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A unique case of mating behaviour in a Malagasy tree frog, *Gephyromantis liber* (Peracca, 1893), with observations on the larval development (Amphibia, Ranidae)

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ABSTRACT

The mating act in *Gephyromantis liber* and in other species of this genus differs from all other mating behaviour patterns known in Anura. The male settles with the ventral side of his thighs on the shoulders of the female, and oviposition starts without delay. The assumption is made that the femoral glands of the male play a rôle in the short mating contact.

G. liber is a small arboreal frog, which is widely distributed in the Malagasy central Highlands. During the rainy season the eggs are deposited in a gelatinous mass on leaves overhanging shady small shallow puddles, in which the hatching larvae drop. The embryo does not develop external gills, and hatches by the time the spiracle and the horny beak are present. The tooth formula of the full grown larvae is in general 1/3 + 3//3.

INTRODUCTION

Field observations on the related endemic Malagasy genera *Gephyromantis* Methuen, 1919, *Mantidactylus* Boulenger, 1895, and *Mantella* Boulenger, 1882, belonging to the subfamily Mantellinae Laurent, 1946, of the Ranidae, are very scarce.

A few field notes on *Gephyromantis* have been published by Millot & Guibé, 1951, the life history of *Mantella aurantiaca* Mocquard, 1900, was studied by Arnoult, 1966, and tadpoles of some *Mantidactylus* species by Arnoult & Razarihelisoa, 1967.

During our stay in Madagascar from November 1970 till May 1973, we collected numerous egg masses, tadpoles, juveniles, and nearly 100 adult specimens of *Gephyromantis liber* (ZMA No. 6634-6639, 6641-6668). We also made notes on several aspects of their life history, of which especially the mating behaviour and embryonic development appear representative for

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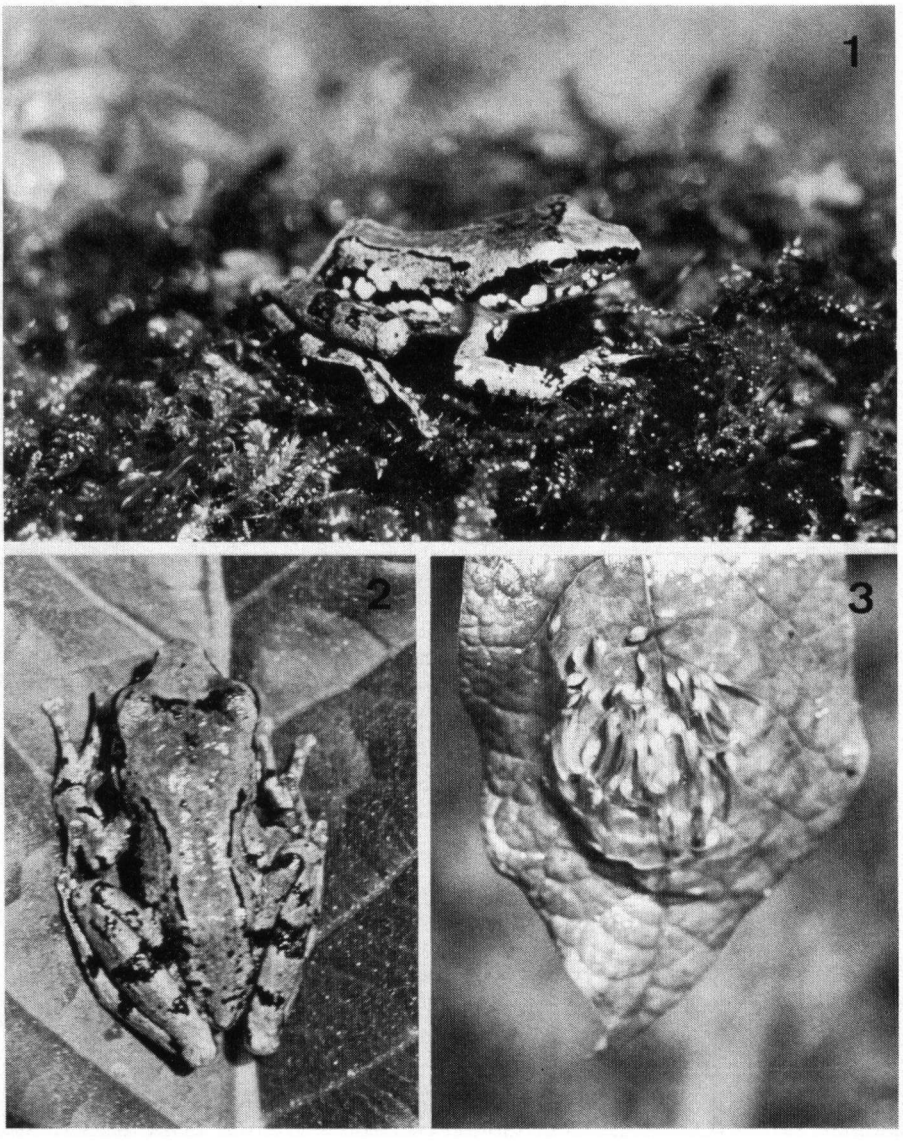


FIGS. 1—3. *Gephyromantis liber*: 1 and 2, male from 20 km south of Moramanga; 3, embryo mass on a leaf.

at least a number of species of the same genus and to a lesser degree for other genera in the same subfamily.

SYNONYMY AND GENERIC ALLOCATION

Gephyromantis variabilis Millot & Guibé, 1951, is a synonym of *Rhacophorus liber* Peracca, 1893 (Guibé in litt.).

Methuen, 1919, has created the Malagasy genus *Gephyromantis* to separate the species with connected lateral metatarsalia from related species in the genus *Mantidactylus*, which have the lateral metatarsalia separated by a web. Guibé (1945) has discovered that the *Gephyromantis* species are also characterized by a bifurcated bony stalk of the sternum on the side of the coracoid, while the stalk in *Mantidactylus* is simple. The bony stalk of the omosternum is bifurcated in both genera. Using this osteological character for discrimination, he noticed that the character used by Methuen is variable in the redefined genus.

Rhacophorus liber shows both the osteological feature emphasized by Guibé and the connected lateral metatarsalia used by Methuen. So this species belongs at any rate to the genus *Gephyromantis*.

Secondary sex characters and size

The only observed external differences between the sexes is the coloration of the ventral side of the body. In live specimens the ventral side of the female is evenly pale green, while the throat of the male is clear white and the belly and the underside of the legs are blackish. This difference is most conspicuous in the breeding season. The size of adult females varies from 23 to 32 mm and of adult males from 21 to 29 mm. A size of 25—27 mm is commonly found for both sexes.

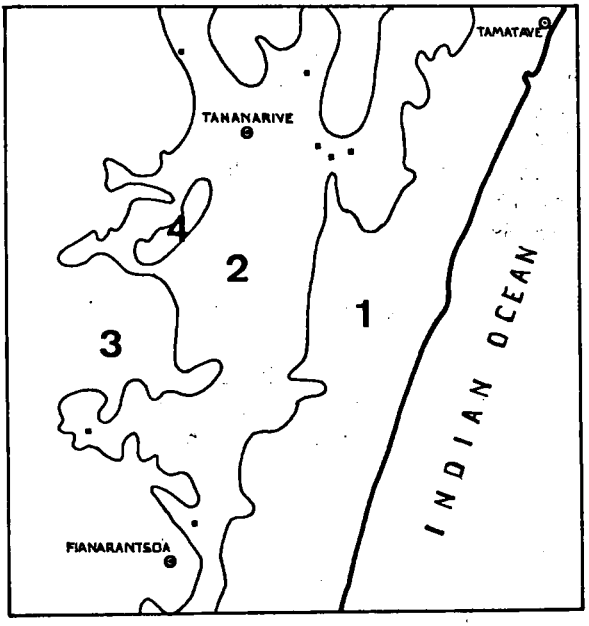


FIG. 4. Distribution of *G. liber*. 1, East Domain; 2, Centre Domain: Central Highlands above 900 m; 3, western slopes of the Centre Domain; 4, High Mountains Domain.

Geographical distribution

G. liber was reported previously only from Perinet and Itremo (Millot & Guibé, 1951). We have collected it in the following localities:

Along the road from Ranomafana to Ifanadiana at 5 km, 800 m; along the road from Moramanga to Anosibe at 25 km, 900 m; Perinet at an altitude of 900—1100 m; Mandraka valley along the road from Tananarive to Moramanga at 69 km, 1200 m; Anjozorobe, altitude 1300 m; and Tampoketsa d'Ankazobe, alt. 1600 m (fig. 4).

According to Humbert's phytogeographical divisions (1955), all these localities belong to the Malagasy Centre Domain, which comprises the central highlands, except the high mountain tops. The altitudes in this Domain range from 800 m up to 2.000 m. *G. liber* was not found in other Domains. From 800 m to 1300 m this area is characterized by the so-called medium altitude dense rain-forest, which is nowadays confined to isolated patches and a fringe on the steep escarpments on the east-side of the highlands. Most of our collections were made in more or less degraded forest of this type. In Tampoketsa d'Ankazobe some of the last vestiges of high altitude forest are preserved.

Climate of the Centre Domain

The annual rainfall amounts to 1.500—2.000 mm, falling almost entirely in the hot season. The start of the rainy season varies from year to year, between the end of October and the beginning of December. The heavy rains brought by the eastwinds fall mostly in intense thunderstorms in the afternoon and early evening. This season lasts till a date between the end of March and mid-May. Although the dry season may extend to several months, its aridity is very much moderated by abundant dew formation, condensation and frequent fogs. The difference between the mean temperatures of January and July is at least 6° C.

Habits and habitat

G. liber is an arboreal frog and inactive during the day. Throughout the year their favoured resting places are various phytotelmes, such as axils of the larger *Pandanus*, *Typhonodorum lindleyanum* (Araceae), *Banana* and *Ravenala madagascariensis* (Musaceae), as well as of some Amaryllidaceae (*Crinum firmifolium*), palms (*Rapphia*) and arborescent ferns. The occurrence of this species in *Pandanus* and *Ravenala* is mentioned already by Millot & Guibé (1951). These phytotelmes contain nearly always some water, even in the dry season. Where these plants are standing close to the waterside, the frogs are frequently found in quantity, always sitting with the heads upwards and frequently accompanied by other *Gephyromantis* species, such as *G. methueni* and *G. pulcher*, and *Megalixalus* species.

G. liber appears to be positively thigmotactic, for also in captivity it prefers hiding-places that fit the body. When threatened it shows a tendency to retreat backwards in its hiding-place. *G. liber* becomes active at dusk and seems to feed primarily on small insects like mosquitoes and flies, which are abundant around their humid resting-places. In captivity they took their flying small preys in a sitting posture or walking.

Reproductive behaviour

Observations about spawning season, breeding sites and reproductive behaviour were made exclusively in Perinet and the Mandraka-valley. In the rainy season the present species congregates on the vegetation near their breeding-sites: small shallow pools, without water-plants and situated in the shade of surrounding shrubs and trees. The bottom is covered with fallen leaves and mud. The soil consists of laterite and the water has a low pH (Roederer, 1972). The greater part of these pools disappear in the dry season.

The males start singing after sunset; the mating call consists of a single short blast, a high and loud "pooo", while the clear white throat becomes about hemispherically inflated. Breeding seems to take place from November to May. Egg masses and gravid females were found in that period, while the males could be heard on rainy evenings.

It is remarkable that we never observed an amplexus in either *Gephyromantis* or *Mantidactylus* species. Even in collections of both sexes made on the height of the breeding season, not one male showed an attempt to embrace a female, contrary to, for example, *Rhacophorus* and *Megalixalus* species under identical conditions.

The evening of the 6th of January 1973 in the Mandraka-valley brought proof of the absence of any sort of amplexus in the mating act of *G. liber*. After sunset at 8 p.m., in pouring rain, I observed a female and a singing male in the same shrub at a distance of about 30 cm from each other. The female moved in the direction of the male and, reaching him, tried to push her head from behind underneath his belly. The male did not seem to notice her at first and continued singing. She tried over and over again and finally after some minutes, he stopped singing and placed his hind legs in such a way that the ventral side of his thighs touched the dorsal side of her head and shoulders (fig. 5). In this posture, the male showed heavy lateral pulsing movements in the flanks, while the female started depositing her eggs without delay. The leaf on which they were sitting, was situated 1.5 m above a shallow pool of 10 cm depth and the first eggs were deposited on the lowest part, each following row of eggs was placed above the former one. She finished the deposition of about sixty eggs within 10 minutes. The male did not wait that long, but left her some minutes before she was ready and started singing at some distance. We took the nest and observed the development of almost all eggs to hatchling stage. Therefore, the observed mating behaviour of *G. liber* appears to be regular for this species. Apparently, the

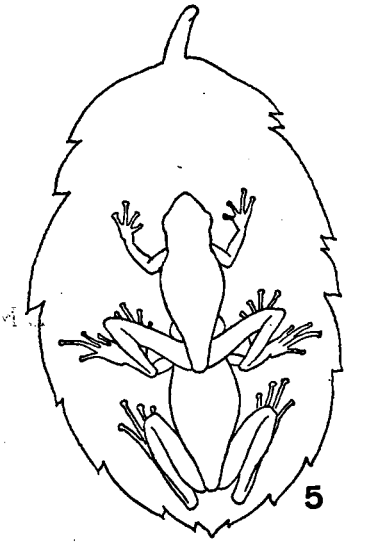


FIG. 5. Mating posture of *G. liber*.

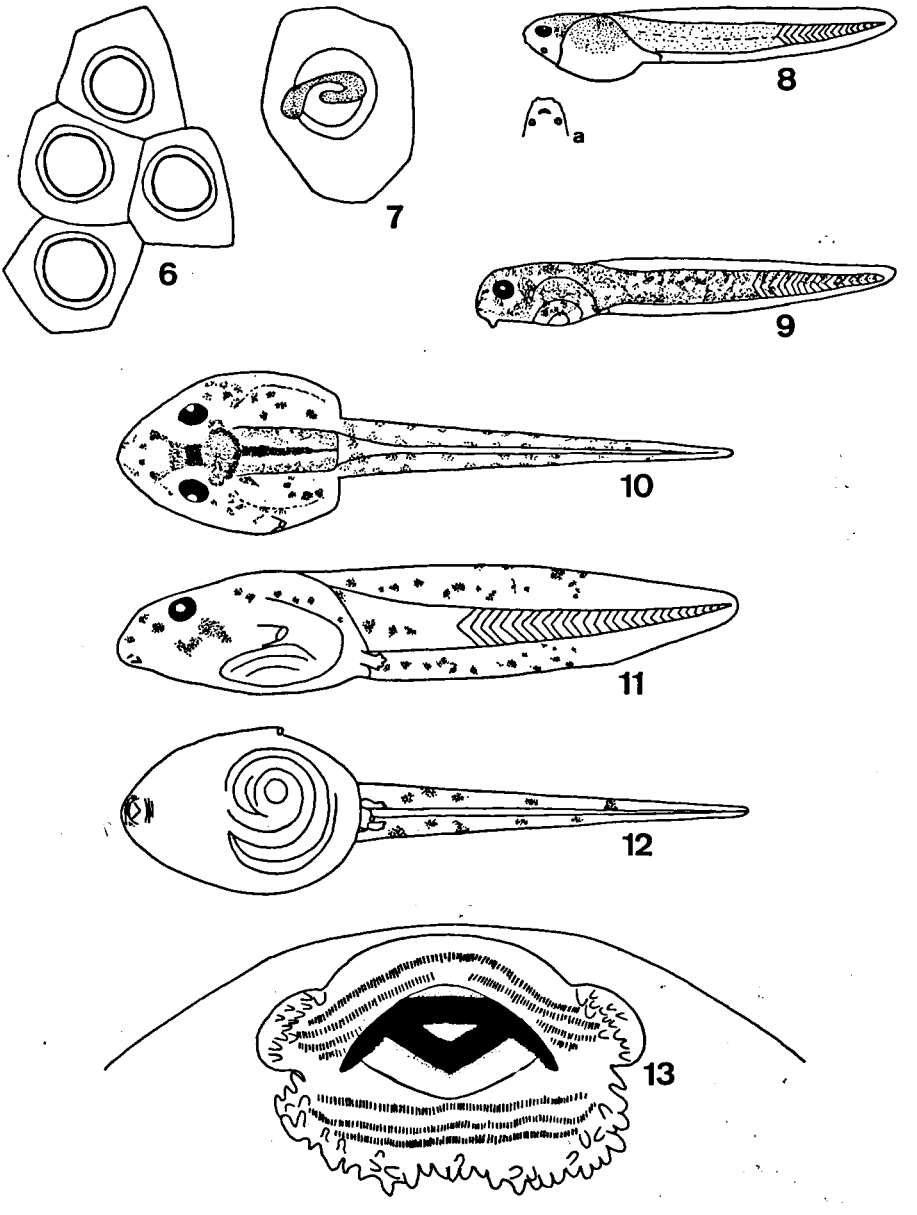
male ejaculates the sperm on the back of the female, leaving it to find its way downwards to the eggs. We observed a similar behaviour in some not yet identified species of the same genus.

EGGS AND EMBRYONIC DEVELOPMENT

One nest may contain 30 to 90 eggs, in general about sixty. Since dissected females show the same egg numbers, a female produces one eggmass at a time. The freshly laid egg measures 1.3—1.5 mm in diameter and has a pale green colour with one brownish pole. Its distance to the vitelline membrane is about 0.16 mm. The contour of the outer envelope is angular, from 2.5 to 4.5 mm in diameter (fig. 6), the outer envelopes of the eggs near the outside of the eggmass are larger than in the centre. The gelatinous mass is completely transparant and colourless and nearly always attached to an almost vertical surface, like hanging leaves, rarely encircling a twig. Initially it is a rather flat mass, round or slightly oval in contour, 2—3 cm in diameter, of a quite stiff consistency. In the following days it reaches a size of 4.5—6 cm as a consequence of liquification. After 5—7 days the developing tadpoles wriggle violently and fall out of the jelly mass into the water below.

Egg masses are located always above the water, from a height of 30 cm upwards, commonly at about 1.5 m. Oviposition takes place only on rainy evenings, the freshly laid eggs have to take up water immediately.

The embryo does not develop external gills at all. Embryos as figured in fig. 7 measure 2—2.5 mm in diameter; in this stage the embryo bursts from the vitelline membrane, the outer envelope is now 4.5—6 mm in diameter.



FIGS. 6—13. Developmental stages of *G. liber*. 6, eggs; 7, embryo bursting from vitelline membrane; 8, embryo with suckers (a: ventral view of mouth area); 9, hatchling stage; 10—12, tadpole in stage 35 of development; 13, mouthpart of the same.

Embryos as figured in fig. 8 measure 7.3—7.7 mm. Two small suckers and a mouth opening are visible (fig. 8a). The pigment cells present a uniformly speckled appearance over the surface of the embryo, the yolk mass is still pale green. The embryos hang now in the liquified jelly mass with the tails downwards (fig. 3). The larvae as figured in fig. 9 hatch and drop into the water below. The hatchling measures 9—9.3 mm. The tail is more than twice as long as the body. The oral suckers have disappeared, and the horny beak and papillae are present. The intestine is coiled and filled with the greenish yolk, the spiracle is sinistral and the vent is dextral. The pigmentation is now less uniform and patterns of grey spots have formed.

TADPOLES

The studied tadpoles originate from different localities: Perinet, the Mandraka-valley and Tampoketsa d'Ankazobe, as well as from own rearings from egg nests from Perinet and the Mandraka-valley. In studying the tadpoles we have used Gosner's (1960) simplified table of developmental stages.

Apart from the size (table I), there is no noticeable difference between the different stages.

TABLE I. Growth of the tadpoles of *G. liber* (in mm); n = number of specimens measured.

Stage	*n*	*Total length*	*Body length*	*Tail length*
25	11	9.5—16.0	3.3— 6.0	6.0—10.0
26	10	16.0—20.0	6.0— 7.5	10.0—12.5
27	9	18.5—26.0	7.0—10.5	11.0—16.0
30	2	25.5—27.0	10.0—10.5	15.0—17.0
35	4	27.5—35.0	10.0—14.0	17.5—22.0
37	9	29.0—35.0	10.0—13.5	18.0—22.0
46	23	10.0—13.0	10.0—13.0	—

For the description we figured a tadpole in stage 35 (figs. 10—13), which can serve as an example, since in this stage the tadpole has reached its maximum length. The body is depressed. The ratio of body-width to length is about 3 : 4. The snout is blunt, and the nostrils are very small, situated at about equal distances from eye and the tip of the snout. The eyes are rather large, placed dorsally at the same distance of the tip of the snout as of the spiracle, which is placed at a distance of 3/5 from the tip of the snout. The ratio of body-length to tail-length is 3 : 5. Measurements of 45 tadpoles of stage 25—39 revealed a mean value body/tail-length = 9/15, with a range from 8/15—10/15 in all stages. The upper crest of the tail is somewhat broader than the lower one, the length of the tail is 3 times its depth.

The coloration of the tadpole in life is grey and rarely brown. The tadpoles are not very agile, they spend most of the time lying on the bottom and feeding there. They are often accompanied by tadpoles of *Mantidactylus betsileanus* (Boulenger, 1882).

Larval mouthparts

The mouth is small and directed downwards, surrounded by small papillae, lacking on the margin of the upper lip.

The rows of labial teeth develop slowly, and the tadpole is relatively large by the time the formula is complete. The tooth formula in tadpoles of stages 25 and 26 amounts to 1/1 + 1//3 and 1/2 + 2//3. During stage 27 the complete formula is reached, from stage 27 onward the tooth formula is most commonly 1/3 + 3//3 (fig. 13), but also 1/2 + 2//3 and 1/4 + 4//3 are found. This variation in tooth formula is present in all our samples. The first row on the underlip is sometimes slightly interrupted.

Seasonal occurrence

Although the spawning season seems to be limited to the rainy season, we found tadpoles the whole year round. From December to May all stages are present. In May we found larvae from stage 27 onward, in August and September from stage 27—36, in October 39—46, in November 1—25 and 40—46.

We observed in captivity and in nature that the development from egg to metamorphosis took two months in the hot rainy season.

May and October are the only months of the dry season in which we observed metamorphosis in nature. Most probably the development is retarded in the dry cool season and a great part of the tadpoles from the last eggs emerge in October and November: the beginning of the hot season. This seasonal metamorphosis yields profit for the young frogs, since food is scarce in the dry season.

Discussion

The embryonic development of *G. liber* appears to be similar to the only species of Mantellinae known in this respect: *Mantella aurantiaca* Mocquard, 1900 (see Arnoult, 1966). In both species the eggs are deposited outside the water, in the bottom-dwelling *M. aurantiaca* on fallen leaves or moss. The size and number of eggs is similar and the embryo does not develop external gills, hatching by the time the spiracle is present.

Mating in *G. liber* is characterized by the shortness of the bodily contact between male and female. The touch of the male on the right moment and in the right place immediately induces the female to oviposition. No amplexus occurs. A similar mating posture, resulting in immediate oviposition, was observed in not yet identified *Gephyromantis*-species, with the difference that the male took the lead to the sexual contact. Short mating contacts seem to be wide-spread among the Mantellinae, for the males of this group never showed any instinct to embrace a female. However, it seems that in *Mantella* (see Arnoult, 1966) and in *Mantidactylus* (see Arnoult & Razarihelisoa,

1967) some kind of fugitive amplexus exists. According to the former author the male of *M. aurantiaca* Mocquard meets and loosely embraces the female, after which both disappear under some leaves and the eggs are deposited immediately.

One might suppose that the mode of fertilization as shown by *G. liber* is not entirely suited for ground-dwelling species, because the latter have to deposit eggs on a more or less horizontal surface, and in the manner of *G. liber* the sperm would not find its way to the eggs.

During the short mating act of *G. liber* the underside of the thighs of the male are in contact with the shoulder region of the female. Within the Mantellinae, the adult males nearly always possess characteristic hypertrophied femoral glands. They are more or less reduced in the females. In *G. liber* the underside of the thighs is glandular in both male and female.

It might well be that the short mating act, without a foregoing preparatory amplexus is connected with the possession of femoral glands. One is tempted to conclude that the femoral glands play an important rôle in the recognition of the male by the female, and provide part of the stimulus to oviposition for the female.

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