# OBSERVATIONS ON THE MALAGASY FROG GENUS HETERIXALUS LAURENT, 1944 (HYPEROLIIDAE) 

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#### Abstract

The colouration in life, some tadpoles and some mating calls of several species of the genus Heterixalus Laurent, 1944, are described. The following taxonomic changes are proposed: Heterixalus rutenbergi (Boettger, 1881), comb. nov. (from Hyperolius) ; Heterixalus betsileo (Grandidier, 1872) is a valid species (syn. Hyperolius renifer Boettger, 1881); Megalixalus boettgeri Mocquard, 1902, is removed from the synonymy of Heterixalus tricolor (Boettger, 1881). The occurrence of Hyperolius Rapp, 1842, in Madagascar is not confirmed.


## INTRODUCTION

Between November 1970 and May 1973, the author and her husband collected five species of the genus Heterixalus Laurent, 1944 in Madagascar. We never collected a species of Hyperolius Rapp, 1842, a genus of which the occurrence in Madagascar was mentioned in the literature.

The main difference between Hyperolius and Heterixalus is the pupil of the eye, which is horizontally elliptical in Hyperolius and vertically rhomboidal in Heterixalius. In life the shape of the pupil is clearly visible, whereas in many preserved specimens it is not at all clear. Therefore I paid much attention to the shape of the pupil in life, and I never observed a species belonging to the family of the Hyperoliidae with a horizontal pupil in Madagascar. Of the six nominal Hyperoliusspecies, I found one belonging to Heterixalus and two to Boophis Tschudi, 1838 (Blommers-Schlösser, 1979 b).
Hyperolius friedrichsi Ahl, 1930, seems also
to belong to the genus Boophis, since Ahl described the male having no gular gland, while the presence of a gular gland is a feature of both Heterixalus and Hyperolius. The specimen in Paris identified by Guibé is a Boophis species (Morère, pers. communication). Hyperolius arnoulti Guibé, 1975, resembles very much Heterixalus madagascariensis (Dum \& Bibr., 1841). This I noticed when I was comparing the type specimens of both in Paris.

Razarihelisoa (1979) described the biology of Hyperolius arnoulti. This identification is not correct, since she also described the male having no gular gland. Her biological observations are a confusion. She found frogs, egg masses and tadpoles separately, which she wrongly connected and assigned to a Hyperolius-species. She did no rearing at all. These observations were made at exactly the same locality in the Mandraka valley, where I made many observations. I reared fifteen different tadpoles in this area. I concluded that her Hyperolius species is in fact Boophis majori (Boulenger, 1896), which has a hyperoliid ap-
pearance, that the eggmasses belong to Mantidactylus depressiceps (Boulenger, 1882), and the tadpoles to Heterixalus betsileo (Grandidier, 1872). Altogether it is clear that more field observations are necessary to solve the question of the dubious occurrence of Hyperolius in Madagascar completely. The morphology is a weak tool to define the taxonomic status of the species in the genus Heterixalus. More field studies on mating calls, colouration in life and geographic variation are necessary. Up to the present time hardly any field information on Heterixalus has been published. My observations can serve as a starting point for further field studies.

## MATERIAL AND METHODS

The material is deposited in the Zoölogisch Museum Amsterdam (ZMA). The ZMA registration numbers are given under each species with the number of specimens in parentheses.

Measurements and characters of both tadpoles and adults and the terminology concerning the sonagrams are in accordance with Duellman (1970). In describing the larvae, I defined the stages according to Gosner (1960). Webbing formula: the numbers x , 2 i , 2e refer to the first toe (or finger), the inner side of the second, the outer side of the second and the numbers in parentheses refer to the number of phalanges free of web. Tooth formula: the tooth rows are numbered from top to bottom both in the upper and lower lip. The separation between both lips is indicated by a double slant line. The bioclimatic areas correspond to those of Koechlin (1972).

## DESCRIPTIONS AND FIELD OBSERVATIONS

Heterixalus Laurent, 1944
Laurent (1944) described Helerixalus for the Malagasy species previously assigned to the genus Megalixalus Günther, 1869. The genus is most closely related to the genus Hyperolius Rapp, 1842. If Hyperolius does not occur on Madagascar, Heterixalus is the only representative of the Hyperoliidae on Madagascar.

Diagnosis. - Vertebral column diplasiocoelous. Second tarsal free. Omosternum with a bony style,
broadly forked at base. Sternum a broad cartilaginous plate. Maxillary teeth present (contrary to Guibé, 1978). Vomerine teeth absent. Tongue heart-shaped and free behind. Pupil vertically rhomboidal (see fig. 9). Intercalary cartilage present between disc and adjacent phalanx. Fingers moderately webbed. Toes nearly fully webbed. A small round tubercle on the base of the fourth toe. Lateral metatarsalia narrowly united. (The following characters are mainly observed by the author, this paper).

Males: Size slightly smaller than females, gular gland present, vocal pouch single not completely overlain by gular gland; weakly developed glandular nuptial pad dorsolaterally on first finger, no nuptial excrescences. Amplexus axillary.

Eggs small, attached to low vegetation over water. Hatchlings with external gills. Tadpoles in stagnant water. Tooth formula $1 / \mathrm{I}+\mathrm{I} / 2$ or $\mathrm{I} / 3$. The frogs are arboreal and live in open areas, like dunes, rice fields and clear-cut forest. Both tadpoles and adults have a high temperature tolerance. The adults are transforming their colour to lighter, when exposed to sunlight (figs. io).

Chromosomes $2 \mathrm{n}=24$, all being meta- or submetacentric (Blommers-Schlösser, 1978). Nuclear DNA amount 8.5 -II.I pg (Bachmann \& Blom-mers-Schlösser, 1975).

Heterixalus betsileo (Grandidier, 1872)
Eucnemis betsileo Grandidier, 1872: 10; Guibé, 1978: 87 (species dubium).
Rappia betsileo; Boulenger, 1882: 471.
Megalixalus betsileo; Ah1, 1931: 426.
Heterixalus betsileo; Laurent, 1944: 112; Liem, 1970: III; Bachmann \& Blommers-Schlösser, 1975 (DNA): 17; Blommers-Schlösser, 1978 (chromosomes) : 37.
Hyperolius renifer Boettger, 188I: 46.
Rappia renifer; Boulenger, 1882: $\mathbf{1 2 0}$.
Megalixalus renifer; Ahl, 1931: 429.
Heterixalus renifer; Guibé, 1978: 87.
Material. - MNHP 1895-267, two syntypes of Eucnemis betsileo. Type locality: Betsileo region. - ZMA 6720(2), 22.III.72; 6723(1), 28.XI.71; 6724(3), 6.X.70; 6727(1), 28.IX.7I; 6735(6), 26.XI.70; 6743(2), XII.70-I.7I; 7040 (tadpoles), III.73; 7007 (tadpoles and young reared from them) 22.IX.7I; 7039 (tadpoles and young reared from them), 16.I.71; 7037 (tad-
poles), 16.I.7r; 7041 (tadpoles), 16.I.7I; 7042 (eggs), I. 72 all collected in Tananarive, Parc de l'O.R.S.T.O.M. Tsimbazaza district, alt. 1300 m . - ZMA 6756(5), 4.XI. 72 collected at Manjakotompo forest station, Ankaratra mts (near Ambatolampy), alt. I800 m. - ZMA 6745(6), 17.II.72; 6744(1), 2I.X.7I; 6738(1), 6.XII.70 all collected near Perinet (highroad R.N. 2 at km 142), alt. 900 m ; 6746(1), $13 . \mathrm{XI}$.72 same locality alt. $1100 \mathrm{~m} .-\mathrm{ZMA} 672 \mathrm{I}(2)$, 15.XI.72; 6740(1), 27.III.72; 6739(1) 2I.III. 72 all collected in the Mandraka valley (highroad R.N. 2 at km 69) , alt. 1200 m. - ZMA 7038 (tadpoles and young reared from them) 2.V. 72 collected near Ampijoroa, Ankarafantsika forest (highroad R.N. 4 at km 465). - ZMA 7225(1), i I.IX. 72 collected along the highroad Tanarive-Majunga at km 555 R.N.4. - ZMA 6742(I), II.IX. 72 collected at Ambalobongo (highroad R.N. 4 at km 396 ).
Description (See Table I and II for metrical data). - The body in the postaxillary region is little narrower than the greatest width of the head. The head is wider than long. The head width is one third of the body length. The snout is bluntly rounded in dorsal and lateral profile. The snout is as long as the horizontal diameter of the eye, and shorter than the distance between the anterior corners of the eye. The nostrils are nearer to the
tip of the snout than to the anterior corners of the eye. The distance from the nostril to the anterior corner of the eye is distinctly shorter than the horizontal diameter of the eye. The canthus is distinct and rounded. The loreal region is slightly concave. The interorbital region is slightly convex. The internarial distance is slightly shorter than the interorbital distance. The interorbital distance is one and a half to two times the width of an upper eyelid. The nostrils are slightly protruding, the opening is laterodorsally. The commissure of the mouth is curved upwards. The pupil is vertically rhomboidal. There is no dermal fold over the tympanum, which is indistinct, covered by skin. Its diameter is about $\mathrm{I} / 6$ of the horizontal diameter of the eye.

There are io-18 tubercles laterally, behind the commissure of the mouth.

The diameter of the discs of the fourth, third and second fingers are twice the diameter of the adjacent phalanx. The diameter of the disc of the first finger is about $I \mathrm{I} / 2$ times the diameter of the adjacent phalanx. The relative lengths of the fingers from shortest to longest are $1-2-4-3$. The subarticular tubercles are round and flat. The distal tubercles on the fourth, third and second finger are sometimes bifid. A small unpigmented glandular nuptial pad is present dorsolaterally on the

Table I. Dimensions in mm of Heterixalus betsileo, H. tricolor, H. alboguttatus, H. mocquardi, H. rutenbergi. $\mathrm{A}=$ snout to vent $; \mathrm{B}=$ length of lower arm $; \mathrm{C}=$ hand length $; \mathrm{D}=$ length of hindlimb; $\mathrm{E}=$ tibia length $; \mathrm{F}=$ length of foot and tarsus $; \mathrm{G}=$ foot length.

|  | A | B | C | D | E | F | G |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| H. betsileo |  |  |  |  |  |  |  |
| 17 ồ ô ZMA | 19-28 | 9-13 | 5-8 | 29-44 | 10-14 | 12-19 | 7.5-12.0 |
| 13.9 ¢ CMA | 19-29 | 9-14 | 5-8 | 29-45 | 10-15 | 12-20 | 7.5-12.0 |
| H. tricolor |  |  |  |  |  |  |  |
| ¢ lectotype SMF | 31 | 14 | 7.5 | 47 | 16 | 20 | 12.5 |
| 8 o of ZMA | 23-26 | 10-11 | 5.5-6.5 | 33-4I | 12-14 | 14-16 | 8.5-10.0 |
| 13 우우 ZMA | 23-30 | 10-14 | 6-8 | 33-45 | 11.5-15.0 | 13.5-19.0 | 8.5-12.0 |
| H. alboguttatus |  |  |  |  |  |  |  |
| $49 \%$ ZMA | 30-33 | 12-14 | 7.5-8.0 | 44-48 | 15-17 | 19-2I | 12-14 |
| H. mocquardi |  |  |  |  |  |  |  |
| \% holotype SMF | 28 | 12 | 6.5 | 41 | 14 | 17 | 10 |
| \% ZMA | 32 | 13 | 7.5 | 44 | 15 | 19 | 12 |
| H. rutenbergi |  |  |  |  |  |  |  |
| \% ZMA | 24.5 | 11.5 | 6 | 35.5 | 11 | 15 | 9.5 |

first finger of the male. The fingers are about half webbed. The formula of the webbing of the hand: $\mathrm{I}(\mathrm{I}), 2 \mathrm{i}(\mathrm{I}), 2 \mathrm{e}(\mathrm{I}), 3 \mathrm{i}(2), 3 \mathrm{e}(\mathrm{I}), 4(\mathrm{I})$. When the limbs are laid along the side, the knee and elbow overlap. The adpressed heels slightly overlap or meet. The tibiotarsal articulation extends just beyond or to the centre of the eye. The inner metatarsal tubercle is small elliptical and flat. There is a very small round tubercle on the base of the fourth toe. The terminal discs are as large as those on the hand. The fifth toe is slightly longer than the third. The subarticular tubercles are round and flat. The formula of the webbing of the foot: $1(\mathrm{r}), 2 \mathrm{i}(\mathrm{I}), 2 \mathrm{e}(\mathrm{o}), 3 \mathrm{i}(\mathrm{I}), 3 \mathrm{e}(\mathrm{o}), 4 \mathrm{i}(\mathrm{I})$, 4 e ( I ), 5 ( O ). The lateral metatarsals are narrowly united. The ventral surface of the foot is granular.
The anal opening is directed posteriorly at upper level of the thighs. The tongue is heart-shaped and free posteriorly. The vocal slits are situated in the floor of the mouth, near the angles of the jaws. The gular gland is broad kidney-shaped. it is free posteriorly and laterally. The width of the gular gland is $5-7 \mathrm{~mm}$. The vocal pouch is subgular single and distensible, posteriorly it consists of extensive folds of skin not overlain by the gular gland (see fig. 3).

The skin on the dorsum and throat is smooth. The skin on the chin and belly is coarsely granular. The posteroventral surface of the thighs, the ventral surface of the hands and feet are finely granular. Elsewhere on the venter the skin is smooth.

In preservative the colour of the dorsum is blue-grey, olive-green, dull brown, light grey or silver and covered with small dark spots; except the thighs and upper arm, which are creamish. Two longitudinal dorsolateral light bands are present from behind the eye to the groin. Sometimes this band starts from the nostril. The light bands are often bordered with black on one or both sides. Light longitudinal bands are present on the shank in some specimens. The venter is evenly cream. The iris is silvery grey with dark pigment and surrounded by a black ring. The upper and lower rim of the palpebral membrane are pigmented in the same colour as the skin.
The general colouration in life is green (or beige). The colour changed to light yellow (or
white) in the sunlight. The dorsolateral bands are yellow (or cream-white). The hands, feet, thighs and ventral surface of the limbs are orange (or yellow). Elsewhere the venter is creamish.

It is possible that $H$. betsileo includes different subspecies. Above an altitude of about 1100 m the colour is green, whereas beneath this altitude the colour is beige.
Taxonomy. - Guibé (1978) rejected the name betsileo, since the type material is in a bad condition. I believe that there is no sufficient reason to reject the name, because Grandidier (1872) described the green colour and lateral yellow bands, which are characteristic. Moreover the name is commonly used up to the present. Ahl (1931) published an extensive description of betsileo. I regard renifer used by Guibé (1978) instead of betsileo, as a synonym. Boettger (188I) described also a green colouration and mentioned already that renifer is possible the same as betsileo. The difference he noticed in the length of the yellow bands, can be present in one population of H. betsileo as I observed.

Natural history. - The species is a real sedge frog. It is very common in the savanna-like areas and cleared parts of the forest of the Centre Domain (central plateau region, the west and east slopes above an average height of 800 m ) and the West Domain (below 800 m alt.).

The following field observations were mainly done in Tananarive, Parc de l'O.R.S.T.O.M. These frogs are active during the wet season from about November till May. After the first rainfall they soon appear. The breeding sites are open stagnant waters, like pools, puddles, ricefields and overflowed grasslands. Breeding starts after a few weeks in the wet season and lasts till about the end of the wet season. During the day the females are found resting on the vegetation with the head up and legs folded in. They are often found exposed to the sunlight. The colour is then changed to light yellow. The males are higher in the trees and start calling softly at 4 p.m. in cloudy weather. After sunset, males and females move to the pools. The males start calling very loudly in large choruses, sitting on vegetation above and near water.
The sonagram (fig. 5) made of a male (ZMA
6743) in December 1970 at 9 p.m., shows that the duration of one call is about 0.5 sec . The dominant frequency is about 3000 Hz . The frequency goes from about $2000-4000 \mathrm{~Hz}$. The call rate is about 30 per minute.
The amplexus is axillary. The eggs, black and white and about $\mathbf{x} .6 \mathrm{~mm}$ in diameter, are deposited around grass blades or other plants in clusters of io to 80 just above the water (fig. 8). When the water rises with further rain, the eggs become submerged. The white part of the egg becomes the belly, and the black part back and tail of the tadpole. External gills are visible after two days. On the third day the embryo hatches and swims, the body is 2 mm and the tail 3 mm . On the fourth day resorption of the external gills starts. The
tadpoles are herbivorous. After two months the metamorphosis is completed and the young frogs emerge. The juveniles are green with two yellow dorsolateral bands. The hands, feet and thighs are light yellow. Some tadpoles of the last batches have to pass the dry winter season, metamorphosis being postponed until September and October.
Tadpoles. - Twenty one tadpoles in stage 25 have body lengths of $3-7 \mathrm{~mm}$ and total lengths of $8.5-21.0 \mathrm{~mm}$. Twenty tadpoles in stages $26-32$ have body lengths of $6-10 \mathrm{~mm}$ and total lengths of $17-30 \mathrm{~mm}$. Thirteen tadpoles in stages 33-39 have body lengths of $10-14 \mathrm{~mm}$ and total lengths of $30-39 \mathrm{~mm}$. Ten tadpoles in stages $40-41$ have body lengths of $14-16 \mathrm{~mm}$ and total lengths of body length in the sixty-four tadpoles listed above


Figs. 1-4. 1, Heterixalus betsileo: tadpole, ZMA 7007, $\times 3 ; 2$, mouth of tadpole, ZMA 7007, $\times 25 ; 3$, gular gland and vocal pouch, ZMA 6756, $\times 3 ; 4$, Heterixalus tricolor, gular gland and vocal pouch, ZMA $6750, \times 3$.
$39-46 \mathrm{~mm}$. The average ratio of tail length to body length in the sixty four tadpoles listed above is 1.9 (range $\mathrm{I} . \mathrm{7}^{-2}$ ).

Ten metamorphosing young have body lengths of $15-20 \mathrm{~mm}$ (mean 17 mm ). The mouth and lateral view of a tadpole in stage 38 (ZMA 7007) are shown in figs. I, 2. The body is ovoid. The nostrils are dorsal, the opening is anterolaterally, situated nearer to the tip of the snout than to the anterior corner of the eye. The eyes are situated laterally. The spiracular opening is
dark brown on the back; the belly is opaque and whitish. The caudal musculature and fin is mottled with brown markings. In life the colouration is the same or dark olive green.

The tadpoles were collected in stagnant waters, often together with tadpoles of Mantidactylus alutus (Peracca, 1893) and Ptychadena mascareniensis (Duméril \& Bibron, 1841). The tadpoles of $I$. betsileo and $P$. mascareniensis were found in the sunny parts of the water, while the tadpoles of M. alutus were found in the more shaded parts,


Fig. 5. Sonagram, filter wide, Heterixalus betsileo.
sinistral, situated at about $2 / 3$ from the tip of the snout and the end of the body. The cloacal tube is short and dextral to the caudal fin. The caudal musculature is rather slender. The caudal fin is moderately developed. At midlength of the tail, the height of the caudal musculature represents $\mathrm{I} / 3$ to $2 / 5$ of the total tail height. The mouth is small and directed anteroventrally. The papillary border has a wide median gap anteriorly. Posteriorly there are two rows of papillae, anterolaterally one row and mediolaterally three rows. The margin of the oral disc is round. The tooth formula is $1 / 1+1 / 2$ or $2 / 3$. The upper row of the lower lip has a very small interruption. The horny beak is robust. The upper beak is narrow and sickle-shaped. The lower beak is broadly V-shaped.
The colour of the tadpole (in preservative) is
close to the shore. Arnault \& Razarihelisoa (1967) described a tadpole as belonging to M. alutus, which in fact belongs to $H$. betsileo (see Blom-mers-Schlösser, 1979).

Heterixalus tricolor (Boettger, 188 I )
Megalixalus tricolor Boettger, 188I : 550; Ahl, 1931: 425. Heterixalus tricolor; Bachmann \& Blommers-Schlösser, 1975: 17 (DNA) ; Blommers-Schlösser, 1978: 37 (chromosomes); Guibé, 1978: 86.
Heterixalus madagascariensis; Bachmann \& BlommersSchlösser, 1975: 17 (DNA).
Material. - SMF 7268 the female lectotype of Megalixalus tricolor, type locality Nosy Bé. Z.MA 6750(4), 2-8.VIII.72; 6734(2), 1I-I7.II. 72; 7132 (tadpoles and young reared from them), VII.72; 7226 (embryos), VII. 72 all collected near Foulpointe (East Coast). - ZMA 6968(5), 13. X.71; 6749(5), r6.X.7I all collected near Fénérive-

Est (East Coast). - ZMA 7224 (tadpoles and young reared from them), io.X.7I collected near Ambila-Lemaitso (East Coast). - ZMA 6772 (12), VII. 72 collected near Ivoloina, 13 km N. of Tamatave (East Coast). - ZMA 675I (3), 22-29. VII. 72 collected 25 km N . of Tamatave. Diagnosis. (See Table I and II for metrical data). - Morphological differences with $H$. betsilco: The snout is slightly acuminate in dorsal profile and round in lateral profile. The snout is as long as the distance between the anterior corners of the eye and somewhat longer than the horizontal
corner of the eye. Often this streak continues over the eye and the tympanic region. Dark spots are present or absent on the back, the forelimbs, on the shank and tarsus, sometimes forming an interrupted band.

In preservative the colouration is about the same. The orange or yellow colour has disappeared. Under the binocular many more very small blackish spots are visible in the dark specimens than in the light specimens.
Taxonomy. - Guibé (1978) synonymised H. boettgeri (Mocquard, 1902) with the present

Table II. Ratios to snout-vent length of : $\mathrm{A}=$ length of lower arm; $\mathrm{B}=$ hand length; $\mathrm{C}=$ length of hind limb; $D=$ tibia length $; E=$ length of foot and tarsus; $F=$ foot length. $\mathrm{m}=$ mean. Heterixalus betsileo, H. tricolor, H. alboguttatus, H. mocquardi, H. rutenbergi.

|  | A | B | C | D | E | F |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| H. betsileo (30 specimens) | $\begin{aligned} & 0.45-0.50 \\ & \mathrm{~m}=0.48 \end{aligned}$ | $\begin{aligned} & 0.26-0.32 \\ & m=0.28 \end{aligned}$ | $\begin{aligned} & 1.48-1.60 \\ & m=1.54 \end{aligned}$ | $\begin{aligned} & 0.48-0.52 \\ & \mathrm{~m}=0.50 \end{aligned}$ | $\begin{aligned} & 0.63-0.70 \\ & \mathrm{~m}=0.66 \end{aligned}$ | $\begin{aligned} & 0.38-0.46 \\ & \mathrm{~m}=0.4 \mathrm{I} \end{aligned}$ |
| H. tricolor (22 specimens) | $\begin{aligned} & 0.43-0.47 \\ & \mathrm{~m}=0.44 \end{aligned}$ | $\begin{aligned} & 0.24-0.28 \\ & \mathrm{~m}=0.26 \end{aligned}$ | $\begin{aligned} & 1.40-1.57 \\ & \mathrm{~m}=1.48 \end{aligned}$ | $\begin{aligned} & 0.48-0.52 \\ & \mathrm{~m}=0.50 \end{aligned}$ | $\begin{aligned} & 0.58-0.64 \\ & m=0.61 \end{aligned}$ | $\begin{aligned} & 0.37-0.40 \\ & \mathrm{~m}=0.38 \end{aligned}$ |
| H. alboguttatus (4 specimens) | $\begin{aligned} & 0.39-0.44 \\ & \mathrm{~m}=0.4 \mathrm{I} \end{aligned}$ | $\begin{aligned} & 0.23-0.25 \\ & \mathrm{~m}=0.24 \end{aligned}$ | $\begin{aligned} & 1.42-\mathrm{I} .50 \\ & \mathrm{~m}=1.47 \end{aligned}$ | $\begin{aligned} & 0.50-0.52 \\ & \mathrm{~m}=0.50 \end{aligned}$ | $\begin{aligned} & 0.63-0.66 \\ & \mathrm{~m}=0.64 \end{aligned}$ | $\begin{aligned} & 0.38-0.42 \\ & \mathrm{~m}=0.40 \end{aligned}$ |
| $H$. mocquardi (2 specimens) | 0.41-0.43 | 0.23 | 1.38-1.46 | 0.47-0.50 | 0.59-0.6I | 0.38 |
| H.rutenbergi ( I specimen) | 0.47 | 0.24 | 1.44 | 0.45 | 0.61 | 0.39 |

diameter of the eye. The canthus is distinct and angular. The ventral surface of the hands and feet is smooth. The posteroventral surface of the thighs is finely granular in the male and smooth in the female. The gular gland in the male is broad and round (see fig. 4). Its diameter is about 6 mm . The gular gland is hardly free posteriorly and laterally. The vocal pouch is single and moderately distensible.

The colour is also changed from dark to light in the sun (figs. io, II). In life the males are brown to grey, the hands, thighs, feet and ventral surface of the limbs are yellow. The females are brown to bright white, the hands, feet, thighs and ventral surface of the limbs are orange. In both sexes the venter is creamy. Dark brown markings are present and variable. In general there is a dark streak from the tip of the snout to the anterior
species. I do not agree with this opinion, since Mocquard (1902) mentioned a green colouration. Morphological differences are so small between species of the genus Heterixalus, that synonymizing in this case without field observations seems unjustified.
Naturalhistory. - The species is a real sedge frog. It is very common in the dunes, savanna-like areas and cleared parts of the forest of the East Coast. There is no real dry season on the East Coast. It appears from our observations that breeding occurs the whole year. The males were heard calling during all our visits: February, July, August and October. Eggs, tadpoles in all stages and metamorphosing young were found in July.

The males call from grasses and herbs in or at the edge of shallow ponds in the evening.

During the day they hide near and in the pond. They disappear under water when disturbed. The females rest on leaves or in the leaf axils of Pandanus, Typhonodorum lindleyanum and other plants. If exposed to the sun they are brightly white. The females move towards the calling males in the evening. The call starts with a long continuing sound followed by numerous short thrills.
$28-31 \mathrm{~mm}$. Seven tadpoles in stages $38-40$ have body lengths of $1 \mathrm{I}-15 \mathrm{~mm}$ and total lengths of $33-45 \mathrm{~mm}$. The average ratio of tail length to body length in the twenty-four tadpoles listed above is 2 (range 1.8-2.1).
Fourteen metamorphosing young have body lengths of $12-15 \mathrm{~mm}$ (mean 14 mm ).
The tadpoles are nearly identical to those of


Figs. 6-7. 6, Heterixalus tricolor: sonagram, filter wide, starting note; 7, sonagram, filter narrow, following notes.

The sonagram (figs. 6, 7) made of a male (ZMA 6968 ) in Octobre 1971 at io p.m. shows that the frequency goes from $2000-5500 \mathrm{~Hz}$. The dominant frequency is about 3500 Hz . The duration of the starting sound is about 2 sec ., the following notes 0.05 sec . with intervals of 0.05 sec .

The eggs are black and white and about 1.5 mm in diameter. The hatchlings have external gills, which soon disappear.
Tadpoles. - Eight tadpoles in stage 25 have body lengths of $4-7 \mathrm{~mm}$ and total lengths of II-I2 mm. Nine tadpoles in stages $26-36$ have body lengths of $9-10 \mathrm{~mm}$ and total lengths of
H. betsileo. Besides the slightly smaller size and slightly longer tail, the caudal musculature is less developed. At midlength of the tail, the height of the caudal musculature represents about $1 / 4$ of the total tail height.

In life the colouration of the young is variable: white with two longitudinal dorsolateral light green bands, light yellow with two longitudinal dorsolateral yellow bands or olive green with two longitudinal dorsolateral yellow bands. Up to a size of 18 mm the dorsolateral bands are present. In alcohol the colour is brownish or whitish covered with numerous blackish spots.


Figs. 8-11. 8, Heterixalus betsileo, eggs, ZMA 7042; 9, Heterixalus tricolor: male, ZMA 6968; 10, female in shade; if, same female in sunlight, ZMA 6968.

Heterixalus alboguttatus (Boulenger, 1882)
Megalixalus madagascariensis var. alboguttatus Boalenger, 1882: 129.
Heterixalus variabilis; Bachmann \& Blommers-Schlösser, 1975: 17 (DNA).
Heterixalus alboguttatus; Guibé, 1978: 86.
Material. - ZMA 6776(2 9 ), 3r.XII.71; 7223 (eggs dissected of 6776) collected on sunexposed Pandanus-leaves in the dunes of Mananjary (East Coast). - ZMA 6730 (I 9 ), 20.II.71;

6722 ( I ) mafana (highroad R.N. 25), alt. 800 m .
Diagnosis (See Table I and II for metrical data). - The species is easy to identify by its characteristic colouration. In morphology the species resembles $H$. madagascariensis (Duméril \& Bibron, 1841). The ventral surface of the thigh is coarsely granular.
Colour in life. - The back is blackish or dark grey with orange spots in the shade and
whitish with yellow spots (bordered with black) in the sun. The thighs, the ventral surface of the limbs, the hands and feet are orange. The venter is creamish.
Eggs. - The eggs dissected from the females are black with white; about 1.5 mm in diameter. Its number is about 500 in one female.

## Heterixalus mocquardi (Boettger, 1913)

Megalixalus mocquardi Boettger, 1913: 280; Ahl, 1931 : 425.

Heterixalus mocquardi; Guibé, 1978: 85.
Material. - SMF 7270 the female holotype of Megalixalus mocquardi, type locality FortDauphin. - ZMA 674I (I 9 ), i.II. 73 collected on a leaf in Fort-Dauphin.
Diagnosis. (See Table I and II for metrical data). - The species differs from $H$. betsileo by the absence of dorsolateral yellow bands and by a clear tympanum, which has a diameter of $\mathrm{I} / 4$ of the eye. The limbs, hand and feet are relatively smaller than those of H. betsileo (See Table II). Colourin life. - The colour on the back is green; the thighs, the ventral surface of the limbs and the hands and feet are orange. The venter is creamish.

Heterixalus rutenbergi (Boettger, 1881)
comb. nov.
Hyperolius rutenbergi Boettger, 1881: 47; Ahl, 1931 : 420; Guibé, 1978 : 89.
Material. - ZMA 6737 ( 1 ) , 4.VI. 72 collected 20 km West of Tananarive in grassland alt. 1300 m .
Diagnosis (See Table I and II for metrical data). - In life the specimen showed the characteristic rhomboidal vertical pupil of the genus Heterixalus. The species is easy to identify by its characteristic colouration. Compared with other Heterixalus-species the discs are small (hardly larger than the horizontal diameter of the penultimate phalanx) and the fifth toe is one phalanx longer than the third. In addition to the descriptions of the previous authors, 14 tubercles are present laterally behind the commissure of the mouth.
Colourin life. - The general colouration
is light green; the thighs, the ventral surface of the limbs, the hands and feet are orange. On the back five longitudinal white bands bordered with dark brown stripes are present. Two parallel longitudinal bands of the same colouration are present on the lateral sides of the lower limb and shank, and one along the tarsus and foot. The belly is creamy and the throat shows white with brown markings.

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