Natural history and distribution of *Agalychnis craspedopus* (Funkhouser, 1957) (Amphibia: Anura: Hylidae)

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Hoogmoed, M.S. & J.E. Cadle. Natural history and distribution of *Agalychnis craspedopus* (Funkhouser, 1957) (Amphibia: Anura: Hylidae).

Zool. Med. Leiden 65 (8), 31.vii.1990: 129-142, figs. 1-8.— ISSN 0024-1652.

Key words: Amphibia; Anura; Hylidae; phyllomedusine; *Agalychnis craspedopus*; life history; distribution; Amazonian lowlands; Neotropics.

Aspects of reproductive behaviour, calls, clutch sizes, and larval morphology are described for *Agalychnis craspedopus* (Funkhouser, 1957). New distributional records extend the range of this species to southern Amazonian Peru. In most respects reproductive behaviour of *A. craspedopus* is similar to that of other phyllomedusine frogs. In southern Peru clutches were suspended above water-filled hollow cavities in logs, but in Ecuador tadpoles were found in a pool on the ground with no directly-overhanging vegetation. *Agalychnis craspedopus* lays small clutches (mean = 17 eggs) with large eggs. Breeding possibly takes place throughout some years in southern Peru, but this undoubtedly varies depending on rainfall. Some aspects of reproductive biology, and tadpole and adult morphology of *A. craspedopus* are similar to those of *A. calcarifer*.

Se describe aspectos del comportamiento reproductivo, las cantas, las masas de huevos, y la morfología larval de *Agalychnis craspedopus* (Funkhouser, 1957). También se presenta nuevos registros que extienden el area de dispersión de la especie hasta el sureste del Perú. En la mayoría de aspectos el comportamiento reproductivo de *A. craspedopus* es similar a aquel conocido de otras ranas phyllomedusinas. En el sur del Perú masas de huevos se colocaron arriba de cavidades en troncos lleno de agua, pero en Ecuador renacuajos se hallaron en un charco sin vegetación sobresaliente. *Agalychnis craspedopus* pone masas pequeñas (por promedio con 17 huevos) de huevos grandes. Possiblemente, la reproducción sucede en todas épocas en el sur del Perú, pero esto varia según la cantidad de lluvia. Algunos aspectos de la biología reproductivo y la morfología de los renacuajos y adultos de *A. craspedopus* son similares a aquellas de *A. calcarifer*.

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Introduction

Agalychnis craspedopus was described by Funkhouser (1957: 23) on the basis of two specimens from Chicherota, Río Bobonaza, Napo-Pastaza Province, Ecuador. Since its original description few specimens have been collected and virtually nothing is known of its natural history. It now has been discovered at two additional Ecuadorian localities: Limoncocha (Napo Province) and Destacamiento Shiona (Pastaza Province); and at the following Peruvian localities: Vicinity of Galilea, Río Santiago (Amazonas Department), Tambopata Reserve, Río Tambopata (Madre de Dios Department), and Cocha Cashu, Río Manu (Madre de Dios Department). The Peruvian records extend the known range of *A. craspedopus* from the Amazonian region of northern Ecuador to southern Peru (fig. 1; see Material studied). All localities are between about 180 m and 400 m elevation.

In 1983-84 JEC made observations on breeding activity and behaviour of *A. craspedopus* at Cocha Cashu, Río Manu, Madre de Dios Department, Peru (about 380 m elevatiom). Goulding (1989) gave a picture of two specimens, that according to a

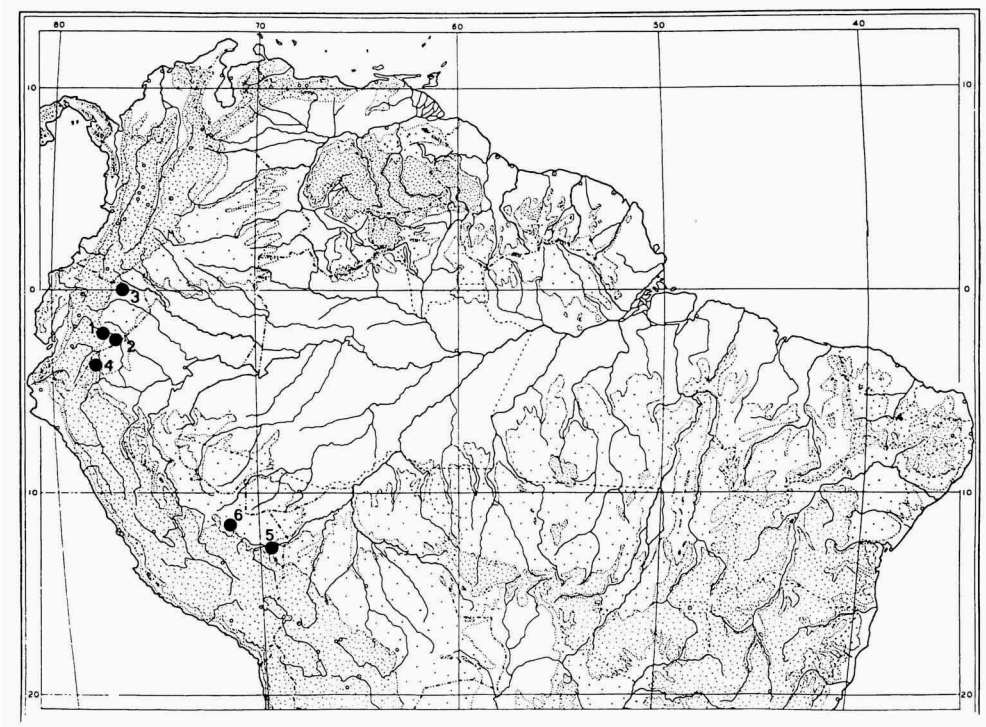

Fig. 1. Map of Ecuador and Peru showing the known localities for *Agalychnis craspedopus*. **Ecuador**: 1. Chicherota, Rio Bobonaza (type locality), 2. Montalvo, 3. Limoncocha. **Peru**: 4. Rio Santiago, 5. Tambopata Reserve, 6. Cocha Cashu, Manu.

personal communication of Russell A. Mittermeier were filmed at Cocha Cashu as well, during the time JEC visited the area. This site is a seasonal lowland rainforest with approximately 2000 mm of rain per year (Terborgh, 1985). In 1983 MSH collected tadpoles eventually determined to be those of *A. craspedopus* at Destacamiento Shiona, Pastaza Province, Ecuador (220 m elevation). Shiona is in an aseasonal lowland rainforest ("Clima uniforme megatérmica muy humedo") with 2000-3000 mm of rain per year (Atlas Ecuador, 1982: 28; Pourrut, 1983: 27, 40). We report here our observations on natural history and development of this poorly known species. References to museum specimens follow abbreviations listed in Leviton et al. (1985). The acronym RMNH now stands for Nationaal Natuurhistorisch Museum, since early 1990 the new name for the former Rijksmuseum van Natuurlijke Historie.

Description of egg-laying sites

Reproductive activity was observed at two sites at Cocha Cashu. At both sites eggs were deposited above water-filled cavities in hollow logs that were approximately 1 m and 1.8 m above the ground (fig. 2). The maximum dimensions of these cavities were 188 x 22 cm (hereafter referred to as site 1) and 163 x 33 cm (site 2). Water depth was 10 cm in the former, and varied from 1 to 8 cm in the latter. Both cavities had a layer of leaf litter and decaying wood in the bottom that varied in depth from about 4 cm to more than 20 cm. Both of these pools were overhung by a

Fig. 2. Egg-laying site (site 1) of *Agalychnis craspedopus* at Cocha Cashu. A pool of water fills the cavity in the log. A clutch of *A. craspedopus* eggs can be seen attached to roots hanging over the far edge of the cavity.

shelf with roots extending down into the water, and all clutches of *A. craspedopus* observed were attached to these roots up to 28 cm above water level. No evidence of breeding activity, including egg masses or tadpoles, was observed at another pool in the same log as site 2, but which lacked overhanging vegetation or shelves. Few *Agalychnis* tadpoles were observed at site 2; the water level in this pool possibly fluctuated, as an egg mass was observed on 16 December 1983 suspended above a dry part of the pool. At both sites the water temperature was measured on various occasions during the day and fluctuated between 24.2° C and 24.4° C.

Because of their dark gray to black colouration, tadpoles of *Agalychnis craspedopus* were strikingly visible against the substrate. Most of their time was spent swimming a few centimeters above the bottom of the pools or suspended vertically at the water surface filtering the surface film. Occasionally they were observed lying on the substrate.

At both egg-laying sites, several adults of a *wagneri*-group *Leptodactylus* (FMNH 228256; species not yet identified, possibly new) were observed on the logs around the pools, at the edge of the water, or under loose bark on other parts of the logs. On numerous occasions individuals of this *Leptodactylus* were seen sitting on the logs and dived into the pool when approached. *Leptodactylus* larvae (USNM 298934), presumably of the same species, were present in pools at sites 1 and 2. The *Leptodactylus* tadpoles were less numerous than were those of *Agalychnis* and, in contrast to *Agalychnis* tadpoles, they generally remained motionless on bottom debris where they were very cryptic. Dragonfly, and mayfly naiads, and mosquito larvae were also present.

In Destacamiento Shiona, near Montalvo, Ecuador, 31 tadpoles were found on 14 August 1983 in a small pool located on bare muddy ground on a gentle slope on a

trail through undisturbed (except for the rather wide trail) primary rainforest. There was no vegetation directly overhanging the pool, though the canopy was closed over the trail. No detailed observations of the surroundings were made, as at the time it was not realized which species was being collected. Some tadpoles (17) were preserved immediately; the remainder was kept alive. The situation at the pool in Shiona differed from that at Cocha Cashu. At Shiona no directly overhanging vegetation or shelves were present until about 4 m above the water surface, which seems to indicate that eggs either were laid high above the water, or were laid directly in the water or on the ground very close to it.

In Limoncocha, Napo Province, Ecuador W.R. Heyer and K. Berven on 16 June 1971 collected five tadpoles in a small pool (1.5 m diameter) on the ground in primary forest.

Description of a mating sequence

The following observations are based on a reasonably complete mating sequence of *A. craspedopus* at site 1 at Manu on 13-14 December 1983, supplemented by other less extensive observations in January 1984. The clutch resulting from the described mating sequence hatched 25-26 December 1983.

When first visiting the site at 2112 h JEC observed one amplexing pair on a branch of a small tree about 2 m from the ground and 0.5 m from the pool. Another smaller male was on another branch of the same tree about 0.3 m from the amplexing pair. The male in amplexus was calling; the other male was not observed to call during the entire period of observation. Another calling male was located about 4 m up in a large tree approximately 4 m from the pool. Within the next 1.5 h three other males were heard calling from high in the trees around the log but could not be located. When not obscured by vegetation, the bright yellow ventral surfaces of these frogs are strikingly visible using a headlamp at night.

The non-amplexing males were calling more frequently than the amplexing male. At 2305 h the amplexing male began calling more regularly and frequently. Between 0005 h and 0030 h all calling males except the amplexing one ceased calling and the male observed high above the log could no longer be seen. During this period the amplexing pair and the small male remained in the same position. Observations were disrupted between 0100 h and 0536 h.

When observations were continued the amplexing pair was now in the pool of water. The small male had moved and could not be located. For the next 45 min the pair moved around in the pool through the female's efforts and several times she attempted to climb the steep sides of the pool without success. Once the male was observed to give a series of quick forelimb contractions, one every 20-25 sec for 3 or 4 repetitions. At 0616 h the female moved quickly to a position where a root mass was suspended above the pool and climbed up the mass until her cloaca was at water level. The body of the female was now observed to be very distended with eggs (not so evident before). The male at this point was still in axillary amplexus. For the next 1.5 h the pair moved up and down on the root mass, during which time the male again gave a series of forelimb contractions. Several times during this period the female splashed water over herself by vigorously kicking her hindlimbs into the water. At 0755 h the female moved from the root mass to the side of the cavity and in response to a disturbance from the observer, retreated to the pool. At 0806 h the female again climbed onto the root mass. At 0842 h and 0857 h the female again

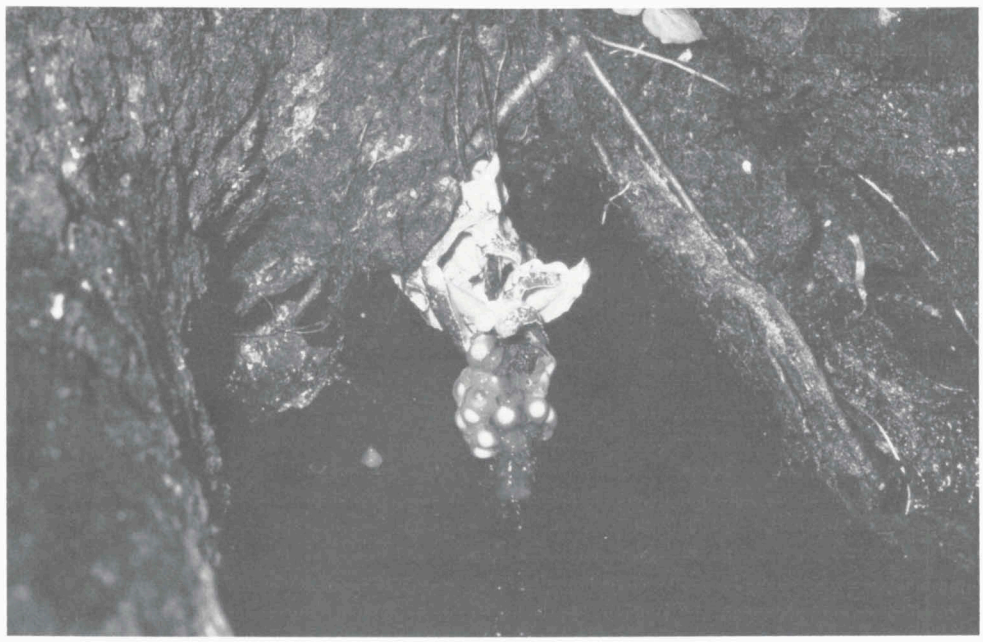

Fig. 3. Amplectant pair of *A. craspedopus* photographed at Cocha Cashu site 1. The pair is suspended at an angle behind the plane of the photography (see text), holding on to the roots hanging over the water, which already have some eggs attached to them.

splashed water onto herself by alternately flicking both feet into the water at about 1 sec intervals. At 0900 h the female pressed her cloaca to the root mass and immediately began laying eggs.

While laying eggs, the female used her hind limbs alternately to push eggs down the root mass as they were being laid. When egg-laying began the male moved his hind legs up onto the trunk of the female rather than resting them on her legs as before. As the eggs were being laid the female gradually raised the position of her cloacal opening along the root mass, bringing the inguinal region in closer proximity to where her forelimbs were grasping the root mass and suspending the pair at an increasingly acute angle from the roots (fig. 3). Numerous empty egg capsules were laid with the clutch. At the end of egg laying, there were 14 eggs and the empty capsules comprised a volume approximately equal to that of the egg mass present.

At 0922 h the male abruptly dislodged himself from the female, dropped into the water, and egg-laying ended. The female remained motionless clutching the root mass for another 10 min, and then dropped into the pool. The male left the pool at 0956 h and jumped to a small tree, ascending to just over 2 m; he remained there until 1023 h when observations were discontinued. The female left the pool between 0952 h and 1001 h.

Mating call

The call of *Agalychnis craspedopus* was recorded at Cocha Cashu, Manu with a Sony ECM-929LT microphone and Walkman Professional cassette tape recorder. A copy of the recording is on file in the Division of Amphibians and Reptiles, U.S. National Museum. The call is similar in sound and intensity to some other species of phyllomedusines in being a soft "cluck." Although the recording was not of suffi-

cient quality to produce a spectrogram, it was analyzed on a Unigon sound analyzer. This analysis indicated a call duration of about 0.06-0.07 s and a dominant frequency in the range 600-800 Hz. The note was repeated at intervals of slightly more than one second. The temperature on the day of the recording was 23-28.5 °C.

Clutch size, eggs, and hatching

Sizes of ten clutches observed at Manu ranged from 14-21 with a mean of 17 eggs. The time between egg-laying and hatching was 11 to 15 days for those clutches with adequate data to determine hatching time, although one clutch possibly hatched as early as eight days. The eggs are large, with ovum diameters of approximately 4 mm and capsule diameters of 10-12 mm. The animal hemisphere is greenish and the vegetal hemisphere is yellowish white; no melanin was observed in the eggs. As in other species of phyllomedusines (e.g., *Phyllomedusa hypocondrialis*; Pyburn, 1980), the embryos of *A. craspedopus* develop long filamentous gills that are appressed to the surface of the egg membranes. The gills are resorbed before hatching. At hatching the tadpoles are 18-20 mm in length. Newly hatched tadpoles are a lighter gray colour than more advanced tadpoles and retain much yolk.

Periodicity of egg-laying

Clutches of eggs were observed at site 1 at Cocha Cashu, Manu sporadically between 7 December 1983 and 27 June 1984. A pair was found in amplexus on 18 October 1986 (fide label attached to specimen) at the Tambopata Reserve, which is near Cocha Cashu, Manu in southeastern Peru (see fig. 1). We have no data for the remainder of the year. It is possible that *A. craspedopus* breeds opportunistically throughout those years in southeastern Peru in which sufficient rain falls to maintain breeding sites and permit activity. Observations of reproductive activity include various parts of two dry seasons (October, December, and May-June), and one entire rainy season (January-April). On several occasions in both wet and dry seasons males were calling without resulting clutches. A plot of timing of clutches relative to rainfall patterns at Cocha Cashu suggests that, at least during the dry season, *A. craspedopus* reproduction tends to follow within a day or two of rains in excess of 10 mm (the pattern is not so evident during the rainy season since the frequency of days with heavy rains is much greater).

Larval development

Part of the tadpoles collected in Shiona on 14 August 1983 were placed in plastic bags with water and (without feeding) transported to the Netherlands where, after some wanderings, they arrived on 27 August 1983. During the trip two specimens metamorphosed (snout-vent length 21 mm) and were preserved. In The Netherlands the remaining tadpoles were placed in an aquarium at room temperature (ca. 20° C) and fed with commercial fish food. On 7 November 1983 the first two specimens left the water, followed by the remainder during the last two weeks of November. The two specimens "metamorphosed" on 7 November (RMNH 24459-60, snout-vent length at time of preservation resp. 27.4 and 27.7 mm) were preserved, together with

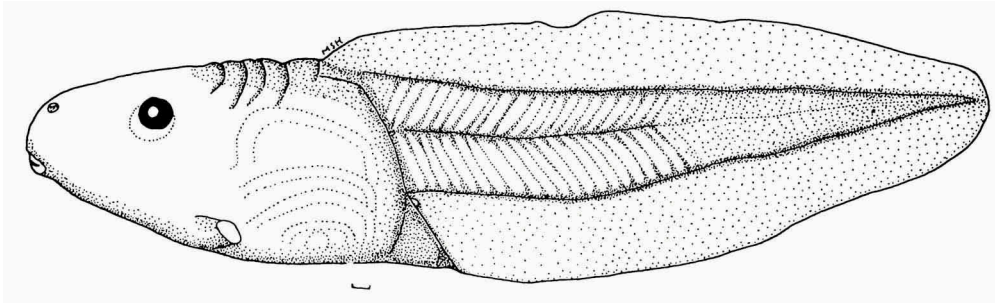

Fig. 4. Tadpole of *Agalychnis craspedopus*, stage 26 of Gosner (RMNH 24451). Bar represents 1 mm.

two well-developed tadpoles in stages 39 and 40 of Gosner (1960) (= stages 25 and 26 of Kopsch [1952]), on 15 November 1983 (RMNH 24461). The remainder was kept alive in a terrarium and, after having been photographed extensively, were preserved 19-21 May 1984, when they stopped eating and it was feared they would starve. At that time they were half-grown (snout-vent length between 34.9 and 44.9 mm).

USNM 300592, recently identified as *Agalychnis craspedopus* for us by Dr Roy W. McDiarmid, consists of five larvae collected by W.R. Heyer and K. Berven at Limoncocha, Napo Province, Ecuador on 16 June 1971. The total lengths and Gosner stages (in parentheses) for these specimens are, respectively, 33 mm (25), 52 mm (27), 52 mm (28), 54 mm (31), and 55 mm (36). As this information only reached us after completion of the manuscript, the metric data for these specimens could not be incorporated in the table.

Description of tadpoles

At the time of collection the sample contained tadpoles in stages 25/26 - 40 of Gosner (1960) (18/19 - 25 of Kopsch (1952)), of which the following were preserved: 25 (5), 26 (5), 28 (1), 30 (1), 31 (2), 34 (1), 38 (1), and 40 (1). Tadpoles in stage 25 and 26 of Gosner are rather variable in size, the body length (measured from the tip of the snout to the end of the cloacal tube) ranging from 13 - 21.5 mm, the total length from 31 - 48.5 mm (figs. 4, 6). The other stages are more or less of the same size, the body length ranging from 20 - 25.1 mm, the total length from 35 (damaged tail), 45 - 65.1 mm (table 1). The following description is based on RMNH 24461, a tadpole in stage 39 (Gosner, 1960). Tadpoles in other stages essentially agree with this description, except for the characters that determine the stage they are in such as development of the limbs and mouth.

Body shape more or less ovoid with a flattened back and deepest point of body posteriorly. Body wider than long, the widest point just behind the eyes. Mouth anteroventral, directed anteriorly. Eyes dorsolateral and directed laterally, diameter 2.4 mm. Area just below the eyes constricted, eyes just barely visible from below. Interorbital distance equal to distance between eyes and tip of snout (7.7 mm). Distance between eye and nostril 4.2 mm, distance between nostril and tip of snout 3.3 mm. Nostrils dorsal, directed anteriorly. Spiracle ventral, sinistral, an oblique slit with a short tube attached to the body, opening 2.4 mm wide, 12.2 - 12.7 mm behind the snout. Cloacal tube dextral to ventral caudal fin, 2.8 mm long. Posterior dorsal part of body with six

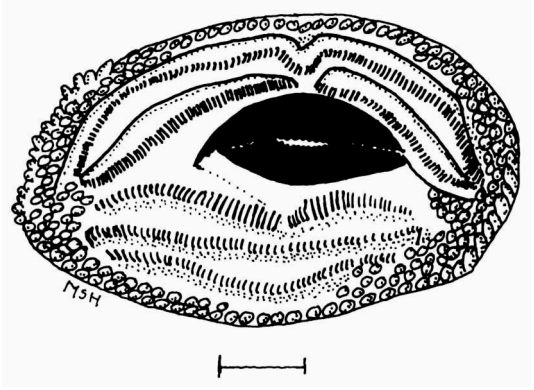

Fig. 5. Mouth of tadpole of *Agalychnis craspedopus*, stage 26 of Gosner (RMNH 24451). Bar represents 1 mm.

transverse furrows, each furrow corresponding to a muscle segment of the tail base, that arises on the back behind the eyes.

Fleshy part of tail from base to midpoint deeper than dorsal and ventral fins. Ventral fin distinctly deeper than dorsal one. Caudal musculature anteriorly robust, gradually tapering posteriorly to the tail tip; depth at midpoint of tail 6 mm, dorsal fin 4.1 mm, ventral fin 4.8 mm. Caudal fin not extending onto body. In life body dark olive grey-green with white canthal lines, belly blue-grey, iris greyish-white. In life tail black with blue-grey spots, in preservative with reticulate brown pattern on anterior muscular part, extending onto adjacent areas of fins.

Oral disc (fig. 5) triangular to oval, completely bordered by papillae; papillae in a single row dorsally and in two rows ventrally, but in many rows laterally, gradually diminishing midventrally, more abruptly diminishing to one row dorsally.

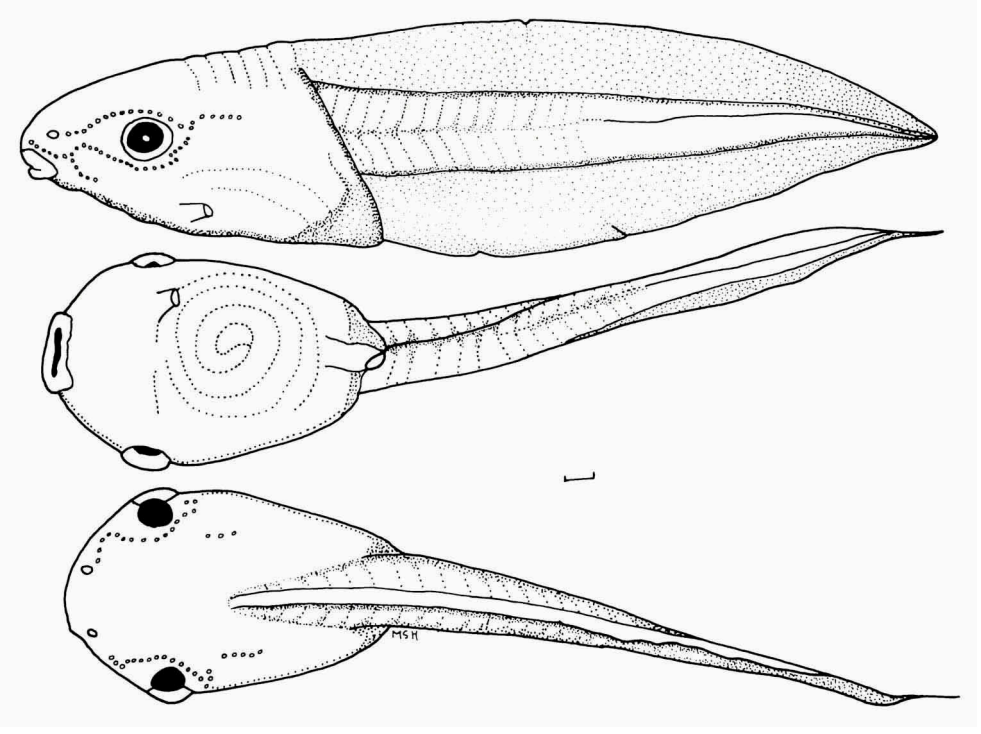

Fig. 6. Tadpole of *Agalychnis craspedopus*, stage 25 of Gosner (RMNH 24451), drawn shortly after preservation and clearly showing the lateral line organs. Bar represents 1 mm.

Exceptionally, the rows of papillae may be interrupted mid-ventrally. Lower jaw U-shaped, with sharp pointed serrations. Upper jaw forming a broad arch. Labial teeth in two anterior and three posterior rows. Labial tooth row formula (Altig, 1970): 2(2)/3(1). Anterior rows equal in length, first row with a median dip, second row interrupted medially. First posterior row narrowly interrupted medially, second posterior row as long as first, third posterior row shorter than the other two. There is no obvious change of body form from stage 25/26 to 40.

In RMNH 24461 stage 39 the hindlimbs are only slightly developed, but the characteristic indentation in the tarsal fold is already visible. In tadpoles in stage 40 the indentation is even more pronounced and the tarsal fold has a white edge.

Shortly after preservation some drawings were made of a specimen in stage 25 (RMNH 24451) and at that time a lateral line system was evident and was drawn. It consisted of a line starting behind the nostril and curving inwards medially of the eye, curving downwards posteriorly of the eye where it entered into contact with another line that had started over the upper lip, running posteriorly below the nostril and shortly after the nostril divided itself into a short ventral branch and a longer branch passing under the eye and entering into contact with the upper line. A short line of lateral line organs was visible at each side of the muscular part of the back (fig.6). At the time of writing this lateral line system is hardly recognisable in any of the specimens.

A tadpole in Gosner stage 32 from Cocha Cashu (USNM 298937) agrees with the above description of Ecuadorian tadpoles except that the body is longer (15 mm) than wide (10 mm), and the ventral fin at the midpoint of the tail is deeper than the dorsal fin and tail musculature, which are approximately the same depth.

Colouration of adults and juveniles in life

Funkhouser (1957) reported only colour notes taken from specimens that had been preserved for one month or more, thus losing some features seen in life. Goulding (1989:94/95) published a nice picture of two specimens of this species taken at Cocha Cashu under the name "*Phyllomedusa* frogs". The following colour notes are based on observations of two males and three females at Cocha Cashu. The entire dorsal surface, including the head, body, forearm, thigh, shank, fifth toe, and all dermal fringes, is dark leaf green. Numerous grayish white splotches are scattered over the dorsum in an irregular pattern and varying from thin cobweb-like patterns to large irregular blotches (fig. 7). The overall effect of these splotches gives the appearance of lichens and/or fungal hyphae, and may function as camouflage when the frogs are resting in canopy vegetation (The tag attached to LSUMZ 37094 from Limoncocha, Ecuador states, "above grass-green mottled blue-gray."). The flanks, upper arms, fingers except for the outer edge of the fifth, toes except for the fifth, and entire ventral surfaces are intense bright yellow or orangeish yellow. The flanks, anterior and posterior surfaces of the thighs and forelimb, dorsal surface of the fourth toe and fifth finger, and ventral surfaces of the dermal fringes of the shank are crossed by a series of thin wavy dark brown/black bars (6-8 on the flank and each posterior limb segment). On the limbs and flank these bars divide dorsally and join to form a thin border between the dorsal green colouration and ventral yellow colouration. The bars do not meet ventrally on either the body or limbs. The ventral surface of the dermal fringe on the tarsus is suffused with dark brown pigment, as is

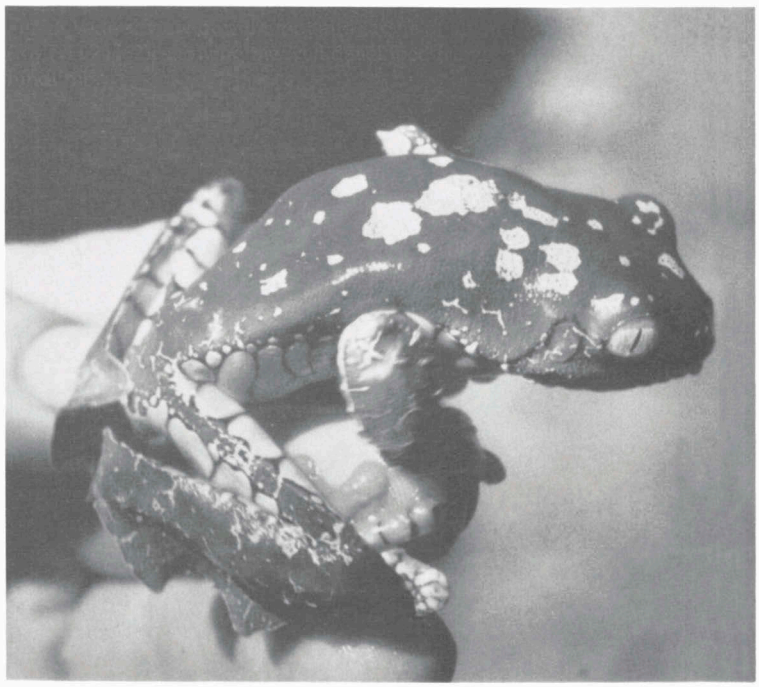

Fig. 7. *Agalychnis craspedopus* from Cocha Cashu, Río Manu, Madre de Dios Department, Perú. This specimen shows the lichen-like markings characteristic of this population (possibly others), the dermal fringes of the hind limbs and lower lip, and the flank and thigh markings.

the plantar surface of the feet to a lesser extent. The iris is grayish white with fine black reticulations and a bright yellow border around the rim. The nictitating membrane is dark green with irregular pale greenish and silver reticulations.

Males have a brown nuptial pad consisting of numerous rounded keratinous denticles on the prepollex (USNM 300572 examined). Adult males observed in the field were smaller than females; measurements of museum specimens were 55 mm and 57 mm for males (holotype (Funkhouser, 1957) and USNM 300572, respectively),

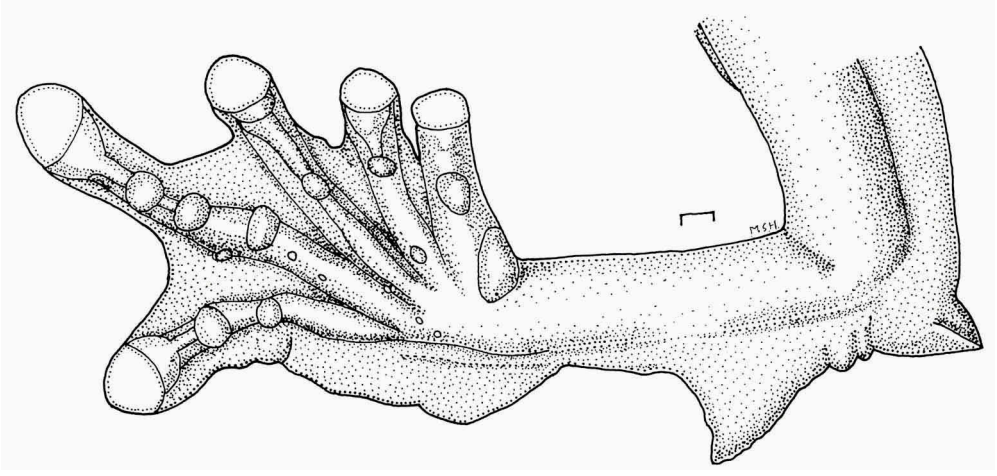

Fig. 8. Ventral view of right foot and tarsus of juvenile *Agalychnis craspedopus* from Montalvo, Ecuador (RMNH 24462), showing the well developed fringes along the posterior margin of the distal part of the hindlimb.

and 69.5 mm, 70.1 mm, and 73 mm for females (LSUMZ 37094, USNM 284270, and paratype (Funkhouser, 1957), respectively). Other than the smaller size and the presence of nuptial pads in males, the only potentially sexually dimorphic feature observed was a somewhat more intense yellow/orangeish colour in females. Larger samples would be necessary to establish this qualitative difference.

At rest against a leaf surface these frogs sit with the limbs drawn close to the body so that only the dorsal green colour is visible, enhancing the camouflage effect of the dorsal splotches.

The juveniles obtained from raising the tadpoles from Shiona generally agree with the above colour description, but some differences can be noted. The dorsal surface of the thighs may show a green stripe throughout its length, or it may be restricted to the area near the knee, with the remainder of the surface orangeish yellow with narrow darker bars. Inner three fingers and toes orange, upper side of fourth finger and fifth toe as dorsum, upper side of fourth finger as flanks, upper side of disc of fifth toe light blue. Throat yellow, with a cream edge along the lower jaw, belly pale orange, underside of limbs flesh-coloured. Edge of ulnar, tarsal, and supra-anal ridges white. Iris grey with small black spots, nictitating membrane clear, without reticulation.

Discussion

Some of our observations support previous suggestions that *Agalychnis craspedopus* and *A. calcarifer* are sister species (Funkhouser, 1957: 8-12; Duellman, 1970 : 93, 123). Donnelly et al. (1987: 249) noted that *Agalychnis calcarifer* tadpoles are unique among *Agalychnis* tadpoles in having a complete row of papillae on the upper labium. The tadpoles of *A. craspedopus* share this putatively-derived character with those of *A. calcarifer*, suggesting a close relationship between these two species. These two species also share a dermal flap (calcar) on the heel (fig. 8 shows the situation in *A. craspedopus*), similar colour patterns on the flanks and limbs (orange with dark vertical bars), and grayish irises rimmed with yellow (orangeish to various shades of brownish or red in other species of *Agalychnis*). One specimen of *A. calcarifer* that JEC observed alive (JEC field number 9414 from Limon Prov., Costa Rica, to be deposited in ANSP) had irregular pale green splotches on the dorsum similar to, but generally smaller than, the lichen-like markings on *A. craspedopus* from southern Peru. Myers & Duellman (1982), reported pale blue spots on specimens of *calcarifer* from western Panama.

Observations at Cocha Cashu and Shiona indicate that *A. craspedopus* inhabits the canopy of lowland rainforest, perhaps at a low density subject to availability of water-filled cavities in old logs or hollows in the ground which are necessary for reproduction. Both egg-laying sites at Cocha Cashu were in fallen logs several years old. These factors possibly account for the sparse records for this species and suggest that it may be more widespread than known at present. Most species of *Agalychnis* lay eggs on vegetation above temporary or permanent forest ponds, although both *A. spurrelli* Boulenger, 1902 and *A. calcarifer* Boulenger, 1913 are also known to use water-filled cavities in logs (*calcarifer* exclusively so) (Duellman, 1970; Donnelly et al., 1987). *Phyllomedusa buckleyi* Boulenger, 1882 is now known to deposit its eggs among vegetation (sedges) at the surface of the water of temporary pools (MSH, personal observations; Cannatella, 1980: 22), whereas all other species of *Phyllomedusa* lay their eggs in a mass which is either deposited on, or enveloped in leaves some dis-

tance above the water surface (Lamotte & Lescure, 1977; Lescure, 1975; Cannatella, 1980; Duellman et al., 1988).

The general features of reproductive behaviour seen in *Agalychnis craspedopus* are similar to other phyllomedusines (see Pyburn, 1970, 1980 for summaries). However, several features observed in *A. craspedopus* are noteworthy. On two occasions amplectant pairs were found in the water, and on one of these occasions this appeared to be a natural preliminary to egg laying (see above). Pyburn (1970) demonstrated for *Pachymedusa dacnicolor* (Cope, 1864) and *Agalychnis callidryas* (Cope, 1862) that this behaviour was associated with filling of the female's bladder with water which was later deposited over the eggs. Although we have no direct evidence that this is the case in *Agalychnis craspedopus* we suspect that it is. Furthermore, *A. craspedopus* lays numerous eggless capsules along with its clutches, an additional mechanism for insuring that sufficient moisture is available for egg development (Pyburn, 1980). Pyburn (1980) suggested that these two alternative means of moisture regulation might be an additional characteristic distinguishing *Agalychnis* (using bladder water) and *Phyllomedusa* (using eggless capsules; *P. buckleyi* was subsequently discovered to deposit eggs in vegetation at water level). *Agalychnis craspedopus* certainly uses eggless capsules and indications are that it possibly also uses bladder water to moisten its clutches. Thus, these two latter species blur the distinction Pyburn thought existed between *Agalychnis* and *Phyllomedusa*. Further understanding of the significance of the different egg-laying behaviours will require establishment of evolutionary polarities for them and observations on additional species.

Our observations at Manu indicate that *A. craspedopus* has a very lengthy courtship. For the sequence described above, the time between initial observation of an amplectant pair and the beginning of egg laying was nearly 12 h. The actual time of egg-laying was 22 min, comparable to the 14 min and 18 min reported by Pyburn (1970) for *Phyllomedusa callidryas* and *Pachymedusa dacnicolor*, respectively. Perhaps the lengthy courtship observed was a response to the presence of the observer. However, the first pair of *A. craspedopus* discovered at Manu was found in amplexus at 1000 h in a pool of water and later laid a clutch of 14 eggs in a collecting bag. This suggests that the pair had begun their courtship the night before and had not yet produced a clutch (none were present on the log at this time). Moreover, a tag attached to USNM 284270, a female, states: "In amplexus on log 10 cm above pool in hole in log, 0830." This also suggests an as-yet-uncompleted courtship that had begun the previous night. All observations indicate that actual egg-laying takes place during daylight hours.

The eggs of *Agalychnis craspedopus* are large and the capsule diameter approaches the largest known in anurans (14 mm in *Gastrotheca cornuta* and 15 mm in *Rana spinosa*; Duellman & Trueb, 1986). The clutch sizes reported here for *A. craspedopus* are smaller than most of those reported for other phyllomedusines. Clutch sizes of 13, 16, and 27 are known for *A. calcarifer* (Donnelly et al., 1987;). [Marquis et al. (1986) reported 30-40 and about 70 for this species, the reason for the disparity in the reported clutch sizes is not clear. We accept the lower values given by Donnelly et al. since they raised the tadpoles to metamorphosis. Also, M. Donnelly (pers. comm.) informed us that the lower values are more trustworthy than the higher ones.]. Mean clutch sizes for other species of phyllomedusines are higher: *A. callidryas*, 26-43 depending on locality; *A. moreleti*, 49; *A. annae*, 106; *Pachymedusa dacnicolor*, 187 (Duellman, 1970; Pyburn, 1970). As in some other phyllomedusines that lay large-yolked eggs (Pyburn, 1980), embryonic development within the egg is relatively long in *A. craspedopus*, and the larvae hatch at a large size.

Material

Ecuador: Napo Province: Limoncocha, 300 m: adult female, LSUMZ 37094 (an additional specimen, not examined, from this locality, originally in LSUMZ, was exchanged to KU); 5 larvae, USNM 300592, 16.vi.1971. Pastaza Province: Shiona, 220 m: 19 larvae, RMNH 24451-57, 24461; 2 recently metamorphosed juveniles, RMNH 24458, metamorphosed viii.1983; 2 recently metamorphosed juveniles, RMNH 24459-60, metamorphosed 7.xi.1983, killed 15.xi.1983; 8 juv., RMNH 24462-69, metamorphosed late xi.1983, killed 19/21.v.1984, all specimens collected 14.viii.1983.
Peru: Amazonas Department: Vicinity of Galilea, Rio Santiago: adult male, USNM 300572. Madre de Dios Department: Cocha Cashu, Río Manu, approx. 70 km NW mouth of Río Manu, about 380 m: metamorphosing larva, USNM 298936; larva (Gosner stage 32), USNM 298937; ca. 30 km (straight line) SSW Puerto Maldonado, Tambopata Reserve, Explorer's Inn, 280 m: adult female, USNM 284270.

Table 1. Measurements of larvae of *Agalychnis craspedopus*. s-vl = snout-vent length; taill = taillength; bodyd = bodydepth; bodyw = bodywidth; orald = width of oraldisc.

Regno RMNH	s-vl	taill	bodyd	bodyw	orald	stage
24451 a	13	18	6.5	6.9	2.6	25
b	15	16	7.2	7.8	3.0	25
c	15	21	6.2	7.2	3.1	25
d	17	19	8.0	8.5	3.5	25
e	18	23	9.0	9.4	3.5	25
f	21.5	27	10.6	11.4	4.1	26
g	20	25	8.5	10.1	3.8	26
h	20	26	9.0	10.1	4.3	26
i	19.7	26	9.3	10.7	4.1	26
j	20	27	8.9	10.2	3.9	26
24452	21	33	9.6	10.7	3.9	28
24453	22	25	10.1	11.2	4.1	30
24454 a	22	35	10.4	12.0	4.4	31
b	20	27	8.5	10.0	4.0	31
24455	23	30	10.6	11.6	4.5	34
24456	22	27	10.4	12.7	4.5	37
24461 a	24.5	40	11.7	14.5	4.8	39
b	25.1	40	11.3	14.6	5.2	40
24457	21	14	9.4	12.7	4.3	40
24458 a	21	3	6.7	8.3	—	43
b	—	—	—	—	—	43
24459	27.4	—	—	—	—	44
24460	27.7	—	—	—	—	45/46

Acknowledgements

P. Sherman located the first pair of *A. craspedopus* at Cocha Cashu and called their attention to JEC. L.H. Emmons conscientiously recorded egg laying at Cocha Cashu from March to June, thus extending observations into the dry season. Field work by JEC at Manu was supported by permit number 069-83-DGFF-DRFF-SDFF from the Dirección General Forestal y de Fauna. The support of that office and of Dra. Nelly Carrillo de Espinoza, Museo de Historia Natural de San Marcos, is greatly appreciated. Fieldwork of MSH in Ecuador was supported by permits number 000001 (1983) and 006-CIC-DINAF-ANVS/000760DNF/ANVS (1987) from the Ecuadorian Ministerio de Agricultura y

Ganadería. The Jefe de la Sección Seguridad Militar del Ejercito- Fuerza Terrestre of the Ministerio de Defenza (Tcrl. de E.M. Jaime R. Silva R.) kindly permitted (no. 830175-E 2c-1) MSH to visit eastern Ecuador and stay in the military camp of Shiona. Ing. Mauro Dávalos Cordero and Iván Bedoya of CEPE (Corporación Estatal Petrolera Ecuatoriana) kindly provided MSH with transportation to and lodging in Shiona (004132). Ana Almendariz was a good field companion who also arranged the perfect logistics in eastern Ecuador. For discussion, comments, and/or other assistance we thank T.C.S. de Avila Pires, D.C. Cannatella, M.A. Donnelly, M. Henzl, W.R. Heyer, R.W. McDiarmid, and R.P. Reynolds.

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Received: 31.xii.1990
Accepted: 17.v.1991
Edited: M.R.R.B. Best