HERPETOZOA 16 (3/4): 133 - 140
Wien, 30. Jänner 2004

The larval hyobranchial skeleton of five anuran species and its ecological correlates

(Amphibia: Anura)

Das larvale Hyobranchialskelett von fünf Anurenarten und seine ökologischen Entsprechungen

(Amphibia: Anura)

MUHAMMAD SHARIF KHAN

KURZFASSUNG

Die Grobmorphologie der hyobranchialen Skelettelemente der Larven von *Bufo stomaticus*, *Euphlyctis cyanophlyctis*, *Limnonectes limnocharis* / *L. syhadrensis*, *Hoplobatrachus tigerinus* und *Microhyla ornata* wird beschrieben. Die Arten unterscheiden sich in der Gestalt ihrer buccopharyngealen Elemente, was die Eigenarten ihrer Ernährung widerspiegelt.

ABSTRACT

Gross morphology of the hyobranchial skeletal elements of the tadpoles of *Bufo stomaticus*, *Euphlyctis cyanophlyctis*, *Limnonectes limnocharis* / *L. syhadrensis*, *Hoplobatrachus tigerinus* and *Microhyla ornata*, is described. The tadpole species differ in details of the morphology of their bucco-pharyngeal elements, which reflects dietary preferences of each species.

KEY WORDS

Amphibia: Anura *Bufo stomaticus*, *Euphlyctis cyanophlyctis*, *Limnonectes limnocharis*, *Limnonectes syhadrensis*, *Hoplobatrachus tigerinus*, *Microhyla ornata*, hyobranchial skeleton, tadpoles, larvae, morphology, feeding ecology, riparian Punjab, Pakistan

INTRODUCTION

Early Paleozoic vertebrates fed on microscopical organic particulate filtrate retrieved from the water as it passed through the oropharyngeal passage (JOLLIE 1982; MALLATT 1986). Even today filter feeding is employed by several vertebrates at adult as well as larval stage (ORTON 1953; STARRET 1973; KHAN 1991). In anuran tadpoles specialized parts of the bucco-pharyngeal passage take part in filtering the particulate suspension as water current passes through it (WASSERSUG 1975; SEALE & WASSERSUG 1979; WASSERSUG & HOFF 1986; VIERTEL 1987; SANDERSON & WASSERSUG 1989; KHAN 1991, 1999; KHAN & MUFTI 1994a).

The morphology of the oral and bucco-pharyngeal structures of anuran tadpole species reflects their dietary preferences (WASSERSUG 1980; INGER 1985; ALTIG & JOHNSTON 1989; KHAN 1991).

The present paper presents comparative studies on the hyobranchial larval skeleton of one bufonid, three ranoid and one microhylid frog species sympatrically living in the riparian Punjab, Pakistan.

MATERIALS AND METHODS

For the present study, five tadpoles of each of the following species were studied at developmental stage 35 (KHAN 1965) [corresponding with stage 35 of GOSNER 1960]: *Bufo stomaticus*, *Euphlyctis cyanophlyctis*, *Limnonectes limnocharis* and/or *L. syhadrensis* (sympatric in the Indus Valley, their larvae cannot be distinguished so far), *Hop-*

lobatrachus tigerinus, *Microhyla ornata*. The tadpoles were picked from the bulk of tadpoles collected and preserved for previous studies (KHAN 1991, 1996; KHAN & MUFTI 1994, 1995) and identified to their species by following the key of KHAN (2002).

The selected tadpoles were washed thoroughly with tap water to remove as much yellow color as possible of Bouin's fixative. Then the tadpoles were placed in Alcian Blue stain and prepared as indicated in HENKEN & WASSERSUG (1981) and KHAN (1991): Alcian Blue 8GX = 9 mg, Absolute alcohol = 60 ml, Glacial Acetic Acid = 40 ml. The tadpoles were left in the stain over night, then washed thoroughly in tap water. This procedure stains the cartilage deep blue, vividly distinguished from the surrounding light blue tissue. Moreover, the tadpole's tissue is softened by the Glacial Acetic Acid in the stain and is easily removed from the cartilage (KHAN 1991). The techniques of preparation developed by KHAN (1991) were followed. The tadpole was pinned on a wax tray, ventral side up, by passing an entomological pin though the thickest part of its tail. The belly skin of the tadpole was cut at mid abdomen and carefully removed by using a pair of fine forceps. Adhering tissue was removed from the exposed deep blue oropharyngeal cartilage.

The outlines of the cartilages were drawn by using a camera lucida attached to a stereo microscope. The cartilage terminology used in the description is that of DE BEER (1937).

Explanations of terms used in the description of the filtering system of tadpoles: branchial basket - the perforated pharyngeal gut including skeletal support and gill apparatus; filter cavity - cavity enclosed by neighboring branchial plates; branchial or visceral ray - the skeletal support of gills; branchial plate or filter plate - functional unit formed by the gill filter apparatus of a visceral arch; filter rows - rows of filter ruffle on a filter plate; tori (singular: torus) - small oval areas with thin folds of buccal lining, along the free edge of which are located fine openings of mucous glands. Tori lie at the base of the filter cavity of microphagus tadpoles.

RESULTS

The bucco-visceral skeletal elements appear to be largely consistent among anuran tadpoles (CHACKO 1965; DE JONGH 1968; GRADWELL 1972). In the present paper, the components of the cartilaginous hyobranchial apparatus which are of functional importance in the maintenance of the flow of water in the bucco-pharyngeal passage, are described.

Bufo stomaticus LÜTKIN, 1862 (fig. 1)
Reference: KHAN (1965)

Meckel's cartilage is fusiform, pointed at both ends, and obliquely placed at the antero-lateral sides of the buccal region. The buccal floor is supported by an ellipsoidal copula (= basihyal), lateral ceratohyals and broad hypobranchial plates. The transverse ceratohyal is broad at its inner end, narrows distally and bends backward at its tip. The hypobranchial plate is the broadest cartilage of the buccopharyngeal region. From its posterolateral sides four delicate ceratobranchial arches are given, which are interconnected distally with each other, enclosing the branchial basket of that side.

The bucco-pharyngeal and branchial regions are subequal. The branchial baskets are prominent posterolateral structures and are typically bowl-shaped, placed at an angle of 45-50° to the longitudinal axis of the body, with two distinct filter cavities: first (outer) is deeper and longer while second (inner) is shallow, and wider.

Limnonectes limnocharis (BOIE, 1835)
L. syhadrensis (ANNANDALE, 1919) (fig. 2)
Reference: KHAN (1996)

The visceral skeleton of this tadpole is typically ranid, with broad thick cartilages. The mesially broadened Meckel's cartilage is produced into an antero-lateral prominent infrarostral process. The transverse ceratohyals are thick with broad massive inner heads, get narrower on side, with distal blunt end. The copula is vase shaped with anteri-

or nicked and posterior gradually tapering pointed end. The broad hyobranchial plate gives off posterolaterally four ceratobranchial arches. The first ceratobranchial is thrice broader than the rest, and is strongly arched out, has four ostia arranged along its midline, while II, III and IVth arches are cylindrical, distally interconnected with each other.

The posterolateral branchial basket, is about half the size of the bucco-pharyngeal region. It bulges out laterally, gradually narrowing mesially, is almost as broad as long. Of the two filter cavities, the first (outer), is longer and deeper, about 1/4th of it is under the velum, it is always packed with floccular matter, while the second (inner) filter cavity is larger, bowl-shaped, shallow, and transversally enlarged.

Euphlyctis cyanophlyctis
(SCHNEIDER, 1799) (fig. 3)
Reference: KHAN & MUFTI (1995)

It is the largest tadpole in the plains, correspondingly its visceral elements are larger and massive. Meckel's cartilage is almost fusiform like that of *Bufo stomaticus*, broadened in the middle, pointed at the ends. The transverse ceratohyals are broad, the inner ends about thrice as broad as the distal parts and partially overlapping the base of the hypobranchial plate. The copula is vase shaped, with nicked anterior end and gradually attenuated pointed posterior end. The hypobranchial plate is broad, ceratobrancial arches I and IV are broadened, thick branchial rays are given out from their outer and inner borders, while II and III are cylindrical simple rods. There are two rows of ostia in the ceratobranchials I and IV.

The postero-lateral branchial basket is about 50-60% the size of the bucco-pharyngeal-region, with three distinct filter cavities: first is longest and deepest, while the second is less so, and the third is shallower and broader than the second.

Hoplobatrachus tigerinus
(DAUDIN, 1802) (fig. 4)
Reference: KHAN (1997)

In this tadpole the buccopharyngeal cartilages are broad and massive. Meckel's cartilage is rectangular, thick, massive, gives medially a short infrarostal process. The transverse ceratohyals are broadest at the inner ends, becoming narrower laterally, ending distally in a hammer-head shape. The copula is large, oval, anteriorly narrower posteriorly broader, lying in an inter-hypobranchial depression. The hypobranchial plate is posterolaterally elongated, while the ceratobranchials are relatively short and cylindrical with extensive outgrowths of branched branchial rays arising from the inner border of branchial arches I and IV, and on both sides of branchial arches II and III.

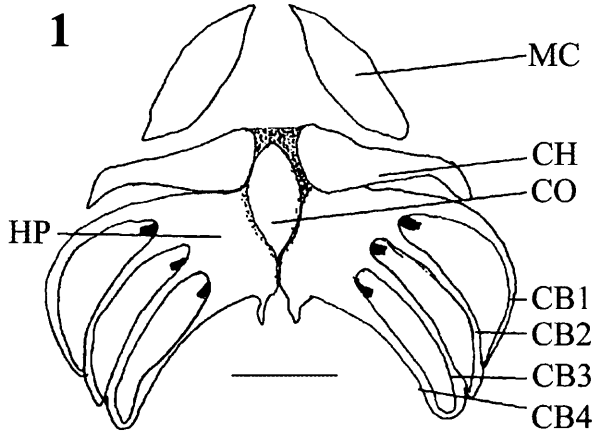
The branchial baskets are in a posterior position and relatively small, about 18-20% the size of the bucco-pharyngeal cavity, enclosing a single shallow bowl-shaped filter cavity.

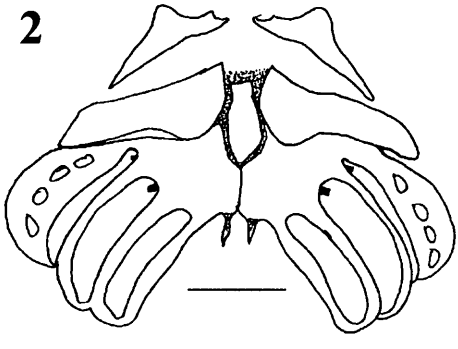
Microhyla ornata
(DUMÉRIL & BIBRON, 1841) (fig. 5)
Reference: KHAN (2000)

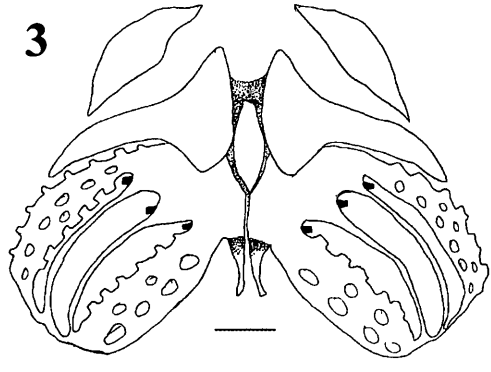
The bucco-visceral skeletal elements of this tadpole consist of typically delicate, cylindrical much elongated, thin cartilages which run parallel to the longitudinal axis of the body.

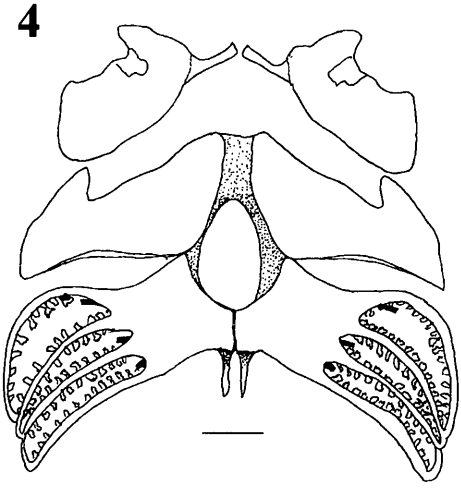
Meckel's and ceratohyal cartilages are thin and elongated, arching out and backwards, are slightly broader at the inner medial end, gradually narrowing at the distal end. The ceratohyals are broader and connected with each other medially, where they slightly overlap the anterior tip of the hypobranchial plate. The hypobrachial plates are narrow, antero-posteriorly elongated, separated from each other throughout their length. The copula is narrow, much elongated, ovoid, with broader anterior and gradually narrowing elongated pointed posterior end; it is in contact with the hypobranchial plates at its anterior end only. Four long, delicate ceratobranchial arches extend latero-posteriorly all along the elongated branchial basket. As in other species they are interconnected with each other at their distal ends.

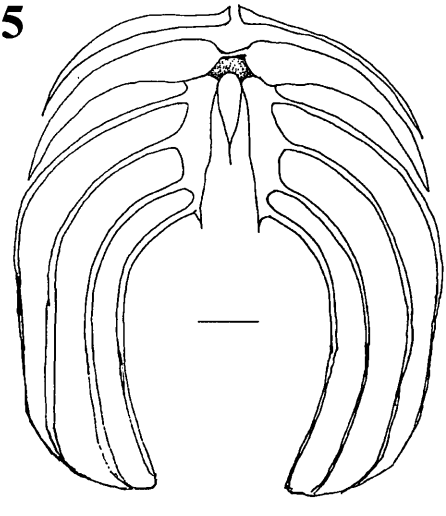
The branchial baskets are in a posterior position, elongated, about 70-75 % the size of the bucco-pharyngeal region, each with three deep filter cavities, which are always clogged with floccular matter.











DISCUSSION

All the five species of tadpoles studied, differ from each other in their external morphology (KHAN 1991, 2002a, 2002b, 2003a, 2003b, 2003c), bucco-pharyngeal morphology (KHAN 1991, 1996, 2000; KHAN & MUFTI 1994a, 1994b, 1995), and in the morphology of the bucco-pharyngeal skeletal elements (present study). Tadpole's buccal apparatus is specialized in entrapment of particulate food, while the pharynx in retrieving the food laden mucous on the filter ruffle of the branchial baskets (KHAN 1999, references therein). Thus each species is a specialized ecomorph with its characteristic morphology, bucco-pharyngeal flow regime, microhabitat selection and mode of feeding (LANNOO et al. 1987; WASSERSUG 1980; HEYER et al. 1990). Based on a variety of ecomorphological features, ALTIG & JOHNSTON (1989) have arranged the exotrophic tadpoles in guilds. The tadpoles from the riparian Punjab can be assigned to two of these guilds:

Guild A. Lentic-Benthic: dorsolateral eyes, suctorial mouth; globular, drab, spotty body; narrow parallel tail-fins.

1. Type 1 Littoral: in early stages, confined to shallow water along soil-water interface; becomes profundal in later stages; macrophagus rasper: *Bufo stomaticus.*

2. Type 1 Littoral: confined to seepage pools along water channels, with moderate emergent vegetation and moderate planktonic growth; microphagus rasper: *Limnonectes syhadrensis.*

3. Type 2 Profundal: inhabit permanent ponds with little or no vegetation; macrophagus detritivorous: *Euphlyctis cyanophlyctis.*

4. Type 2 Profundal: inhabits ephemeral puddles with little or no vegetation; macrophaguous, carnivorous: *Hoplobatrachus tigerinus.*

Guild B. Lentic-Suspension Feeder: anterodorsal non-suctorial mouth; lateral eyes; dorsoventrally depressed head, laterally compressed transparent body; long, broad finnned, with long terminal tail flagellum; mid stream-swimming microphagus suspension feeder: *Microhyla ornata.*

The Lentic-Benthic-Littoral *Bufo stomaticus* and *Limnonectes syhadrensis* tadpoles are almost similar in the size, external morphology, disposition and size of their branchial baskets (28-36% the size of the bucco-pharynx) (KHAN 1991, 1996; KHAN & MUFTI 1994a, 1994b). *Bufo stomaticus* has larger branchial plates than *L. syhadrensis*, but the number of filter rows is higher in *L. syhadrensis* and its filtring grid is tighter with one torus; moreover, the visceral elements are more robust, and the first ceratobrancial arch is broader with ostia. The outer filter cavity of this tadpole is always found almost clogged with fine floccular organic matter (KHAN 1996, 1999). The compact filter grid suggests that water is forcefully expelled through its branchial mesh. Despite having a suctorial oral disc *L.syhadrensis* is microphaguous, relaying little on scrapings from beak and teeth (KHAN 1996), while *Bufo stomaticus* is macrophaguous and relies primarily on scrapings. The branchial basket of the detritus feeding tadpole of *Euphlyctis cyanophlyctis* of the Benthic-Lentic-Profundal type is about 38-40% the size of the total bucco-pharynx, with three deep filter cavi-

Figs. 1-5 (opposite page): Ventral views of the hyobranchial skeletal elements of tadpoles of developmental stage 35 (KHAN 1965) [corresponding with stage 35 of GOSNER 1960] from riparian Punjab, Pakistan. Bars represent 0.5 mm; CB1–CB4 – Ceratobranchials I through IV; CH - Ceratohyal; CO - Copula; HP - Hypobranchial Plate; MC - Meckel's Cartilage.

Abb. 1-5 (gegenüberliegende Seite): Ventralansichten der hyobranchialen Skelettelemente von Larven des Entwicklungsstadiums 35 (Khan 1965) [entsprechend Stadium 35 von GOSNER 1960] aus dem Punjab-Stromland, Pakistan (Balkenlängen entsprechen 0,5 mm); CB1–CB4 – Ceratobranchialia I bis IV; CH - Ceratohyale; CO - Copula; HP - Planum Hypobranchiale; MC - Meckelscher Knorpel.

1 - *Bufo stomaticus* (LÜTKIN, 1862)
2 - *Limnonectes limnocharis* (BOIE, 1835) / *Limnonectes syhadrensis* (ANNANDALE, 1919)
3 - *Euphlyctis cyanophlyctis* (SCHNEIDER, 1799)
4 - *Hoplobatrachus tigerinus* (DAUDIN, 1802)
5 - *Microhyla ornata* (DUMÉRIL & BIBRON, 1841)

Table 1: Comparative morphology of the hyobranchial elements of five species of anuran tadpoles. cyl - cylindrical; broad + - broad with ostia; - - absence; * - arrangement of tori respective to branchial filter plates; I - filter cavity; ^ - arrangement of branchial rays respective to branchial filter plates; I-III - branchial filter plates.

Tab. 1: Morphologische Gegenüberstellung der hyobranchialen Elemente bei 5 Arten von Anurenlarven. cyl - cylindrisch; broad + - breit mit Ostien; – - fehlt; * - Anordnung der Tori bezüglich der Kiemenfilterplatten; I - Filterkammer; ^ - Anordnung der Kiemenstrahlen bezüglich der Kiemenfilterplatten; I-III - Kiemenfilterplatten.

	M. ornata	*B. stomaticus*	*E. cyanophlyctis*	*L. limnocharis / H. syhadrensis*	*H. tigerinus*
Branchial basket size in % of bucco-pharynx / Kiemenkorbgröße in % der Buccopharynxgröße	70-73	34-36	38-40	28-30	18-20
No. of filter cavities / Anzahl Filterkammern	3	2	3	2	1
Arrangement of tori (*) respective to branchial filter plates (I) / Anordnung der Tori (*) bezüglich der Kiemenfilterplatten (I)	I*I*I*	–	–	I*I–	–
Size of Meckel's Cartilage / Größe des Meckelschen Knorpels	long lang	short kurz	large groß	short kurz	large groß
Hypobranchial plates / Planum hypobranchiale	separate geteilt	fused verbunden	fused verbunden	fused verbunden	fused verbunden
Ceratobranchial I	cyl	cyl	broad +	broad +	cyl
Ceratobranchial II	cyl	cyl	cyl	cyl	cyl
Ceratobranchial III	cyl	cyl	cyl	cyl	cyl
Ceratobranchial IV	cyl	cyl	broad +	cyl	cyl
Arrangement of branchial rays (^) respective to branchial filter plates (I) / Anordnung der Kiemenstrahlen (^) bezüglich der Kiemenfilterplatten (I)	–	–	^I^I–I^I	–	I^I^I^I
Lagest branchial filter plate / Größte Kiemenfilterplatte	II	I	III	I	III
No. of filter rows on largest branchial filter plate / Filterreihen auf der größten Kiemenfilterplatte	20-23	10-12	12-14	13-14	9-10

ties. Its elongated buccal apparatus is heavily armed with papapillae and mucous secreting glands, to process heterogeneous particles of sand, girt and rotten organic matter contained in the ingested detritus. The tadpole ingests large quantities of detritus to meet its nutritional needs, since most of the stuff, on which it feeds, is of no food value. The filter plates are large (length 2.5 mm, breadth 1.12 mm) and have a high number of filter rows (12-14 on the largest branchial plate) (KHAN & MUFTI 1995). Moreover, the bucco-visceral skeletal elements are comparatively stout broad and heavily built, the branchial basket is supported by broad, strong visceral arches with perforations indicating the heavy pressure under which water is expelled through the filter ruffle.

In the carnivorous tadpole of *Hoplobatrachus tigerinus*, the second representative of the Benthic-Lentic-Profundal type, the branchial basket is smallest (18-20% the size of the bucco-pharynx), the visceral arches are rather weak, the poorly organized filter ruffle is attached on branchial rays, the buccal and subvelar secretary tissue is poorly organized and the buccal papillation is almost nonexistent, while the circum-oral structures, buccal musculature (KHAN 1997) and the buccopharyngeal skeletal elements are much thickened and exaggerated. The specialized circumoral structures suggest that the food is cut in large chunks, the thickened oropharyngeal musculature generates a strong suction force to draw the chunks in the buccopharyngeal passage. The smallest particle, which is filtered on the filter ruffle of this tadpole, is of the size of *Daphnia* and *Cyclops*, common fresh water crustaceans (KHAN 1991, 1997).

The obligate filter feeder *Microhyla ornata* has the most enlarged branchial baskets, about 70-73% of the size of the buccopharyngeal cavity, with three deep, most

extensive filter cavities, each with a distinct torus. It has the largest and broadest (length 1.97-3.7 mm, breadth 1.2-1.8 mm) branchial plates, with dense filter rows (20 - 23 on the largest branchial plate). The filter cavities are always found clogged with ultramicroscopic floccular organic matter. The tadpole processes large amount of water to meet its dietary requirements (KHAN 1991).

The five species of anuran tadpoles of riparian Punjab, though found sympatric in common habitat, occupy different flow regimes, differ markedly in the morphology of their buccal and branchial organization which delimits their filtering capabilities.

REFERENCES

ALTIG, R. & JOHNSTON, G. F. (1989): Guilds of auran larvae: relationships among developmental modes, morphologies. and habitats.- Herpetol. Monogr., Pittsburgh; 3: 81-109.

CHACKO, T. (1965): The development and metamorphosis of the hyobranchial skeleton in *Rana tigerina* the Indian bull frog.- Acta Zool., Stockholm; 46: 311-328.

DE BEER, G. R. (1937): The development of the vertebrate skull. London (Oxford Univ. Press), 552 pp.

DE JONGH, H. S. (1968): Functional mophology of the jaw apparatus of larval and metamorphosing *Rana temporaria* L.- Netherlands J. Zool., Leiden; 18 (1): 1-103.

GRADWELL. N. (1972): Gill irrigation in *Rana catesbeiana* Part I. On the anatomical basis.- Canadian J. Zool., Ottawa; 50:481-499.

HANKEN, J. & WASSERSUG, R. J. (1981): The visible skeleton. A new double-stain technique reveals the native of the "hard" tissues.- Functional Photography, Hempstead; 16: 22-26.

HEYER, W. R. & RAND, A. S. & GONCALVES DA CRUZ, C. A. & PEIXOTO, O. L. & NELSON, C. E. (1990): Frogs of Boraceia. Arq. Zool., Mus. Zool., Univ., São Paulo; 31 (4): 231-410.

INGER, R. F. (1985): Tadpoles of the forested regions of Borneo.- Fieldiana Zool., N. S., Chicago; 1365 (26): 1-89.

JOLLIE, M. (1982): What are the 'Calcichordata'? and the larger questions of the origion of chordates.- Zool. J. Linnean Soc., London; 75: 167-188.

KHAN, M. S. (1965): A normal table of *Bufo melanostictus*.- Biologia, Lahore; 11: 1-39. [describes *Bufo stomaticus*].

KHAN, M. S. (1982): Key for the identification of amphibian tadpoles from the plains of Pakistan.- Pakistan J. Zool., Lahore; 14: 133-145.

KHAN, M. S. (1991): Morphoanatomical specialization of the buccopharyngeal region of the anuran larvae and its bearing on the mode of larval feeding. Ph.D. diss., University of the Punjab, Lahore, Pakistan, pp. 99.

KHAN, M. S. (1996): Oropharyngeal morphology of tadpole of southern cricket frog *Rana syhadrensis* ANNANDALE, 1919, and its ecological correlates.- Pakistan J. Zool., Lahore; 28:133-138.

KHAN, M. S. (1997): The oropharyngeal morphology and feeding habits of tadpole of tiger frog *Rana tigerina* DAUDIN.- Russian J. Herpetol., Moskva; 2:163-171.

KHAN, M. S. (1999): Food particle retrieval in amphibian tadpoles.- ZooPrint J., Dahli; 14 (5): 17-20.

KHAN, M. S. (2000): The oropharyngeal morphology and feeding habits of tadpole of *Microhyla ornata*.- Asiatic Herpetol. Res., Berkeley; 9: 130-138.

KHAN, M. S. (2002a): A checklist and key to the Amphibia of Pakistan.- Bull. Chicago Herpetol. Soc., Chicago; 37 (9): 158-163.

KHAN, M. S. (2002b): Riparian tadpoles of Punjab, Pakistan - *Bufo stomaticus* LÜTKIN, 1862.- Bull. Chicago Herpetol. Soc., Chicago; 37 (12): 216-219.

KHAN, M. S. (2003a): Morphology of the tadpole of *Microhyla ornata*, with notes on its feeding ecology and breeding habits.- Bull. Chicago Herpetol. Soc., Chicago; 38 (3): 40-51.

KHAN, M. S. (2003b): Morphology of riparian tadpoles: *Euphlyctis cyanophlyctis* (SCHNEIDER, 1799).- Bull. Chicago Herpetol. Soc., Chicago; 38 (5): 95-98.

KHAN, M. S. (2003c): Morphology of the *Limnonectes* tadpole, with notes on its feeding ecology and on the breeding habits of *Limnonectes* frogs in riparian Punjab.- Bull. Chicago Herpetol. Soc., Chicago; 38 (9): 177-179.

KHAN, M. S. & MUFTI, S. A. (1994a): Oral disc morphology of amphibian tadpole and its functional correlates.- Pakistan J. Zool., Lahore; 26: 25-30.

KHAN, M. S. & MUFTI, S. A. (1994b): Buccopharyngeal specializations of tadpole of *Bufo stomaticus* and its ecological correlates.- Pakistan J. Zool., Lahore; 26: 285-292.

KHAN, M. S. & MUFTI, S. A., (1995): Oropharyngeal morphology of detritivorous tadpole of *Rana cyanophlyctis* SCHNEIDER, and its ecological correlates.- Pakistan J. Zool., Lahore; 27: 43-49.

LANNOO, M. J. & TOWNSEND, D. S. & WASSERSUG, R. J. (1987): Larval life in the leaves: arboreal tadpole types, with special attention to the morpology, ecology, and behaviour of the oophagus *Osteophilus brunneus* (Hylidae) larva.- Fieldiana Zool. N.S., Chicago; 1381 (38): 1-31.

MALLATT, J. (1986): Reconstructiong the life cycle and the feeding of ancestral vertebrates; pp. 59-68. In: FOREMAN, R. & GORBMAN, A. & DODD, J. & OLSSON, R. (eds.): Evolutionary biology of primitive fishes. New York (Plenum Publishing Corp.).

ORTON, G. L. (1953): The systematics of vertebrate larvae.- Syst. Zool., New York; 2: 63-75.

SANDERSON, S. L. & WASSERSUG, R. J. (1989): Convergent and alternative designs for vertebrate suspension feeding; pp. 37-112. In: HALL, B. K. & HANKEN, J. (eds.): The vertebrate skull: Vol. 3 Function and evolutionary mechanisms. Chicago (Univ. Chicago Press).

SEALE, D. B. & WASSERSUG, R. J. (1979): Suspension feeding dynamics of anuran larvae related to their functional morphology.- Oecologia, Berlin; 39: 259-272.

STARRETT, P. H. (1973): Evolutionary patterns in larval morphology; pp. 251-271. In: VIAL, J. L. (ed.): Evolutionary biology of the anurans. Contemporary research on mayor problems. Columbia (Univ. Missouri Press).

VIERTEL, B. (1987): The filter apparatus of *Xenopus laevis*, *Bombina variegata*, and *Bufo clamita* (Amphibia, Anura): a comparison of different larval types.- Zool. Jb. Abt. Anat. Ontog., Jena; 115: 425-452.

WASSERSUG, R. J. (1975): The adaptive significance of the tadpole stage with comments on the maintenance of complex life cycles in anurans.- American Zool., Chicago; 15 (2): 405-417.

WASSERSUG, R. J. (1976a): Oral morphology of anuran larvae: terminology and general description.- Occ. Pap. Mus. Nat. Hist. Univ. Kansas, Lawrence; 48: 1-23.

WASSERSUG, R. J. (1976b): Internal oral features in *Hyla regilla* (Anura: Hylidae) larvae: an ontogenetic study.- Occ. Pap. Mus. Nat. Hist. Univ. Kansas, Lawrence; 49: 1-24.

WASSERSUG, R. J. (1980): The internal oral features of larvae from eight anuran families: Functional, systematic, evolutionary, and ecological considerations.- Univ. Kansas Mus. Nat. Hist. Misc. Publ., Lawrence; 68: 1-146.

WASSERSUG, R. & HOFF, J. K. (1979): A comparison of the buccal pumping mechanism of tadpoles.- Biol. J. Linnean Soc., London; 12: 225-229.

DATE OF SUBMISSION: February 28th, 2003 Corresponding editor: Heinz Grillitsch

AUTHOR: Muhammad Sharif KHAN, Ph. D., Herpetological Laboratory, 15/6 Darul Sadar North, Rabwah 35460, Pakistan. Address for communication: Apt # A17, 151-S. Bishop Ave. Secane, PA 19018, USA < typhlops99@hotmail.com >