Molecular identifications and descriptions of the tadpoles of *Rhacophorus kio* Ohler & Delorme, 2006 and *Rhacophorus rhodopus* Liu & Hu, 1960 (Amphibia: Anura: Rhacophoridae)

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ABSTRACT
The knowledge of the development is important in organisms with a biphasic life cycle, as in anuran amphibians, particularly in families in which the developmental modes greatly vary between genera and are used for their systematics. This is the case of the family Rhacophoridae Hoffman, 1932. The tadpoles of *Rhacophorus kio* Ohler & Delorme, 2006 and *Rhacophorus rhodopus* Liu & Hu, 1960, two sympatric species of the genus *Rhacophorus* Kuhl & Van Hasselt, 1822 found in syntopy in Northwestern Thailand are molecularly identified, morphologically described and illustrated. The buccal anatomy is documented and described. These two tadpoles are compared to the known tadpoles of their species group as here newly defined based on the latest molecular results. Additionally they are compared to the known tadpoles of the *Rhacophorus* species that can be found in sympatry with them.

KEY WORDS
Rhacophoridae,
Thailand,
tadpole,
morphology,
buccopharyngeal anatomy,
molecular identification.

RÉSUMÉ
Identification moléculaire et description des têtards de Rhacophorus kio *Ohler & Delorme, 2006 et* Rhacophorus rhodopus *Liu & Hu, 1960 (Amphibia: Anura: Rhacophoridae).*
La connaissance du développement des organismes à cycle de vie biphasique, tels que les amphibiens anoures est importante, particulièrement dans les familles pour lesquelles le mode de développement varie énormément entre les genres et est utilisé pour leur systématique. C'est le cas de la famille des Rhacophoridae Hoffman, 1932. Les têtards de *Rhacophorus kio* Ohler & Delorme, 2006 et de *Rhacophorus rhodopus* Liu & Hu, 1960, deux espèces sympatriques appartenant au genre *Rhacophorus* Kuhl & Van Hasselt, 1822 collectés en syntopie dans le nord-ouest de la Thaïlande, sont identifiés par des données moléculaires, décrits morphologiquement et illustrés. L'anatomie buccale est documentée et décrite. Ces deux têtards sont comparés aux têtards connus de leur groupe d'espèces tel qu'il est ici défini à la lumière des résultats moléculaires les plus récents. De plus, ils sont comparés aux têtards connus des espèces de *Rhacophorus*, qui peuvent être potentiellement trouvées en sympatrie avec eux.

MOTS CLÉS
Rhacophoridae,
Thaïlande,
têtard,
morphologie,
anatomie bucco-pharyngée,
identification moléculaire.

INTRODUCTION

The larval stages of many amphibian species are still yet not known. Furthermore old descriptions are at present obsolete because they are often too succinct to accurately describe subtle congeneric variations among species and so larval characters cannot be included in taxonomic and systematic studies. In addition some tadpole descriptions are based on a nominal species that has since been found to be a species complex and further split in several new species without means to link unambiguously the described specimen to one of these species (for example because localities are not clearly stated). At last, some of these old descriptions are done on a mix of individuals of several populations further revealing to be different species (e.g., Bourret 1942). The larval forms need to be molecularly identified and linked to voucher adult specimens which would allow their taxonomic reassessment in the future.

Tadpole stages and modes of development are of importance in the taxonomy of frogs, especially in the family Rhacophoridae Hoffman, 1932 whose members developed a great variety of developmental strategies, from a "common" development with deposition of a clutch in water (in the genus *Buergeria* Tschudi, 1838) to direct development (in the genera *Philautus* Gistel, 1848; *Pseudophilautus* Laurent, 1943 and *Raorchestes* Biju, Shouche, Dubois, Dutta & Bossuyt, 2010; but see Hertwig *et al.* 2012) through several other developmental adaptations such as the deposition of a foam nest in vegetation which shelter developing embryos until the just hatched tadpoles drop in the water to complete their larval development (in the genera *Chiromantis* Peters, 1854; *Ghatixalus* Biju, Roelants & Bossuyt, 2008; *Polypedates* Tschudi, 1838, *Rhacophorus* and *Taruga* Meegaskumbura, Meegaskumbura, Bowatte, Manamendra-Arachchi, Pethiyagoda, Hanken & Schneider, 2010). The evolution of these complex modes of development have been actively studied in these last years (Grosjean *et al.* 2008; Li *et al.* 2009; Hertwig *et al.* 2012, 2013) and have led to the generic reassignment of a number of species.

Fieldwork in Thailand in 2005 allowed us to collect in the same locality (Doi Chiang Dao, Chiang Mai Province, Thailand) the tadpoles of two *Rhacophorus* species, *Rhacophorus kio* Ohler & Delorme, 2006 and *Rhacophorus rhodopus* Liu & Hu, 1960. *Rhacophorus kio* is a sibling species of *R. reinwardtii* (Schlegel, 1840) (Ohler & Delorme 2006) with which it has been confounded until its description. It is distributed in China (southern Yunnan and southern Guangxi), northern Thailand, Laos, and Vietnam (Frost 2015). Contrary to the statement of Frost (2015) this species has not been reported in Cambodia to our knowledge. So all mentions and descriptions referring to *R. reinwardtii* from these areas apply in fact to *R. kio*. However the mention of *R. reinwardtii* in eastern India (Das & Dutta 1998; Frost 2015) seems to be erroneous. Pillai & Chanda (1979) reported *R. reinwardtii* from the Khasi Hills, Meghalaya and noted the presence of several spots on the flanks (whereas *R. kio* has consistently only one on each side; Ohler & Delorme 2006; Bordoloi *et al.* 2007). These specimens refer then to *R. bipunctatus* Ahl, 1927. *Rhacophorus rhodopus* is a species which has been frequently confounded with *R. bipunctatus* and whose taxonomic status has only recently been clarified (Bordoloi *et al.* 2007). This is a common species distributed in northeastern India (Arunachal Pradesh), Myanmar, Thailand, Laos, Cambodia, Vietnam, and southern China (Xizang, Yunnan, Guangxi, Hainan) (Ohler *et al.* 2002; Frost 2015). So these two species have a roughly sympatric distribution (Fig. 1) and are commonly found in the same locality. They have even been collected from the same water body in two occasions in Thailand (in the Phu Hin Rong Kla National Park, Phitsanulok Province, North central Thailand and in the Kui Buri National Park, Prachuap Khiri Khan Province, northern Peninsular Thailand). Furthermore one probable case of introgressive hybridization has been reported corroborating the fact that these two species are close phylogenetically (Grosjean *et al.* 2015). This dubious specimen has not been included in the present study and is not discussed further as it is beyond the scope of this paper.

Although these two species are commonly reported and listed (*R. kio*: Smith [1917, 1930: 115]; Bourret 1942; Liu & Hu 1960 "1959"; Taylor 1962; Yang 1991, 2008; Ye *et al.* 1993; Nguyen & Ho 1996; Fei 1999; Inger *et al.* 1999; Orlow & Cuc 2000; Ohler *et al.* 2000; Tordoff *et al.* 2000; Orlov *et al.* 2001; Ziegler 2002; Stuart 2005; Ohler & Delorme 2006; Fei *et al.* 2009, 2012; Nguyen *et al.* 2009; *R. rhodopus*: Liu & Hu 1960 "1959"; Sarkar & Sanyal 1985 [as *R. namdaphaensis* Sarkar & Sanyal, 1985]; Yang 1991, 2008; Fei 1999; Inger *et al.* 1999 [as *R. bipunctatus*]; Ohler *et al.* 2002; Chan-ard 2003; Inthara *et al.* 2005 [as *R. bipunctatus*]; Wilkinson *et al.* 2005 [as *R. bipunctatus*]; Stuart & Emmet 2006 [as *R. bipunctatus*]; Bordoloi *et al.* 2007; Nguyen *et al.* 2008, 2009; Fei *et al.* 2009, 2012; Mathew & Sen 2010), only the tadpole of *R. rhodopus* has been briefly described or drawn (Yang 1991; Fei 1999; Inger *et al.* 1999 [as *R. bipunctatus*]; Inthara *et al.* 2005 [as *R. bipunctatus*]; Fei *et al.* 2009, 2012).

Tadpoles of congeneric species are usually very difficult to discriminate and specific allocation is often impossible for a non-trained herpetologist especially where several species can occur syntopically. The DNA barcoding method is an easy, fast and reliable mean to unequivocally allocated tadpoles to an adult frog and it has already proved to be a powerful tool (Vences *et al.* 2005; Randrianiaina *et al.* 2012; Grosjean *et al.* 2015). We verified the specific allocation by DNA barcoding and provided in this paper accurate descriptions of the external morphology and of the buccopharyngeal features of the tadpoles of these two rhacophorid species.

MATERIAL AND METHODS

Specimens

The tadpoles of *Rhacophorus rhodopus* and *R. kio* were collected during a field trip in the Wildlife Sanctuary of Chiang Dao, Chiang Mai Province, Thailand (Fig. 1).

Tadpoles were collected in the field and euthanized by immersion in chlorobutanol, and subsequently divided into series based on their morphology. A small portion of the

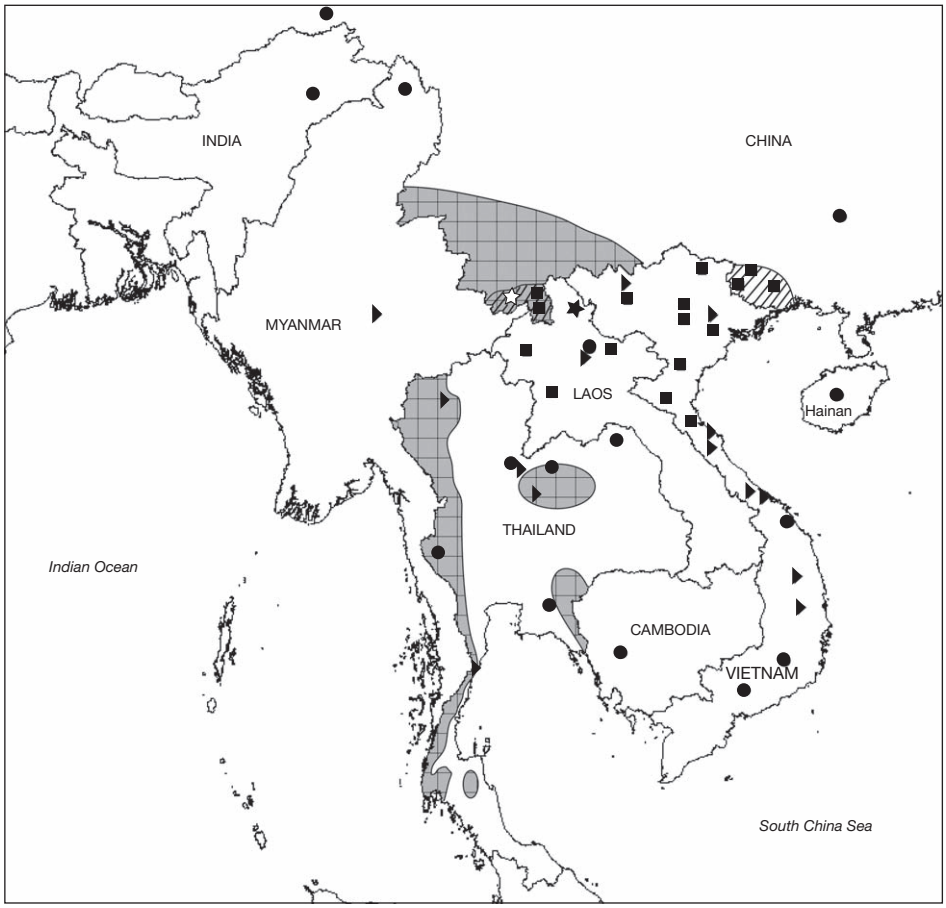

FIG. 1. — Known distributions of *Rhacophorus kio* Ohler & Delorme, 2006 and *Rhacophorus rhodopus* Liu & Hu, 1960. Symbols: ⋆, type locality of *R. kio*; ☆, type locality of *R. rhodopus*; ■, and **hatched areas**: localities and areas where *R. kio* has been found; ●, and **grey squared areas**: localities and areas where *R. rhodopus* has been found; ▶, localities where both species have been encountered. Note that both species are present in the type locality of each species. Data from Sarkar & Sanyal 1985; Yang 1991; Nguyen & Ho 1996; Fei 1999; Fei *et al.* 2009; Inger *et al.* 1999; Ohler *et al.* 2000, 2002; Tordoff *et al.* 2000; Ziegler 2002; Chan-ard 2003; Stuart 2005; Inthara *et al.* 2005; Wilkinson *et al.* 2005; Ohler & Delorme 2006; Bordoloi *et al.* 2007; Nguyen *et al.* 2008; Nguyen *et al.* 2009; Grosjean *et al.* 2015.

caudal muscle was removed from one specimen of each series for molecular analysis. This specimen (the DNA voucher) was used for the detailed description given below. All specimens were fixed and preserved in a solution of equal part of 4% formalin and 70% alcohol. Tadpoles were subsequently checked again in regard to the characteristics of the voucher specimens. All specimens were deposited in the Herpetological collections of the Muséum national d'Histoire naturelle (*R. kio*, MNHN 2010.1072-2010.1104, 2010.1142, 1143; *R. rhodopus*, MNHN 2010.1106-2010.1139).

MOLECULAR DATA

The sequences of tadpoles and adults used in this paper, a partial sequence of the 16S rRNA gene, have been generated for another project (Grosjean *et al.* 2015) and have been deposited in GenBank under the accession numbers KR828037-39 and KR828043-45, and KR828048-49 and KR828066-71. For molecular procedures refer to Grosjean *et al.* (2015). The sequence of the tadpole of *R. kio* MNHN 2010.1072 had an uncorrected pairwise sequence divergence of 0% with the syntopic adult MNHN 3033K whereas the other syntopic rhacophorid species (*Chiromantis doriae* (Boulenger, 1893) MNHN 3006K; *Polypedates megacephalus* Hallowell, 1861 MNHN 3032K; *Raorchestes parvulus* (Boulenger, 1893) MNHN 3056K; and *R. rhodopus* MNHN 3046K and MNHN 3085K; accession numbers KR827715, KR828013, KR828034, KR828066 and KR828067) all had pairwise divergences of more than 8.21%. The sequence of the tadpole of *R. rhodopus* MNHN 2010.1124 had an uncorrected pairwise sequence divergence of 0-0.59% with the syntopic adults MNHN 3046K and MNHN 3085K whereas the other syntopic rhacophorid species (*Chiromantis doriae* (Boulenger, 1893) MNHN 3006K; *Polypedates megacephalus* Hallowell, 1861 MNHN 3032K; *Raorchestes parvulus* (Boulenger, 1893) MNHN 3056K; and *R. kio* MNHN 3033K accession number KR828043, for the others see above) all had pairwise divergences of more than 8.50%.

MORPHOLOGY

Morphological terminology follows Altig & McDiarmid (1999), Keratodont Row Formula (KRF) follows Dubois (1995) and developmental stages were determined according to Gosner (1960). Measurements were taken with a graduated ocular

attached to a stereomicroscope except for the total length which was measured with a hand calliper, and are rounded to the nearest 0.1 mm except for the gaps in the keratodont rows which are rounded to the nearest 0.01. The landmarks are those shown in Altig & McDiarmid (1999:26, fig. 3.1), for others see Grosjean (2001). Drawings were made with a camera lucida.

Preparation for SEM examination (JEOL JSM-840A) comprised dehydration (ethanol), critical-point-drying (liquid carbondioxide) and gold sputter surface coating. Terminology of buccopharyngeal features follows Wassersug (1976).

We hereafter give a detailed description of *Rhacophorus kio*. The external morphology of *R. rhodopus* being very similar, its description is therefore abbreviated, mainly mentioning differences with the former species.

ABBREVIATIONS

BH	maximum body height;
BL	body length;
BW	maximum body width;
DG	maximum size of dorsal papilla gap;
ED	maximum eye diameter;
KG A-2	length of the gap in the keratodont row A2;
KG A-3	length of the gap in the keratodont row A3;
KR A-2	length of the keratodont row A2;
KR A-3	length of the keratodont row A3;
KRF	keratodont row formula;
LF	maximum height of lower tail fin;
MTH	maximum tail height;
NN	internarial distance;
NP	naro-pupilar distance;
ODW	oral disc width;
PP	interpupilar distance;
RN	rostro-narial distance;
SS	distance from tip of snout to opening of spiracle;
SU	distance from snout to beginning of upper tail fin;
TAL	tail length;
TL	total length;
TMH	tail muscle height;
TMW	tail muscle width;
UF	maximum height of upper tail fin.

RESULTS

The two tadpoles belong to the exotrophic lentic benthic ecomorphological guild (Altig & Johnston 1989).

Genus *Rhacophorus* Kuhl & Van Hasselt, 1822

Rhacophorus kio Ohler & Delorme, 2006 (Figs 2; 3A, B)

Rhacophorus kio Ohler & Delorme, 2006: 90.

MATERIAL EXAMINED. — A series of 37 tadpoles (MNHN 2010.1072-1104, MNHN 2010.1142-1143) were identified as belonging to *Rhacophorus kio*. The specimens were collected in the Wildlife Sanctuary of Chiang Dao, Chiang Mai Province, Thailand (19°17'N, 98°57'E), 13.VII.2005, S. Grosjean, C. Inthara and Y. Chuaynkern. Tadpoles were collected in a large puddle (10 m × 2 m and 50 cm depth) on the roadside. The pool was bordered by grass all around, and by shrubs and bamboos on the side opposite to the road where adults were observed high-perched. Tadpoles of *Polypedates megacephalus* and *R. rhodopus* were collected in the same pool. The description is based on a DNA voucher specimen at stage 36 (MNHN 2010.1072, BL 20.3 mm). Because the end of the tail was taken for molecular determination and was also damaged, information upon tail fin and tip of tail was taken from another individual at stage 36 (MNHN 2010.1073, BL 21.0 mm, TL 54.4 mm) as well as the ratios given in text.

DESCRIPTION

External morphology

In dorsal view (Figs 2A; 3A), body elliptical, widest at level of gills, snout rounded. In lateral view (Figs 2B; 3B), body slightly depressed, BW 116% of BH, snout rounded. Eyes moderately sized, ED 8.3% of BL, bulging and not visible in ventral view, positioned dorsolaterally with an anterodorsolateral direction. Pineal ocellus present, at level of the anterior border of eyes. Nares round, moderately sized, rimmed, positioned almost dorsally but directed anterolaterally with an opening direction horizontal, closer to snout than to pupils, RN 62% of NP; NN 46% of PP. Spiracle sinistral, square, of moderate size, positioned ventrolaterally and situated before half of body length, SS 42% of BL; opening at a height intermediate between apex of caudal myotomes and hind limb insertion, oriented posterodorsally and entirely attached to body wall (inner wall present as a slight ridge). Tail musculature moderate; TMH 71% of BH and 60% of MTH, TMW 55% of BW, slightly tapering in proximal part then gradually tapering, reaching tail tip. Tail fins of moderate size; UF 34% of MTH, LF 28% of MTH, upper fin not extending onto body, SU 72% of BL, convex, lower fin straight on more than the proximal half then curved to form the tail tip; point of maximum height of tail located just after proximal third, MTH 120% of BH, tail tip finely rounded. Anal tube short, tubular, medial and directed posteriorly, entirely attached to ventral fin, opening lateral. Lateral line present onto body.

Oral disc. (Fig. 2C) Oral disc positioned and directed anteroventrally, emarginated, of moderate size; ODW 18% of BL and 40% of BW. A row of marginal papillae largely interrupted medially on upper labium, DG 66% of ODW, two rows on the lower labium (submarginal row shortly interrupted medially leaving only one row on a small portion), one or two submarginal papillae laterally on upper labium; papillae moderately small, round. No denticulate papillae. KRF 1:4+4/3, upper rows subequal, A2 with a short gap, lower rows subequal. Keratodonts (Fig. 2D) spoon-shaped bearing 12 to 16 cusps. Jaw sheaths moderately-sized, finely serrated, upper half black and lower half white; upper sheath flat on its most part medially; lower sheath V-shaped.

Colour in life. Back and flanks light olive, anterior part of ventral side very light yellow-grey, abdomen white. Caudal muscle very light olive, fins colourless except a fine light grey area at their edge near middle of tail.

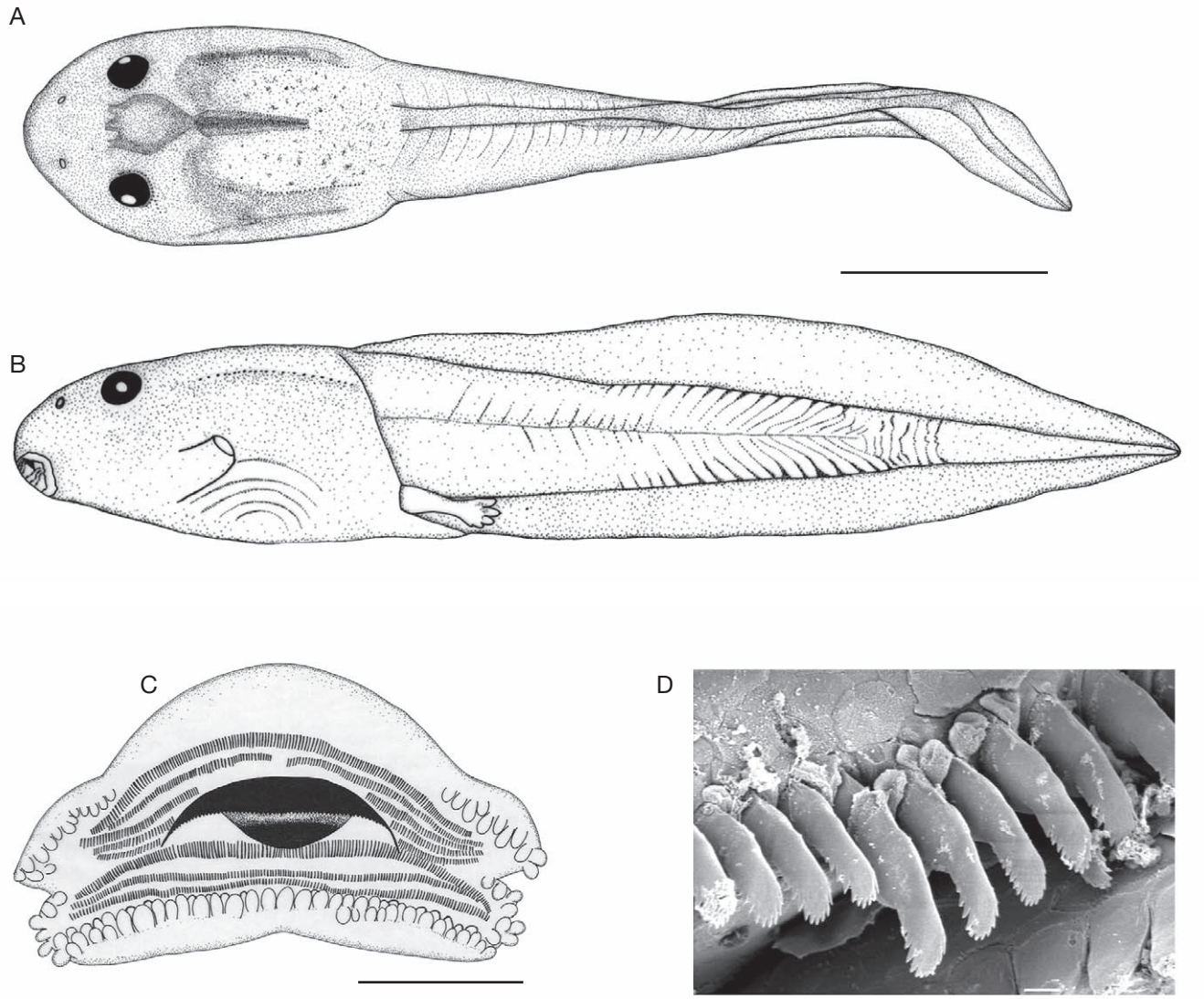

FIG. 2. — Drawings and scanning electron micrographs of the tadpole of *Rhacophorus kio* Ohler & Delorme, 2006, MNHN 2010.1072, stage 36: **A**, dorsal view; **B**, lateral view; **C**, oral disc; **D**, some keratodonts of the row A3 of the tadpole MNHN 2010.1142, stage 40. Scale bars: A, B, 10 mm; C, 1 mm; D, 10 µm.

Colour in preservative. Entirely yellowish.

Variation. Variation of KRF was assessed based on 28 other tadpoles in stages 25-41 (MNHN 2010.1073-1087, 2010.1090-1094, 2010.1097-1100, 2010.1142-1143, and two tadpoles lost since the description). Different collective KRF can be found: 1:(3+3)-(4+4)/3 (14%); 1:(3+3)-(5+5)/1+1:2 (75%); 2:3+3/1+1:2 (11%). TL and BL of 36 tadpoles in stages 25-41 (MNHN 2010.1073-1104, 2010.1142-1143, and two lost tadpoles) are respectively 18.7-58.9 mm and 8.6-21.2 mm. The ratios of 10 tadpoles (MNHN 2010.1073-1082) in stages 34-36 vary in the following proportions: BW 108-120% of BH; ED 7.8-10.7% of BL; RN 50-76% of NP; NN 46-50% of PP; SS 42-47% of BL; TMH 63-78% of BH; TMH 55-70% of MTH; TMW 54-65% of BW; UF 33-36% of MTH; LF 24-29% of MTH; SU 73-81% of BL; MTH 96-122% of BH; ODW 17-20% of BL; ODW 38-42% of BW; DG 62-73% of ODW. Basic measurements and KRF are provided for all available stages (Table 1) whereas detailed measurements are provided for the stages 34-36 (Table 3). The lower row of marginal papillae can be shortly interrupted medially.

Buccopharyngeal features

Description based on a tadpole in stage 34 (MNHN 2010.1143, BL 13.9 mm, TL 34.4 mm) verified on a tadpole in stage 36 (MNHN 2010.1091, BL 13.5 mm).

Buccal floor. (Fig. 4A). Buccal floor roughly diamond-shaped. Prelingual arena hourglass-shaped, very narrow bearing five pairs of cylindrical papillae pustular on top: most anterior one lying on the floor of the arena and directed dorsally; second pair arising from sides of lower beak at about mid-length of arena and dorsomedially directed; third and fourth pairs at

TABLE 1. — Keratodont row formula (**KRF**), body length (**BL**), tail length (**TAL**) and total length (**TL**) for all available stages of *Rhacophorus kio*. Mean in mm ± standard deviation, range in mm between parentheses and number of specimens (**N**).

Stage	KRF	BL	TAL	TL
25	1:3+3/1+1:2	8.6	10.1	18.7
N = 1				
28	2:3+3/1+1:2	11.4	17.8	29.2
N = 1				
33	2:3+3/1+1:2	14.6	22.6	37.2
N = 1				
34	1-2:(3+3)-(4+4)/	17.9 ± 3.63	27.1 ± 5.71	45.0 ± 9.2
N = 3	(0+0)-(1+1):2-3	(13.9-21.0)	(20.5-30.5)	(34.4-51.3)
35	1:4+4/1+1:2	16.4 ± 2.60	26.4 ± 5.8	42.8 ± 8.33
N = 5		(14.0-20.7)	(20.1-35.2)	(34.1-55.9)
36	1:(4+4)-(3+3)/1+1:2-3	20.0 ± 1.42	33.9 ± 1.90	53.9 ± 3.06
N = 9		(16.5-21.2)	(32.2-37.8)	(48.7-58.9)
39	1:4+4/1+1:2	18.4	26.5	45.0
N = 1				
40	1:(4+4)-(5+5)/1+1:2	17.4 ± 1.60	28.4 ± 0.82	46.1 ± 1.75
N = 5		(15.9-20.1)	(27.4-29.4)	(44.1-48.3)
41	1-2:(3+3)-	18.0 ± 0.84	30.9 ± 2.80	48.9 ± 2.71
N = 6	(4+4)/1+1:2-3	(17.2-19.4)	(27.3-35.2)	(44.9-52.3)
42	/	19.6	29.9	49.5
N = 1				
43	/	18.2	19.1	37.3
N = 1				
44	/	19.6	7.1	26.6
N = 1				
45	/	19.6 ± 0.21	1.9 ± 0.26	21.4 ± 0.47
N = 3		(19.4-19.8)	(1.7-2.1)	(21.1-21.9)

TABLE 2. — Keratodont row formula (**KRF**), body length (**BL**), tail length (**TAL**) and total length (**TL**) for all available stages of *Rhacophorus rhodopus*. Mean in mm ± standard deviation, range in mm between parentheses and number of specimens (**N**).

Stage	KRF	BL	TAL	TL
25	1:(1+1)-(4+4)/1+1:2	8.3 ± 0.85	12.0 ± 0.55	20.6 ± 0.45
N = 5		(7.2-9.4)	(11.6-12.8)	(20.0-21.1)
26	1:4+4/1+1:2	12.8 ± 0.49	15.9 ± 1.49	28.7 ± 2.43
N = 2		(12.4-13.1)	(14.5-17.3)	(26.9-30.4)
27	1:(4+4)-(5+5)/1+1:2	13.4 ± 1.36	17.2 ± 1.79	30.6 ± 3.01
N = 8		(10.6-14.4)	(14.5-19.7)	(25.8-34.1)
28	1:5+5/1+1:2	15.9 ± 1.05	22.8 ± 0.18	38.2 ± 1.22
N = 2		(15.2-16.7)	(22.6-22.9)	(37.8-39.6)
30	1:4+4/1+1:2	15.1	22.0	37.1
N = 1				
34	1:5+5/1+1:2	16.5	25.9	42.1
N = 1				
35	1:4+4/1+1:2	17.3	26.2	43.5
N = 1				
36	1:(4+4)-(5+5)/1+1:2	18.4 ± 0.82	27.3 ± 3.08	45.7 ± 3.77
N = 8		(17.3-19.3)	(23.5-30.5)	(41.5-49.3)
37	1:(4+4)-(5+5)/1+1:2	19.1 ± 0.58	28.7 ± 2.99	47.8 ± 2.91
N = 6		(18.2-19.7)	(23.8-32.4)	(43.2-51.9)

end of prelingual arena, at its narrowest part, one above the other and both transversely directed; fifth pair, the shortest, erupting low from wall bordering arena, behind previous ones, at level of anterior part of tongue anlage. Tongue anlage oval with a posterior protuberance, bearing two small lingual papillae with tiny pustulations at top, dorsally oriented. Buccal floor arena round, delimited by about 30 small buccal floor arena papillae, biggest in front of buccal pockets, flattened and slightly pustular; interior of arena with 35-40 pustules and small papillae regularly arranged. Buccal pockets oblique, anteromedially-posterolaterally oriented, with a wide opening, deep, closer to tongue anlage than to medial end of ventral velum; numerous pustules and small papillae in front of the buccal pockets, posterior part smooth. About 10 pustules between posterior part of buccal floor arena and end of ventral velum. Ventral velum with spicular support, four projections on margin of velum, one above first and second filter plates, four above third, at last two median projections forming median notch; secretory pits present on projections and on margin of ventral velum; glottis below velum almost entirely covered by it. Branchial baskets large and well exposed, wider than high, with three oblique filter plates on each side, filter rows dense with tertiary folds.

Buccal roof. (Fig. 4B). Prenarial arena square, bearing a discontinuous prenarial ridge making up three sides of a square, anterior side composed of four coarse papillae, lateral sides composed of three smaller papillae on each. Choanes moderately fine, transversely oriented; anterior wall pustular bearing a pustulose prenarial papilla positioned on external half of anterior narial wall; narial valve smooth. Postnarial arena hardly observable, at least two pustules in tadpole in stage 36; a pair of postnarial papillae pustular on their tip, curved and oriented medially. Medial ridge rounded, wider than high, pustular on its free edge. Lateral ridge papillae small, pustular anteriorly and oriented transversely. Buccal roof arena round and big, delimited by seven or eight fine buccal roof arena papillae on each side, oriented anteriorly and pustular at tip; interior of arena occupied by about 90 faint pustules arranged slightly more densely posteriorly. Posterolateral ridges present laterally, a small bunch of four-five papillae at each extremity (the groove observed in this specimen is absent from two other and considered for now as an abnormality). Glandular zone wide, about 13 or more secretory pits wide laterally, finer medially; size of secretory pits decreasing anteroposteriorly. Dorsal velum pustular on its free edge, interrupted in its medial part.

Rhacophorus rhodopus Liu & Hu, 1960
(Figs 3C, D; 5)

Rhacophorus rhodopus Liu & Hu, 1960: 525.

MATERIAL EXAMINED. — A series of 34 tadpoles (MNHN 2010.1106-1139) were identified as belonging to *Rhacophorus rhodopus*. The specimens were collected at Den Ya Khad, Chiang Dao, Chiang Mai Province, Thailand (19°20'42"N, 98°39'45"E; altitude about 1470 m above sea level), 14.VII.2005, S. Grosjean, C. Inthara & Y. Chuaynkern. The tadpoles were collected in a pool with very clear water in a small stream. This round pool was small (2 m in diameter) but deep (1.5 m), the bottom was covered by a layer of decaying leaves and it was bordered by shrubs. The tadpoles were associated with those of *Microhyla heymonsi* Vogt, 1911. The description is based on a DNA voucher specimen at stage 36 (MNHN 2010.1124, BL 17.3 mm). Because the end of the tail was taken for DNA barcoding and was also damaged, information upon tail fin and tip of tail was taken on another individual at stage 36 (MNHN 2010.1125, BL 17.9 mm, TL 41.7 mm).

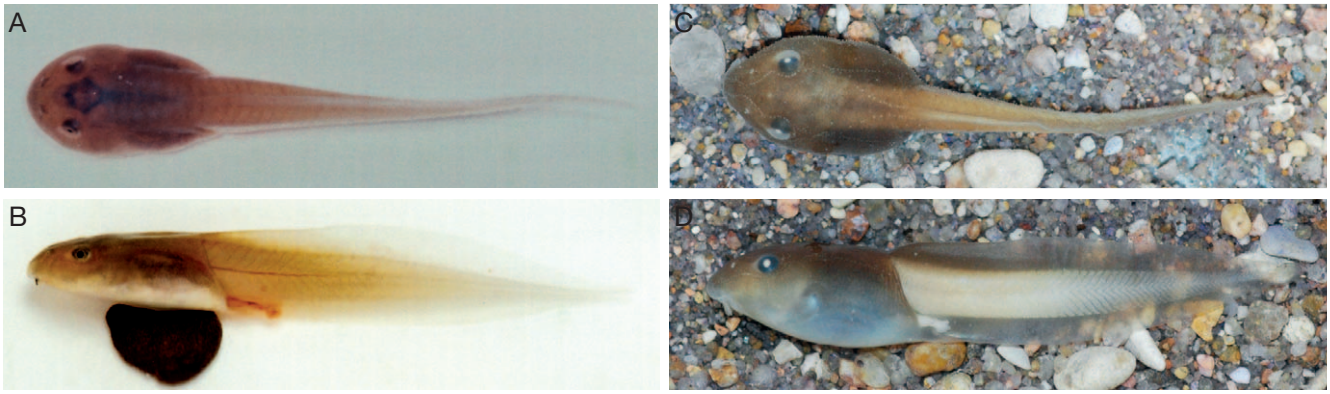

FIG. 3. — **A**, **B**, photographs of dorsal (**A**) and lateral (**B**) views of *Rhacophorus kio* Ohler & Delorme, 2006 (MNHN 2010.1072, stage 36, BL 20.3 mm, voucher DNA) with life coloration; **C**, **D**, photographs of dorsal (**C**) and lateral (**D**) views of *Rhacophorus rhodopus* Liu & Hu, 1960 (MNHN 2010.1131, stage 36, TL 44.4 mm) with colours in preservative.

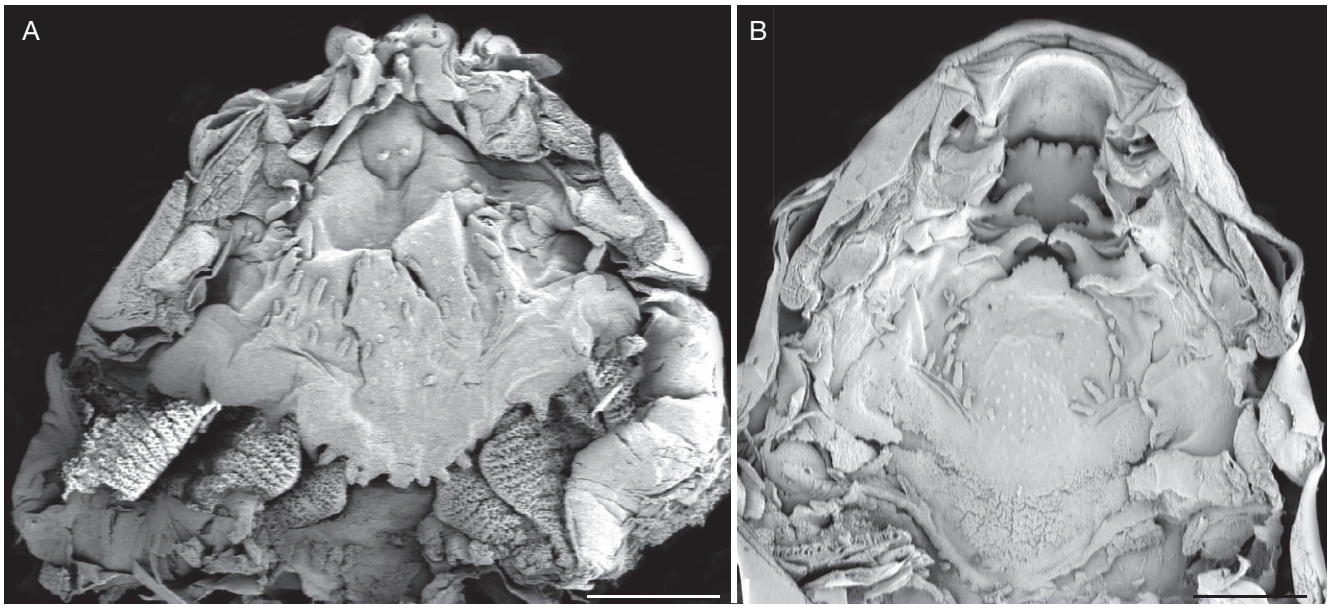

FIG. 4. — *Rhacophorus kio* Ohler & Delorme, 2006 (MNHN 2010.1143, stage 34): **A**, buccal floor; **B**, buccal roof. Scale bars: 1 mm.

DESCRIPTION

External morphology

In dorsal view (Figs 3C; 5A), snout subovoid. In lateral view (Fig. 3D; 5B), BW 114% of BH. Eyes positioned slightly more dorsally than dorsolaterally, ED 8.1% of BL. Pineal ocellus between anterior part of eyes. Nares elliptical, RN 78% of NP; NN 51% of PP. Spiracle slightly conical, positioned slightly ventrolaterally, opening at a level situated just below apex of caudal myotomes, SS 47% of BL. Tail musculature parallel in proximal half then gradually tapering, TMH 52% of BH and 54% of MTH, TMW 46% of BW. Upper fin slightly convex, UF 34% of MTH, lower fin straight, LF 22% of MTH, SU 71% of BL; point of maximum height of tail located at proximal quarter, MTH 96% of BH. Lateral line present onto body and tail.

Oral disc. (Fig. 5C) Oral disc of moderately large size, ODW 24% of BL and 50% of BW. DG 75% of ODW; papillae cylinder-shaped. KRF 1:5+5/1+1:2, A2 formed of two parts overlapping medially; P1 with a very short gap. Keratodonts (Fig. 5D) spoon-shaped bearing 16-20 cusps. Jaw sheaths black coloured; upper sheath almost flat.

Colour in life. Back and upper part of flanks olive. Lower part of flanks and ventral side transparent with iridescent coiled gut and red gills visible. Caudal muscle olive, fins transparent smoked with diffuse melanophores.

Colour in preservative. Upper part brownish, flanks grey, lower part dirty white translucent. Caudal muscle yellowish on anterior ⅓, posterior ⅔ white, becoming transparent at

TABLE 3. — Morphometric measurements of tadpoles in stages 34-36 and 34-37 of *Rhacophorus kio* and *Rhacophorus rhodopus* respectively. Measurements are provided as mean in mm ± standard deviation, range in mm between parentheses and number of specimens (**N**).

Stage	SS	SU	UF	LF	MTH	TMH	BH
Rhacophorus kio Ohler & Delorme, 2006							
34	8.5 ± 0.51	15.0 ± 1.33	2.9 ± 0.41	2.4 ± 0.51	8.7 ± 1.23	5.9 ± 0.51	7.9 ± 0.31
N = 2	(8.1-8.9)	(14.1-16.0)	(2.6-3.2)	(2.0-2.8)	(7.8-9.6)	(5.5-6.2)	(7.7-8.1)
35	8.1 ± 0.83	14.4 ± 1.95	2.8 ± 2.23	2.2 ± 1.27	8.1 ± 1.74	5.4 ± 0.82	8.0 ± 1.23
N = 2	(7.5-8.7)	(13.1-15.8)	(2.3-3.3)	(1.7-2.6)	(6.8-9.3)	(4.8-6.0)	(7.1-8.9)
36	8.7 ± 0.51	15.2 ± 1.06	3.1 ± 0.40	2.5 ± 0.38	9.1 ± 0.99	5.7 ± 0.70	8.0 ± 0.49
N = 7	(7.5-9.0)	(13.1-16.1)	(2.3-3.3) N = 6	(1.7-2.8) N = 6	(7.1-9.7) N = 6	(4.5-6.2)	(7.1-8.4)
Rhacophorus rhodopus Liu & Hu, 1960							
34 N = 1	7.3	13.1	2.3	2.0	7.3	6.8	8.0
36	8.0 ± 0.47	13.2 ± 0.50	2.4 ± 0.17	1.9 ± 0.17	7.5 ± 0.31	7.9 ± 0.55	9.1 ± 0.53
N = 7	(7.5-8.7)	(12.6-14.1)	(2.2-2.6) N = 6	(1.6-2.0) N = 6	(7.0-7.8) N = 6	(7.0-8.7)	(8.3-9.7)
37	8.4 ± 0.51	13.8 ± 0.21	2.6 ± 0.24	2.0 ± 0.35	7.6 ± 0.62	8.1 ± 0.28	9.2 ± 0.44
N = 5	(7.5-8.9)	(13.5-14.1)	(2.3-2.9)	(1.6-2.5)	(6.8-8.4)	(7.7-8.4)	(8.6-9.6)

Stage	BW	PP	NN	RN	NP	TMW	ED
Rhacophorus kio							
34	9.0 ± 0.62	5.9 ± 0.51	2.8 ± 0.10	1.8 ± 0.10	2.8 ± 0.21	5.0 ± 0.51	1.6 ± 0.21
N = 2	(8.6-9.4)	(5.5-6.2)	(2.8-2.9)	(1.7-1.9)	(2.6-2.9)	(4.6-5.4)	(1.5-1.7)
35	8.7 ± 1.23	5.7 ± 0.8	2.6 ± 0.41	1.6 ± 0.62	2.5 ± 0.31	5.2 ± 0.41	1.7
N = 2	(7.8-9.6)	(5.1-6.2)	(2.3-2.9)	(1.2-2.0)	(2.3-2.8)	(4.9-5.5)	(1.7-1.7)
36	9.2 ± 0.49	6.0 ± 0.35	2.9 ± 0.20	1.8 ± 0.40	2.8 ± 0.34	5.4 ± 0.38	1.7 ± 0.12
N = 7	(8.4-9.6)	(5.4-6.2)	(2.5-3.1)	(1.2-2.3)	(2.2-3.1)	(4.8-5.8)	(1.6-1.9)
Rhacophorus rhodopus							
34 N = 1	5.4	2.8	1.5	2.6	3.5	3.9	1.5
36	5.5 ± 0.20	2.7 ± 0.10	1.8 ± 0.23	2.6 ± 0.15	4.1 ± 0.35	4.3 ± 0.28	1.6 ± 0.10
N = 7	(5.2-5.8)	(2.6-2.9)	(1.5-2.0)	(2.3-2.8)	(3.8-4.5)	(3.9-4.8)	(1.5-1.7)
37	9.2 ± 0.44	5.7 ± 0.27	2.7 ± 0.12	1.9 ± 0.30	2.8 ± 0.13	4.4 ± 0.19	1.7 ± 0.12
N = 5	(8.6-9.6)	(5.4-5.9)	(2.6-2.9)	(1.5-2.2)	(2.6-2.9)	(4.2-4.6)	(1.6-1.9)

Stage	ODW	DG	KR A-2	KR A-3	KG A-2	KG A-3
Rhacophorus kio						
34	3.7 ± 0.26	2.4	3.0 ± 0.22	2.8 ± 0.26	0.09 ± 0.04	1.23 ± 0.09
N = 2	(3.5-3.9)	(2.4-2.4)	(2.8-3.1)	(2.6-3.0)	(0.06-0.12)	(1.17-1.29)
35	3.4 ± 0.35	2.3 ± 0.48	2.6 ± 0.22	2.5	0.25	0.25
N = 2	(3.1-3.6)	(2.0-2.6)	(2.4-2.7)	N = 1	N = 1	N = 1
36	3.6 ± 0.13	2.5 ± 0.12	2.9 ± 0.22	2.9 ± 0.22	0.11 ± 0.07	1.18 ± 0.28
N = 7	(3.4-3.8)	(2.3-2.7)	(2.5-3.2)	(2.6-3.2)	(0.06-0.25) N = 6	(0.55-1.35)
Rhacophorus rhodopus						
34	4.2	2.9	3.1	3.2	/	0.18
N = 1						
36	4.8 ± 1.28	3.0 ± 0.15	3.1 ± 0.20	3.3 ± 0.17	0.12	0.42 ± 0.11
N = 6	(4.2-7.7) N = 7	(2.8-3.2)	(2.8-3.4)	(3.1-3.5)	N = 1	(0.25-0.55) N = 7
37	4.5 ± 0.39	2.8 ± 0.42	3.1 ± 0.30	3.3 ± 0.26	/	0.43 ± 0.13
N = 5	(4.1-5.0)	(2.3-3.4)	(2.9-3.6)	(3.1-3.8)		(0.31-0.61)

end of tail. Caudal muscle covered by numerous dots of melanophores. Fins grey transparent with small melanophores. Upper part of hind limbs with very small melanophores.

Variation. The variation of KRF ranges from 1:(0+0)/1+1:2 to 1:(4+4)/1+1:2 in stage 25 (five specimens) and from 1:(4+4)-(5+5)/1+1:2 in stages 26-37 (24 specimens). TL and BL of 33 tadpoles in stages 25-37 are respectively 20.0-51.9 mm and 7.2-19.7 mm. The ratios of 11 tadpoles in stages 34-37 vary in the following proportions: BW 107-122% of BH; ED 8.3-9.7% of BL; RN 56-75% of NP; NN 45-51% of PP; SS 39-45% of BL; TMH 50-66% of BH; TMH 54-68% of MTH; TMW 40-49% of BW; UF 31-34% of MTH; LF 23-29% of MTH; SU 69-79% of BL; MTH 85-106% of BH; ODW 22-26% of BL; ODW 46-53% of BW; DG 41-75% of ODW. Basic measurements and KRF are provided for all available stages (Table 2) whereas detailed measurements are provided for the stages 34-37 (Table 3).

Buccopharyngeal features

Description based on one tadpole (MNHN 2010.1107; stage 37, BL 19.2 mm) verified with another tadpole (MNHN 2010.1123, stage 36, BL 17.9 mm).

Buccal floor. (Fig 6A). Buccal floor triangular. Prelingual arena narrow, bearing four pairs of papillae, one on floor of arena oriented dorsally, one pair of small pustular papillae at same level than previous pair but originating from lateral

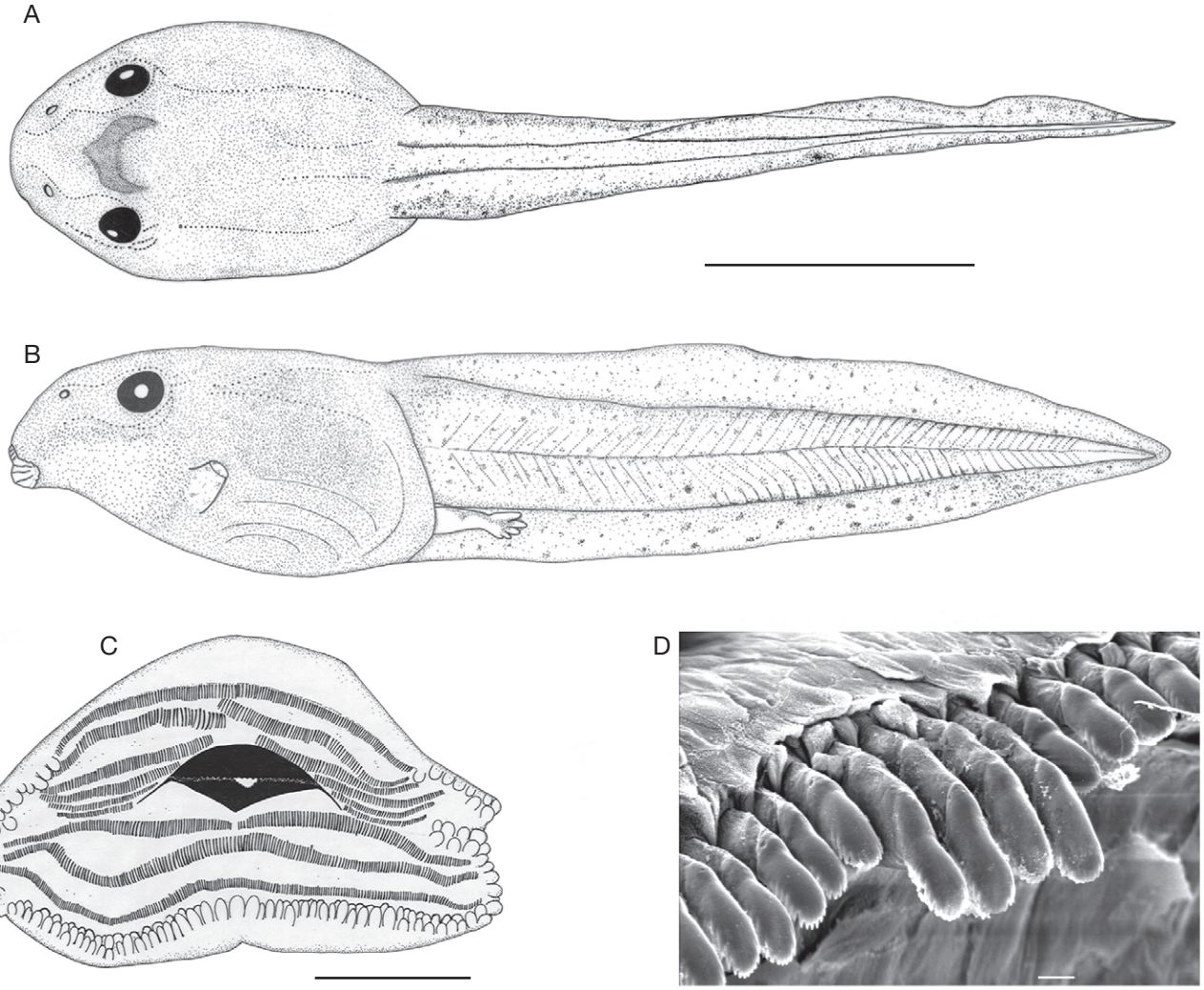

Fig. 5. — Drawings and scanning electron micrographs of the tadpole of *Rhacophorus rhodopus* Liu & Hu, 1960, MNHN 2010.1125, stage 36: **A**, dorsal view; **B**, lateral view; **C**, oral disc; **D**, some keratodonts of the row A2 of the tadpole MNHN 2010.1106, stage 36. Scale bars: A, B, 10 mm; C, 1 mm; D, 10 µm.

sides of arena, the two other pairs located in posterior part of arena, originating at lateral sides of arena, one pair above other, papillae pustular on their dorsal part and at tip, oriented transversely. Tongue anlage round with a posterior protuberance, bearing two fine lingual papillae without pustulations at top, dorsally oriented. Buccal floor arena round, delimited by about 13 small buccal floor arena papillae, biggest bifid, flattened and slightly pustular in front of buccal pockets, others fine and smooth more or less flattened; interior of arena with about 50 pustules and small papillae diamond-shaped arranged and regularly spaced in posterior part of arena. Buccal pockets anteromedially oriented, with a wide opening, deep slightly closer to tongue anlage than to medial end of ventral velum; numerous pustules and small papillae in front of the buccal pockets, posterior part smooth. About 10-15 faint pustules between posterior part of buccal floor arena and end of dorsal velum. Dorsal velum with spicular support, 18 projections on margin of velum (Fig. 7), one above first and second filter plate, 14 above third, medial notch little developed and made up by two most medial projections; secretory pits present on projections and margin of velum; glottis partly visible below velum, branchial baskets large, longer than wide, with three filters cavities; filter rows dense with tertiary folds.

Buccal roof. (Fig. 6B). Prenarial arena trapezoidal, bearing a discontinuous prenarial ridge making up three sides of a trapeze, anterior side composed of three coarse papillae, lateral sides composed of three smaller papillae on each. Choanae moderately fine, transversely oriented; anterior wall smooth surmounted by a prenarial papilla pustular on its anterior face, positioned on external half of anterior narial wall; narial valve smooth. Postnarial arena with three pustules aligned transversely; a pair of postnarial papillae slightly pustular, transversely oriented. Medial ridge truncate, wider than high, pustulose on its free edge. Lateral ridge papillae small, cylindrical, pustular anteriorly and anteriorly oriented. Buccal roof arena round and big, delimited by six fine buccal roof

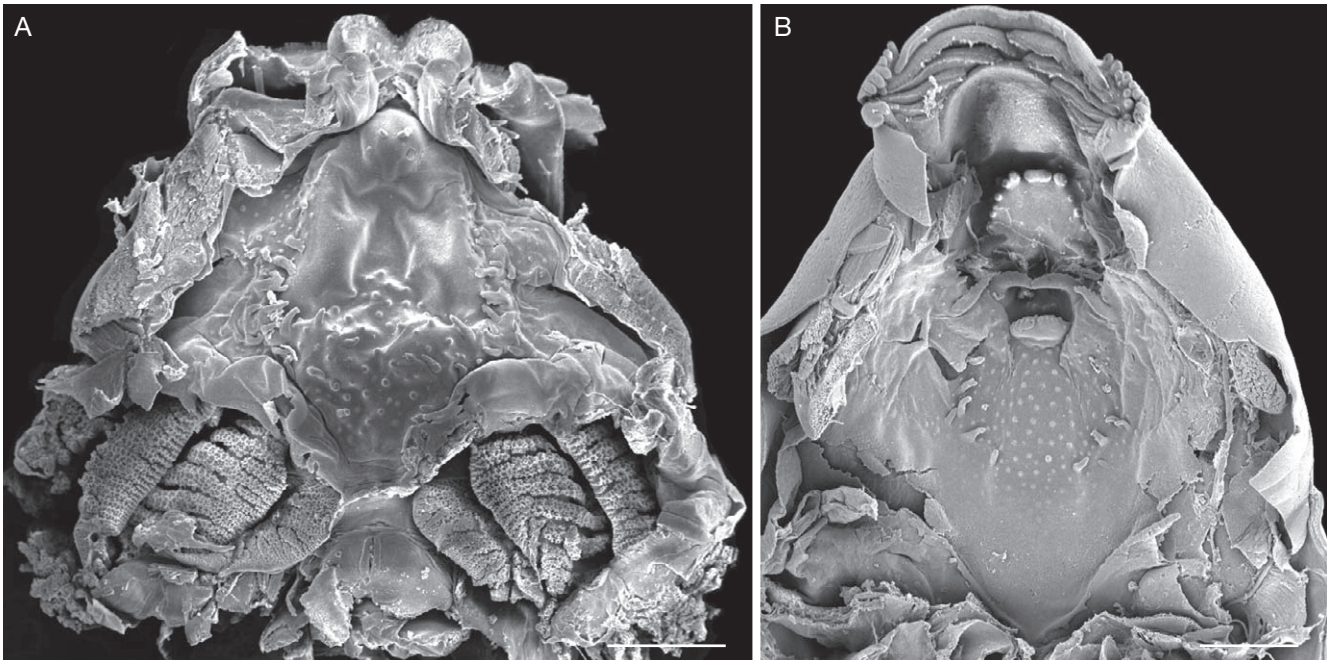

Fig. 6. — *Rhacophorus rhodopus* Liu & Hu, 1960 (MNHN 2010.1107, stage 37): **A**, buccal floor; **B**, buccal roor. Scale bars: 1 mm.

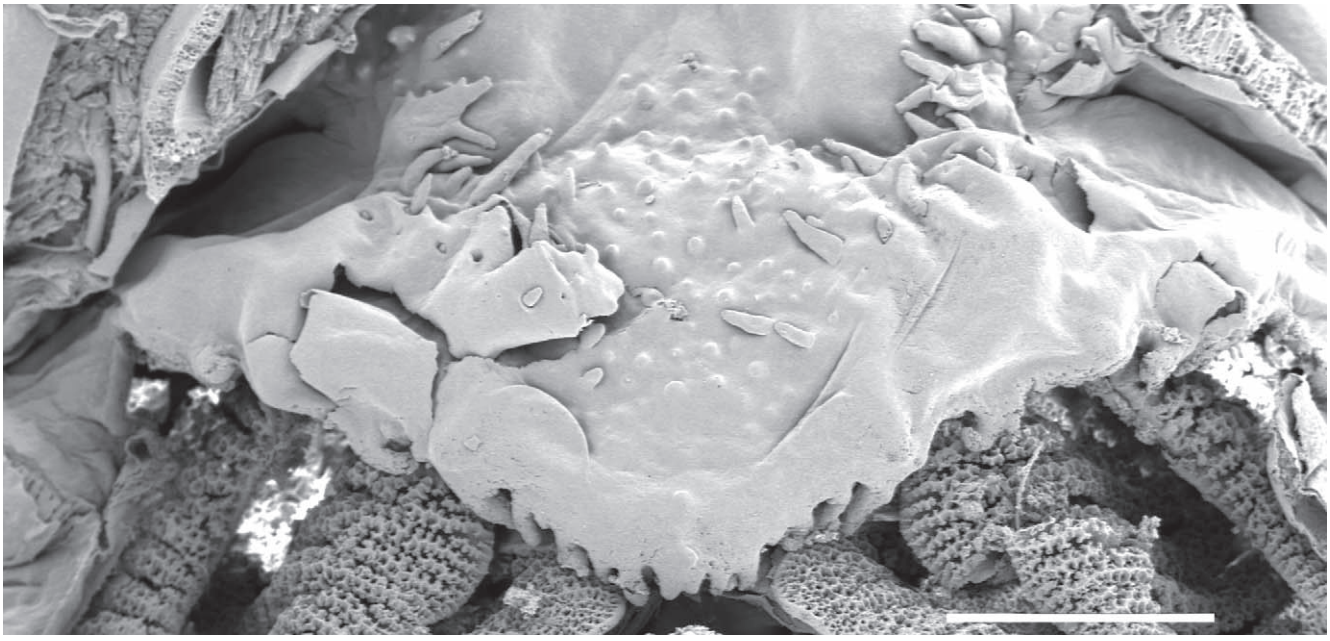

Fig. 7. — Ventral velum of *Rhacophorus rhodopus* Liu & Hu, 1960 (MNHN 2010.1123, stage 36) showing the 18 projections. Scale bar: 1 mm.

arena papillae on each side, oriented anteromedially; interior of arena occupied by about 100 pustules regularly arranged. Posterolateral ridges present laterally, a small bunch of 2-4 papillae at each extremity. Glandular zone wide with more than 10 secretory pits laterally, finer medially; size of secretory pits increasing anteroposteriorly. Dorsal velum pustular, not or very slightly interrupted in its medial part, its lateral parts curved forward.

DISCUSSION

A genus is a subjective grouping (but see Dubois 1988) of monophyletic, ecologically and morphologically similar species (Inger 1958; Ohler *et al.* 2015). This is the case for the adults within the genus *Rhacophorus*. The tadpoles of this genus should present a morphological and ecological uniformity too. This is the case for the great majority of species

except for the species in the subgenus *Leptomantis* Peters, 1867 whose tadpoles are adapted to running water and for the recently described species *R. vampyrus* Rowley, Le, Thi, Stuart & Hoang, 2010, which has a tree-hole dwelling larva with an oophagous feeding mode and that is highly derived from the typical *Rhacophorus* tadpoles (Rowley *et al.* 2012; Vassilieva *et al.* 2013). The larval forms of all the other species of *Rhacophorus* share the following characters: tadpoles of lentic benthic morphotype with an ovoid body, dorsolateral eyes, a sinistral spiracle attached to body wall, a moderately muscled tail with moderately elevated fins, an anteroventrally emarginated oral disc with a row of marginal papillae largely interrupted medially on the upper labium and a complete row of marginal papillae and a row of submarginal papillae shortly interrupted medially or not on the lower labium, and a KRF 1-2:(3+3)-(6+6)/3 or 1-2:(3+3)-(6+6)/1+1:2.

The comparison of the tadpoles of *R. kio* and *R. rhodopus* is particularly relevant as they are frequently found in syntopy and even in the same water body, and closely related phylogenetically. Differences are tiny and the most obvious character for discrimination is the coloration which is yellow in *R. kio* but brownish in *R. rhodopus*. *Rhacophorus kio* is slightly larger than *R. rhodopus* and has a higher and wider caudal muscle (resulting in broader *dorsalis trunci* muscles onto body) and a higher tail relative to body height, relatively larger and more laterally directed eyes, and a larger oral disc with less developed lower labium. The KRF of *R. kio* displays a large amplitude of variation which encompasses the KRF of *R. rhodopus*. However the presence of five interrupted keratodont rows on the upper labium seems to be occasional in *R. kio* (observed only in stage 40) whereas the KRF of *R. rhodopus* varies only slightly and its first keratodont row of the lower labium (P1) is always interrupted (at least in our sample). To our knowledge the tadpole of *R. kio* has never been reported. The tadpole of *R. rhodopus* has been briefly described: Yang (1991) and Fei (1999) gave a KRF 1:(4+4)-(5+5)/1+1:2 for Chinese specimens. Later Fei *et al.* (2009, 2012) provided a drawing of the oral disc and a lateral view of a tadpole as well as measurements and a KRF array which closely fitted our data. Inger *et al.* (1999) gave the same KRF, reported a continuous papilla row on the lower labium, BL 16.7-18.3 mm and TL 45.4-55.4 mm (stages 31-40) for tadpoles from southern Annam, Vietnam as *R. bipunctatus*. In our sample the tadpoles are smaller with a proportionally larger body length (BL 15.1-19.7 mm, TL 37.1-51.9 mm, stages 30-37). Inthara *et al.* (2005) provided a drawing of the oral disc for specimens from Loei and Kanchanaburi Provinces, western and northeastern Thailand (as *R. bipunctatus*), with a double papilla row (the submarginal row being not interrupted medially contrary to our sample) and three continuous rows of keratodonts on the lower labium. It is important to note that two divergent populations of *R. rhodopus* have been reported, one from Yunnan and Xizang, and the other one from Vietnam and Hainan (Yu *et al.* 2007; Li *et al.* 2012). The latter probably represent a new taxon.

In a concern of clarification and as a basis for further taxonomical works, Dubois (1987) proposed 10 species groups within the genus *Rhacophorus* including the genus *Polypedates* (*R. leucomystax* group) and some representatives of the genus *Kurixalus* Ye, Fei & Dubois, 1999 (in the *R. appendiculatus* group) but excluding species of the subgenus *Leptomantis*. The tadpoles of the two species described in this paper belong to the *Rhacophorus* (*Rhacophorus*) *reinwardtii* species group, along with *R. bipunctatus*; *R. borneensis* Matsui, Shimada & Sudin, 2013; *R. dulitensis* Boulenger, 1892; *R. georgii* Roux, 1904; *R. helenae* Rowley, Tran, Hoang & Le, 2012; *R. laoshan* Mo, Jiang, Xie & Ohler, 2008; *R. maximus* Günther, 1859; *R. nigropalmatus* Boulenger, 1895; *R. norhayatii* Chan & Grismer, 2010; *R. prominatus* Smith, 1924; *R. reinwardtii*; and *R. suffry* Bordoloi, Bortamuli & Ohler, 2007. Two decades later several molecular works challenged the Dubois' groups (Grosjean *et al.* 2008; Yu *et al.* 2008, 2009; Wiens *et al.* 2009; Pyron & Wiens 2011; Hertwig *et al.* 2012, 2013; Li *et al.* 2012; Abraham *et al.* 2013; Nguyen *et al.* 2014). Although most of the species originally included in the *reinwardti*-group are recovered as monophyletic some changes in its composition occurred: *Rhacophorus dulitensis* and *R. maximus* are systematically found outside the clade grouping *R. kio*, *R. rhodopus*, *R. bipunctatus*, *R. reinwardtii* and *R. nigropalmatus* (Grosjean *et al.* 2008; Yu *et al.* 2008, 2009; Wiens *et al.* 2009; Pyron & Wiens 2011; Haas *et al.* 2012; Hertwig *et al.* 2012, 2013; Li *et al.* 2012; Nguyen *et al.* 2014). On the other hand, a bunch of species is recovered in the clade encompassing the species of the *reinwardtii*-species group: *R. annamensis* Smith, 1924; *R. baluensis* Inger, 1954; *R. calcaneus* Smith, 1924; *R. lateralis* Boulenger, 1883; *R. malabaricus* Jerdon, 1870; *R. orlovi* Ziegler & Köhler, 2001; and *R. pardalis* Günther, 1858 (Grosjean *et al.* 2008; Wiens *et al.* 2009; Pyron & Wiens 2011; Hertwig *et al.* 2012, 2013; Abraham *et al.* 2013). If we consider these latter species being included in the *reinwardtii*-species group then *R. exechopygus* Inger, Orlov & Darevsky, 1999; *R. translineatus* Wu, 1977; and *R. verrucopus* Huang, 1983 should be included too (Li *et al.* 2012; Abraham *et al.* 2013; Nguyen *et al.* 2014). The new genus erected for *R. translineatus*, *Huangixalus* Fei, Ye & Jiang, 2012, based on a new type of development, is thus a subjective synonym of *Rhacophorus* sensu stricto as it is in the *Rhacophorus reinwardtii*-species group. A recent molecular phylogeny of mostly Vietnamese species of *Rhacophorus* (Nguyen *et al.* 2014) proposes a different species group composition. However this result is based only on 434 bp long sequences of the mitochondrial 16S rRNA gene whereas all other molecular phylogenies (quoted above) are all based on several mitochondrial and nuclear genes and are all congruent. We have then chosen to retain the species group composition given by these robust phylogenetic hypotheses. However despite that much of the internal (and suprageneric) nodes are not statistically supported in the tree of Nguyen *et al.* (2014), the sister group relationship between *R. annamensis* and *R. exechopygus* is strongly supported corroborating the results of Abraham *et al.* (2013).

Of these 22 species of the *R. reinwardtii*-species group as newly defined by molecular phylogenies, the larval forms of 13 species are known and more or less accurately described

(Table 4). The accounts provided by Inger (1966, 1985) under the heading *R. dulitensis* most probably belong to *R. reinwardtii* (Haas *et al.* 2012). However, the results of Matsui *et al.* (2013) suggest than only one species of parachuting frog is present in Borneo, *R. borneensis*. We then assign the characteristics of the tadpole *R. dulitensis* described by Inger to the latter species.

Among these 13 species only the larval stages of *R. annamensis*, *R. georgii*, *R. helenae*, *R. orlovi* and *R. prominatus* are fully described and can be compared with the tadpoles of *R. kio* and *R. rhodopus*. Of these, only *R. annamensis*, *R. helenae* and *R. orlovi* can be found in sympatry with *R. kio* and/or *R. rhodopus*. The tadpole of *R. kio* can be distinguished from that of *R. annamensis* by its bigger size (44.9-52.3 mm vs 39.4-41.7 mm in stage 41, respectively), its coloration (yellow in *R. kio* and dark in *R. annamensis*), its KRF (five upper keratodonts rows in *R. kio* vs seven in *R. annamensis*) and more finely by the place of nares on the snout and of spiracle opening along the body axis, and by a stronger caudal muscle in *R. kio*. The tadpole of *R. rhodopus* can be distinguished from that of *R. annamensis* by its bigger size (43.2-51.9 mm in stage 37 vs 39.4-41.7 mm in stage 41, respectively), its KRF (six upper keratodont rows in *R. rhodopus* vs seven in *R. annamensis*, always one uninterrupted keratodont row in *R. rhodopus* vs two in *R. annamensis*) and more finely by the place of nares on the snout and of spiracle opening along the body axis. The tadpole of *R. helenae*, which is the sister species of *R. kio* (Matsui *et al.* 2013; Vassilieva *et al.* in press), shows only slight variation with the latter. The tadpole of *R. helenae* is smaller than the one of *R. kio* or in the lower limit of its size range at equivalent stage, their KRF are similar, as well as their global coloration in preservative that is yellowish. The eyes are bigger in *R. helenae* (11% of BL vs 8.3% in *R. kio*), the nares closer to snout in *R. kio* (although the ranges of the two species are overlapping: 63-93% in *R. helenae* vs 50-76% in *R. kio*), and the spiracle situated in the anterior half of the body in *R. kio* (SS 42-47% BL) but in the posterior part in *R. helenae* (SS 64-69% BL). However in the light of the data available the two species have an allopatric distribution. The differences are more marked between the tadpoles of *R. helenae* and *R. rhodopus* (which can be found in sympatry): the tadpole of *R. rhodopus* is bigger than that of *R. helenae* at equivalent stage without overlap, it often possesses six keratodont rows on the upper labium (vs five in *R. helenae*) and P1 is always divided (vs undivided in *R. helenae*), and it is brownish in preservative (vs yellowish in *R. helenae*). Variations relative to the eye size, and nares and spiracle position are the same that those of *R. kio* relative to *R. helenae*. The tadpole of *R. kio* can be distinguished from that of *R. orlovi* by its bigger size (44.1-48.3 mm vs 24.5 mm in stage 40, respectively), relatively smaller eyes and its coloration (yellow in *R. kio* and grey in *R. orlovi*). The tadpole of *R. rhodopus* can be distinguished from that of *R. orlovi* by its bigger size (43.2-51.9 mm in stage 37 vs 24.5 mm in stage 41, respectively), relatively smaller eyes and its KRF (six upper keratodont rows in *R. rhodopus* vs five in *R. annamensis*).

The known larval forms of the species included in the *reinwardtii*-species group are clearly homogeneous and differ especially by the maximum number of keratodont rows on the upper labium, the presence or not of a gap in the first row of the lower labium (P1, although the two conditions can exist within a single species), the size and the coloration (Table 4). A double row of papillae is a constant in the tadpoles of these species, except for *R. georgii*. However this latter species has not been included in molecular works to test its phylogenetic affinity with the *reinwardtii*-species group.

Additional 23 *Rhacophorus* species belonging to other species groups can be found sympatrically with *R. kio* and *R. rhodopus*: *R. burmanus* (Andersson, 1939); *R. dennysi* Blanford, 1881; *R. dorsoviridis* Bourret, 1937; *R. duboisi* Ohler, Marquis, Swan & Grosjean, 2000; *R. dugritei* (David, 1872); *R. feae* Boulenger, 1893; *R. hoanglienensis* Orlov, Lathrop, Murphy & Ho, 2001; *R. jarujini* Matsui & Panha, 2006; *R. larissae* Ostroshabov, Orlov & Nguyen, 2013; *R. leucofasciatus* Lui & Hu, 1962; *R. maximus* Günther, 1858; *R. minimus* Rao, Wilkinson & Liu, 2006; *R. nigropunctatus* Liu, Hu & Yang, 1962; *R. omeimontis* (Stejneger, 1924); *R. puerensis* (He, 1999); *R. robertingeri* Orlov, Poyarkov, Vassilieva, Ananjeva, Nguyen, Sang & Geissler, 2012; *R. spelaeus* Orlov, Gnophanxay, Phimminith & Phomphoumy, 2010; *R. tuberculatus* (Anderson, 1871); *R. turpes* Smith, 1940; *R. vampyrus*; *R. viridimaculatus* Ostroshabov, Orlov & Nguyen, 2013; *R. yaoshanensis* Liu & Hu, 1962; and *R. yinggelingensis* Chou, Lau & Chan, 2007. Of these the larval forms of the following species have been at least partially described: *R. dennysi* (Pope 1931; Liu & Hu 1961), *R. dugritei* (Liu & Hu 1961; Fei *et al.* 2012), *R. jarujini* (Stuart *et al.* 2006), *R. maximus* (Wildenhues *et al.* 2010), *R. minimus* (Rao *et al.* 2006), *R. nigropunctatus* (Fei *et al.* 2012), *R. omeimontis* (Liu & Hu 1961), *R. vampyrus* (Rowley *et al.* 2012; Vassilieva *et al.* 2013). The tadpole of *R. burmanus* differs from the tadpole of *R. kio* in having one keratodont row more on the upper labium (Fei *et al.* 2009 as *R. gongshanensis*). The tadpole of *R. dennysi* bears one keratodont row less than *R. rhodopus* on the upper lip. The tadpoles of *R. dugritei* and *R. nigropunctatus* differ from both *R. kio* and *R. rhodopus* in having a smaller KRF (1:3+3/1+1:2) and a clear papilla gap on the lower labium. The tadpole of *R. jarujini* differs from *R. kio* and *R. rhodopus* mainly by its particular coloration pattern (tail covered by big black spot with its posterior three-fourths bright red) and by the absence of gap in the submarginal papilla row of the lower labium; this species possesses a keratodont row less than *R. kio* on the upper labium. The tadpole of *R. maximus* and *R. minimus* differ from the ones of *R. kio* and *R. rhodopus* mostly by their smaller size and by the presence of a small median gap in the papilla row of the lower labium, and specifically from *R. rhodopus* by their KRF (1:4+4/1+1:2, i.e. in having one keratodont row less on the upper labium). Furthermore the tadpole of *R. minimus* differs from the one of *R. kio* by its black coloration. The tadpole of *R. omeimontis* differs from *R. kio* in having one keratodont row more on the upper labium and from both species in having a gap in the papilla row on the lower labium (Liu & Hu 1961; Fei *et al.* 2012).

TABLE 4. — List of tadpoles of the *Rhacophorus reinwardtii*-species group as defined by recent phylogenetic results including some morphological characteristics and references for the known tadpoles. Note that only final stages of KRF are reported in this table to avoid providing entire ontogenetic series of the KRF (as provided in certain descriptions) which is not the scope of this paper and which can hamper the comparisons.

Species	KRF	Papilla row on lower labium	Maximum known total length	References
R. annamensis Smith, 1924	2:5+5/3	Double uninterrupted	43.3 mm (stage 41)	Hendrix *et al.* 2007
R. baluensis Inger, 1954	1:6+6/1+1:2	?	75 mm (maximum size)	Malkmus *et al.* 2002; Inger & Stuebing 2005
R. bipunctatus Matsui, Shimada & Sudin, 2013	1:5+5/3 1:5+5/1+1:2	?	?	Fei 1999 Fei *et al.* 2009
R. borneensis Matsui, Shimada & Sudin, 2013	1:(4+4)-(5+5)/1+1:2	Double uninterrupted	42.7 mm (stage 35)	Inger 1966, 1985 (as *R. dulitensis*, see discussion)
R. calcaneus Smith, 1924	?	?	?	Tadpole unknown
R. exechopygus Inger, Orlov & Darevsky, 1999	?	?	?	Tadpole unknown
R. georgii Roux, 1904	1:4+4/1+1:2	Single uninterrupted	41.2 mm (stage 35)	Gillespie *et al.* 2007
R. helenae Rowley, Tran, Hoang & Le, 2012	1:4+4/3	Double only the submarginal row interrupted	36.6-43.6 mm (stages 35-39)	Vassilieva *et al. in press*
R. kio Ohler & Delorme, 2006	1:(3+3)-(4+4)/3; 1:(3+3)-(5+5)/1+1:2; 2:3+3/1+1:2	Double only the submarginal row interrupted	58.9 (stage 36)	This paper
R. laoshan Mo, Jiang, Xie & Ohler, 2008	?	?	?	Tadpole unknown
R. lateralis Boulenger, 1883	2:(4+4)/1+1:2	Double interrupted	31.9 mm (stage 40)	Prudhvi Raj unpublished data
R. malabaricus Jerdon, 1870	2:(4+4)-(6+6)/1+1:2 2:(4+4)-(6+6)/3	Double uninterrupted row	41.0 mm (hindlimb stage)	Ferguson 1904; Sekar 1990; Prudhvi Raj unpublished data
R. nigropalmatus Boulenger, 1895	1:(3+3)-(5+5)/1+1:2 2:4-4/1+1:2	Double interrupted or uninterrupted	39.0 mm (stage 36) 43.0-50.0 mm (stage 40)	Inger 1966, 1985
R. norhayatii Chan & Grismer, 2010	1:(5+5)-(6+6)/1+1:1-2 (5-5)-(6-6)/1+1:2	Double uninterrupted	?	Berry 1972 (as *R. nigropalmatus*)
R. orlovi Ziegler & Köhler, 2001	1:(3+3)/1+1:2	Double only the submarginal row interrupted	24.5 mm (stage 40)	Wildenhues *et al.* 2011
R. pardalis Günther, 1858 from Borneo	2:5+5/3	Double uninterrupted row	43.2 mm (stage 37)	Inger 1966
R. prominanus Smith, 1924	1:(5+5)-(6+6)/3	Double uninterrupted	30 mm (maximum size)	Berry 1972; Manthey & Grossmann 1997; Leong 2004 (under *R. tunkui* Kiew, 1987)
R. reinwardtii (Schlegel, 1840)	1:5+5/3	?	?	Iskandar 1998
R. suffry Bordoloi, Bortamuli & Ohler, 2007	?	?	?	Tadpole unknown
R. rhodopus Liu & Hu, 1960	1:(4+4)-(5+5)/1+1:2	Double only the submarginal row interrupted	51.9 mm (stage 37)	This paper
R. translineatus Wu, 1977	1:5+5/1+1:2	?	48.4 mm (stage 43)	Fei *et al.* 2009
R. verrucopus Huang, 1983	?	?	?	Tadpole unknown

The tadpole of *R. vampyrus* is easily distinguishable from any other *Rhacophorus* tadpole by its very derivate morphology, in particular its oral disc with modified labia without keratodonts, with hook-shaped serrations borne by the upper beak and two large hooks on the lower labium (Rowley *et al.* 2012; Vassilieva *et al.* 2013).

However all these data are given for information only because the larval stages of numerous species are yet not known and additional characters will be needed to fully discriminate the tadpoles of *R. kio* and *R. rhodopus* from all other sympatric species. In such speciose genera with morphologically similar species accurate descriptions are needed (such as in Haas *et al.* 2012) including colour and coloration pattern. Furthermore, these descriptions should be based on molecularly determined specimens (DNA barcoding) to avoid publication of misidentified tadpole descriptions. Then several works are hardly usable because of misidentification (e.g., Inger 1966) or because of mixing of species (e.g., the genus *Rhacophorus in* Bourret 1942). So another challenge is to clearly delimit species boundaries to avoid reporting exaggerated intraspecific variation due to mixing of specimens belonging to close species.

Larval stages of the other species group do not differ in general KRF nor in arrangement of papilla rows and no clear characters allow to diagnose them.

The systematics of the Rhacophoridae is not yet stable as showed by the recent erection of new genera (Delorme *et al.* 2005; Frost *et al.* 2006; Biju *et al.* 2008, 2010; Li *et al.* 2008; Meegaskumbura *et al.* 2010; Fei *et al.* 2012; Abraham *et al.* 2013). In the Rhacophoridae, in which the adults could be largely similar (e.g., *Rhacophorus* and *Polypedates*), the knowledge of the larvae and of the reproductive modes could be of great help in defining and delimiting the genera boundaries.

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