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Reproductive behaviour of *Polypedates taeniatus* (Boulenger 1906) (Anura: Rhacophoridae)

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ABSTRACT. We studied the breeding and nesting behaviour of the endemic terai tree frog, *Polypedates taeniatus* in Uttar Pradesh state of India. We describe amplexus, spawning, unique ground nesting behaviour, and larval developmental stages of the species. Comparative reproductive behaviour of foam-nesting rhacophorids from India is also provided. The present study emphasises the conservation of this obligate grassland species in the Terai Arc Landscape.

KEYWORDS. Rhacophoridae, breeding behaviour, grassland, endemic.

Introduction

Over 40 different reproductive modes are known among the anurans (Gururaja et al. 2014; Seshadri et al. 2014; Meegaskumbura et al. 2015). The family Rhacophoridae exhibits the most diverse reproductive modes in both aquatic and terrestrial habitats (Bahir et al. 2005; Iskandar et al. 2014; Seshadri et al. 2014; Meegaskumbura et al. 2015; Biju et al. 2016; Khongwir et al. 2016). Terrestrial breeding rhacophorids deposit their eggs in a gelatinous matrix (*Beddomixalus, Feihyla, Gracixalus, Kurixalus, Mercurana, Nasutixalus, Nyctixalus* and *Theloderma*), a foam nest above or near water bodies (*Polypedates*, *Rhacophorus, Chiromantis* and *Chirixalus*), or in a bubble nest (*Rohanixalus*) (Meegaskumbura et al. 2015; Biju et al. 2016; Biju et al. 2020). Other terrestrial breeders (*Philautus*, *Pseudophilautus* and *Raorchestes*) undergo direct development with lecithotrophic larvae except for *Philautus macroscelis* (Hertwig et al. 2012, Meegaskumbura et al. 2015; Biju et al. 2016). Foam nesting rhacophorids construct their nests on a variety of substrates such as under vegetation, on the ground, or on branches or leaves hanging over standing water where free swimming and ectotrophic tadpoles undergo development (Biswas 2000; Deuti 2001; Biju 2009; Hooroo et al. 2017).

Foam nesting rhacophorids of the Himalayan terai region are represented by six species, viz, *Polypedates teraiensis*, *P. maculatus*, *P. taeniatus*, *P. zed, Chirixalus dudhwaensis*, and *Chirixalus simus*. The terai tree frog, *Polypedates taeniatus* was described from Purneah, Bihar, India (Boulenger 1906) and is currently restricted to the grasslands along the Ganga and Brahmaputra rivers in India and Nepal (Fig. 1). Despite several reports of the species from Nepal and India (Ray, 1991; Anders et al. 1998; Ahmed and Dutta 2000; Schleich and Kästle 2002; Hedge et al. 2009; Das et al. 2012; Deuti et al. 2018) very little is known about the ecology and reproductive biology of *Polypedates taeniatus*.

Material and Methods

Study area and data collection. During August 2018, we observed the breeding behaviour of *P. taeniatus* along the River Ganga at Bidurkuti (29.28301º N and 78.10165º E, elevation 208 m a.s.l.) of Bijnor district, Uttar Pradesh. The area is characterized by a large patch of *Typha angustifolia* with temporary water pools created by rain and river flooding. The vegetation of the

area is fragmented by a few roads connecting fringe villages.

We observed the breeding activity from 17 August to 22 August 2018 between 18:00 h and 01:00 h. We actively searched for calling males, a pair in amplexus or a female until it engaged in amplexus. All observations were made with red light or a dim torch from about 1 m distance. The duration of amplexus and foam nesting was recorded with a stopwatch. The perch height (distance from the ground to the height at which individuals were roosting or calling) of the individuals and the distance of the nests from the nearest waterbody was measured using a 5 m tape. After spawning, the body size (snout-vent length, SVL) of the amplectant pair and size (length, width and height) of the nest were taken in the natural habitat using a digital calliper (Mitutoyo®) to the nearest 0.1 mm. In addition to nocturnal surveys, we opportunistically searched for foam nests by thoroughly inspecting the ground under the vegetation during the day. We collected nests (n = 2) to determine the clutch size and egg size. Egg extraction from the foam nest follows Coe (1974). Collected nests were placed on the water surface in a glass jar; carefully shaking the nest until all the eggs separated from the foam and settled down at the bottom of the jar. After the complete dispersal of the foam, the fluid and water were poured out and the eggs were counted. The diameter of the eggs was taken within 24 h of foam nest construction using a digital calliper. We photographed and video-recorded the behavioural activities in the field and analysed them in the lab for additional data. We also collected tadpoles from temporary water puddles of the same habitat to study the developmental stages. Collected tadpoles were reared in a plastic tray (50 cm × 30 cm × 8 cm) in the laboratory. We provided rainwater with algae and debris from similar habitats (Chakravarty et al. 2011; Lalremsanga 2017). Tadpoles were preserved at different stages. Developmental stages were identified using Gosner (1960). Collected adults, eggs and tadpoles of *P. taeniatus* were fixed in 4% formalin, washed and finally stored in 70% ethanol. Specimens were housed in the repository of the Wildlife Institute of India, Dehradun. Microscopic observations of tadpoles were made under a stereo microscope (LEICA MZ 125) and measurements were obtained in ImageJ software.

Abbreviations used

SVL- snout-vent length (for adult individuals), IOS- inter-orbital space (minimum distance between upper eyelids), BL- body length, TL- tail length, MTH- maximum tail height, TMW- tail muscle width, TMH- tail muscle height, LTRF- labial tooth row formula. Tadpole morphometry follows Altig (2007), except for IOS.

Results

Calling activity and perch height of *Polypedates taeniatus*

Males started calling after 18:30 h. Initially, the males called from the ground and as time progresses, they gradually exposed themselves, calling from the perch above ground (Figure 2). The maximum perch height of the calling male was 126 cm above the ground (mean perch height= 23.24 ± 36.21 cm, n = 118). Calling intensity decreased after 22:00 h. Occasionally, a call could be heard in the early morning. The female perch height observed was 60–110 cm (88.33 ± 25.66 cm, n = 3).

Sexual dimorphism

During the present study, we found the body size (SVL) of the adult male of *P. taeniatus* to be smaller than that of the female. SVL of the male individuals varies between 35.8–40 mm (37.28 ± 1.48, n = 8) and SVL of the female individuals ranges between 42.4–44.1 (43.46 ± 0.92, n = 3).

Amplexus and nesting

We encountered six pairs in amplexus between 17 August to 22 August 2018. Our observation on breeding behaviour is based on four amplectant pairs (Table 1). Amplexus and nesting behaviour ensued in the following steps:

1. Females slowly moved on grass blades towards the calling male.
2. The female slowly descended to the ground at a distance of 110–140 cm from the calling male (n = 2).
3. The female carefully entered the grass (n = 2) or came to the same perch (n = 2) where the male is calling. The total distance travelled by the female to reach the mate was 160–610 cm (n = 3) within a

time range of 30–115 min (n = 3) (Table 1).

4. When the female approached very close, the male quickly mounted the female and engaged in axillary amplexus.
5. Amplexus occurred on the ground (n = 2) or above ground up to a height of 70 cm (48.33 ± 18.93 cm, n = 3). As soon as amplexus was initiated, the amplectant male stopped calling.
6. The amplectant pair remained in the same place where the male was calling (n = 2) or if amplexus occurred on grass blades then the amplectant pair descended to the ground after 5–15 min (n = 2) to find a suitable place to construct foam nest. The distance travelled by the amplectant pairs was 13–305 cm (n = 2).
7. After 28–125 min (n = 2) (Table 1) of amplexus, the pair started constructing a foam nest at the same place where the amplectant male was calling. Foam nests were constructed on the ground at the base of *Typha* or under the grass (Figure 4E). Before initiating foam nest construction, the female moved in a semi-circular way with the amplectant male for a few seconds. This is probably to clear the obstacles for foam nesting.
8. Then with the amplectant male, the female stood on the hind limbs grasping the surrounding grasses (Figure 4D).
9. The female initiated the foam nest construction by rubbing her hind limbs below the vent. The female moved her hind limbs 6–8 times (6.64 ± 2.09, n = 11) with an interval of 4–11 sec (6.44 ± 1.93 sec, n = 16). The male also showed similar hind limb movements and pelvic thrusts during spawning. But this behaviour was not as frequent as in the female. Initially, the male shook its hind limbs once, and later increased it to twice, and sometimes thrice. This movement is probably to spread the sperm for effective fertilization of the egg mass, as mentioned by Biswas (2000). This process continued until the construction of the foam nest was completed. The time taken to complete the foam nest was 29–57 min (n = 2) (Table 1).
10. After spawning, the amplectant male slowly moved out of the amplexus and left the place (n = 2).
11. The female stayed on the nest for 3 minutes (n = 1) or left the nest just after the male (n = 1).

In one case (20.08.2018) the amplectant pair dislodged after 25 min of coming to the ground and moved away from each other (Table 1). Within 15 min, the same male grasped another female which was at a distance of 110 cm and a perch height of 35 cm. We followed the pair up to 01:00 h but the pair didn't start foam nesting (Table 1).

Nest size and egg clutch

The foam nest was nearly rounded and cream-coloured (Figure 3E). The size of the foam nest was L = 48.64 ± 6.71 mm, W = 48.98 ± 7.51 mm, and H = 39.34 ± 7.21 mm (n = 6). The distance between the foam and the nearest water body was 47–410 cm (224.33 ± 124.9 cm, n = 6). The eggs numbered 220 and 308 in the two collected clutches. The eggs were round, unpigmented, and cream-coloured. The diameter of the egg was 1.35 ± 0.06 mm (n = 27).

Larval description

The hatchlings of *P. taeniatus* develop in temporary water pools created by rain or overflow from the river (Figure 3). Tadpoles were elliptical and elongated in shape. Tail long, muscular, and laterally compressed with a pointed tip (Figure 5A-C, E, H). Snout rounded in dorsal view and oval in lateral view. Eyes lateral. Nostril lateral, small, closer to the snout. Pineal ocellus not distinct. Single rectangular shaped spiracle ventro-laterally placed on the left side (Figure 6G). Tail fin broad; dorsal fin originated at the junction of body and tail; ventral fin originated from anterior of the vent tube. Vent tube dextral. Oral disc anteroventral. Marginal papilla with a wide gap on anterior labium and small gap at the middle of the posterior labium. Labial tooth row formula (LTRF) observed at Gosner stage 31 was 4(2-4)/3(1) (Figure 6H) and at Gosner stage 27 was 3(2-3)/3(1). Jaw sheaths serrated, upper jaw sheath arch shaped and lower jaw sheath "V" shaped. Marginal papillae, jaw sheath and labial tooth started degenerating at stage 41. Details of tadpole stages (Gosner 1960) of *P. tae-*

Table 1. Details of the breeding and foam nesting behaviour of *P. taeniatus*. (M-male, F- female, L- length, W- width, H- height, measurements are given in mm).

Date	Temp. (°C) / humidity (%)	Perch height		Dist. Between M and F	Amplexus start time	Foam nesting		M dislodge time	F leaving time	Nest size (L/W/H)	Dist. from water	Clutch size	SVL	
		F	M			Start time	Finished time						F	M
19 August 2018	29.2/96.0	1100	ground	2300	21:15 h	23:20 h	23:49 h	As soon as the nest was completed	00:04 h	43/49.5/35.4	1800	eggs eaten by maggots	44.1	36.6
21 August 2018	28.4/96.1	950	ground	1600	20:56 h	21:24 h	22:21 h	22:24 h	22:25 h	50.7/43.1/38.8	470	220	42.4	35.8
20 August 2018	27.3/98.0	-	400	-	21:15 h	Dis-lodged	-	-	-	-	-	-	-	-
20 August 2018	27.3/98.0	600	350	6100	21.55 h	Not com-menced	-	-	-	-	-	-	-	-

niatus observed in the present study are given in the Table 2.

Live colouration of the tadpole

Dorsal body and the muscular part of the tail is dark or light brown (Figure 7). Ventral and lateral parts of the body below the level of the eyes is creamy white, sometimes with dark brown patches. Eyes red with black rounded pupils. Lateral line present on body and tail. A faint mid-dorsal line may be visible. A lateral golden stripe runs up to the tail tip radiating at the middle of the body, broader at the base of tail. Fins of the tail transparent with dark brown irregular markings.

Discussion

Polypedates taeniatus is locally abundant in the study area (Bijnor, Uttar Pradesh), mostly restricted to the fragmented grasslands like *Typha angustifolia*, and *Saccharum spontaneum*. We also observed the species in crop fields, sugarcane cultivations, and marsh lands along the Ganga river, albeit rarely. Earlier, Hegde et al. (2009) reported the species from Ravali forest of Bijnor, Hastinapur forest, and Ram-Ganga river bank. Also, Boruah et al. (2018) recorded the species in the riverine vegetations along the River Ganga between Bijnor and Narora (Ramsar conservation site), Uttar Pradesh.

Earlier documentation of larval development of Indian foam nesting rhacophorids includes *P. teraiensis* (Chakravarty et al. 2011; Tamuly and Dey 2014), *P. maculatus* (Mishra and Dash, 1984; Mohanty-Hejmadi & Dutta 1988; Girish and Saidapur 1998), *P. megacephalus* (Tesia et al. 2017), *P. leucomystax* (Kiyasetuo and Khare 1986; Iangrai 2007), *R. malabaricus* (Sekar 1990), *Z. smaragdinus* (= *maximus*) (Khongwir et al. 2003), and *R. bipunctatus* (Iangrai, 2007). Although, development of *R. rhodopus* and *R. smaragdinus* (= *maximus*) is reported from Thailand (Grosjean and Inthara 2016) and Vietnam (Wildenhues et al. 2010), respectively. Postembryonic development of *P. taeniatus* is described by Deuti et al. (2018). (Table 3). However, Deuti et al. (2018) have not provided information on breeding behaviour of the species. In the present study, we provided information on amplexus, spawning, clutch size, and also live colouration of the tadpole. *Polypedates taeniatus* breeds for a short period between mid-July and end of August. The duration of amplexus (85–154 min), foam nesting (29–57 min) and clutch size (220–308) is nearly similar with that of congeneric species (Table 3). The diameter of the egg is smaller than that of other foam nesting rhacoph-

Table 2. Morphological measeurements (given in mm) and characteristics of *P. taeniatus* tadpole in different stages (Gosner 1960).

Gosner Stage	BL	TL	MTH	TMH	TMW	IOS	ED	Characteristics
27 (n = 1) (Figure 5A)	3.6	6	-	1.1	0.7	1.1	0.6	Hind limb bud length greater than half of its diameter. Melanophores spread along lateral side of the body, tail muscle and fins; dense on dorsal side of the head.
28 (n = 1) (Figure 5B)	4.3	8.4	1.85	1.2	1	1.3	0.7	Hind limb bud greater than its diameter. Melanophores denser than previous stage. On fins melanophore forms irregular lines.
31 (n = 3) (Figure 5C-D)	5.5 ± 26	10.6 ± 0.5	3.6 ± 0.1	1.6 ± 0.1	1.3 ± 0.05	1.7 ± 0.06	0.9 ± 0.06	Hind limb bud becomes spatula shaped. Toe development starts. Melanophore pigmentation more dispersed.
33 (n = 1) (Figure 5E-F)	6	11.8	3.7	2.1	1.5	1.9	1	Three toe nubs of 3rd, 4th and 5th toe develops. Melanophore spread on base of the hind limb.
35 (n = 3) (Figure 5G)	7.1 ± 0.2	14.1 ± 0.3	4.7 ± 0.1	2.6 ± 0.3	1.9 ± 0.06	2.2 ± 0.1	1.1 ± 0.06	Hind limb more elongated. 5 toe nubs well defined.
36 (n = 1) (Figure 5H)	6.6	12.4	4	2	1.7	1.9	1.1	3rd, 4th and 5th toe separated. Melanophores concentrated on distal part.
37 (n = 2) (Figure 5I)	7.9 ± 0.4	15.7 ± 0.04	4.4 ± 0.1	2.5 ± 0.1	2 ± 0.1	2.4 ± 0.2	1.3 ±0.01	Thigh, tibia and tarsus distinct; all toes separated and elongated. Webbing clearly visible. Melanophore pigmentations more prominent on gular and abdomen.
39 (n = 2) (Figure 5J)	8.3 ± 0.4	16.4 ± 0.5	4.8 ± 0.1	2.7 ± 0.08	2.3 ± 0.1	2.4 ± 0.3	1.3 ± 0.03	Inner metatarsal tubercle visible; subarticular tubercles appeared as clear round patch.
40 (n = 2) (Figure 6A)	8.4 ± 0.4	16.4 ± 0.8	4.5 ± 0.7	2.6 ± 0.05	2.2 ± 0.1	2.3 ± 0.1	1.4 ± 0.05	Subarticular tubercle, circum-marginal groove distinct with well-developed toes. Fold of skin present between thighs. Forelimb bulges slightly visible.
41 (n = 2) (Figure 6B)	8.3 ± 0.02	17.4 ± 0.8	4.1 ± 0.2	2.5 ± 0.05	2.3 ± 0.01	2.2 ± 0.01	1.4 ± 0.04	Cloacal tail piece disappeared. Forelimb bulges clearly visible.
42 (n = 3) (Figure 6C-D)	8.6 ± 0.3	17.3 ± 0.8	3 ± 1.1	2.5 ± 0.4	2.2 ± 0.2	2 ± 0.05	1.5 ± 0.04	Forelimb emerges with well-developed fingers; left forelimb emerges first. Granules on thigh and posterior part of the abdomen prominent.
43 (n = 2) (Figure 6E-F)	8.9 ± 0.3	14 ± 2.8	2.2 ± 0.9	2 ± 0.05	2.3 ± 0.1	1.8 ± 0.1	1.4 ± 0.2	Lateral margin of the mouth reaches between nostril and eye. Tail and fins reduced.

Table 3. A comparative chart of foam nesting and breeding behaviour in Rhacophorids of India.

Species Name	Duration of Amplexus (min)	Duration of Foam Nesting (min)	Size of Nest (L/W/H) (mm)	Substratum	Clutch Size	Diameter of Egg (mm)	Locality	Reference
Chirixalus simus **(Annandale 1915)**	-	-	52–73/19–36/16–28	On grass, 6–58 cm above water, 17–89 cm above land	153–234	-	West Bengal	Deuti (2001)
Chirixalus dudhwaensis **(Ray 1992)**	-	-	30–67/27–55/13–17	On leaves 0.6–1.8 m above water	201–231	-	WII, Uttarakhand	Biswas (2000)
Rhacophorus bipunctatus **Ahl 1927**	-	-	60–80 (diameter)	On grass near water, tree branches overhanging water	45–76	3	Meghalaya	Iangrai (2007)
Zhangixalus smaragdinus **(= *maximus*) (Blyth 1852)**	-	-	155–205 (L)	On vegetation 2–3 cm above water, earthen bank, Rock 30 cm above water	809–2059	2	Cherrapunjee, Meghalaya	Khongwir et al. (2016)
Rhacophorus malabaricus **Jerdon 1870**	120–180	15–20	-	Overhanging branches, on ground with leaf litter	160–192	2.62 (n=10)	Western Ghats	Kadadevaru and Kanamadi (2000)
Rhacophorus lateralis **Boulenger 1883**	35–50	17–29	53–80 (L), 28–64 (diameter)	Single leaf	43–72	-	Western Ghats	Biju (2009)
Polypedates leucomystax **(Gravenhorst 1829)**	-		60–120 (diameter)	Vegetation along pond or on concrete 5–40 cm above water	250–530	1.5	Meghalaya	Iangrai (2007)
Polypedates leucomystax **(Gravenhorst 1829)**	270	60	58–63/58–61/65–80	On Branch 5.6 ft above water	-	-	Meghalaya	Banerjee and Deuti (2006)
Polypedates maculatus **(Gray 1830)**	150	-	-	Concrete above water	210–448	-	South India (locality not specified)	Girish and Saidapur (1999)
Polypedates himalayensis **(Annandale 1912)**	-	-	-	Earthen hole, under moist vegetation		-	Meghalaya	Hooroo et al., (2017)
Polypedates megacephalus **Hallowell 1861**	-	-	-	Vegetation and twigs overhanging water	500–600	2.1–2.9	Arunachal Pradesh	Tesia et al., (2017)
Polypedates taeniatus **(Bpoulenger 1906)**	85–154	29–57	39.6–58.3/37.2–57.3/27.2–44.7	On ground; under grass or base of Typha	220–308	1.2– 1.4 (N= 27)	Uttar Pradesh	Present Study

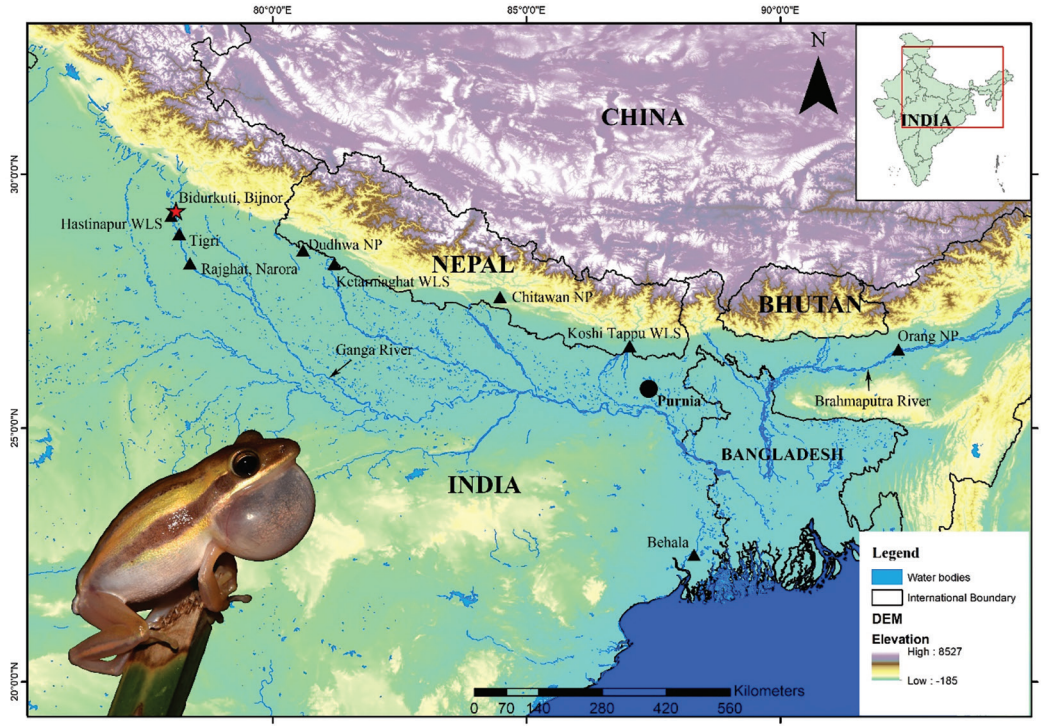

Figure 1. Distribution of *P. taeniatus* in India and Nepal. Recorded locality of *P. taeniatus* based on available literature (black triangle), type locality (black circle), study site (red star).

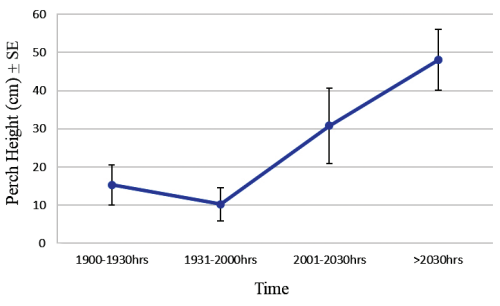

Figure 2. Perch height of the male individuals (*P. taeniatus*) with respect to time, N = 145.

Figure 3. A typical breeding habitat of *Polypedates taeniatus*. Scale bar = ~ 1 m. and Das 03.tif

orids (Table 3). Size of the foam nest found in the present study was smaller than that observed by Deuti et al. (2018); i.e. 60 mm × 60 mm. Like in other rhacophorid frogs (*C. dudhwaensis, R. malabaricus*, *R. lateralis*, *C simus*, *Z. smaragdinus* (= *maximus*)), (Biswas 2000; Kadadevaru and Kanamadi 2000; Biju 2009; Banerjee 2010, 2014; Khongwir et al. 2016), we did not find any satellite male disturbing the amplectant pair. The reproductive mode of *P. taeniatus* belongs to the type 28 (i.e. foam nest on ground and after flooding, exotrophic tadpoles develop in standing water body) as delineated by Haddad and Prado (2005). During the study period, foam nests of *P. taeniatus* were found at a distance of 47–410 cm from the nearest water puddle. Another congeneric species from Northeast India, *P. himalayensis*, is known to construct the foam nest inside earthen holes or under vegetation, 50–100 cm away from waterbodies (Hooroo et al. 2017). This could be to minimize the predation risk from aquatic predators. Moreover, the possible reasons for avoiding arboreal foam nesting could be: (1) to prevent the desiccation of the egg mass from sunlight as desiccation is the main threat to larval development in tropical

Figure 4. Breeding behaviour of *Polypedates taeniatus*. A. calling male on its perch, B. an amplectant pair in arboreal habitat, C. an amplectant pair on the ground, D. foam nesting on the ground, E. a completed nest, F. male and female after leaving the nest.

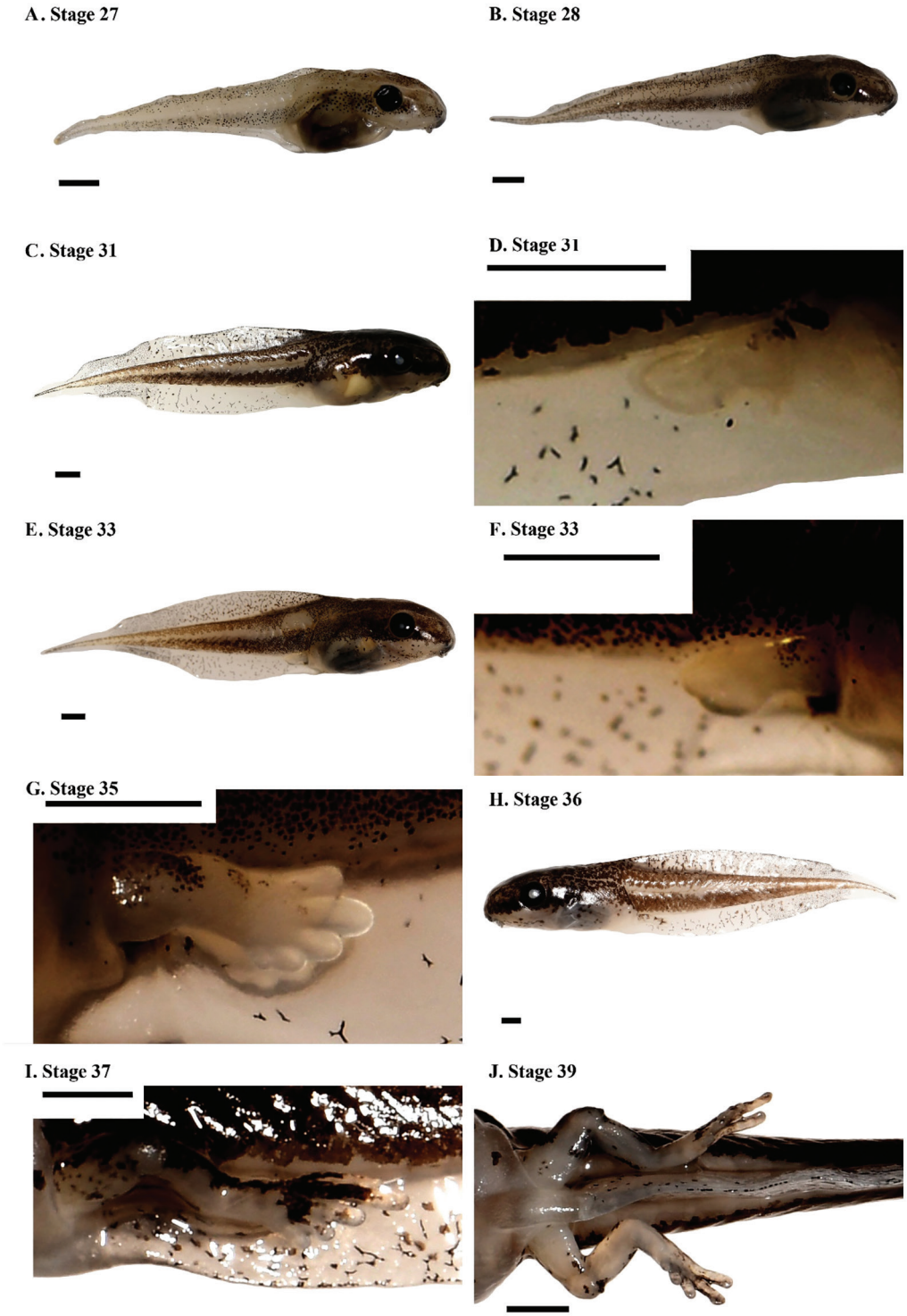

Figure 5. Gosner stages of P. taeniatus. A- stage 27, B- stage 28, C-D- stage 31, E-F- stage 33, G- stage 35, H- stage 36, I- stage 37, J- stage 39. (Scale- 1 mm).

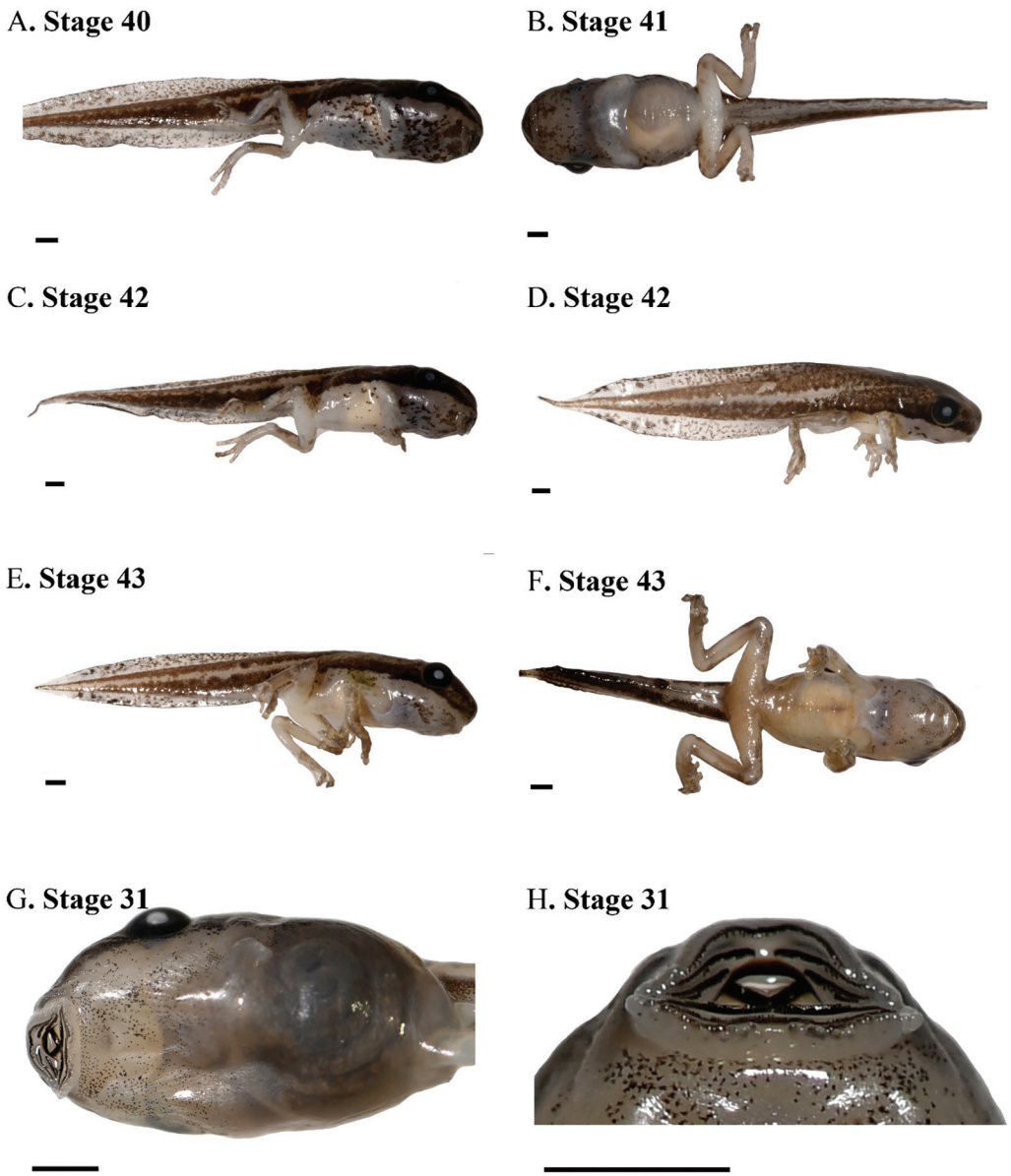

Figure 6. Gosner stages of *P. taeniatus*. A- stage 40, B- stage 41, C-D- stage 42, E-F- stage 43, G- stage 31 showing spiracle, H- stage 31 showing LTRF. (Scale- 1 mm).

region (Mohanty-Hejmadi and Dutta 1988), (2) dependency on overflow water of the river rather than rain for larval development.

The external morphology of the tadpole of *P. taeniatus* is similar to that of the congeneric species from India. The LTRF of *P. taeniatus* is similar to that of *P. teraiensis* [4(2-4)/3(1)]. Additionally, there is no interruptions in the first tooth row in the posterior papilla (i.e., 4(2-4)/3) as seen in *P. maculatus* (Mohanty-Hejmadi & Dutta 1988) and *P. himalayensis* (Gogoi and Sengupta 2017). The LTRF of *R. malabaricus, Z. smaragdinus* (= *maximus*) and *P. megacephalus* is 5(2-5)/3(1) (Sekar 1990; Wildenhues et al. 2010; Tesia et al. 2017). The LTRF of *R. rhodopus* is 6(2-6)/3(1) (Grosjean and Inthara 2016). The tadpole of *P. teraiensis* does not have the lateral line which is present in the tadpoles of *P. taeniatus* and *R. rhodopus*.

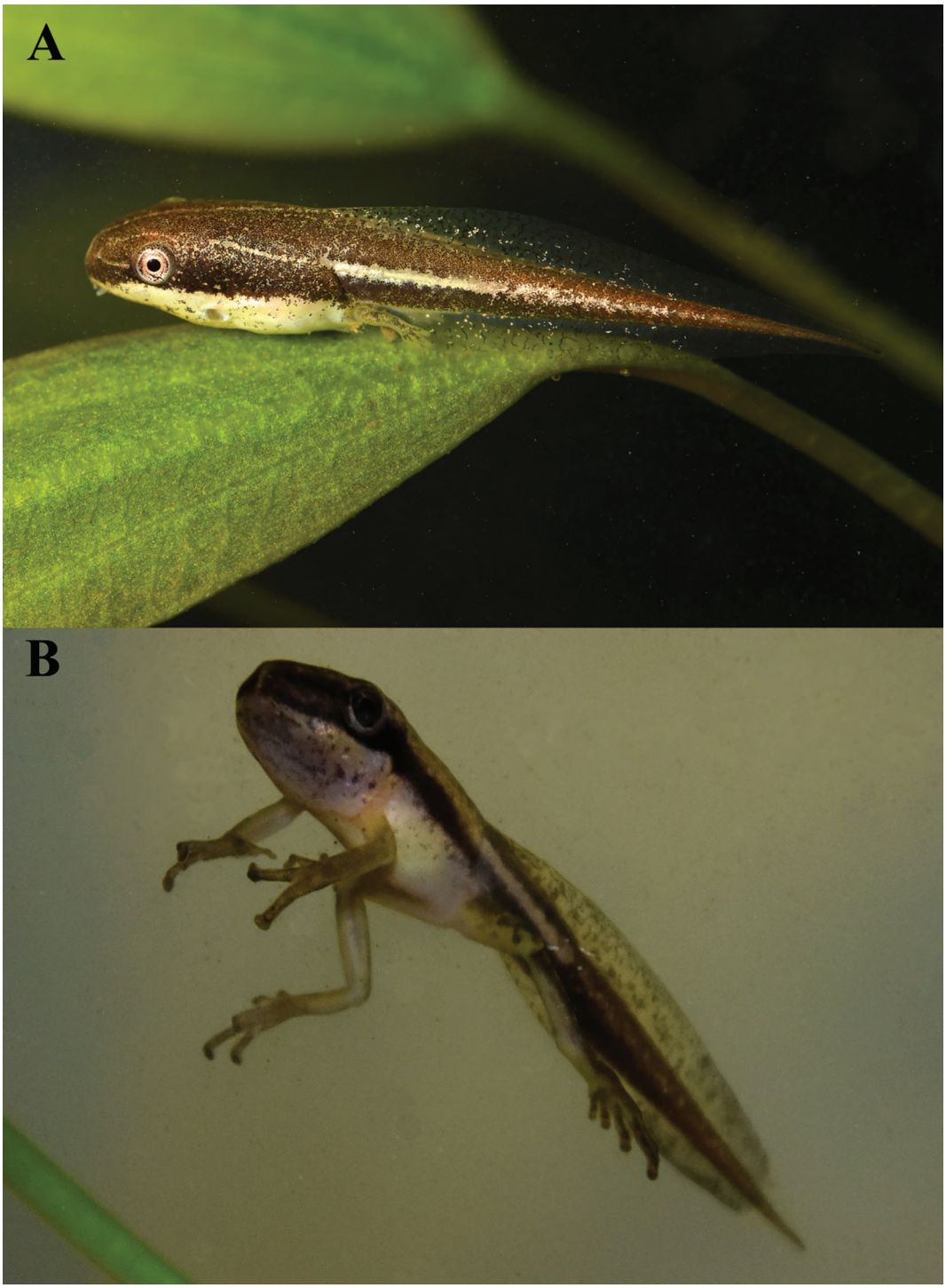

Figure 7. Tadpole of *P. taeniatus* in life. A. stage- 37, B. stage- 43.

Polypedates taeniatus appears to have the narrowest distribution range at an elevation below 500m a.s.l., inhabiting the fragmented grassland and *Typha* patches of the Gangetic and Brahmaputra plains. Rapid conversion of these natural habitats to agricultural land and settlement may lead to a decline in the populations of this species. Therefore, immediate conservation of the species is vital.

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