

MORPHOLOGY AND BUCCOPHARYNGEAL ANATOMY OF THE TADPOLE OF *RANA (NASIRANA) ALTICOLA* (ANURA: RANIDAE)

Stéphane Grosjean, Mélanie Pérez and Annemarie Ohler

Laboratoire de Zoologie des Reptiles et Amphibiens, Muséum national d'Histoire naturelle,
25 rue Cuvier, 75005 Paris, France
Email: sgrosjea@mnhn.fr; ohler@mnhn.fr

ABSTRACT. - The external morphology and the buccopharyngeal features of the tadpole of *Rana (Nasirana) alticola* are described. Morphometric data are provided. This tadpole is easily distinguishable from other ranid species by its large size, high number of keratodont rows, coloured ocelli on tail, and large glands such as parotoid glands, supracaudal and infracaudal glands. A comparison with tadpoles from other populations is done.

KEY WORDS. - Tadpole, *Rana (Nasirana) alticola*, external morphology, buccopharyngeal features, India, Thailand, *Rana (Clinotarsus) curtipes*.

INTRODUCTION

Rana alticola Boulenger, 1882, was described on the basis of four specimens from Shillong (Khasi Hills District, Meghalaya State, India) under the name *Hylorana pipiens* Jerdon, 1870. This is a poorly studied species distributed widely in latitude, longitude and elevation, from the Hills of Assam (India) to southern Thailand [the specimen mentioned as *Hylorana alticola* by Bourret (1939: 59) from Mao Son (Northern Vietnam) proved to be an *Amolops nasicus* (Boulenger, 1903) (Bourret, 1942: 350); it should therefore be removed from the species list of Vietnam (see Frost, 1985)]. Although adults are rare in herpetological collections, the tadpoles have been known for a long time (Boulenger, 1882; Annandale, 1912; Smith, 1924a, b; review by Bourret, 1942). These tadpoles bear conspicuous features such as large size, entirely black coloration with red ocelli, large parotoid glands, supracaudal gland, several other glands as well as secretory pores spread over ventral surface and caudal fin, and numerous keratodont rows. We redescribe the external morphology of *Nasirana* tadpoles from Thailand, and we give for the first time a description of the buccopharyngeal features of a specimen.

MATERIALS AND METHODS

A total of 69 *Rana alticola* tadpoles were collected from a quiet area of a stream bordering a primary forest, at the base of a waterfall in the Ramon Forest Park (8°27' N, 98°32' E, about 30 m above sea level), Phang Nga Province, Thailand. The tadpoles in developmental stages 25 to 41 (Gosner,

1960), preserved in a mixture of equal parts of 4% formaldehyde and 70% ethanol (Grillitsch, 1984), were deposited in the collections of the Muséum national d'Histoire naturelle of Paris (MNHN 2000.4594-4661). A specimen in stage 43 (MNHN 2000.8402) allowed us to ensure the identity of the species. Morphological terminology follows Altig & McDiarmid (1999), terminology of oral disc follows Altig (1970), keratodont formula (KF) follows Dubois (1995), developmental stages were determined according to Gosner (1960) and terminology of internal buccal features follows Wassersug (1976). Total length (TL) and distance from opening of vent to tip of tail from stage 26, distance from tip of snout to insertion of upper tail fin and snout-vent length from stage 27, and distance from tip of snout to opening of spiracle and distance from opening of vent to point of maximum height of tail from stage 28 were measured with a hand calipers. All other measurements were taken with a graduated ocular attached to a stereomicroscope. For exact location of measurement landmarks, see Grosjean (2001: Fig. 2). Drawings were made using a camera lucida.

RESULTS

Diagnosis of tadpole. – A large-sized tadpole (TL 16.4-92.7 mm, stages 25-38) beige-grey with black spots in tadpoles in stage 25 and uniformly black from stage 26, a large black ocellus with a red halo on caudal muscle at base of tail (followed by two smaller ones of decreasing size often poorly visible); a pair of large parotoid glands behind eyes, a pair of pectoral glands and a pair of ventroposterior ones, a

supracaudal and an infracaudal gland; KF 1-2:(3+3)-(7+7)/1+1:4-8.

Larval morphology. – The following description is based on a tadpole in stage 36 (MNHN 2000.4630). Morphometric data are presented in Table 1. In dorsal view (Fig. 2A), body elliptical, widest at the posterior third; snout semi-circular. In profile (Fig. 2B), body depressed; body width 1.2 of body height; snout rounded. Eyes slightly bulging, directed almost laterally and positioned dorsolaterally, not visible in ventral view, diameter about 0.1 times snout-vent length. Nares oval, relatively small-sized, rimmed, with one anterolateral projection, positioned almost dorsally and directed slightly anterolaterally, distance between nares about 0.5 times interpupilar distance, closer to snout than to pupils. Spiracle sinistral, bulb-shaped, attached to body wall except at its extremity, positioned ventrolaterally, oriented more horizontally than posterodorsally; snout-spiracle distance 0.6 times snout-vent length. Spiracular opening oval, situated above level of hind limb. Tail musculature robust, gradually tapering, almost reaching tail tip. Tail fins moderately high, not extending onto body, riddled with numerous white pores on whole surface with secreted white mucus. A gland on the ventral fin, posterior to vent, the infracaudal gland; another at the beginning of dorsal fin, the supracaudal gland, slightly extending on body. Upper fin convex, slightly higher than lower; lower fin straight in proximal quarter, then slightly

convex. Maximum tail height located 20-30 % from anterior end, tail tip rounded. Vent tube moderately large, roughly conical, opening with bevelled edge hidden by large flap of skin, directed posteriorly, linked to ventral tail fin, opening dextral. Presence of a pair of large parotoid glands behind eyes with pores visible without magnification, a pair of grey pectoral glands ventrally and a pair of ventral glands posteriorly situated at the level of hind limbs. Ventral surface also riddled with numerous white pores. All the pores secrete white mucus (probably produced under the stress of capture), particularly the parotoid glands (Fig. 3) and the supracaudal gland but also pores of caudal fins and ventral surface. Neuromasts not observed.

Oral disk large (Fig. 4), anteroventral, slightly emarginated, directed ventrally. Papillae of moderate size, finger-shaped, some bifid. Single row of papillae on median part of lower labium and at extremities of large medial gap of upper labium (five papillae on each side); up to five rows of submarginal papillae laterally; transverse row of submarginal papillae between accessory keratodont rows and lower keratodont rows; accessory keratodont rows present on submarginal papillae and short ridges oriented at right angle to the keratodont rows. KF 2:6+6/1+1:8; keratodonts about 80 µm long with a curved spatulate apical portion bearing 26-29



Fig. 1. Natural habitat of the tadpoles of *Rana alticola*.

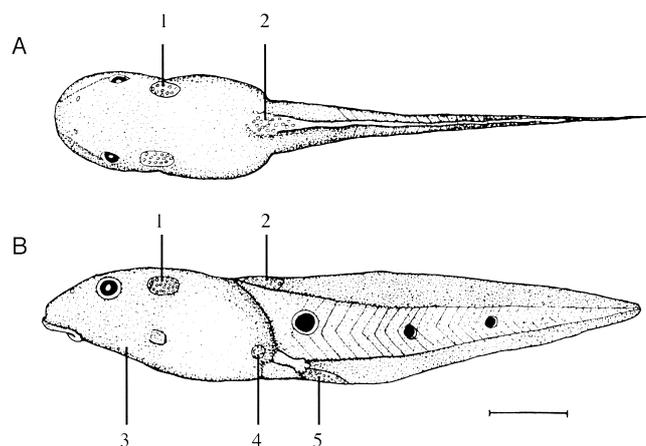


Fig. 2. Tadpole of *Rana alticola* in stage 36 (MNHN 2000.4630) showing its glands and three ocelli. A, dorsal view; B, profile. 1 = parotoid gland; 2 = supracaudal gland; 3 = pectoral gland; 4 = posteroventral gland; 5 = infracaudal gland. Scale bar = 10 mm.

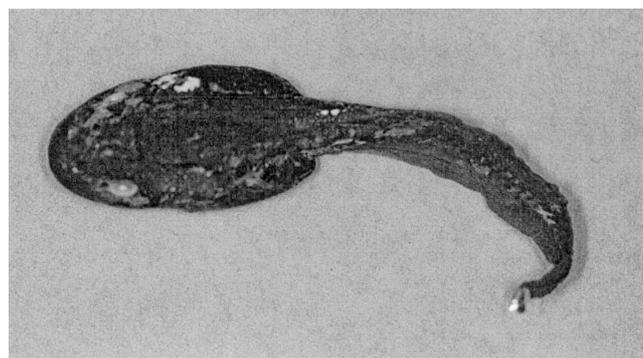


Fig. 3. Tadpole of *Rana alticola* in stage 35 (MNHN 2000.4660) showing venom expelled by parotoid and supracaudal glands. Total length = 76.3 mm.

(counted from six keratodonts from row P6) marginal denticles. Jaw sheaths slightly serrated, serrations black, distal half of sheaths dark brown, lower part white; upper sheath in wide flat arch slightly convex medially, lower sheath V-shaped.

In life, tadpole entirely brown-black, fins opaque, a black ocellus at the base of tail surrounded by a red halo. In preservative, back and flanks dark grey, ventral surface light grey with white pores; tail fins dark grey with white pores, caudal muscle dark brown with a black ocellus surrounded by a light orange halo.

Variation through ontogeny. – Coloration of tadpoles in stage 25 differs greatly from that of tadpoles in older developmental stages. Colour in life of tadpoles in stage 25: anterior half of back light beige-grey with a darker blotch between eyes, posterior half of back dark brown-grey; iris all black, ventral part beige-grey transparent. Caudal muscle sandy transparent with small black spots and an ocellus at the base with a red halo. In preservative (Figs. 5A, B): back transparent with internal organs visible through the skin, a black dot behind each nare posteromedially, a large brown spot medial between eyes and nares, another behind eyes; posterolaterally a pair of parotoid glands with white pores. Background colour of back and upper flanks studded with melanophores giving a grey colour; lower flanks and ventral surface transparent. Caudal muscle off-white, with a black ocellus without a halo at its base and few black spots. Caudal fins opaque grey with white pores concentrated at the base of upper fin and a few on the rest of lower and upper fins. From stage 26 tadpoles have the typical coloration described for the tadpole in stage 36. However slight differences in colour can occur between individuals: in preservative, two tadpoles in stage 34 (MNHN 2000.4658-4659) have back and upper flanks black brown, parotoids red brown; lower flanks and belly light red brown with white pores posteriorly, branchial area yellow grey with white pores. Caudal muscle red brown with a black ocellus surrounded by a yellow orange halo; tail fins black brown with white pores.

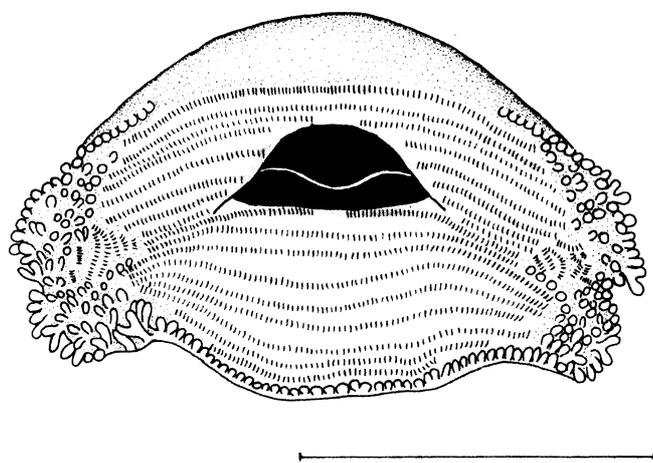


Fig. 4. Oral disk of *Rana alticola*, MNHN 2000.4630, stage 36. Scale bar = 5 mm.

A great increase in size of tadpoles takes place between stages 25 and 27 (Table 1). The number of keratodont rows increases during ontogeny. KF of tadpoles below stage 27 ($n = 14$): 1-2:(3+3)-(5+6)/1+1:4-6 and KF of tadpoles in stage 27 and above ($n = 11$): 1-2:(6+6)-(7+7)/1+1:7-8. The pair of pectoral glands and the pair of posteroventral glands are not always evident.

Description of the internal buccal features. – The description is based on a tadpole in stage 35 (MNHN 2000.4629).

Buccal floor (Fig. 6A): prelingual arena narrow with two pairs of large pustulose infralabial papillae, the first pair directed transversely, the second one directed posteriorly. Tongue anlage rounded and truncate anteriorly, scarcely prominent, without lingual papillae but with a pustule on each side anterolaterally. Buccal floor arena wide, defined by 5-6 pustulose papillae on each side; interior of arena without papillae anteriorly, with about 30 little pustulose papillae posteriorly. Buccal pockets wide, transverse, roughly oval, closer to tongue anlage than to medial end of ventral velum; about five prepocket papillae; no papillae posteriorly to buccal pockets. Ventral velum continuous, with spicular support; margin with six projections on each side, the three medial ones closer together, the two medial making up the medial notch, glottis not visible; medial projections with small-sized secretory pits. Branchial baskets oblique; three gill chambers on each side; filter ruffles with tertiary folds; lungs big (1.5 time length of buccal floor), fine and elongate, with their distal third inflated giving the lung a club shape.

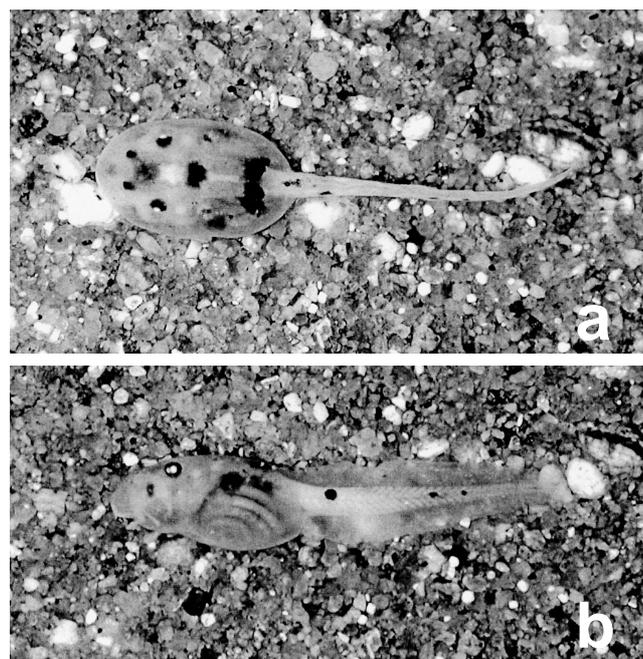


Fig. 5. Tadpole of *Rana alticola* in stage 25 (MNHN 2000.4656). A, dorsal view; B, profile. Total length = 20.0 mm. Note the striking difference of coloration and glands much less developed (supracaudal gland visible in dorsal view) in comparison with older stages.

Table 1. Morphometric variation among tadpoles of *Rana alticola* before and from stage 27. Mean value (mm) \pm standard deviation, range (mm) in parentheses.

Variable	Stage 25 and 26 <i>n</i> = 14*	Stage 27 and beyond <i>n</i> = 11*
Distance from tip of snout to opening of spiracle	4.8 \pm 0.79 (3.8-6.5)	16.4 \pm 1.84 (12.6-19.7)
Distance from tip of snout to insertion of upper tail fin	7.5 \pm 1.51 (5.4-11.7)	24.7 \pm 8.13 (20.0-30.0)
Snout-vent length	9.0 \pm 1.64 (7.3-13.7)	29.3 \pm 9.60 (25.3-35.8)
Distance from opening of vent to point of maximum height of tail	2.73 \pm 1.09 (1.8-5.9)	9.4 \pm 5.63 (3.0-16.3)
Distance from opening of vent to tip of tail	12.1 \pm 6.34 (9.3-14.5)	42.7 \pm 15.86 (36.6-59.6)
Total length	18.1 \pm 1.87 (16.4-28.5)	71.0 \pm 25.28 (61.8-92.7)
Maximum height of upper tail fin	1.3 \pm 0.25 (1.1-2.1)	4.2 \pm 0.67 (2.5-4.9)
Maximum height of lower tail fin	1.2 \pm 0.23 (1.0-1.9)	3.2 \pm 0.47 (2.3-3.9)
Maximum tail height	3.7 \pm 0.87 (3.0-6.4)	13.7 \pm 1.33 (11.5-15.8)
Maximum height of caudal muscle	1.3 \pm 0.42 (1.0-2.6)	8.7 \pm 2.37 (5.3-12.9)
Maximum body height	4.2 \pm 0.84 (3.3-6.7)	13.9 \pm 2.08 (9.7-16.4)
Maximum eye diameter	0.9 \pm 0.17 (0.7-1.3)	2.9 \pm 0.97 (2.1-3.2)
Maximum body width	4.8 \pm 1.00 (3.7-7.8)	15.2 \pm 2.33 (11.6-18.4)
Interpupilar distance	3.26 \pm 0.73 (2.6-5.4)	10.2 \pm 1.14 (8.1-11.7)
Internarial distance	2.0 \pm 0.29 (1.7-2.8)	4.5 \pm 0.35 (4.0-5.1)
Rostro-narial distance	0.1 \pm 0.15 (0.8-1.3)	2.7 \pm 0.48 (1.8-3.4)
Naro-pupilar distance	1.56 \pm 0.53 (1.3-3.1)	4.8 \pm 0.54 (3.8-5.6)
Oral disk width	2.5 \pm 0.56 (2.1-4.1)	8.7 \pm 0.89 (7.2-10.4)
Length in transverse plane of dorsal papillae gap	1.6 \pm 0.30 (1.3-2.4)	4.6 \pm 0.38 (4.1-5.4)

*except when specified

Buccal roof (Fig. 6B): prenarial arena rectangular, strongly concave, with a transversal prenarial ridge at the base of beak, occupying almost the entire width of the arena. Prenarial papillae present, long, rising in the middle of the anterior narial wall. Choanae transverse, with two short papillae on each lateral side. Posterior narial wall smooth, with a postnarial papilla on the medial end. Postnarial arena with three pustules anteriorly and a short papilla posteriorly. Medial ridge slightly prominent, wider than high, smooth. Lateral ridge papillae absent. Buccal roof arena with about 80 little pustules uniformly distributed, no buccal roof arena papillae. Posterolateral ridge poorly-marked, defined by a few pustules. Glandular zone of about 12 secretory pits wide, continuous across the roof. Dorsal velum smooth, interrupted on a short portion in its medial part.

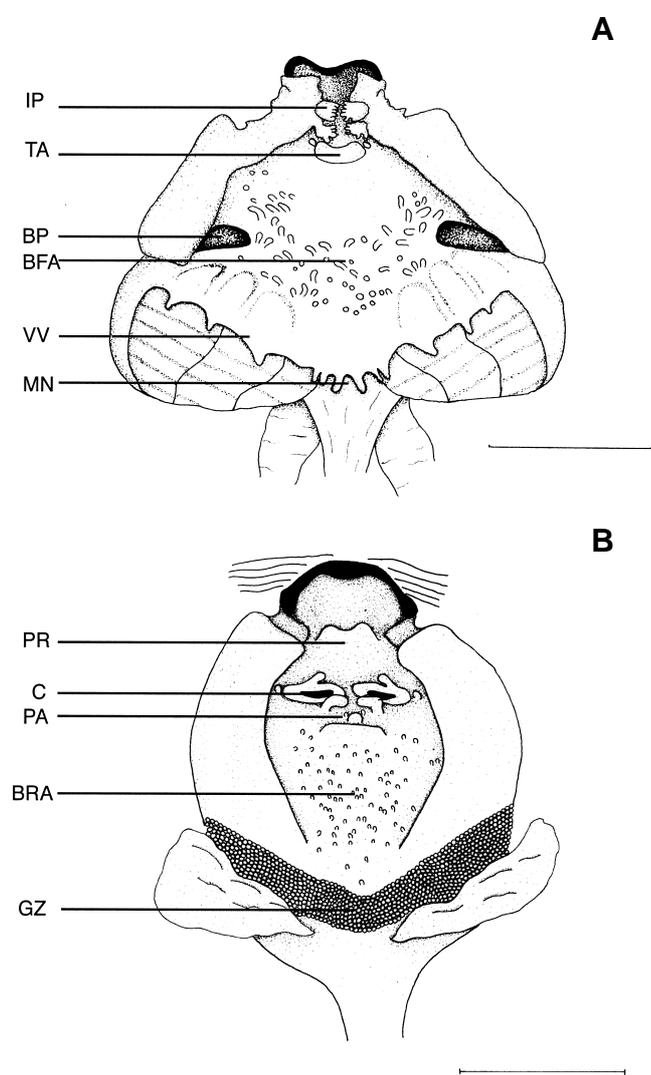


Fig. 6. Buccal cavity of the tadpole of *Rana alticola* (MNHN 2000.4629, stage 35). A, buccal floor; B, buccal roof. BFA = buccal floor arena; BP = buccal pocket; BRA = buccal roof arena; C = choana; GZ = glandular zone; IP = infralabial papilla; MN = medial notch; PA = postnarial arena; PR = prenarial ridge; TA = tongue anlage; VV = ventral velum. Scale bar = 5 mm. Note the rather simple structure of buccal cavity: simple structure of most papillae, absence of tongue anlage papillae, lateral ridge papillae as well as buccal roof arena papillae.

Ecology. – The present tadpoles were collected from a large pool under a waterfall of a river (about 10 m wide) running through a primary forest (Fig. 1). This quiet pool was 30 cm deep and sun-exposed. The tadpoles did not gather in schools, and stayed still on the substrate where they were conspicuous due to their black coloration and large size. They belong to the lotic-benthic ecomorphological guild of Altig & Johnston (1989).

DISCUSSION

Tadpoles of *Nasirana* possess several conspicuous features, including the tail ocellus, which is unique among ranid tadpoles. As far as known, no other ranid species have a similar feature, and that is sufficient to differentiate this tadpole species from all other ranid species. Other conspicuous features such as parotoid glands and other dermal glands are shared by the tadpoles of subgenera *Clinotarsus* Mivart, 1869, *Glandirana* Fei, Ye & Huang, 1990 and *Sanguirana* Dubois, 1992. Previous descriptions of the tadpole of *Rana* (*Clinotarsus*) *curtipes* Jerdon, 1853 (Sekar, 1990; Hiragond et al., 2001) show an animal with parotoid glands, a supracaudal gland and an oral disk which presents great similarities with that of *R. alticola* in shape of jaw sheaths, number of keratodont rows (including the divided ones), number of marginal rows of papillae, and submarginal papillae. (Note that the diagram of Hiragond et al. (2001) does not correspond to the text description). These two taxa appear to be close phylogenetically based on tadpole morphology.

The caudal ocelli and the glands could be interpreted as means of defence. Although the tadpoles live in a stream, they occupy quiet areas where the current is slow and are therefore conspicuous because of their large size and black coloration. Glands secreting noxious substances are known to be efficient against predators (Liem, 1961) whereas the largest red ocellus is thought to mimic the eye of a larger animal (Altig & Channing, 1993) and could misdirect predator attacks. Black coloration associated with cutaneous toxicity (as in many bufonid tadpoles) are traits indicative of aposematic coloration. Usefulness of the numerous keratodonts rows present in this species is more difficult to explain since these tadpoles inhabit slow water areas. However, this occurs frequently in stream living tadpoles (Altig & Johnston, 1989).

Tadpoles from different localities referred to *Rana alticola* have been described by previous authors from northeastern India [Abor, Arunachal Pradesh (Annandale, 1912), Shillong, Khasi Hills (Annandale in Smith, 1924b) and northeastern hill region (Sahu & Khare, 1983)], and peninsular Thailand (Smith, 1924a). The measurements of total length given by these authors fit well with our observations: a maximum size of 98 mm for the population of northeastern hills region (Sahu & Khare, 1983), 96 mm for the peninsular Thailand population (Smith, 1924a) and 93 mm in our sample. Annandale (1912) reported a size of at least 57 mm without specifying the developmental stage of the tadpole.

Differences in coloration and number of ocelli have been noted by most of the previous authors. Although the centres of ocelli are invariably black, the coloration of the outer ring varies from yellow (Annandale, 1912) to red (our sample) to orange (Smith, 1924a). Previous authors did not indicate if this coloration was from living or fixed tadpoles. It is thus not possible to establish if these differences in coloration are due to interpopulational variation or, more likely, to a fading in preservative. Boulenger (1882), Smith (1924a), Bourret (1942) and Sahu & Khare (1983) reported one ocellus on each side of the tadpole whereas Annandale (1912) reported the presence of several ocelli. Several ocelli are also present on the tail of our specimens but they were not easily noticeable because the small ocelli are darker and the outer ring is very slightly marked or non-existent.

Slight differences occur in KF reported in the previous descriptions. The highest number of rows in our sample is 2:7+7/1+1:8 (stage 38), but it is reported to be 2:5+5/1+1:8 (Annandale, 1912) and 2:5+5/1+1:6 (Sahu & Khare, 1983) in the northeastern Indian tadpoles. The tadpoles from peninsular Thailand (Smith, 1924a) possess nine rows in the upper labium which is similar to the number observed in the tadpoles studied in this paper [Smith's diagram (1924a) is wrong in lacking submarginal papillae and accessory keratodont rows and with misinterpretation of KF]. However ontogenetic variation is common in species having high number of keratodonts rows such as North American pelobatids (Bresler & Bragg, 1954; Gosner & Black, 1954; Bragg & Hayes, 1963; Bragg et al., 1963; Hampton & Volpe, 1963), tadpoles of *Hoplobatrachus*, a ranid genus (Lamotte & Zuber-Vogeli, 1954; Dutta & Mohanty-Hejmadi, 1984) and *Leptobranchium (Vibrissaphora) echinatum*, a megophryid species (Grosjean, 2001).

ACKNOWLEDGMENTS

This publication is a part of an active collaborative research program between the Royal Forest Department of Thailand (Bangkok) and the Muséum national d'Histoire naturelle (Paris). Thanks to W. R. Heyer for his helpful criticism of early version of the manuscript. This is publication N° Publication N°03-74 see Keith (2003) of PPF "Faune et flore du sud-est asiatique".

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