Buccopharyngeal Morphology and Feeding Ecology of *Microhyla ornata* Tadpoles

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Abstract.- The oropharyngeal morphology of *Microhyla ornata* tadpoles is described. Anatomical peculiarities are correlated to feeding ecology. Microhylid anatomical features are discussed and compared with ranoid tadpoles.

Key words.- Amphibia, Salientia, Microhylidae, *Microhyla ornata*, larval oropharyngeal morphology, feeding ecology.

Introduction

The common southeast Asian narrow-mouth frog *Microhyla ornata* is widely distributed throughout Punjab, Sindh, N.W.F.P. and Azad Kashmir (Khan, 1974; 1979; 1988; Khan and Tasnin, 1987). Normally, its small size makes it inconspicuous and difficult to detect in the field. However, after a summer heavy downpour, the characteristic rasping call of *Microhyla ornata* is easily distinguishable from rest of the local amphibians (Khan and Malik, 1987b). *Microhyla ornata* readily takes refuge under vegetation, leaf litter, logs, stones, in holes and fissures in the ground, and often is mistaken as a juvenile of some larger species.

At mid-monsoon, *M. ornata* invades large water bodies, which, by this time, are filled with water and have developed thick planktonic growth. Solitary males perch well away from water among marginal vegetation to call. Eggs are laid in patches of jelly, which float at water surface as "egg-rafts" (Khan, 1982b).

The present study describes oropharyngeal morphology of *Microhyla ornata* tadpole, at Stage 35 and correlate it to the tadpole's feeding ecology. Moreover, it is compared with already known morphologies of sympatric tadpoles belonging to the genera *Bufo* and *Rana* (Khan and Malik, 1987a; Khan and Mufti, 1994b, 1995).

Material and Methods

Tadpoles for the present study were collected during the summers of 1986-88 from different localities along the northwestern border of Rabwah City (Khan and Malik, 1987b). They were netted at midstream with a hand net. *Microhyla ornata* tadpoles from Ghakkhar, District Gujranwala, Punjab, Pakistan (Khan, 1974) and Azad Kashmir (Khan, 1979), were used as comparative material.

Collection, preservation and storage methodology followed Khan (1982b), while surgical procedures and descriptive terminology are from Khan and Malik (1987a) and Khan and Mufti (1994b, 1995), except that for *M. ornata* tadpole, the lateral cuts through buccopharyngeal walls, must pass through mid-eye, unlike ranoid tadpoles where cuts pass below the eye. Fine particulate mucilage-trapped material accumulating in the filter cavities is cleared by a jet of water from an ordinary eyedropper. Drawings of the buccopharyngeal surfaces were made with the help of camera lucida.

Tadpoles at Stage 35 were selected, since at this stage, they have already attained maximum size and their characteristic organs are fully developed and functional. The tadpole at this stage is voraciously feeding and its digestive system is functioning at its full capacity. Shortly after this stage, metamorphic changes start occurring.

For identification of Stage 35, tadpoles were compared with Khan's (1965) table of normal development. Data for present study are recorded from 10 specimens.

Description

External morphology

The tadpole's body is perfectly streamlined; the head is dorsoventrally depressed while its belly is laterally compressed and oval in dorsal profile. The snout is countersunk, displacing mouth anterodorsally. The tail is more than twice the length of the head and body. Broad caudal fins narrow abruptly in the poste-

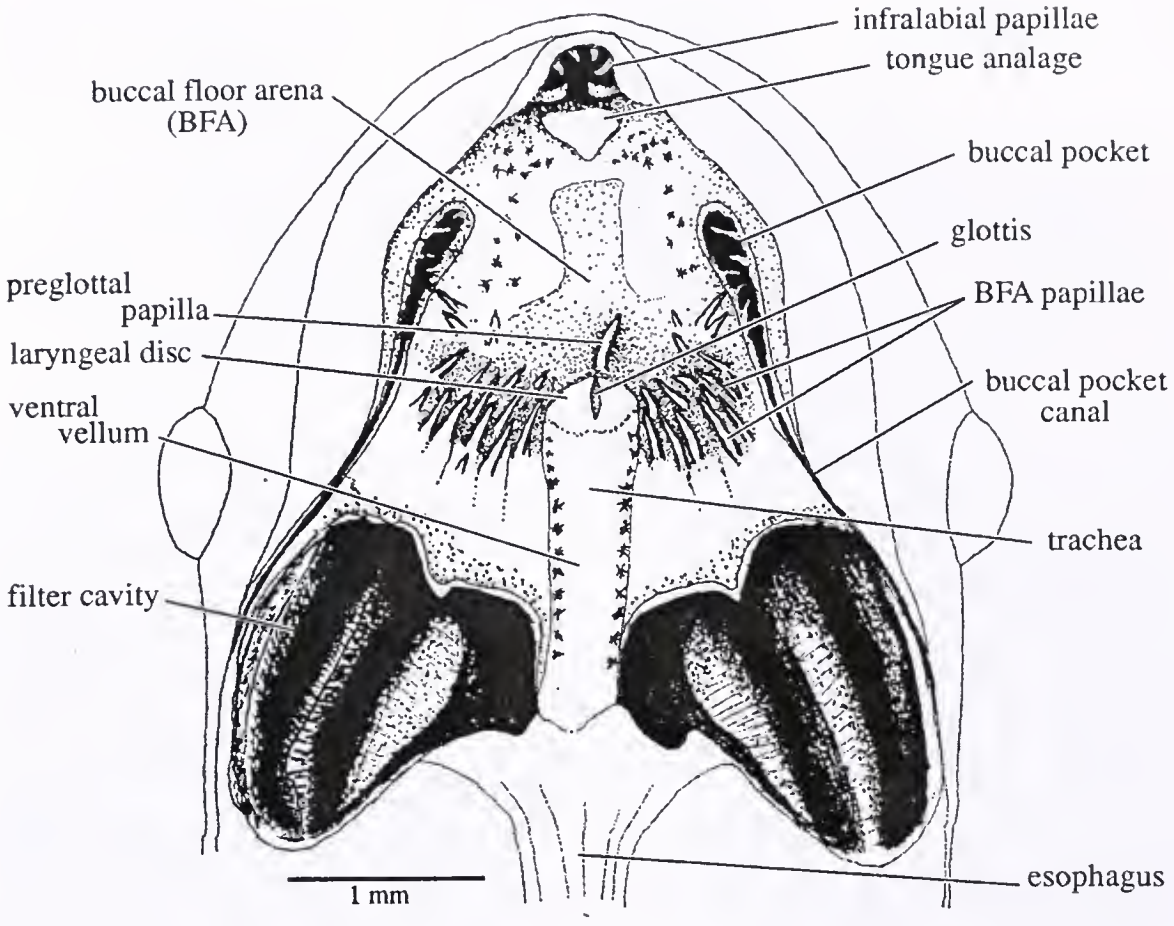

Figure 1. Morphology of surgically exposed buccopharyngeal floor of *Microhyla ornata* tadpole at Stage 35 (scale 1 mm).

rior half of the tail, passing into a delicate long flagellum.

The body is widest at the level of laterally disposed small eyes. The nostrils are imperforate; their position is marked by heavily pigmented anterolateral pits lying just anterior to eyes. The mid-ventral spiracle is close to posterior ventral end of the abdomen, with a distinct prespiracular valve (Khan 1982b).

The horizontal mouth has a median U-shaped cleft in the middle of the lower lip which remains permanently open (Khan and Mufti, 1994a, Fig. 2). Presence of iridiocytes in the abdominal wall, give it a characteristic silvery shine, which is lost within two to three weeks, on preservation. A median dorsal band of melanophores covers the brain and extends onto the base of eyes and the nasal pits.

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 0.5-1.95; 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.

Internal Morphology

Buccal region. Khan and Mufti (1994b; 1995) distinguished a tadpole's buccal cavity in two functional units: anterior food gleaning part and posterior food retrieving part. The dorsoventrally depressed head and peculiar position of the mouth in *M. ornata* tadpoles have affected the form and shape of the tadpole's buccal cavity; reducing the food gleaning part and widening the food retrieval part which occupies most of the buccal region.

Ventral buccal (Fig.1). The floor of the food gleaning part consists of vertical U-shaped prelingual chamber which opens out through mouth at snout top and is lined by a series of three simple infralabial papillae. Posteriorly, it opens in food retrieval part of

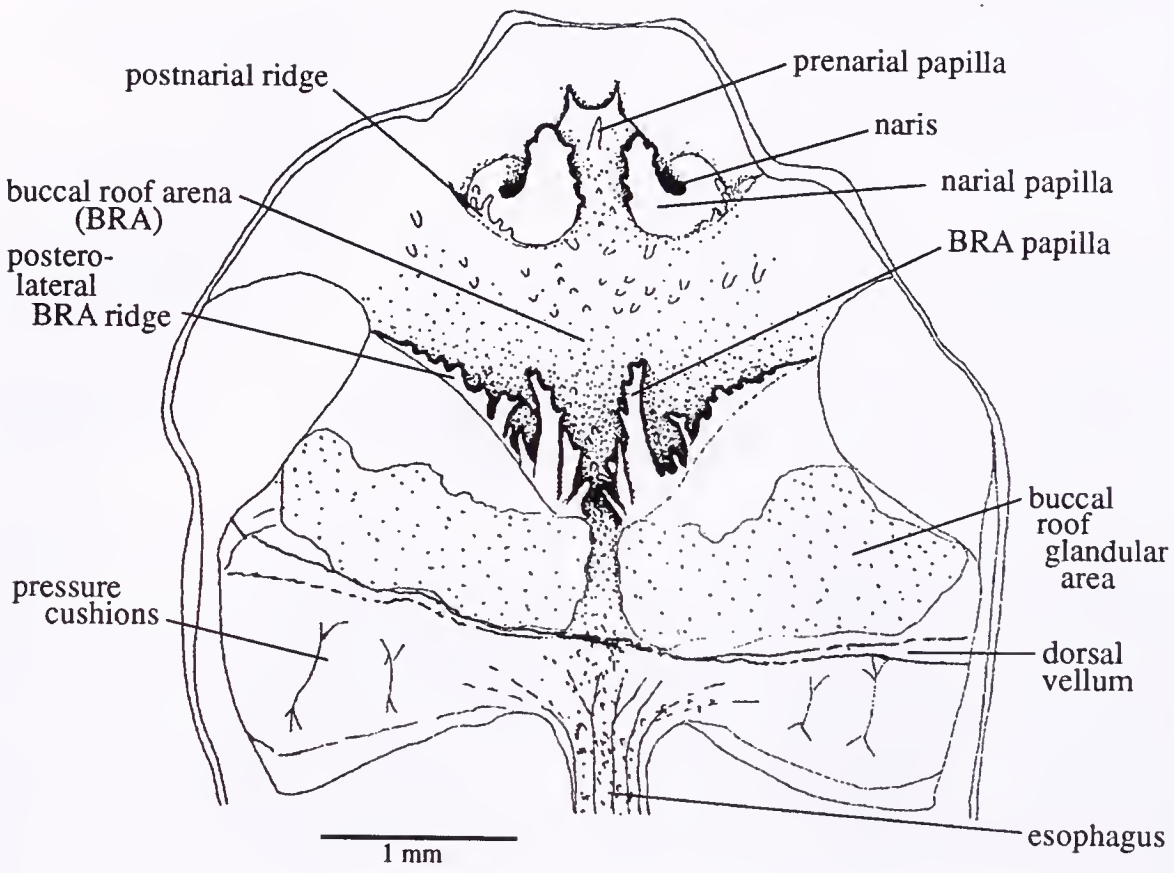

Figure 2. Morphology of surgically exposed buccopharyngeal floor of *Microhyla ornata* tadpole at Stage 35 (scale 1 mm).

the buccal. A non-papillated tongue analage, a conical thickening which is broader anteriorly pointed posteriorly, guards the opening of the food gleaning part into the food retrieval part. The spacious food retrieval part forms the main buccal cavity. The buccal floor arena (BFA) is rectangular, laterally raised with a median shallow passage. A group of 12-14 fine tipped, large, flat BFA papillae lie on lateral sides of anterior end of trachea. A pair of smaller midpocket papillae lie at the level of mid-pockets. A buccal pocket is a long, narrow, club shaped longitudinal slit running anteroposteriorly on each lateral side of the BFA with a posterior narrow canal connecting it with the pressure cushions. Anterior, wider, parts of buccal pockets have 3-6 pre- and 5-8 post pockets, small, conical papillae.

The trachea is a long cylindrical pipe that extends medially to the base of the BFA, carrying the glottis far anterior to the ventral velum and dividing it into lateral halves. The thin lipped glottis is 100% exposed, lies on a bulbous laryngeal disc, and is guarded by a long preglottal papilla which is tipped left.

The broad ventral velum has a strong spicular support. It covers about 1/2-1/4th of the underlying branchial baskets and consists of three distinct long and deep filter cavities. The free margin of the velum is smooth, with a single broad projection above third filter plate and is covered by a narrow strip of minute secretory pits. Rows of melanophores run along the lateral sides of the buccal arena and are aggregated on the sides of the tongue analage; a row runs along lateral sides of trachea.

Dorsal buccal (Fig. 2). The food gleaning part of the buccal is roofed by a broad prenarial arena, which has a median V-shaped depression with an anterior prenarial papilla and several pustules. The position of the imperforate naris is marked by a shallow depression from which a flat ribbon like twisted narial papilla hangs down in the buccal cavity. A thin delicate, narrow, papillated, postnarial ridge dorsally delimits narial region and the food gleaning part of the buccal.

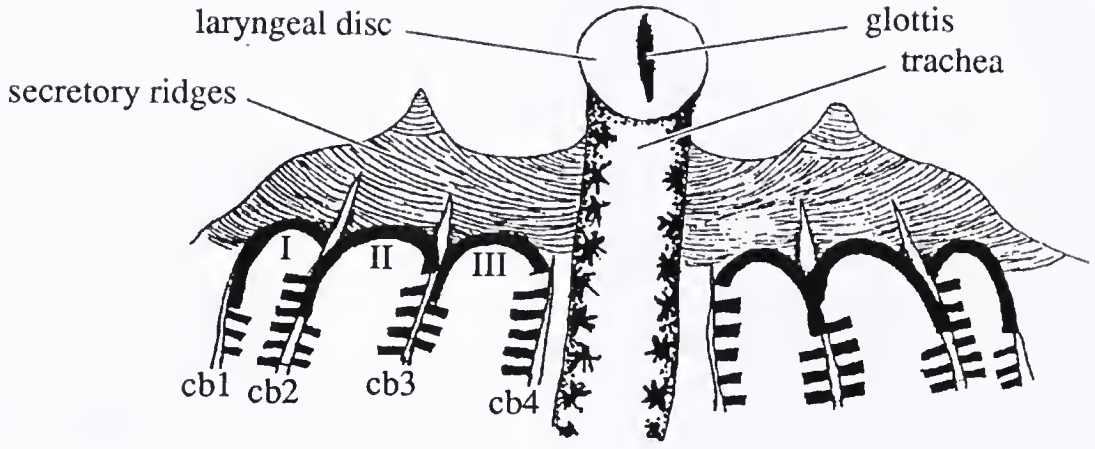

Figure 3. Underside of ventral velum showing details of filter cavities (diagramatic).

The food retrieval part is roofed by a spacious, broader than long, buccal roof arena (BRA), which is featured mainly by a distinct posterolateral BRA ridge, the free margin of which is cut into flat fine tipped BRA papillae, increasing in length from out smallest, to inside longest, with blunts on their inner sides, while smaller are without blunts. The BRA surface is pustular.

The broad glandular area of the buccal roof is divided into lateral rectangular halves and is covered with dense minute secretory pits. The dorsal velum narrows gradually mesoid, at mid-BRA it staggers to continue with that of other side.

Branchial region. Branchial baskets are more than twice the length of the buccal. Three filter cavities are distinct in each branchial basket. The first filter cavity is largest while the third is smallest. The filter cavities are always packed with fllocular matter. The third is tilted outwards, partially blanketing the second. About half to one third of the filter cavities are covered with velum. A distinctly ridged oval torus (Fig.3:I, II, III) is present in each filter cavity. The subvelar surface is profusely ridged with fine transverse secretory ridges (Fig. 3) that run in line with toric ridges, which are edged with fine secretory pores.

A tight filter ruffle cover the surface of filter plates. The number of filter rows on filter plates vary from minimum 9 on the 4th ceratobranchial to 23 on second (Table 1). The filter ruffle is 3° dense with tertiary foldings. Successive filter rows abut across fully canopied deep filter canals. The filter ruffle covers both sides of second and third filter plates (Fig.3: cb2, cb3).

Three pressure cushions are distinct on posterolateral sides of the dorsal pharynx (Fig. 4). The first and second are four times longer than broad. The first, and outer-most, is continuous anteriorly with the buccal pocket of its side through a buccal pocket canal. Meanwhile, the third, innermost, is broadest and has a median hook-like appendage. Deep ciliary groove runs along posterior border of the pressure cushions towards esophageal orifice along posterior sides of the pressure cushions.

The lungs at Stage 35 are well developed, each running along the dorsolateral sides of the abdominal cavity, extending to the posterior end of the abdomen. Anterior half of the lung is broad, with well-devel-

Table 1. Branchial elements of *Microhyla ornata* tadpoles at Stage 35 (Ant=anterior aspect; B=breadth; cb=ceratobranchial; L=length; Post=posterior aspect). Data from 10 specimens, all measurements in mm.

Ceratobranchial	Filter plate		Filter rows/side	
	L	B	Anterior	Posterior
cb. 1	3.5	1.8	0	15-18
cb. 2	3.7	1.5	13-16	20-23
cb. 3	2.5	1.4	16-17	13
cb. 4	1.9	1.2	8-9	0

Table 2. Comparison of microhylid and ranoid tadpole.

Character	Microhylid	Ranoid
Head	depressed	depressed
Belly	compressed	depressed
Color	transparent	Drab + pattern
Tail length	2-3 times body	2-2.5 times
Tail muscle	narrow	broad
Tail fins	broad	moderate
Tail tip	produced in a flagellum	round/pointed
Spiracle	median ventral	dextral
Belly wall	silver-shiny	transparent or drab
Mouth	antero-dorsal	anterior/antero-ventral
Oral disc	absent	present
Nostrils	imperforate	perforate
Narial flap/papillae	flap	papillae
Infralabial papillae	simple	palmate
Lingual papillae	absent	present
Postnarial papillae	small on a membrane	long solitary
Lateral ridge papilla	absent	present
Median ridge	absent	present
Buccal musculature	poor	well developed
Branchial basket	longer than broad	broader than long
Pharyngeal/buccal ratio	75 %	45-50 %
Prenarial ridge	absent	pustules or ridge
BRA/BFA papillae	flat fine tipped	short forked blunted
BRA/BFA papillae	form membranes	distinct no membranes
Glottis	100% exposed	not or partiall exposed
Glottal disc	bulbous	concealed
Glottal position	anterior to vellum	posterior to vellum
Glottal papilla	present	absent
Trachea	long	absent
Secretory tissue	single celled	multicellular
Subvelar secretory tissue	ridged	ridged/pitted
Filter cavities	3	2/3
Maximum filter rows	15-23	10-14
Position of tori	all filter cavities	absent or first cavity
Filter cavity depth	as long as deep	longer than deep

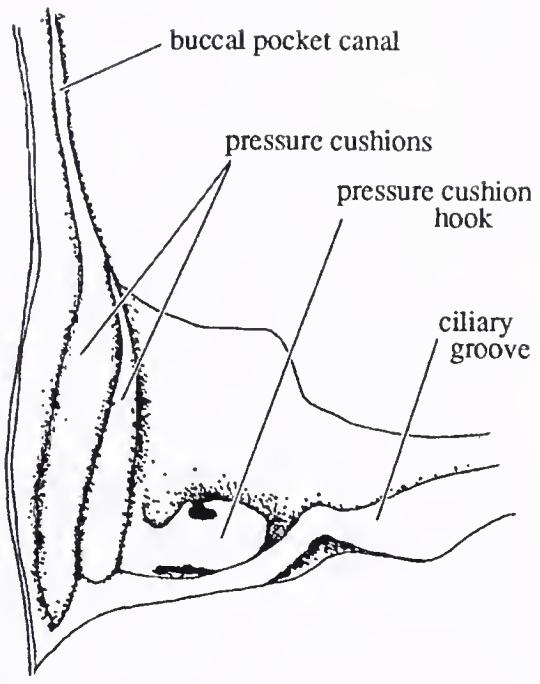

Figure 4. Morphologyofposterolateralpartofdorsal buccopharyngeal region, showing details.

oped air sacs, it gradually narrows down caudally and its terminal part is a dark pigmented cord.

Ecological Correlates

The adult *Microhyla ornata* is sharply contrasted from its sympatric ranoids in its choice of breeding site and mode of egg deposition. Usually its breeding sites are deep ponds, which develop rich planktonic bloom during summer. Such sites are quite restricted and rare in temperate Punjab, unlike sympatric ranoids who breed in temporal sites that dry in the summer. Intermittent unpredictable rains or irrigation seepage saves such populations of tadpoles (Khan and Malik, 1987b).

Table 1 and 2 summarize peculiar features of *M. ornata* tadpole necessary to suit its lentic habits: perfectly streamlined transparent body and long broad finned tail with independently vibratile terminal flagellum, lateral eyes, median ventral spiracle, abdominal silver-shine, are adaptations to nektic habits of the *M. ornata* tadpole. A school of tadpoles swimming at midstream is almost invisible from above the water due to tadpole's transparent bodies. Meanwhile abdominal coloration makes them invisible in water since the water surface viewed from inside appears shiny due to reflection of light from water. A vibrating tail flagellum and the jet of water from median ventral spiracle supports the microhylid tadpole at midstream, while its buoyancy is maintained by dorsally placed air filled lungs. A long broad finned tail helps the tadpole to react quickly to any stimulus including enemies and food in the water column above and below.

Microphagous tadpoles are characterized by an exaggerated oropharyngeal region (Wassersug, 1980). All oropharyngeal modifications distinguishing microhylid tadpoles from bufonids and ranids are adaptations to microphagy: reduction of infralabial cartilage, corresponding reduction in prelingual and prenarial arenas; displacement of mouth to snout top; simple infralabial papillae; absence of lingual papillae; membranous postnarial and BRA papillary ridges; divided fine pitted buccal glandular zone; fine ridged subvelar and toric glandular surfaces; broad medially divided spicularly supported ventral velum; compact thick filter ruffle on broad and deep filter plates; deep filter cavities with distinct tori. These microhylid structures are part of obligate microphagus filter feeding technology. Similarly long tubular trachea, bulbous laryngeal cartilage, distinct anteriorly displaced glottis with a preglottal papilla, and dorsal, long, air filled lungs are not only efficient parts of an efficient pulmonary aeration system, but at the same time, serve to maintain hydrostatic balance of the tadpole at mid-stream position. The complex morphology of pressure cushions and their connection with buccal pockets are a part of a system which maintains a sustained drainage of excessive buccal water in pressure cushions, providing necessary turgidity during each stroke of bucco-pharyngeal pumping. Turgid cushions act as pharyngeal valves in the process and play key role in sustained pumping of food-laden water current in buccopharyngeal passage.

Morphologically, the *Microhyla ornata* tadpole is a perfect model suited for sustained midstream swimming. It has all the necessary oropharyngeal technology to filter and feed on the planktonic bloom in deeper ponds in temperate Punjab.

Microhylid Tadpole Characters

The microhylid tadpole is ranked as Type 2 in Orton's (1953) classification. It markedly differs in morphologically from ranoid Type 4 macrophagus tadpole (Table 2). Microhylid is the only tadpole, in Punjab riparian ecosystem, occupying unique midstream feeding niche, while rest of the sympatric ranoid tadpoles are bottom grazers and in no way compete with microhylid tadpole. Distinguishing morphological characteristics of *Microhyla ornata* tadpoles are:

External morphology

1. Transparent body and tail, silver-shine on abdomen.

2. Head dorso-ventrally depressed, body and tail laterally compressed.

3. Antero-dorsal mouth, without keratinized oral disc and other associated organs.

4. Eyes prominent, laterally disposed on head.

5. Tail broad finned, its tip produced into a terminal vibratile flagellum.

6. Spiracle median-ventral, mid-abdominal, squarish opening, with a prespiracular flap.

7. Anal tube straight, median-ventral anal opening.

8. Schools of tadpoles swim at midstream schools, never rest at bottom. Capable of making spontaneous movements from midstream to darker parts of the pond to avoid intruders, shortly reappearing at the same midstream site.

Internal morphology

9. Opercular chamber extending to vent.

10. Smooth broad ventral vellum, divided into right and left halves.

11. Long pipe like trachea carries, bulbous glottal cartilage,

for forward in buccal cavity. Glottis thin lipped, 100% exposed.

12. Preglottal papillae guarding glottis.

13. No lingual papillae.

14. No lateral ridge papilla and median ridge.

15. Pharyngeal region exaggerated, about 75 % of oropharyngeal region, branchial baskets large with distinct, deep filter cavi ties, which are usually full of fllocular matter in dissected tadpoles.

16. Tight filter mesh, maximum number of filter rows 13-23 on either sides of the ceratobranchials.

17. Branchial food traps with microscopic openings of secretory glandular tissue borne on fine parallel ridges forming distinct crescentric torus in each branchial cavity.

18. Imperforate nares with a foliaceous broad narial palp, descending into the buccal cavity.

19. Ceratohyal with a ventrally directed lateral arm, and an an tero-posterior median arm.

20. Broad based BRA and BFA papillae, which usually coalesced to form fine membranes.

21. Narrow lateral buccal pockets with distinct connection with pressure cushions, forming an elaborate system to control function of pressure cushions.

Microhylids are phylogenatically connected with ranoids through tadpoles with intermediate morphologies like *Psedohemisus granulosa* (Wassersug, 1984) and *Otophryne robusta* (Wassersug and Pyburn, 1987).

Discussion

Independent vibratile distal caudal flagella are characteristic of mid-stream swimming microphagus tadpoles (Wassersug, 1980, 1989; Wassersug and Sperry, 1977; Nishikawa and Wassersug, 1988, 1989; Hoff and Wassersug, 1986). Maintenance of midstream position is made possible by independent movements of the caudal flagellum and ventrally directed continuous water from the spiracle giving a sustained upward thrust (Khan, 1982a, 1991). Apart from morphological differences in structure of notochord and arrangement of caudal nerves, microhylids and ranoids differ in the site of generation of propulsive locomotory waves. In ranoids, waves are generated at the tail; the tip acts as a steer. In microhylids, waves are generated at the end of the caudal flagellum.

The limited tail musculature and bulky form of the amphibian tadpole restricts its movements so that it cannot evade its potential enemies, fishes, niads, etc., (Khan and Mufti, 1994b; 1995). Amphibian tadpoles rely on a reduced conspicuousness. Its drab spotted pattern blends well against natural aquatic background with moderate to thick vegetation (Caldwell, et al., 1981; Gatten et al., 1984; Kehr and Basso, 1990; Khan and Mufti, 1994 b, 1995). The microhylid tadpole, which is exposed at midstream, solves this problem differently. Transparency of its body reduces its shadow at pond bottom and its abdominal shine blends well against water surface reflecting sun rays, making it invisible from inside pond as well from out side, to its predators.

Microhyla ornata has a larger buccal volume than ranoids. It constantly pumps large amounts of water to get food (Seale and Wassersug, 1979; Wassersug, 1980). Due to its specialized feeding habits, several elements universally present in ranoid tadpoles are missing in its oropharyngeal morphology: median ridge, lateral ridge papillae and lingual papillae. Moreover, papillae in the food retrieval part are a part of particulate food guiding membrane rather particulate food retrieving sieves. Moreover, microhylids have fine-ridged oral and branchial glandular system with fine pits, a specialization to entrap finest particulate food. Deep filter cavities, long filter plates and tight filter mesh are more a part of food retrieval system rather respiratory in function (Wassersug and Murphy, 1987). Particulate food filtering capacity of

filtering system is enhanced by development of a fine-ridged torus in each filter cavity. A well-developed pulmonary system with long tubular trachea, a totally exposed guarded glottism, and inflated dorsal functional lungs are adaptations to the midstream sustained swimming and are efficient respiratory organs (Khan, 1991).

Tadpoles of the microhylid genera *Otophryne* and *Psdudohemisus* show both ranoid as well as microhylid characteristics. Frogs of Family Microhylidae and Ranidae have distinctive adult morphology, however definition of microhylid larva stands only on imperforate naris, since the ranoids have always perforated naris (Wassersug, 1989).

Tadpoles of *M. ornata* from Pakistan differ in morphological details from those collected from Thailand by Inger (1985) in having longer infralabial papillae, more filter rows, presence of postnarial membranous ridge, BRA and BFA membranous papillae, mesially divided dorsal buccal glandular zone, and a single preglottal papilla. Moreover, no silver shine is reported on the belly of tadpoles from Thailand, as is reported from India (Rao, 1917; Azad Kashmir (Khan, 1979) and District Jhang, Punjab Pakistan (Khan 1982a). Flower (1899) reported morphological differences among adults and larvae of this species from Malay peninsula and Siam, while Liu (1950) has reported dextral anal tube in tadpoles from China, which is straight in Pakistani tadpoles. These morphological differences may refer to geographical races within this widely distributed southeast Asian species of narrow-mouth frogs.

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