969 a; Gradwell, 1974; DeJongh, 1968; Khan and Malik, 1987 a). The posterior margin of the ventral velum presses against buccal floor preventing regurgitation of

water. Moreover, the velar surfaces support secretory tissue, branchial food traps and hold the filter plates in position, which are attached to them.

In tadpoles specialized to trap fine particles, all filter plates are attached with the subvelar side of the ventral velum, so that there are three distinct filter cavities, as in *M. ornata* and *R. cyanophlyctis*. Tadpoles of *B. stomaticus* and *R. syhadrensis* feed on intermediate sized food particles, and here first two plates cb 1, cb 2 are attached, while cb 3 and cb 4 are free. The first filter cavity is distinct while third and fourth are confluent with each other. In *R. tigerina* none of the filter plates is attached, and the filter cavity is single and bowl-shaped.

### Pharyngeal region

All the five species of tadpoles differ in the morphology of their pharyngeal region (Table X). Pharyngeal region of a tadpole is attached to the posterolateral sides of its buccal region. It is mainly concerned with the entrapment of fine food material, retrieval of food laden mucous cords by filtering them from water current on the filter ruffle of the filter cavities and directing them to the esophageal orifice. Primarily pharyngeal region is concerned with respiration.

The part of the branchial baskets lying under the ventral velum (branchial food trap of Wassersug and Rosenberg, 1979) is a region of specialized secretory tissue concerned with the entrapment of food particles in mucous. In microphagous tadpoles it is particularly specialized to trap fine food particles, since here it is in the form of thickened tori which are capable of secreting copious amount of mucous. Such an arrangement is lacking in macrophagous tadpoles (Wassersug, 1972, 1980; Kenny, 1969 a; Viertel, 1984, 1989).

Table X summarizes the differences in some morphological criteria of the pharyngeal region of the tadpoles studied. *M. ornata* has most enlarged branchial basket, about 70-73% of the buccopharyngeal cavity. It has three deep, most extensive filter cavities and largest branchial plates (length 1.97-3.7, breadth 1.2-1.8), with dense filter rows, 8-23. Branchial food traps are very well developed, deep with distinct three tori, one in each branchial food trap, covered with fine secretory ridges, all over. Ultramicroscopical food material entangled in mucous almost clogs the three filter cavities in the form of floccular material, whole of the branchial basket is filled with it.

Both *B. stomaticus* and *R. syhadrensis* tadpoles have second largest branchial cavity

(28-36% of the buccopharyngeal region). *B. stomaticus* tadpole has larger branchial plates than that of *R. syhadrensis*, but the number of the filter rows are higher in *R. syhadrensis*, and this tadpole has a distinct torus with fine secretory ridges associated with its first filter cavity, on each side. It has made filtering system of *R. syhadrensis* more efficient than that of *B. stomaticus*. First filter cavity of *R. syhadrensis* is always clogged with floccular material. Moreover, these tadpoles differ in the morphology of their subvelar secretory tissue. *B. stomaticus* tadpole has both ridged as well as pitted pattern. Ridges lie on the first filter cavity, while pitted secretory tissue is mesially located on the subvelar surface. *R. syhadrensis* tadpole has only the ridged pattern (Figs. 6, 24).

*R. cyanophlyctis* tadpole has relatively larger branchial basket, which is about 28-30% of the total buccopharyngeal region. Moreover, unlike other ranid tadpoles, its branchial basket has three distinct filter cavities. Its filter plates are larger (length 2.5, breadth 1.12) and have more filter rows (12-14). Detritus food of this tadpole is composed of heterogenous particles, including sand and earth particles. The subvelar secretory tissue has ridged pattern. This tadpole has to ingest large quantity of detritus to get required food, since most of the stuff it eats contains inorganic material having no food value. On the other hand, carnivorous tadpole of *R. tigerina*, despite its large size, has smallest branchial basket (18-20%), and has poorly organized filter plates due to loose filter ruffle. This tadpole is capable of filtering only large food particles, smaller particles pass easily through its loose branchial filter. It has been observed that smallest plankton which this tadpole is able to filter is of the size of *Daphnia* or *Cyclops*, common crustaceans in the pond water. Its buccal as well as subvelar secretory tissue consists of large pits, arranged in 2-5 rows along the velar margin. The secretory pits are elevated from the general surface of the velum and are largest observed in the tadpoles studied. Entrapment of large sized food is done by secretion of copious mucous. There are no ridges in the secretory tissue.

The five anuran tadpoles, which have been studied, are morphologically different in their buccal and branchial organization and filter grid, with different filtering capabilities, thus each species is able to feed on a particular part of the common food base available in the sympatric habitat.

### Pressure cushions

The part of the dorsal buccal, lying over the branchial baskets, plays an important role in

regulation of the passage of water current through the branchial basket. The pressure cushions are in the form of a delicate loose membrane. Kenny (1969 a) reported that the pressure cushions were composed of alveolar tissue. Present study, like other studies (Gradwell and Paztor, 1969; Gradwell, 1972 a, 1975 b; Wassersug, 1980), has shown that buccal cavity has connection with the pressure cushions, through which the water is pumped into the pressure cushions at the time of the buccal contraction. Turgid pressure cushions push the velum forwards which shuts the buccopharyngeal orifice, while the pressure cushions fit tightly on the branchial basket. In this way the branchial basket is tightly sealed from the buccal cavity.

To maintain appropriate pressure in the cushions, buccal pockets of *Bufo* and *Rana* tadpoles are thick-lipped, which keep their oral orifices closed in low pressure. In microphagus *M. ornata* tadpole, the buccal pockets are without valves and remain open. However, the pressure cushion of this tadpoles has complicated morphology, indicating some complicated arrangement which maintains a constant pressure in the pressure cushions (Fig. 13).

## Physiographic Background of the Amphibian Fauna of Pakistan

Present and past ecological conditions, geographical accessibility, and long term physiographic events have shaped out present day fauna of Pakistan. All these factors as well as recent human activity have played key role in creating habitat suitability and have affected the evolutionary history of each amphibian familial unit. Cosmopolitan amphibian genera *Bufo*, *Microhyla* and *Rana* are represented in Pakistan by few species (Khan, 1980, 1990; Khan and Tasnim, 1987). The historical physiographic events which have been taking place in the subcontinent are documented in fossil and floral history of Miocene (Axelrod, 1960). The Indian plate broke off from Africa during Cretaceous, due to fragmentation of Gondwanaland (Holmes, 1965; King, 1967; Courtillot and Vink, 1983). It drifted northwards and collided with Eurasia during Eocene, resulting in the uplift of Himalayas (Buffetaut and Ingawat, 1985; Jaeger et al., 1989).

The deep trench which appeared between Himalayas and the peninsular part of the Indian plate under Eurasian plate, was filled by the detrital deposits washed down from the Himalayan heights by the ancient rivers. By Miocene the trench was replaced by vast tracts of plain land the Indo-gangetic plains (Wadia, 1966; Khan, 1980). Himalayan heights had far reaching effects on the geology, geography, hydrology and climatology of Indo-Pakistan subcontinent. The original wetter and warmer climate, evenly distributed rainfall throughout the year and the ever green and warm deciduous forests were gone from the subcontinent. These ecophysiographic changes were mainly due to entrapment of water in polar ice caps, which had already started a wave of dryness throughout the continents. By the Oligocene extreme regions of temperature and precipitation developed, and the dryness prevailing at this time in western Eurasia extended on to the subcontinent. Vast grasslands appeared with subtropical temperate climate and low rainfall. Aridity resulted in the establishment of Cholistan and Thar deserts and it is main ~~major~~ feature of the climates of Pakistan even today (Ahmed, 1951). East-west strike of the Himalayan ranges, overlooking the Indo-Gangetic plains, has profound effect on the annual rainfall of the area, by creating barometric vacuum and attracting water vapour laden winds from the sea in the South. It started the monsoons, the main annual feature of the subcontinent. By the Pliocene, the physiographic conditions of the plains were right for colonization by amphibians and other groups of animals, which by this time had invaded Eurasia from different sources (Savage, 1973).

Patterns and correlates of genetic diversity in amphibians strongly implicate environmental selection as an important evolutionary force causing divergence of heterozygosity (Nevo, 1976 a, b; 1988; Nevo and Yang, 1979; Nevo and Bailes, 1988, 1989, 1991; Nevo and Filippucci, 1988). The tropical species are more heterozygous with much diversified habitats available. World tropics have played important role in the evolution of main amphibian genetic lines (Savage, 1973; Nevo and Bailes, 1991). The three main familial units, constituting main stock of amphibian fauna of Indo-Pakistan subcontinent, are most diversified in tropics.

The Cretaceous fauna of the India plate was probably similar to that of Africa, but it soon became extinct without leaving any trace. Family Microhylidae most probably had already separated from family Ranidae before the breaking off of the Indian plate from Africa. It was the only amphibian which was transported and survived on the Indian plate (Savage, 1973; Rabinowitz et al., 1983; Wassersug, 1984). Now-a-days the microhylids occur throughout most of the world, with the greatest diversity in the tropics and subtropics (Vanzolini and Heyer, 1985). These frogs are now represented in the peninsular India by four genera and ten species (Parker, 1934; Savage, 1973). These small anurans have radiated out from India to nearby landmasses (Savage, 1973). One species *Microhyla ornata* has extended in the temperate environs of northern Punjab, Pakistan (Khan, 1974). Darlington (1957, Figs. 23:139) and Savage (1973, Figs. 13.8: 366) do not include Pakistan in the distribution maps of Family Microhylidae. Khan (1974) discovered *M. ornata* from Punjab and subsequently has shown that this frog has a wide distribution in the subHimalayan ranges and Punjab, Pakistan (Khan, 1980; Khan and Tasnim, 1987).

The bufonid frogs are distributed throughout the world except Australia, Papua and New Guinea (excluding *Bufo marinus* which has been recently introduced in Australia). Evolution of family Bufonidae has taken place in tropical South America, during upper Cretaceous, from where these toads radiated out to North America (Blair, 1968, 1972; Reig, 1972; Maxon, 1984). American toads invaded Eurasian landmass in two waves through Bering land bridge. First invasion took place in Upper Cretaceous by tropical South American broad-skulled toads. They mainly colonized the southeast Asian tropics, however, one line invaded western Himalayas, and now is represented in Pakistan by two species *Bufo himalayanus* and *B. melanostictus*. The later toad though is wide spread in southeast Asia but do not extends in the plains of Punjab. The second invasion was by narrow-skulled temperate North American toads, during Oligocene. They established in temperate Eurasia, from where they radiated out. Four of

these toads are represented in fauna of Pakistan, *Bufo olivaceous*, *B. viridis*, *B. surdus* and *B. stomaticus*. Of these toads only *B. stomaticus* is represented in Punjab plains (Mertens, 1969, 1970; Khan, 1972, 1976; 1980, 1990).

View differ among herpetologists about the origin of frogs of the family Ranidae. Savage (1973) has evidenced from present distribution pattern that they originated in tropical Africa, while Darlington (1957) believes southeast Asian tropics. Present day data favours the former view. From Africa, ranid frogs radiated out northwards during Cenozoic, and by Oligocene they had established a secondary evolutionary center in southeastern tropical Asia. In Asia, they underwent extensive differentiation and radiated out to surrounding areas (Boulenger, 1920; Dubois, 1984, 1986). By the mid Tertiary the physiographic conditions in the subtropical North became habitable; ranid as well as microhylid frogs invaded peninsular Indo-China, nearby islands and Indo-Pakistan subcontinent (Savage, 1973). Present day ranid fauna of Pakistan mainly belongs to two subgenera *Rana*, and *Paa* of genus *Rana*. Frogs of subgenus *Paa* colonized the torrents of northern and western highlands (Dubois and Khan, 1979; Khan 1990; Khan and Tasnim, 1989), while frogs of subgenus *Rana*: *R. cyanophlyctis*, *R. syhadrensis* and *R. tigerina*, are widely distributed throughout the Indo-Gangetic plains (Khan, 1980; Khan and Tasnim, 1987).

Punjab plain was invaded by the amphibians from northern highland through tadpoles washed down by the rain water. In mid-Tertiary, while metamorphic changes were taking place in the extra peninsular part of Indian plate, ranid and microhylid frogs had already established themselves in the waters of the foothills of Himalayas. At this time the Punjab plain was land of swamps. Courses of the rivers were not yet determined. The streams of the run-off water from Himalayan heights, meader through the plains. They had rush of water only during short torrential monsoon rains. During rest of the year the plains remained in the form of swamps with water trapped in lakes, ponds and puddles. The water had heavy planktonic bloom, the emergent vegetation was in the form of algae and pond grasses. The scenario provided ideal situation to the amphibian larvae from Himalayas to develop and metamorphose. Soon Punjab plain was colonized by audlt amphibians. Khan (1984, 1985) has shown that Himalayan river system has played important role in carrying down and distribution of different mountain species of amphibians and snakes in the plains of Punjab. Annual flooding of the plains has also contributed

activity, in the plains, has made conditions suitable for this small frog, which is relatively recent entrant in our amphibian fauna (Khan and Tasnim, 1987, Khan, 1990).

Starrett (1973) has emphasized the importance of basic morphological features of the anuran tadpole as a key to our understanding of frog's evolution. The xenoanurans (rhinophrynids, pipids) and scoptanuran (microhylids) frogs have mid-stream filter feeding microphagus nektic larvae. Several authors like Orton (1953, 1957), Starrett (1973) and Savage (1973) have argued that xenoanuran and scoptanuran tadpoles radiated out in the tropical waters and occupied most of the filter feeding niches, long before the arrival of acosmanuran (bufonid and ranid) larvae. Late arriving acosmanuran larvae radiated into different tropical adaptive larval types, except the midstream filter feeding, due to its pre-emptive occupancy by microphagus tadpoles. Though acosmanuran larva is more advanced than midstream filter feeding one, but the presence of a specially adapted primitive stock prevented invasion of its adaptive zone by a more advanced line (Savage, 1969).

Species rich fauna of scoptanuran and xenoanuran frogs coexist with acosmanuran frogs in the tropics, species do not come in direct competition with each other at any stage of their life (Toft, 1981, 1985; Heyer et al., 1990). In the plains of Punjab, same harmony exists between species of these two groups at adult as well larval stages. The acosmanuran frogs, *Bufo stomaticus*, *Rana cyanophlyctis*, *R. syhadrensis*, *R. tigerina* and scoptanuran *Microhyla ornata* are sympatric both at feeding as well as at breeding sites. Their reproductive activity is triggered by the presence of different ecological conditions which prevail at different times of breeding season. They call from different positions, deposit their eggs in different ways and at different sites in a common habitat. Their eggs and larvae differ morphologically, ecologically and in feeding habits. They occupy different niches in a sympatric habitat (Khan, 1982 a,b; Khan and Malik, 1987 b, and present study). An anuran larva is an important constituent of the food chain in a pond ecosystem in the plain of Punjab, and plays important role in the regulation of the pond vegetation. Except carnivorous larva of *R. tigerina* all other four larvae are primary consumers, feeding on different parts of the common available food base.

## GUILD STRUCTURE

In this concluding part of the discussion, ecological adaptations of the anuran larvae inhabiting plains of Punjab are being ecologically categorized. Each species of the larvae is distinct from the other, not only in its morphology but also in its microhabitat.

Ecologically similar anuran larval assemblages —the ecomorphs, have recently been categorized into ecological guilds (Lannoo et al., 1987; Wassersug, 1980; Toft, 1981; Wassersug and Heyer, 1983, 1988; Heyer et al., 1990). Altig and Johnston (1989) have developed a generalized scheme of anuran tadpole guilds, taking into account their mode of feeding. Sufficient data now has accumulated for the five anuran tadpoles inhabiting waters of Punjab, to allow to categorize them following Altig and Johnston's (1989) scheme.

None of the five tadpoles is endotrophic and lotic. All of them are exotrophs and lentic. They fall in Section II of the scheme of the guilds. These tadpoles inhabit non-flowing lakes, ponds, puddles and seepage pools.

- A. Lentic-benthic tadpoles; dorsolateral eyes, suctorial mouth; globular, drab coloured spotty body; narrow parallel tail-fins.
1. Benthic-littoral in early stages, confined to shallow water along soil-water interface; becomes profundal in later stages; macrophagous rasper.....  
.....*Bufo stomaticus*.
  2. Lentic-littoral, confined to seepage pools with moderate emergent vegetation and moderate planktonic growth; microphagous rasper.....*Rana syhadrensis*.
  3. Lentic-profundal, inhabit permanent ponds with little or no vegetation; macrophagous detritivorous.....*Rana cyanophlyctis*.
  4. Lentic-profundal, inhabit ephemeral puddles with little or no vegetation; macrophagous, carnivorous.....*Rana tigerina*.
- B. Lentic-nektic tadpoles, with anterodorsal non-suctorial mouth, lateral eyes; dorso-ventrally depressed head and laterally compressed transparent body; long tail, broad fins, long terminal tail flagellum; microphagous suspension feeder.....  
.....*Microhyla ornata*.

## SUMMARY AND CONCLUSIONS

Following is the summary and conclusions drawn from the ecomorphological studies of the anuran tadpoles from Punjab, Pakistan.

1. The tadpoles studied belong to five taxa, *Bufo stomaticus*, *Microhyla ornata*, *Rana cyanophlyctis*, *R. syhadrensis* and *R. tigerina*. They differ from each other in external as well as in their internal buccopharyngeal morphology.
2. The morphological differences among five species of tadpoles can be sorted out at familial, generic and specific levels.
3. Interfamilial and intergeneric differences in morphology of tadpoles are of prime importance, since the tadpoles belong to three families and three genera. microhylid tadpoles have reduced buccal and hypertrophied pharyngeal region, while conditions in *Bufo* and *Rana* tadpoles are reverse.
4. Differences among three species of genus *Rana* are significant and are sufficient to differentiate them from each other.
5. Once a tadpole has developed specific external as well as internal oropharyngeal features, ontogenetic variations in its morphology are slight from Stage 26 to Stage 38, beyond which metamorphic changes take place.
6. Morphological features which vary little within a species but vary considerably among species are of great systematic value. These characters are:
 

Number, size, shape and position of the infratrabial, lingual, buccal, lateral ridge and postnarial papillae; shape and size of buccal pockets, ventral velum and presence, shape and size of median ridge; morphology of buccal and subvelar secretory tissue, and of branchial food traps; size and shape of the filter plates, number of filter cavities, number and density of filter rows; the ratio between buccal and pharyngeal cavities and extent of the lung development.

7. The external morphology of a tadpole categorizes its ecological preferences. the peculiar transparent, broad-finned tadpole with long vibratile terminal tail filament, anterodorsal non-suctorial mouth with median ventral spiracle of *Microhyla ornata*, is lentic-nektic. Tadpoles of *Bufo* and *Rana* are lentic-benthic in habits, and have suctorial mouth, muscular tail with low fins.

8. Feeding ecology of the tadpole is best reflected from its oropharyngeal morphology. Imperforate nares, membranous BRA and BFA papillae, broad flattened BRA and BFA, absence of lateral ridge papilla and median ridge, hypertrophied pharyngeal and abbreviated buccal region of *Microhyla ornata* tadpole indicate its obligate microphagus suspension feeding habits. Broad BFA and BRA and rudimentary papillae, hypertrophied buccal and abbreviated pharyngeal region of *Rana tigerina* tadpole indicate obligatory macrophagus carnivorous habits. Few simple BRA and BFA papillae, almost equally developed buccal and pharyngeal regions of *Bufo stomaticus* and *R. syhadrensis* tadpoles, suggest generalized, macrophagus, suspension feeding habits. However, presence of distinct torus in branchial food trap reflects that *R. syhadrensis* tadpole can filter much finer food particles than *B. stomaticus*. Long and narrow-BRA and BFA with rich papillation, three distinct filter cavities and peculiar teeth of *R. cyanophlyctis* tadpole indicate its detritivorous macrophagus habits.

9. Microphagus tadpole of *M. ornata* prefers to live in calm ponds, with little or no emergent vegetation but rich in planktonic bloom. *R. cyanophlyctis* tadpole prefers permanent ponds with rich detritus accumulated at the bottom. *Bufo stomaticus*, *R. syhadrensis* and *R. tigerina* breed in shallow water pools, with little vegetation. The larvivorous tadpole of *R. tigerina* feeds on sympatric tadpoles.

10. All tadpoles inhabiting plains of Punjab are voracious feeders, as if wishing to complete development as quickly as possible, which is another adaptation to the temperate and unpredictable environs.

11. The physiographic data, when viewed in prespective of the idea of continental drift, indicates that peninsular India was first colonized by microhylids and later by bufonids and ranids.

12. Punjab plains were colonized through the bufonid and ranid larvae washed down from

Himalayan heights, while microhylids invaded through their adults.

13. Recent and past human activity has played a key role in creating suitable habitat for wide distribution of frogs in the plain of Punjab and throughout Indo-Pakistan subcontinent.

14. Differences in the morphological accounts in literature pertaining to the tadpoles of the same species, described from different parts of subcontinent, are due mainly to misidentifications of tadpoles.

15. Ecological changes during tadpole's ontogeny do not affect its oropharyngeal morphology.

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