

Kalikasan, Philipp. J. Biol. 11(2-3): 203-226 (1982)

Printed in the Philippines

Received for publication: 21 August 1982

DEPARTMENT OF HERPETOLOGY
CALIFORNIA ACADEMY OF SCIENCES

Reproductive biology of some species of *Philautus* (Rhacophoridae) and other Philippine anurans

ANGEL C. ALCALA
Biology Department, Silliman University,
Dumaguete City 6501
and WALTER C. BROWN
Menlo College,
Menlo Park, California 94025,
and California Academy of Sciences,
Golden Gate Park, San Francisco,
California 94118, U.S.A.

Relatively complete data on the reproduction of two Philippine anurans are presented, viz., *Pelophryne brevipes* and *Philautus lissobrachiatus*. Inger's hypothesis that *Philautus* species probably exhibit a direct mode of development is confirmed. Some new data on reproduction of several other Philippine frogs as follows are also presented: *Rana microdisca parva*, *R. sanguinea*, *Edwardtayloria spinosa*, *Rhacophorus zamboangensis*, *R. appendiculatus*, and two undetermined species of *Philautus*.

When we began in 1958 our field studies of Philippine amphibians and reptiles, data on reproduction of most of the anuran species were lacking or very limited. Relatively complete life history data were available for only two species (1, 2). Also available were some information on the

0115-0553/82/02-30203-24\$2.00

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eggs, larvae, or both for another dozen or so species (3-7). Since that time relatively complete life history data have been obtained for 14 species as well as some information on eggs, larvae, or both for all but ten of the 67 known species of Philippine anurans. Parts of the data have been published (8, 9); the second paper summarizes the modes of reproduction exhibited by Philippine anurans. In addition, data for Bornean populations of several species have also become available (10, 11). We now record the previously unpublished information on the life histories of *Pelophryne brevipes* and *Philautus lissobrachius* and the new data on the reproduction of several other little-known Philippine frogs.

Study areas and methods

The materials used in this study were collected in the rainforests of Mt Malindang, Zamboanga del Norte and Misamis Occidental provinces in northern Mindanao, in March-May, 1959; Mt Hilong-Hilong, Agusan del Norte in northeastern Mindanao, in May, 1971 and April, 1979; Thumb Peak and Central Peak, Puerto Princesa area in Palawan, in March-April, 1961; Mt Barawan, Mindoro Oriental Province, in March-April, 1963; and Negros Island at various times.

Large aquatic tadpoles were collected by means of dip nets and reared in plastic buckets in the field camps and later in the laboratory in Silliman University, Dumaguete City. These were fed with green algae and bottom sediments from ponds. The embryos and larvae of *P. brevipes* and *Philautus* spp. were taken from leaf axils of *Pandanus* and bird's nest ferns (*Asplenium nidus*). These arboreal sites of egg deposition, generally 2-10 m above the ground, were brought down and examined on cleared ground or on canvas material laid on the forest floor. The eggs or larvae were allowed to metamorphose but were not fed in plastic bags containing water (for *Pelophryne*) or root masses of ferns (for *Philautus*). Samples of the developing embryos and larvae were preserved in formalin at various times to record different developmental stages.

The measurements are given in millimeters and were made from preserved materials. In measuring, a pair of dividers and a steel ruler, graduated in tenths of a millime-

ter, were used. Eggs, embryos and small larvae were measured under a stereoscope. The following measurements were taken: *diameter*, for eggs and early embryos; *total length*, from tip of snout to tip of tail of tadpoles (Stage I to Stage XXIV), or from tip of snout to vent (Stage XXV); *body length*, from tip of snout to base of tail (point of origin of hind limbs); *body width*, at point of greatest width; *body depth*, at point of greatest depth; *tail length*, from base to tip of tail; and *tail depth*, at point of greatest depth from edge of dorsal fin to edge of ventral fin.

Taylor & Kollros' (12) and Gosner's (13) classifications of the larval stages were followed. In the description, the stages given in Arabic numerals correspond to those of Gosner, whereas stages given in Roman numerals correspond to those of Taylor & Kollros.

Embryos and larvae of Philippine anurans which we collected, including those serving as bases for this paper, are deposited in the California Academy of Sciences, San Francisco, U.S.A. and Silliman University Natural History Museum, Dumaguete City, Philippines.

***Pelophryne brevipes* (Peters)**

Five groups of embryos and larvae were collected in the mid-mountain forest, about 1500-1800 m in altitude, on Dapitan Peak, Zamboanga Peninsula, Mindanao, in March-May, 1959. One group consisted of 15 early embryos in the same stage of development. The second group consisted of nine tadpoles also of a similar stage. The third group was composed of 26 whitish undeveloped eggs and embryos in various states of development. The remaining two groups had less than five tadpoles each. The embryos and larvae were reared at the field camp in plastic bags without food being added. The data on tadpoles that were preserved at various intervals during the rearing period are summarized in Table 1.

Oviposition sites. All five groups of embryos and larvae were found in leaf axils of the screw pine (*Pandanus*), at heights of 3-5 m above the ground. The leaf axils held water varying from about 15 to 80 cc (mean of 11 determinations, about 35 cc). Because of the continual rainfall (not

Table 1. Summary of data on tadpoles of *Pelophryne brevipes* collected on Mount Malindang, Mindanao Island, Philippines, April, 1959. Measurements in mm.

Field no. ^a	Date collected	Date preserved	Stage ^b	B o d y			T a i l		Hind limb length
				length	width	depth	length	width	
2639	4/8	4/8	II[27]	4.0	2.5	1.0	5.7	1.8	0.4
3780	4/8	4/30	X[35]	4.5	3.0	2.6	7.8	2.5	1.8
4321	4/8	5/9	XIX	4.1	2.9	2.3	9.0	2.7	4.0
2789	4/8	4/14	21	4.0-4.5 (4.1) ^c	—	—	2.6-3.0 (2.8) ^c	—	—
3776	4/8	4/30	V[30]	4.0	2.8	2.0	7.0	2.0	1.5
4323	4/8	5/9	X[35]	4.2	3.0	2.5	7.9	2.8	2.3
4341	4/8	5/20	XXI-XXII	4.8-4.9 (4.8) ^d	—	—	2.9-6.0	—	—
2790	4/14	4/14	IV[29]	4.3	3.0	1.9	7.0	2.0	0.8
3785	4/14	4/30	VIII[33]	3.7	2.7	2.5	6.7	2.0	1.8
3779	4/8	4/30	X[35] or XI[36]	4.5	3.0	2.5	7.5	2.7	3.0
3226	4/10	4/10	XII[37] or XIII[38]	5.5	—	—	—	—	—

^aNumbers within parallel horizontal lines are from the same developmental series.

^bStages in Arabic numbers after Gosner (13); stages in Roman numerals after Taylor & Kollros (12).

^cMean of five measurements.

^dMean of three measurements.

measured) and the high relative humidity (mean, 88%) at all times in the mountain forests, these oviposition sites probably contain water at all times. Water temperatures in the leaf axils, between 8 a.m. and 5 p.m., ranged from 16 to 22.8 C (mean, 18.7 C). At no time during the day were these sites exposed to direct sunlight.

Eggs and clutch size. The eggs of *P. brevipes* are probably non-pigmented and ivory white when newly laid, judging from the early embryos. Because we lacked gravid females in our collections the size of the eggs was not determined. However, the size probably does not differ very much from those for *P. lighti* and *P. albotaeniata*, both of which have moderately large eggs measuring about 1.5-2.5 mm in diameter (10). Clutch size in these two species is apparently small, large ovarian eggs numbering 4-6 in one ovary. Our clutches of *P. brevipes* embryos and larvae are also small, 5-15.

Embryonic development. One of our five series was collected not long after oviposition, since the embryos that were preserved five days after collection were still in Stage 20 or 21. Unfortunately, however, all of the embryos preserved at collection time were lost, precluding knowledge of their developmental stage. At Stage 20 or 21, the embryos measure 4.0-4.5 mm in body length and 2.6-3.0 mm in tail length (Table 1). The eye primordia appear as faint, unpigmented lateral bulges in the head region. The stomodeum is distinct. The oral suckers are clearly seen but apparently not functional, as no secretion material is visible. One of the five embryos has a minute, rudimentary external gill on the left side of the head region. The tail fins appear translucent.

Description of the tadpole. This description is based on the tadpoles in Stages II [27], V [30], X [35], and XIX in the first two series in Table 1. Body (Fig. 1) ovoid, 4.0-4.5 mm long, 2.5-3.0 mm wide, 1.0-2.6 mm deep; eye diameter in tadpoles older than Stage II [27] about equal to or slightly shorter than distance between eye and tip of snout; oral disk (not developed in Stage II) anteroventral, circular, diameter (0.8-1.2 mm) larger than eye diameter; lips feebly

crenulate; one row of horny teeth on upper lip, none on lower lip; labial teeth unequal in size, 7 in Stage V [30], 13-26 in Stage X [35], 4 in Stage XIX; beaks degenerate, serrated, whitish with brown edges; operculum without spiracle; youngest tadpole (Stage II or 27) with one minute gill filament protruding from left posterior region of head and with primordia of oral suckers on ventral part of head; gut feebly coiled (about 2 coils) clearly seen in Stages V [30] and X [35]; gut still yolky at Stage XIX; anal tube median, fused with ventral fin, with median slit-like opening in Stages X [35] and XIX; hind limb length 0.4-4.0 mm; fore limb buds in Stage II [27] recognizable as faint projections; tail 5.7-9.0 mm long, 1.8-2.8 mm deep at deepest point, tip rounded. upper and lower fin margins subparallel; tail fins originating at base of tail, heavily vascularized but not expanded, dorsal and ventral fins equal in depth in all specimens except one where dorsal is slightly deeper.

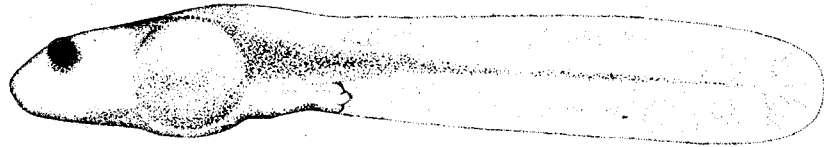


Fig. 1. *Pelophryne brevipes*. Lateral view of larva.

The above description supplements the brief description of Inger (10), which was based on only five larvae taken from a broken bottle in a forest on Mt McKinley (altitude 900+ m) in Davao Province on Mindanao Island. We confirm Inger's suggestion that the larva of this species is non-feeding for the following reasons: (1) there is a large amount of yolk in the early embryos; (2) the yolk persists even in Stage XIX; (3) the gut is only faintly coiled; and (4) the mouthparts are degenerate. Furthermore, it is improbable that the small volumes of water in the leaf axils of *Pandanus* contain enough food organisms for the larvae to subsist on. The larvae apparently depend primarily upon the vascularized tail fins for respiration since the gills are not well developed.

The metamorphosing tadpoles tend to show an hourglass figure on the back and the dark lateral bands, both of which are features serving to distinguish adults of *P. brevipes* from those of *P. lighti*, the only other species of *Pelophryne* occurring on Mindanao Island. It took 42 days for the earliest embryos (younger than Stage 20) to reach Stage XXIII, with tails partly resorbed.

***Rana microdisca parva* Taylor**

Seven lots of 46 larvae in various stages of development from pre-limb bud to Stage XXV were taken from quiet and slow-flowing mountain streams at 700-1700 m elev. on Mt Malindang, Mindanao on five occasions between April 15 and May 1, 1959.

Eggs and clutch number. No eggs or early embryos were collected in the field. However, one female (CAS-SU 20410) measuring 27.0 mm snout-vent length, had seven enlarged eggs in one ovary. The eggs were dark-brown in the animal hemisphere and yellowish in the vegetal hemisphere and measured about 2.2-2.3 mm in diameter.

Larvae. The tadpoles resemble those of *Rana microdisca* from Sarawak in such features as ovoid shape of head and body, dorsolateral placement of the eyes and nostrils, sinistral spiracle, dextral opening of the anal tube, common dental formula I:1-1/1:II, low dorsal fin originating near tail base, pigmentation patterns, and head-body length (9.5-13.0 mm in Stages XX-XXV in our sample; 8.8-9.9 mm in Inger's Bornean sample). Our tadpoles, however, differ somewhat in the shape of the dorsal tail fin, being less convex than is characteristic of the Sarawak examples.

The presence of almost a complete series of developmental stages leaves no doubt about the identification of these tadpoles. Tadpoles in Stage XIX and onwards show the webbing characteristic of the adults, and beginning from Stage XX the crossbars on the limbs are clearly seen.

***Rana signata moellendorfi* Boettger and**

***R. s. grandocula* Taylor**

Twenty tadpoles of *R. signata moellendorfi* were taken from mud pools of mountain streams on Thumb Peak, Pala-

wan in April, 1961, and 61 tadpoles of *R. s. grandocula* in Stages I through XIX were collected from a pool of Dapitan River at 700 m elev., Mt Malindang, Mindanao on April 30, 1959.

The complete series of larval stages, including completely metamorphosed young, leaves no doubt about the identity of the tadpoles of *R. s. moellendorfi*. The extent of webbing of the toes and the crossbar pattern on the limbs exhibited by the transformed young were typical of the adults collected from the same locality. The tadpoles of *R. s. grandocula*, though failing to metamorphose completely, possess characters such as the tooth formula and white glandules which characterize the tadpoles of ssp. *signata* from Sabah, Borneo (10) and ssp. *moellendorfi* from Palawan. There is, therefore, no doubt of their identity.

Our Palawan and Mindanao series agree closely with the Bornean material in most characters, such as body shape, tail shape, mouthparts, placement of anal opening and spiracle, and presence of distinctive whitish glandules. The commonest labial teeth formula in our Palawan material is I:2-2/1-1:II; those in the Mindanao sample are I:2-2/1-1:II and I:3-3/1-1:II in equal frequency. Inger's (10) Sabah tadpoles have a tooth formula identical with that of our Mindanao sample. The head and body lengths of our samples at Stages XIX, XX and XXV range from 13.0 to 14.2 mm.

***Rana sanguinea* Boettger**

A total of 94 tadpoles of this species were collected from shallow, rocky and muddy pools of mountain streams at 90-125 m elev. in the Thumb Peak area, Palawan Island, April 16-24, 1961. The tadpoles were disturbed readily by our presence and were observed to hide beneath rocks when we approached. The water temperature of the pools reached a maximum of about 26 C at mid-day and a low of 21 C in early morning.

The tadpoles were reared in plastic buckets in the field camp and some of them reached Stage XXIII. These froglets show clearly the crossbars on the anterior and posterior limbs. The digits and webs approximate those of the adults, of which several specimens were taken in the same locali-

ties. However, the rhomboid temporal spot, one diagnostic character of the adults, is not yet present.

Eggs and clutch size. No freshly laid eggs were collected, but based on the earliest stages these were apparently laid in the water. One female with a snout-vent length of 59 mm had about 180 pigmented eggs in the two ovaries. The eggs measured 1.5-1.6 mm in diameter.

Description of larvae. The following description of the tadpoles is based on 94 individuals (Stages I to XXIII). Body ovoid, depressed (Fig. 2a); body width about 60% of body length (based on 10 larvae); snout broadly rounded; eyes and nostrils dorsolateral; interorbital distance equal to internarial; nostril-eye distance shorter than nostril-snout distance and shorter than internarial; spiracle sinistral, tubelike, low on left lateral surface, diameter of tube about $2/3$ eye diame-

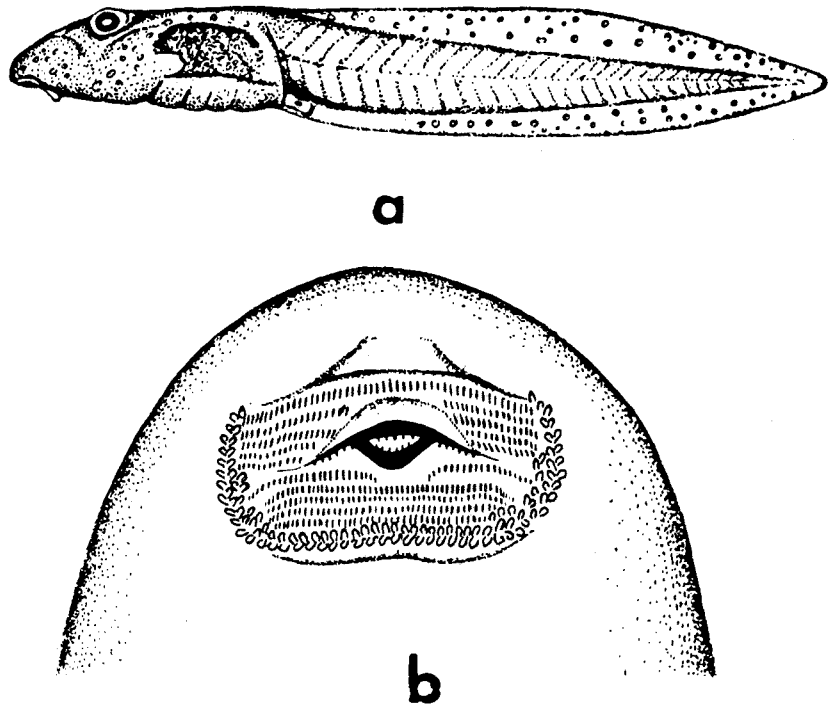


Fig. 2. *Rana sanguinea*. a. Lateral view of larva. b. Mouthparts of larva.

ter, its opening nearer posterior end of body than tip of snout; anal tube opening to the right of ventral fin (dextral).

Oral disk (Fig. 2b) ventral; lower lip bordered by one or two rows of continuous papillae; upper lip and lateral corners of upper and lower lips with three or four rows of papillae; beaks strong, serrated, edged with black; upper lip at maximal development of the tooth rows with one continuous row (outermost) and four medianly interrupted rows; lower lip with one broadly interrupted row (innermost) and four continuous rows, the outer shortest and weakest; of 94 tadpoles, 38 have labial tooth formula I:4-4/1-1:IV; other formulas: II:3-3/1-1:IV (7 specimens), 1:3-3/1:III (6 specimens), II:4-4/1-1:IV (5 specimens), I:4-4/1-1:III (5 specimens), 4-4/1-1:III (5 specimens), rest of tadpoles usually lack one or more divided rows on upper lip.

Tail moderately high, arched dorsally, its tip bluntly pointed; tail muscles well-developed, anterior half deeper than

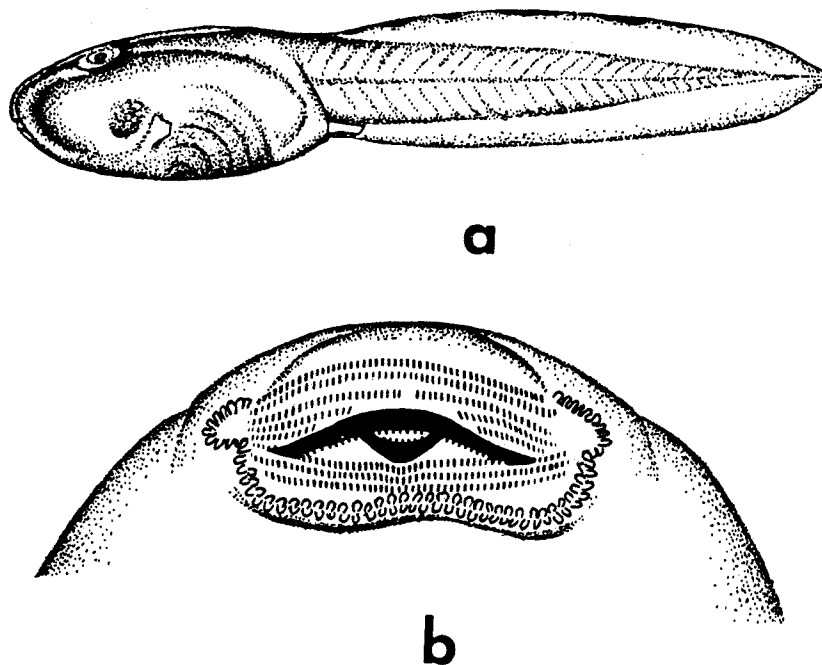


Fig. 3. *Edwardtayloria spinosa*. a. Lateral view of larva. b. Mouthparts of larva.

dorsal or ventral fin; fins fairly high, dorsal deeper than ventral; ratio of tail depth to length 0.23-0.29 (mean of 20 specimens, 0.26); upper fin low near base of tail, shallower than tail muscles at their deepest points; ratio of tail length to body length 1.73-2.12 (mean of 20 specimens, 1.96).

In life, the tadpoles are dark-colored with a greenish tint. In preservative, they are brownish gray, with dusting of black and brown pigments on head, body and tail. The head and body are darker than the tail. There is gradual diminution of the melanophore concentration from the base to the tip of tail. White glandular granules, often with melanophores, are distributed on head, body and ventral portions of body and tail fins.

The data on the total length (mm) of the 94 larvae of this frog are as follows: Stage I, 17.3-25.4 (mean of 11 larvae, 21.9); Stage II, 22.4-29.0 (mean of 15 larvae, 26.4); Stage III, 25.9-31.4 (mean of 23 larvae, 28.7); Stage IV, 26.5-31.3 (mean of 12 larvae, 29.6); Stage V, 28.2-32.3 (mean of 9 larvae, 30.2); Stage VI, 33.0; Stage IX, 31.9; Stage X, 30.5-33.7 (mean of 5 larvae, 32.3); Stage XII, 33.3-34.6 (2 larvae); Stage XIII, 31.8-35.0 (2 larvae); Stage XIV, 31.1-32.5 (mean of 3 larvae, 31.7); Stage XIX, 31.2-36.7 (mean of 5 larvae, 33.6); Stage XXI, 37.6; Stage XXIII, 16.1-21.6 (mean of 4 larvae, 18.3). Head and body length of Stages XX-XXIII ranges from 12.2 to 13.5 mm (mean of 3, 12.7).

Edwardtayloria spinosa (Taylor)

About 120 tadpoles in various stages of development and three adults were found inside a tree hole near the base of a broad-leaved conifer (*Agathis alba*), which was about 1.5 m in diameter. The locality was in the upper dipterocarp forest at about 1100 m on Dapitan Peak, Zamboanga Peninsula, Mindanao Island, May 6-7, 1959. Part of the central, woody portion at the base of this tree had been burned but the tree had survived. Rain water, charcoal and rotting leaves had collected in the cavity. The water in which the tadpoles were found was about 1.5 to 2 ft deep. The temperature, taken in the late afternoon, was 21 C. The adult frogs were clinging to the charred inner walls of the cavity near the

water level. A very low, diffused light penetrated the hole during the daylight hours. No permanent body of water was observed in the vicinity of the tree. Dapitan River was about a thousand feet below the site.

Taylor (3, p. 95-96) mentions finding adults and tadpoles of this species, including a newly metamorphosed individual, in a similar water-filled tree hole on Basilan Island. His description of the larvae, however, is very limited and our series of stages provide additional data.

Description of larvae. Body oval, depressed (Fig. 3a), dorsal surface flattened, body length twice its depth and slightly more than $1\frac{1}{3}$ times its width (based on 20 specimens); snout broadly rounded, internarial distance shorter than interorbital, equal to eye-nostril distance; nostrils about equidistant from eye and from snout tip; eyes dorsal; spiracle slit-like, ventro-lateral in position, in line with corner of mouth and ventral edge of tail muscles, nearer anus than tip of snout; anus forming short tube, opening medianly; gut highly coiled.

Mouth (Fig. 3b) anteroventral or subterminal, two continuous rows of papillae of about equal size bordering lower lip and lateral corners of upper lip; beaks well-developed, serrated, black; at maximal development of teeth, upper lip with five rows, two outer ones usually continuous and about equal in length, other three rows medianly interrupted; lower lip with three continuous rows, subequal in length; dental formulas II:3-3/III (62 specimens), II:3-2/III (9 specimens), II:2-2/III (8 specimens), I:4-4/III (5 specimens), and I:3-3/III (4 specimens); typical formula (II:3-3/III) observed at Stage I; some tadpoles in Stages I and II lack one or both series of the short, innermost row on the upper lip; teeth and beaks lost at Stage XX.

Tail moderately high, blunt, deepest at point near base; ratio of tail depth to length 0.31-0.41 (mean of 20 specimens, 0.35); upper fin originating near base (point level with origin of hind limbs) of tail, about equal in depth to lower fin, tail muscles well-developed, deeper than both fins in the anterior half or two-thirds of tail; ratio of tail length to body length 1.29-1.66 (mean of 20 specimens, 1.47).

In Stage XXIII the spinules on the dorsal surface are well-developed, and the toe webbing approximates that of adults.

In formalin, the head, body and tail muscles are reddish brown; tail fins are light gray. The crossbars on the hind limbs are clearly seen at Stage XVI, and the white, roundish spots on the dorsum, characteristic of adults, are first seen at Stage XX.

The data on total length (mm) of the tadpoles are as follows: Stage I, 26.2-34.1 (mean of 13 larvae, 33.6); Stage II, 31.0-44.1 (mean of 15 larvae, 39.7); Stage III, 38.7-47.7 (mean of 16 larvae, 45.1); Stage IV, 44.9-49.7 (mean of 4 larvae, 46.9); Stage V, 46.9 (1 larva); Stage VI, 47.8-51.9 (mean of 6 larvae, 51.1); Stage VII, 46.7-48.8 (2 larvae); Stage VIII, 49.0-49.7 (2 larvae); Stage IX, 47.3-48.5 (2 larvae); Stage X, 48.9-52.0 (mean of 3 larvae, 47.6); Stage XI, 50.7-52.3 (mean of 3 larvae, 51.3); Stage XII, 48.9-53.6 (mean of 3 larvae, 50.0); Stage XIII, 48.4-51.2 (mean of 3 larvae, 50.0); Stage XIV, 52.6-54.7 (mean of 5 larvae, 53.8); Stage XV, 55.0-56.0 (mean of 3 larvae, 55.9); Stage XVI, 52.0-54.4 (2 larvae); Stage XVIII, 49.9-55.1 (6 larvae); Stage XIX, 52.3-52.5 (2 larvae); Stage XX, 49.5 (1 larva); Stage XXI, 44.4 (1 larva); Stage XXIII, 29.2 (1 larva). The head and body length of tadpoles in stages XIX-XX is about 19.5-20.5 mm.

Since our series contained nearly complete larval stages (Stages I-XXIII), there is no doubt about the identity of the tadpoles. Inger (11, p. 351) described the larvae of *Edwardtayloria* (under *Hazelia*) *picta* from Borneo. [*Edwardtayloria* (Marx, 1975) (14) is the substitute name for *Hazelia*, which is preoccupied.] The larvae of this species and *E. spinosa* are similar in the characteristics of the body, mouthparts, and tail. The similarity of the labial-tooth formulas in the two species is especially striking.

***Rhacophorus zamboangensis* (Taylor)**

Oviposition site. In May, 1971, we observed a pair in amplexus on a rock in a stream bed at 700 m elev. on Mt Hilong-hilong, Mindanao. The amplexic pair was collected and placed in a plastic bag, and a foamy mass containing a few non-pigmented eggs was found the next morning. The embryos, unfortunately, died before reaching the laboratory.

The species lays eggs in a foamy nest which is probably attached to substrates above mountain streams.

Larvae. On April 13, 1979 a metamorphosing young, still with a long tail, was observed and photographed on a leaf overhanging a mountain stream at 1100 m elev. in the Mt Hilong-hilong area. The tadpole was brought to the laboratory where it continued to develop to nearly full transformation. Most probably, the species normally utilizes streams for larval development.

***Rhacophorus appendiculatus* (Gunther)?**

Inger (11, p. 286) tentatively referred to this species a series of larvae collected from a small, temporary, forest pond in North Borneo, primarily on the extent of the webbing of hands and feet. He noted especially the lack of horny beaks and teeth, as in *R. hosei*.

Although we have not observed the breeding behavior of *R. appendiculatus*, 11 adult specimens of this frog were collected in the original dipterocarp forest at about 1,000 feet elev. in the Bagtik River Valley, near Dungga, in southwestern Negros on April 12-16, 1957. These were picked up at night on the leaves of *Pandanus* trees growing above the pools of a mountain stream. The males were calling at the time of collection. On May 22, 1959, six larvae were collected from a pool in a small stream emptying into the Bagtik River in the same locality. The larvae ranged from Stage XVII to XXIII. Based on the nature of the disks, the complete webbing of the toes, the crossbars on the hind limbs, and the tooth formula (which differs from that of *R. pardalis*, the only other species of the genus known from Negros Island), we have little doubt that these larvae belong to *R. appendiculatus*.

The data on total length (mm) of the six larvae available for study are as follows: Stage XVII, 44.9 (1 larva); Stage XVIII, 48.1 (1 larva); Stage XIX, 45.5 (1 larva); Stage XX, 40.1-42.4 (2 larvae); and Stage XXIII, 31.3 (1 larva). The last larva possesses crossbars on the limbs and complete webbing on the toes. Some broken lines are generally evident, running in an anterior-posterior direction on the body, and small round white spots are distributed all over the body and the tail.

Larvae. Body depressed, with dorsal surface slightly sloping; body length twice its depth and one and a half times its width (based on 3 specimens); snout rounded; nostrils about midway between eye and tip of snout and dorsolateral in position; spiracle tube-like, on left side, in line with ventral edge of tail muscles and tip of snout and about midway between tip of snout and anus; anal tube opens medianly.

The mouth is ventral in position with papillae of unequal sizes bordering lower lip and lateral corners of upper lip; those on lower lip arranged in a single row in median part but in double rows toward corners of mouth; beaks serrated and edged with black; dental formulas of three larvae I:3-3/1-1:III (2 specimens) and I:4-5/1-1:III (1 specimen). The latter larva shows symmetrical breaks in the two lower rows on the lower lip.

The most striking difference between these larvae and those from Borneo identified by Inger (11) as *R. appendiculatus* is the absence of beaks and teeth for the Bornean series and the presence of these structures in the Philippine series. Since neither Inger's nor our series contained fully metamorphosed individuals, the data may be interpreted in various ways: (a) One of us or both of us may be in error as to identification. (b) If the larval series in both instances are correctly associated with adult populations, the population in Borneo must represent a different species; the type locality for *R. appendiculatus* is Philippines. Further field work is necessary before these questions can be answered.

PHILAUTUS

Data on life histories of species assigned to this genus by Liem (15) have not been previously published except those for *Rhacophorus* (= *Philautus*) *hosei* from Borneo. Inger (11, p. 306) states:

The absence of the usual larval oral apparatus and of gills and operculum at early limb bud stages suggests that larvae of *hosei* have an abbreviated free swimming stage if that stage is not in fact completely suppressed.

At various times from 1959 to 1979 we collected clutches of amphibian eggs from arboreal sites similar to those used

for egg deposition by *Platymantis* spp. In April and May, 1959, 15 clutches of frog embryos (seven from leaf axils of *Pandanus* and eight from aerial ferns) were collected in the forests at 1,700 to 2,000 m elev. on the upper slopes of Dapitan Peak, Zamboanga Peninsula, Mindanao. On April 28, 1963, 2 clutches of embryos, also undergoing direct development, were taken from bird's nest ferns in the submontane forest at 1,400 to 1,500 m elev. on Mt Halcon, Mindoro Island. On May 19-25, 1971, we collected 15 clutches of 148 frog embryos and larvae in the forest on Mt Hilong-hilong in Agusan del Norte Province, Mindanao Island. One clutch was taken from the ground at an altitude of 400 m, one from the leaf base of a wild banana at 900 m, one from a bird's nest fern (*Asplenium nidus*) at 1,900 m, and 12 from the leaf axils of the screw pine (*Pandanus*) at 1,500-2,000 m. These arboreal egg-laying sites were 5 to 25 ft above the ground. The collecting locality in Mt Hilong-hilong was revisited in April, 1979, and two more clutches of embryos were taken from bird's nest ferns at an altitude of 1,550-1,700 m. One of the two clutches had 17 larvae and the other had 19 embryos.

A number of the clutches were placed in plastic bags and observed to continue in the direct development mode. It soon became evident that these were not *Platymantis* eggs, however, as the larval respiratory structure was a greatly expanded, vascularized tail rather than consisting of expanded abdominal sacs typical of *Platymantis*.

On the basis of the toe structure, webbing, color pattern, and rugosity of the skin for the fully metamorphosed froglets in some of the Mt Hilong-hilong series, the clutches from this locality can be assigned tentatively to *Philautus lissobrachius*. These clutches were from *Pandanus* leaf axils. The series from Mindoro are referred to *P. schmackeri*, the only species of the genus known from that island. Others from northeastern Mindanao and those from Zamboanga Peninsula, western Mindanao, are identified only as *Philautus* spp.

***Philautus lissobrachius* (Inger)**

Oviposition sites. Two clutches of embryos and larvae, on which the following description is based, were taken from

leaf axils of *Pandanus* and bird's nest ferns at 1200-1500 m elev. on Mt. Hilong-hilong, Mindanao on April 8, 1979. Earlier, in May, 1971, in the same locality at 1500-1800 m elev., 10 other clutches were collected, also from leaf axils of *Pandanus*.

Eggs and clutch number. The eggs are non-pigmented and uniformly creamy in color in life. Freshly laid eggs are about 3.0 mm in diameter exclusive of the three layers of gelatinous capsules. Oviducal or ovarian eggs of two females (Field Nos. 33866 and 33719) measure 2.5-3.0 mm in diameter. The diameter of the eggs inclusive of the capsules is 8.5-9.0 mm. Clutch number in the material collected in 1979 varies from 17 to 19; that in the material, 5 to 13 (mean, 10.7). To further verify the clutch number, two females were dissected: No. 33866 had 6 enlarged eggs in the right ovary, and No. 33719 had 5 eggs in the left oviduct. This suggests that clutch number is probably at least a dozen.

Development. We arbitrarily divide development into *embryonic*, *limb bud*, *hind limb paddle* and *operculum*, and *metamorphosis stages*. The data on a series of specimens are summarized in Table 2.

Embryonic stages. The earliest stage, blastula stage, is represented by one embryo in one of the 1971 series. One embryo in the 1979 series is in the pre-limb bud stage. The body at the latter stage is seen as a dorsal thickening. The head is distinguishable and heavily pigmented. Optic primordia are also evident. Age is estimated at 10+ days.

Limb bud stage. Five larvae in the 1971 series and two in the 1979 series are in this stage (Fig. 4a). Head, body and tail are elevated above the yolk; the head forms an obtuse angle with the yolk. The body is slightly curved over the yolk. The eye and nose primordia are clearly indicated. The primordia of the upper and lower jaws are well-developed, enclosing a fairly deep stomodeum. The gut shows no coiling. There is no evidence of external gills. Head and body length is 3-4 mm. The fore and hind limb buds are developed. Hind limb buds may begin to flatten. An opercular fold at base of fore limbs is evident. The length of the fore limb buds is 0.1-0.2 mm, of hind limb buds, 0.2-0.3

Table 2. Measurements (in mm) of 24 embryos and larvae of *Philautus lissobranchius* from Mt Hilong-hilong, Agusan del Norte. Numbers in parentheses refer to tail length.

Stage	Estimated age (days)*	Field number							
		34189	34190	34192	34194	34196	34199	34200	34201
Late cleavage diameter	?	—	—	—	—	—	2.8	—	—
Limb bud									
body length (tail length)	5-10+	—	—	3.0(1.8) 3.0	—	3.0(2.0)	3.4(2.0)	—	3.0(2.0)
Hind limb, paddle, and operculum									
body length (tail length)	10-15+	4.0(5.6)	3.9(4.3)	—	3.5(3.9)	—	—	3.2(2.8)	—
Early metamorphosis									
body length (tail length)	15-25+	—	—	4.5(6.0)	4.4(5.2)	—	4.4(6.7)	3.7(4.4)	—
Late metamorphosis									
body length (tail length)	25-46+	4.6(4.9) 5.5(2.1) 5.0(1.2)	4.6(4.8) 5.2	—	5.2(2.4)	—	5.0(2.3) 4.9	4.7(1.6)	—

*Age calculated from late cleavage stage (Field No. 34199).

mm. The tail is curved over the latero-ventral side of the yolk and fins are beginning to expand. The tail length is 2.0-3.0 mm, tail breadth 1.0-1.5 mm. Melanophores are evident on all surfaces except on the tail fins and ventral part of yolk. The age of the early limb bud stage is 12+ days, the late limb bud stage, 15+ days.

Limb paddle and operculum stages. Two larvae in the 1979 series and five in the 1971 series exhibit these stages. The head and body axis is straight (Fig. 4b). The mouth is developed, its angles level with anterior margin of eye in the late stage. Eyes are well-developed, the lens being clearly visible. Nostrils are indicated by pigment-free patches anterior to eyes. The head and body length is 3.2-4.0 mm. Fore and hind limb paddles have two indentations in the early stage (Fig. 4b). An operculum develops from the lower jaw region, ultimately completely covering fore limbs in the late stages (Fig. 4c). The completed operculum is without a median opening. The hind limb paddles in the late stage have four indentations, separating all five toes, and measure 1.5-1.7 mm in length. In the 1971 series, development of indentations in the hind limb paddle appears asynchronous with development of the operculum; for example, larvae with complete opercula may have 2, 3, or 4 indentations on the hind limb paddle. No internal gills are evident inside the operculum.

The tail in the late stage is longer than head and body, is curved over left or right lateral side of body and yolk, and has a rounded tip, with expanded or broad fins that are highly vascularized (Fig. 4c). The tail length is 2.5-2.8 mm in the early stage, 5.6-6.5 mm in the late stage. Melanophores are present except on tail fins in the late stage. Age of the early stage is 17+ days, and of the late stage, 18+ days.

Metamorphosis stages. The first step in metamorphosis is the thinning of the operculum at the sites of fore limb eruption. The operculum becomes almost completely resorbed resulting in the full exposure of the fore limbs (Fig. 4d). Fingers and toes are dilated at the tips. The tail is at its maximum development, curved over the left lateroventral side

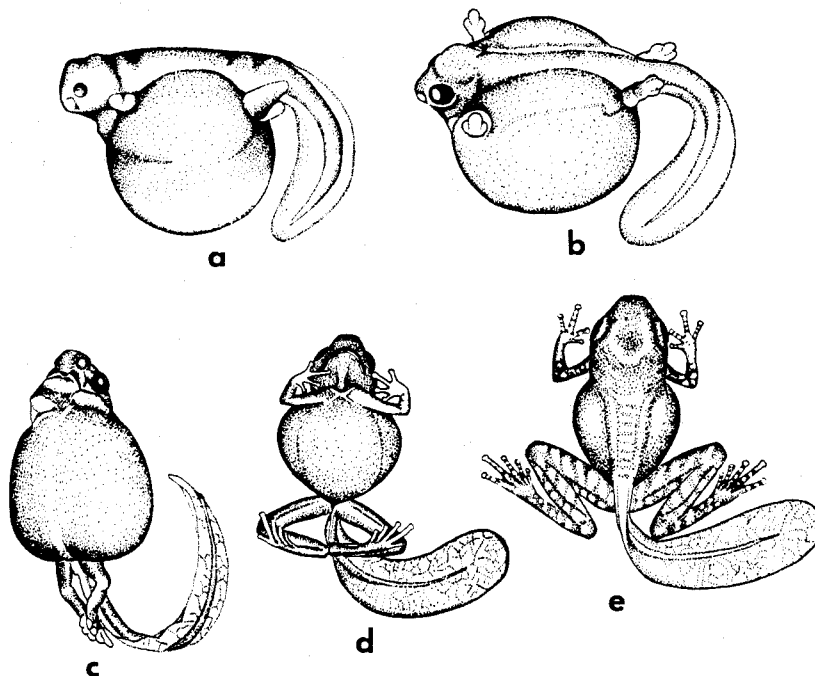
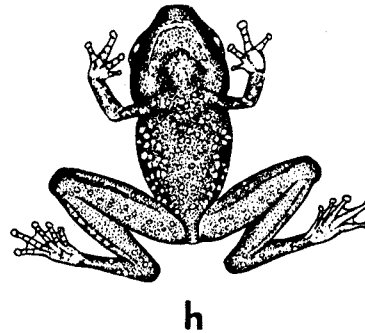
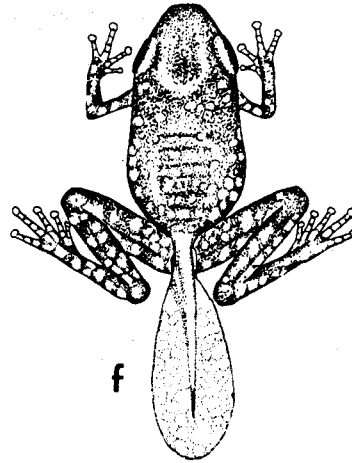


Fig. 4. *Philautus lissobranchius*. a. Lateral view of larva in limb bud stage. b. Dorsolateral view showing operculum developing around fore limbs. c. Ventrolateral view of operculum enclosing fore limbs. d. Ventral view showing resorbed operculum and fully exposed fore limbs. e. Dorsal view of transforming froglet with fully developed tail. f. Dorsal view of froglet with partly resorbed tail. g, h. Completely transformed froglet, dorsal (g) and ventral (h) views. i. Undersurface of foot of transformed froglet showing extent of webbing.

of body. The ventral surface of the body and yolk are pigmented. The head and body length is 3.6 mm; the tail length, 6.3 mm. Age is 19+ days.

The next older stage in the 1979 series has the operculum completely resorbed (Fig. 4e). The yolk is noticeably decreased in amount but still substantial. Fingers and toes have subarticular tubercles, and the tips are dilated. The tail, still near maximum development, is curved over left lateroventral side of hind limb and body. Head and body length is 4.0-4.5 mm, and tail length, 4.6-5.6 mm. Age is 24+ to 26+ days.



Two individuals which are a few days older than the preceding ones have small roundish spots on dorsum (Fig. 4f). The angle of mouth is level with the middle or posterior margin of eye. Yolk is still present, but the body does not bulge ventrally. Crossbars are faintly indicated on the hind limbs. The tail is somewhat reduced in length, curved over right hind limb along the side of body. Head and body length is 5.2 mm; tail length, 4.2-5.0 mm. Age is 29+ to 31+ days.

Seven froglets at about time of hatching have completely or almost completely resorbed tails (Fig. 4g-h). All except one froglet have distinct crossbars on limbs and white circular spots on dorsum. Fingers are webbed at base only. Webbing on toes is more extensive than on the fingers, nearly

as extensive as in adults (Fig. 4i). Hatching froglets show no visible yolk. Head and body length is 4.8-5.6 mm. The age of completely transformed froglets is 38+ to 41+ days.

***Philautus schmackeri* (Boettger)**

Oviposition site. Two clutches of larvae undergoing direct development were collected from leaf axils of bird's nest ferns which were growing on trees a few meters above the ground at 1280-1370 m elev. on Mt Barawan, Mindoro Island, April 28, 1963. There were 15 larvae in one clutch and 12 in the other. Unfortunately, only two larvae, both in the hind limb paddle and operculum stage, were alive at collection time; the rest of the larvae had died earlier.

Eggs and clutch size. Ovarian eggs are uniformly creamy and unpigmented. The largest ovarian eggs measure 2.5-2.8 mm in diameter. Five undeveloped eggs or very early embryos in the two clutches mentioned above vary from 2.7-3.0 mm in diameter, exclusive of the capsules. With the capsules they measure 4.5-5.2 mm. Five gravid females collected from the same locality as the two clutches of larvae were dissected. One had 3 enlarged eggs in one ovary, two had 5, one had 6, and one had 7. Clutch number for this series ranges from about 6 to 15.

Limb paddle and operculum stages. In the paddle stage represented by this series, the head and body are arched over the yolk (Fig. 5), with the head somewhat elevated and

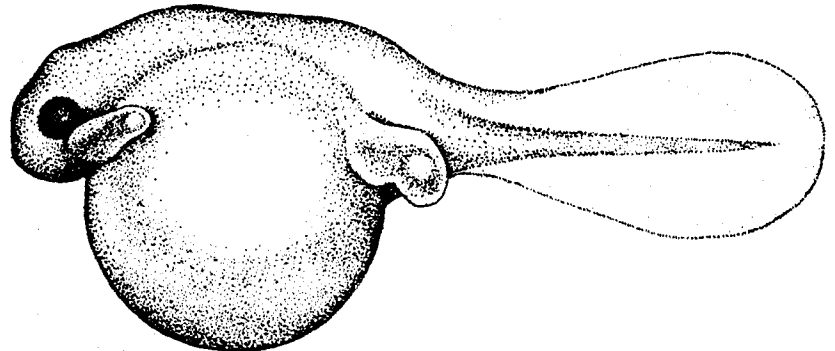


Fig. 5. *Philautus schmackeri*. Lateral view of larva in the limb paddle and operculum stage.

forming an acute angle. Mouth, eyes, and nasal pits are well-developed. The usual tadpole mouthparts — beaks, lips and labial teeth — are absent. Two visceral arches are evident. There is no sign of coiling of the gut. Head and body measure about 3.0 mm long in both larvae. Hind limb paddle, without indentations, measure about 1.0-1.2 mm in length. Fore limb buds are about 0.5-0.7 mm long. In both larvae, the operculum has begun to develop at the base of the fore limbs. The tail is somewhat expanded, curved and closely applied to one side of the yolk. Tail fins and muscles are beginning to differentiate and the tail tip is rounded. Melanophores occur on the head, body and dorsal part of yolk but not on the tail.

The close similarity of the developmental pattern of this series to that of the larvae of *Philautus lissobrachius* and the fact that there is only one species of *Philautus* recorded from Mt Barawan, Mindoro make it almost a certainty that the two clutches belong to *Philautus schmackeri*.

Philautus spp.

Two clutches of eggs were taken in 1971 from the leaf axils of wild banana and aerial ferns at about 1000 m elev. on Mt Hilong-hilong. Earlier in 1959, we collected 15 clutches of similar eggs from *Pandanus* and aerial ferns at 1500-1800 m elev. on Mt Malindang. We are not sure of the identity of these 17 clutches as yet. All exhibit direct development similar to that of *Philautus schmackeri* and *P. lissobrachius*. We suspect that these clutches belong to at least two different species of *Philautus*, but identification is held in abeyance pending the availability of a more complete series of stages.

Illustrations were prepared by Mr Walter Zawojski at Stanford University and Mr Moses Alcala at Silliman University.

Literature cited

- (1) D.V. Villadolid and N. del Rosario (1930). Philipp. Agric. 18: 475.
- (2) S.M. Cendaña and D.V. Fermin (1940). Philipp. Agric. 28: 626.
- (3) E.H. Taylor (1921). Amphibians and Turtles of the Philippine Islands. Bur. Sci., Manila, Publ. 15. 193 p.
- (4) R.F. Inger (1954). Fieldiana, Zool. 33: 183.
- (5) R.F. Inger (1956). Fieldiana, Zool. 34: 389.

- (6) A.C. Alcalá (1955). *Silliman Jour.* 2: 175.
- (7) A.C. Alcalá and W.C. Brown (1957). *Herpetologica* 13: 182.
- (8) A.C. Alcalá (1962). *Copeia* 1962: 679.
- (9) W.C. Brown and A.C. Alcalá (1982). Modes of reproduction of Philippine anurans. In *Advances in Herpetology and Evolutionary Biology. Essays in honor of Ernest E. Williams, A.G.J. Rhodin and K. Miyata, Eds.* (Mus. Comp. Zool., Harvard Univ., Cambridge, Mass.)
- (10) R.F. Inger (1960). *Fieldiana, Zool.* 39: 415.
- (11) R.F. Inger (1966). *Fieldiana, Zool.* 52: 1.
- (12) A.C. Taylor and J.J. Kollros (1946). *Anat. Rec.* 94: 7.
- (13) K.L. Gosner (1960). *Herpetologica* 16: 183.
- (14) K.W. Marx (1975). *Sci. Publ. Sci. Mus. Minnesota* 2(3): 1.
- (15) S.S. Liem (1970). *Fieldiana, Zool.* 57: 1.