RÉPUBLIQUE DÉMOCRATIQUE DU CONGO

INSTITUT DES PARCS NATIONAUX

Exploration du Parc National de la Garamba

MISSION H. DE SAEGER

en collaboration avec

P. BAERT, G. DEMOULIN, I. DENISOFF, J. MARTIN, M. MICHA, A. NOIRFALISE, P. SCHOEMAKER, G. TROUPIN et J. VERSCHUREN (1949-1952).

FASCICULE 52

AMPHIBIA

BY

ROBERT F. INGER (Chicago)

KINSHASA

1968

Etude réalisée avec la
collaboration de l'Institut royal des Sciences naturelles
de Belgique.

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GENERAL DESCRIPTION OF THE PARK

The Parc National de la Garamba has been described in detail by DE SAEGER (1954) in the introductory volume of this series. This brief summary, based mainly on De Saegers's publication, will deal only with those environmental features of direct relevance to amphibian distribution, amplified by our own observations on particular habitats.

The Garamba park lies in the extreme northeastern corner of the Congo and covers an area of 480.000 hectares. The general topography is an undulating plain (710 to 860 m) with a few inselbergs having elevations of 900 to 1.061 m.

The average annual rainfall at Faradje, 8 km from the park, during the decade 1940-1949 was 1.424,5 mm (BULTOT, 1951). The months January, February, March, November, and December each had less than 100 mm of rain (fig. 1). At Nagero, park headquarters, the total rainfall in 1958 (1) was 1.357 mm. The monthly distribution of precipitation (fig. 2) follows that at Faradje rather closely. The months November through March may be considered the dry season. Although March is somewhat intermediate, 83-100 % of the rainfall recorded for that month in 1958 and 1959 fell in the last two weeks.

(1) Data from files at park headquarters. This was the last year of complete data at the time of our arrival in March, 1959.

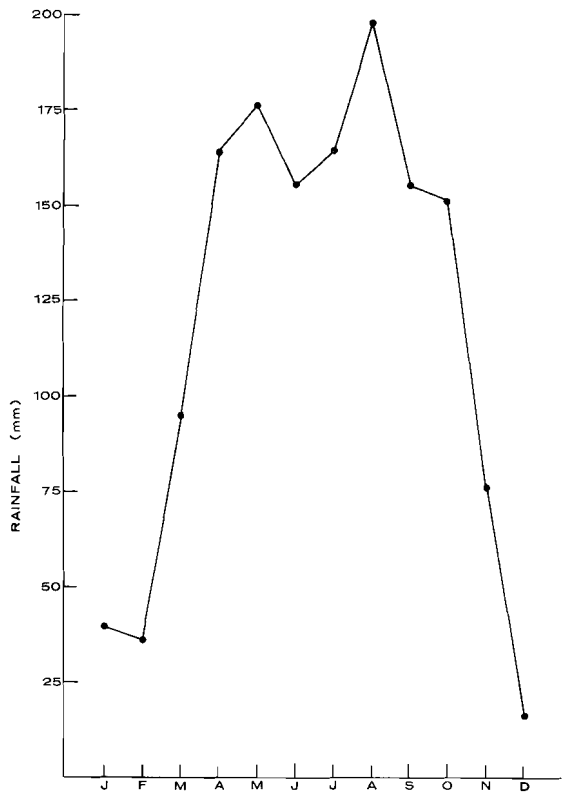


FIG. 1. — Rainfall at Faradje, Province Orientale, Congo, 1940-1949 (BULTOT, 1951).

Relative humidity at night is high (i.e.>80 %) throughout the year. However, in the dry season, it drops to low levels during the afternoons (fig. 2). Extremely hot, dry winds blow out of the northeast from November to March. During the first 15 days of March, 1959, the relative humidity remained below 30 % at 1500 hrs and on four days fell below 20 %. The recurrent low day time humidities during the dry season may affect the activity of even nocturnal frogs by forcing them into deeper retreats (see comments under *Bufo latifrons*, p. 37). NOIRFALISE (1956, Table 11) shows mean daily evaporation in the Garamba above 3,4 mm from November to March and below 2,8 from April to October. He also shows that total monthly evaporation was above 100 mm from November to March and below 90 mm from April to October.

The mean annual temperature is 25° C. The absolute temperature range at Nagero in 1958 was 9,1-38,6°. The range within months was 13-18° during

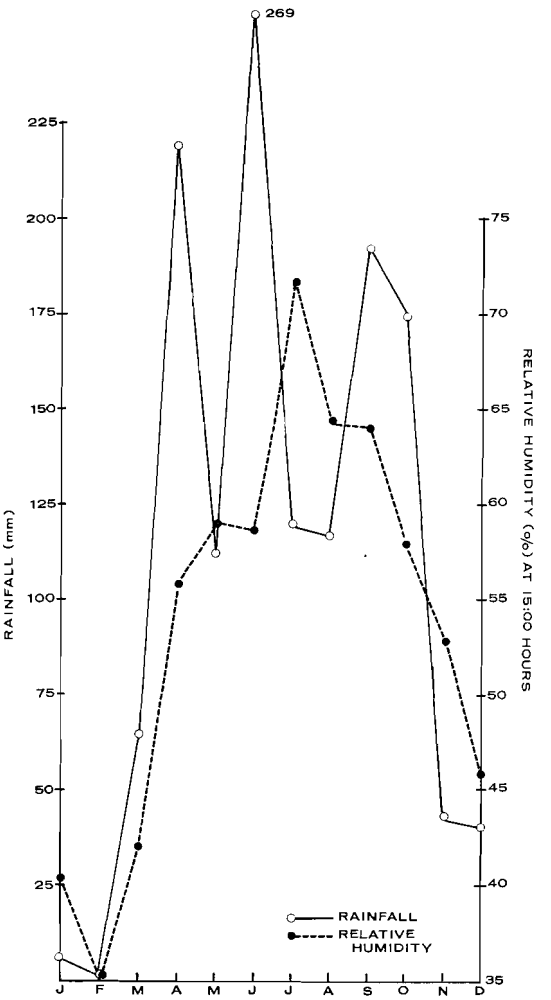


FIG. 2. — Rainfall and relative humidity at Nagero.
Data courtesy Parc National de la Garamba.

the period April-October and 23-29° in December-March. In November the range was 20° C.

DE SAEGER and NOIRFALISE conclude that the Garamba has a three-month dry season from December through February, and for most purposes that interpretation is satisfactory. The dependence of amphibian activity on relatively high humidities, however, makes months like March and November, with their recurrent, excessively low humidity, effectively part of a larger dry season. Hence, for the purposes of this report, I am considering that the dry season extends from November to the latter part of March.

VEGETATION.

The Garamba park lies in an area of mixed woodlands and savanna of a relatively moist type (1). Most of it is covered by savana of three types wich grade into one another. Grass savanna (fig. 3) typically has woody plants widely spaced. Trees and bushes may be as much as 200 m apart. In shrub savanna (fig. 4) woody vegetation is much denser and consists mainly of shrubs less than 2 m tall. Tree savanna (fig. 5) differs from the preceding type only in the height of the woody plants.

Photo: H. DE SAEGER.

FIG. 3. — Grass savanna in Parc National de la Garamba.

Open woodlands (2) dominated by the tree, *Isoberlinia doka*, occur in the northeastern corner of the park (fig. 6). Scattered through the park, but more abundant in the northern half, are gallery forest. The best

(1) Category 16 on the *Vegetation Map of Africa*, Assoc. Étude Tax. Flora Afr. Trop., 1959.

(2) Category 17 on the *Vegetation Map of Africa.*

Photo: H. DE SAEGER.

FIG. 4. — Shrub savanna in Parc National de la Garamba.

Photo: H. DE SAEGER.

FIG. 5. — Tree savanna in Parc National de la Garamba.

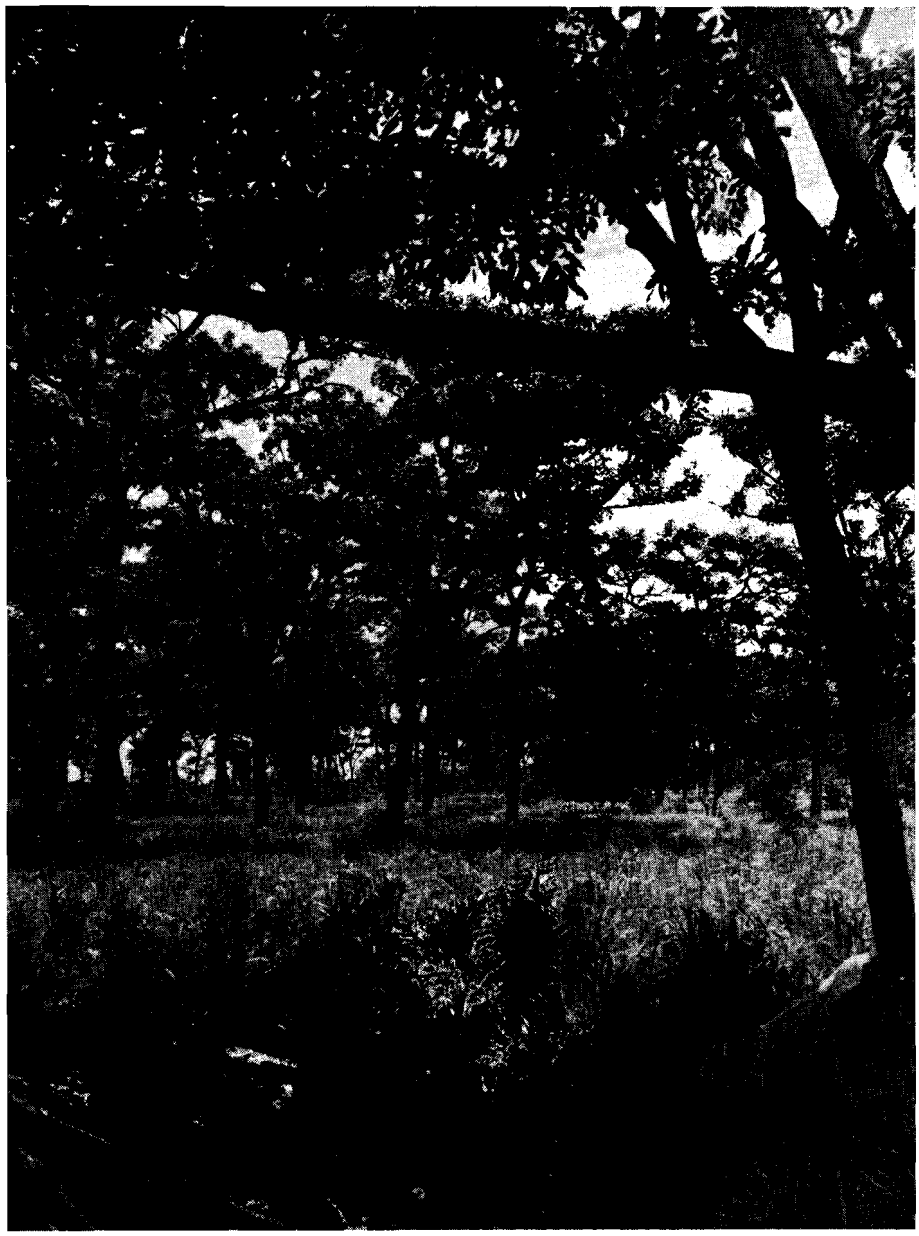


Photo: H. DE SAEGER.

FIG. 6. — *Isoberlinia* woodland in Parc National de la Garamba.

developed ones are in narrow, deeply entrenched ravines (fig. 7) and have dark, humid interiors. The gallery forest generally have higher relative humidities and lower daytime temperatures than the neighboring savanna (Table 1; see also NOIRFALISE, 1956, fig. 12).

Table 1. — **Differences between interior and exterior of two gallery forests in the Parc National de la Garamba on April 5, 1959.**

Locality	Time	Position	Air temperature	Relative humidity
Akawa.	10 : 40	In gallery	25,5 °C	79 %
	10 : 50	In savanna	30,0 °C	54 %
Pidigala	11 : 50	In gallery	28,3 °C	58 %
	12 : 20	In savanna	31,7 °C	38 %

More open but continuous gallery forests border the larger streams (fig. 8). From this condition the gallery forests grade downward to a few trees in line along the smallest water courses.

This part of Africa was apparently more heavily forested and Keay (1959) suggests that the climax vegetation is probably closed woodland with little grass. DE SAEGER concludes that a general impoverishment of the vegetation is now under way. He attributes this to the destruction by man of the original forest cover in much of the area, followed by annual man-made fires. Many gallery forests, according to DE SAEGER, are in process of degradation. Conceivably this important habitat of some species of frogs will disappear from the Garamba in the not too distant future.

AQUATIC HABITATS.

Aquatic environments are of five major types : rivers, small streams, marshes, ponds, and springs. The three principal rivers in the park, Dungu (fig. 8), Garamba, and Aka, have a narrow fringe of trees but varying types of banks and bottoms. Several species of frogs live along their banks or breed in pot-holes formed where the rivers flow over bed rock (fig. 9). Smaller streams (fig. 10) frequently have wide marshy edges.

Marshes may be permanent or temporary. Permanent marshes in open savanna are of two general types. One, known locally as « ndiwili », forms in slight depressions over impermeable rock or subsoil and characteristically

Photo: R. F. INGER.

FIG. 7. — Crown of gallery forest in ravine at Nabakoyo, Parc National de la Garamba.

Photo: R. F. INGER.

FIG. 8. — Open gallery forest along Dungu River, Parc National de la Garamba.

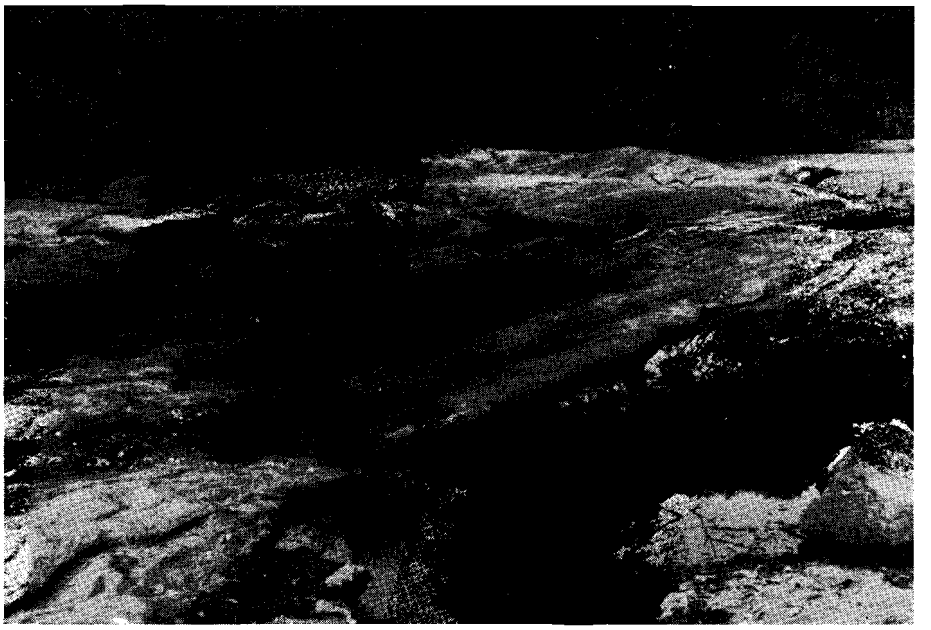


Photo: R. F. INGER.

FIG. 9. — Pot-holes in bed of Dungu River,
Parc National de la Garamba.

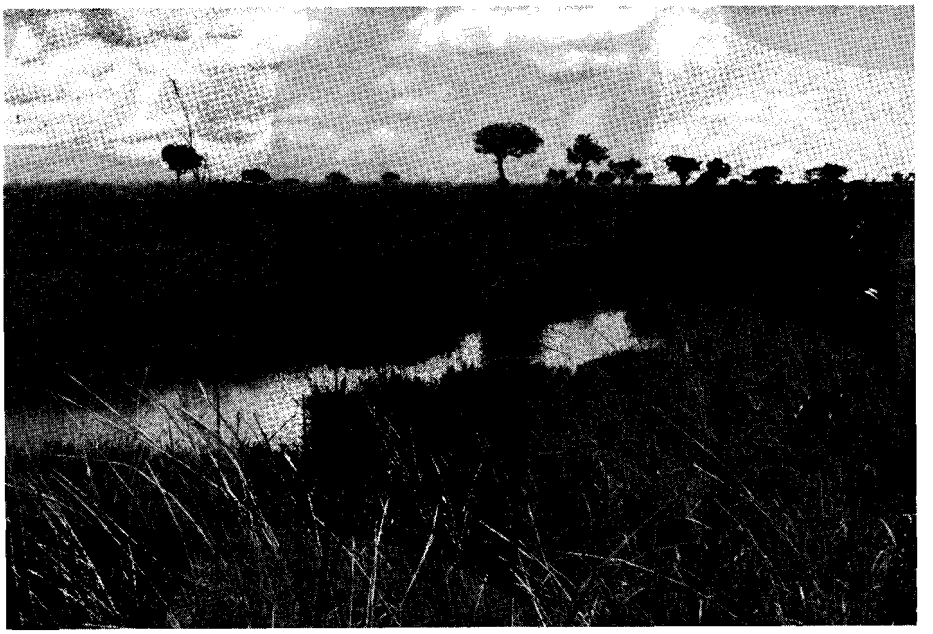


Photo: R. F. INGER.

FIG. 10. — Nambirima, a stream with marshy edges.
Parc National de la Garamba.

supports a vegetation of grasses and low Cyperaceae (fig. 11). The second type has much taller vegetation, often consisting of papyrus (fig. 12), and is usually in the drainage of a spring and small stream. Marshes also form in gallery forest or in the outflow of streams from gallery forest (fig. 13).

Temporary marshes develop in the rainy season, either in open savanna away from rivers (fig. 14) or in the flood plains of rivers.

Photo: R. F. INGER.

FIG. 11. — A permanent marsh (« ndiwili ») near Nagero, Parc National de la Garamba.

Permanent ponds occupy a few cut-off meanders of the larger rivers or semi-isolated depressions in the course of smaller streams (fig. 15). They also form in the rainy season in flood plains as well as in areas far from streams and seemingly without any drainage pattern (fig. 16).

Some of these aquatic environmental types grade into one another. The distinction between a marsh and a pond is often a fine one. In general, I have applied the term marsh to those aquatic environments in wich a current is virtually absent and in which emergent vegetation occupies more than half of the surface area. As marshy areas frequently border small streams (fig. 10) and may even be interposed along the length of a stream,

Photo: R. F. INGER.

FIG. 12. — Papyrus marsh in Parc National de la Garamba.

the boundary between a marsh and a stream may be indefinite. Springs in the Garamba flow out into marshy areas or from small ponds.

Parts of shallow marshes are modified by elephants, buffalo, and hippos into pools considerably deeper than the adjacent water. *Phrynobatrachus natalensis*, *P. parkeri*, and *P. scapularis* were caught in such pools as were unidentifiable frog eggs.

Photo: R. F. INGER.

FIG. 13. — Marsh at opening of gallery forest at Nabakoyo, Parc National de la Garamba.

Photo: R. F. INGER.

FIG. 14. — Temporary marsh in open savanna 1 Km north of Nagero, Parc National de la Garamba.

Photo: R. F. INGER.

FIG. 15. — Permanent pond near Nagero, Parc National de la Garamba.

Photo: R. F. INGER.

FIG. 16. — Temporary pond on hill at Ndelele, Parc National de la Garamba.

MATERIAL.

The great bulk of this collection was obtained by the DE SAEGER Mission which was in the field from October, 1949 to October, 1952. Detailed habitat notes were made for most specimens and were available for this study. My wife and I were in the field from the end of February to mid-May, 1959. Most of our observing and collecting was done at night with the hope that we might complement the work of the DE SAEGER Mission which was conducted mainly during the day.

The collection of the DE SAEGER Mission can be viewed as a random set of daylight samples. Every specimen seen was caught if possible and preserved. As our major field goals were the study of behavior of the frogs and an analysis of their habitats, we did not attempt to catch every frog seen. Our activities were centered at the aquatic environments around which frogs were likely to be concentrated. Our collection, therefore, is a somewhat biased, representatieve sample.

ACKNOWLEDGMENTS.

It is a pleasure to acknowlegde the cooperation and assistance of the Institut des Parcs Nationaux du Congo. A grant from the Institut made our trip to the Garamba possible. In particular, I am grateful to M. HENRI DE SAEGER and the late M. VICTOR STRAELEN for the opportunity to study this material and for the many arrangements they made to smooth the way for our work. In the field, we would have accomplished nothing without the constant help of M. A. ORY, Conservateur, and his wife M^me^ H. ORY. Their many kindnesses made our brief stay in the Garamba pleasant as well as scientifically profitable.

I also wish to express my gratitude to my wife, MARY LEE INGER, who was a full partner in all aspects of the field work.

Sonograms of many of the frog calls we recorded were prepared by D^r^ W. F. BLAIR, University of Texas. M^r^ C. M. BOGERT, American Museum of Natural History, loaned me comparative material collected by the Lang-Chapin Expeditions in the Garamba area 50 years ago.

FIELD MUSEUM OF NATURAL HISTORY.
Chicago, Illinois.

XENOPUS

Four species occur in the Parc National de la Garamba. They may be distinguished by means of the following key.

1A. — Inner metatarsal tubercle armed with a black claw 2

B. — Inner metatarsal tubercle clawless 3

2A. — Lower eyelid covering most of the eye ..... *X. fraseri.*

B. — Lower eyelid covering about one-eighth of eye ..... *X. tropicalis.*

3A. — Orbital tentacle more than half diameter of eye; inner metatarsal tubercle elevated, digitiform ..... *X. muelleri.*

B. — Orbital tubercle about one-third diameter of eye; inner metatarsal tubercle low, not digitiform ..... *X. laevis.*

Xenopus fraseri and *X. tropicalis* are more or less confined to the belt of tropical rain forest, whereas *X. laevis* and *X. muelleri* are distributed outside of the forest. As is true of other rain forest amphibians, the forest species of *Xenopus* penetrate into the surrounding savannas using especially the corridors afforded by gallery forest; this is true, for example, of *X. tropicalis* in northeastern Angola (LAURENT, 1961). Conversely, *X. muelleri* has been reported a short distance inside the rain forest belt in Nigeria (SCHIOTZ, 1963).

In the Garamba park, which lies just a short distance north of the rain forest belt and at the southern edge of the drier woodland extending across the Sudan-Guinea area, *Xenopus tropicalis* occurs mainly in bodies of water in grass savanna. The two *X. fraseri* and the 16 *X. laevis* were found only in the northwestern, more heavily wooded portion of the park. Though *X. muelleri* was collected in gallery forest, it was more abundant in tree savanna, and still more numerous in grass savanna (Tabel 4).

The Garamba collection includes 101 samples of *Xenopus* (metamorphic or post-metamorphic), of which only eight consist of two species. Five samples include *muelleri* and *laevis;* four of these are from tree savanna and one from gallery forest. Two samples consist of *muelleri* and *tropicalis*, one from grass savanna and one from an uncertain site. One sample from shrub savanna consists of *laevis* and *tropicalis*.

Xenopus muelleri (PETERS).

Dactylethra muelleri PETERS, 1844, Monatsber. Akad. Wiss. Berlin, **1844**, p. 37 — Mozambique.
Xenopus muelleri PETERS, 1875, Monatsber. Akad. Wis. Berlin, **1875**, p. 201.

Descriptive notes. — Head moderately large, axilla to snout distance about 3 1/2 times in snout-vent; diameter of eye more than half width of interorbital; lower eyelid covering half of eye; orbital tentacle more than half diameter of eye; three inner toes clawed; inner metatarsal tubercle without black horny claw, distinctly projecting; ventral surface yellowish brown, variously spotted with black. In life underside of legs yellow or orange with pale silvery gray spots.

Secondary sex characters. — Females are distinctly larger than males (Table 2), though there is much overlap between the sexes. Adult females have conspicuous anal flaps, which differ from those of *X. laevis* by lacking papillae.

The nuptial asperities on the arms of adult males are like those found in *laevis* (SCHMIDT and INGER, 1959).

Larvae and development. — Fifteen lots of larvae from scattered localities in the park agree with descriptions of larval *Xenopus laevis* (BEDDARD, 1894; WEISZ, 1945). Transforming tadpoles in several of these series have prehalluxes projecting as in *X. muelleri* and completely metamorphosed juveniles in the same series have long orbital tentacles as in *X. muelleri.* On the basis of these characters of metamorphosing juveniles, I think the present series should be identified as *X. muelleri.* Another reason for the identification is the far greater abundance and wider distribution of adult *muelleri* in the Parc de la Garamba as compared to *laevis* (pp. 17 and 22).

Larvae from the Ivory Coast identified by GUIBÉ and LAMOTTE (1958) as *Xenopus tropicalis* differ from the present tadpoles in coloration. The entire lateral surface of the tail is dotted with melanophores in *tropicalis* whereas the tail of *muelleri* tadpoles has a lateral strip devoid of melanophores.

As larvae attributed to *muelleri* have not been described in detail, descriptive notes are presented here.

Head broad, flattened from level of eyes forward; eyes lateral, visible from above and below; oral tentacles reaching level of hind limbs; spiracles ventral, oblique, situated anterior to level of developing fore limbs; limb buds not in branchial (or opercular) chamber; vent median, anal tube curving backwards; tail muscle anteriorly forming a compressed, raised mass over body; tail long, attenuate; dorsal fin thick, low; ventral fin much deeper than dorsal, beginning opposite fore limb buds.

Table 2. — **Monthly frequency with respect to breeding condition of adult** Xenopus muelleri **from Parc National de la Garamba.**

	Males (1)		Females (2)		
	Nuptial pads		Ova		
	absent	present	immature	intermediate	mature
January	8	7	11	—	1
February	3	1	4	1	—
March	3	16	5	2	5
April	2	12	2	—	22
May	1	24	2	2	17
June	4	18	3	2	10
July	4	8	4	1	4
August	2	12	4	4	2
September	4	1	2	1	1
October	1	3	—	—	2
November	1	—	—	—	—
December	1	—	—	—	—
Total number ...	34	102	37	13	64
Range	35,8–50,3	35,6–52,5	38,8–58,4	50,2–61,7	39,6–62,7
Mean ± SE	42,14 ± 0,72	43,53 ± 0,34	48,19 ± 0,86	55,32 ± 1,07	52,25 ± 0,57

Dorsal and lateral surfaces heavily dusted with melanophores; a lateral chromatophore-free streak beginning at the rear of the head and running posteriorly to the distal third or fourth of the tail.

The fore limbs erupt from the pouch in which they develop when the three claws appear on the hind limb. One tadpole having black claws on the first two toes only does not have erupted fore limbs. However, all nine having three black claws have the fore limbs exposed.

(1) Only those at least 35 mm long are included. None below that size had nuptial pads.

(2) All have mature oviducts.

The orbital tentacle appears as a small bud in front of the eye in two larvae in which the oral tentacles have been reduced to stubs. These two individuals, 17,4 and 19,3 mm head plus body, have erupted fore limbs.

Variation in length is given in Table 3.

Table 3. — **Size at various stages of larvae of** Xenopus muelleri **from Parc National de la Garamba.**

Stage of development of hind limbs	Toes with black claws	Fore limbs erupted	Length of oral tentacle	Head plus body	Number
Intermediate	0	0	Full	13,5–24,3	7
Complete	+	+	Full	13,8–24,6	4
Complete	+	+	Half length	25,1–27,5	3

Ecological notes. — *Xenopus muelleri* lives in every type of aquatic environment found in the Garamba park (Table 5), in whatever type of vegetation these environments occur though most commonly in savannas (Table 4). The habitat data of 35 specimens do not refer to aquatic situations, but to grass savanna (14), tree savanna (19), shrub savanna (1), and gallery forest (1). Some of these 35 may actually have been caught in aquatic environments that were not recorded.

Table 4. — **Frequency distribution of** Xenopus muelleri **with respect to habitat in the Parc National de la Garamba.**

Aquatic habitats	Location of aquatic habitats		
	Grass savanna	Tree savanna	Gallery forest
Marsh	40	2	10
Stream	36	83	6
Spring	12	9	5
Temporary pond	39	—	1
Permanent pond	48	—	—
	175	94	22

This species does occur in isolated, temporary bodies of water. Specimens were seen in and around the hill-top pond at Ndelele (fig. 16). At our visit to this site on April 2 the pool, 4×5 m at that time, contained *Xenopus* tadpoles and adults were seen and caught (RFI 3320) at night. The pool had dried up by April 6. Following a rain at 10 : 30 P.M. April 12, the pool reformed and two hours later clasping pairs of *X. muelleri* were seen. One individual (RFI 3494) was caught under a rock 8 meters from the pool at 9 the next morning. Another (RFI 4093) was caught several nights later. The nearest permanent body of water is a spring located approximately 200 m away and 25 m below the level of the pool on the steepest side of the hill.

Table 5. — **Seasonal frequency distribution of** Xenopus muelleri **in aquatic habitats in the Parc National de la Garamba.**

	Wet season	Dry season	Total
Marsh	25	27	52
Stream	111	18	129
Spring	32	12	44
Temporary pond	71	1	72
Permanent pond	50	23	73

All 15 of the larval series were taken at aquatic sites in savanna. Eight of them were collected in temporary ponds and marshes and three in sluggish, marshy streams. Three others were taken in moderately flowing streams.

Females with mature ova are most frequent early in the rainy season, i.e. from April to June (Table 2). Adult males in breeding condition (nuptial pads present) were relatively more abundant from March to August, or from the end of the dry season to past the middle of the wet season. On this basis, breeding seems to take place mainly in the first half of the rainy season. The monthly proportions of juveniles (Table 6), highest after the middle of the rainy season, are in agreement with this hypothetical breeding cycle. Larvae were collected from March through December with about equal frequency before and after July.

Range. — Southern Sudan and Kenya to Transvaal and Angola (Loveridge, 1957), westward from the Sudan to Nigeria (Schiotz, 1963) and Dahomey (Chabanaud, 1919).

Table 6. — **Frequency distribution with respect to age groups of** Xenopus muelleri **in the Parc National de la Garamba. Percentages in parentheses.**

	Juveniles (1)	Adults (2)	Total
January	8 (21)	30	38
February	8 (47)	9	17
March	7 (18)	31	38
April	2 (4)	46	48
May	6 (11)	49	55
June	18 (33)	37	55
July	46 (68)	21	67
August	11 (32)	24	35
September	31 (76)	10	41
October	18 (75)	6	24
November	1	1	2
December	1	1	2

Garamba localities and specimens : Cellule Biologique I (97), Cellule Biologique II (165), Aka (2), Akawa River (4), Bagunda (4), Beredwa (3), Garamba River (3), Inimvua (29), Iso River (1), Kalikimvua (11), Kassi (9), Km. 17 south of Bagbele (1), Mabanga (31), Morubia (8), Nabakoyo (4), Nagbarama (3), Nambia (3), Napokomweli (3), Ndelele (22), Pali (2), PFS Km 21 (6), Pp Km 14 (2), Tikadje (1).

Xenopus laevis (DAUDIN).

Bufo laevis DAUDIN, 1803, Hist. Nat. Rainettes,, p. 85, pl. 30, fig. 1.
Xenopus laevis STEINDACHNER, 1867, Reise Novara, Amph., p. 4.

Descriptive notes. — Head large, axilla to snout distance 3-3 1/2 times in snout-vent; diameter of eye half interorbital width; lower eyelid covering half of eye; orbital tentacle about one third diameter of eye;

(1) All having erupted fore limbs and not meeting criteria for adults given in Table 2.

(2) Criteria in Table 2.

three inner toes clawed; inner metatarsal tubercle without black horny claw, tubercle not digitiform or projecting; ventral surfaces yellowish brown or brown, with numerous small black spots.

Secondary sex characters. — These have been described in detail (SCHMIDT and INGER, 1959) and do not differ appreciably from those of *Xenopus muelleri*.

The only two adult females in this sample measure 59,4 and 61,8 mm Males having nuptial pads measure 40,7-56,4 mm (mean 50,46; N=6).

Ecological notes. — Twelve of the 16 were caught in streams in tree savanna. One was caught in a stream fringed by a gallery forest and three were collected in bush savanna.

Both adult females, caught in August, contain enlarged ova.

Range. — From northeastern Congo southward to Cape Province and westward to Angola.

Garamba localities and specimens : Cellule Biologique I (13), Nagbarama (3).

Xenopus tropicalis (GRAY).

Silurana tropicalis GRAY, 1864, Ann. Mag. Nat. Hist., (3), **14**, p. 316 — Lagos, Nigeria.

Xenopus tropicalis MÜLLER, 1910, Abh. Bayer. Akad. Wiss., (2), **24**, p. 625.

Descriptive notes. — Head small, narrow, axilla to snout distance 4 times in snout-vent; diameter of eye about one-third of interorbital width; lower eyelid covering anterior lower eighth of eye; orbital tentacle one-third to one-half of eye; three inner toes and inner metatarsal tubercle with black, horny claws; ventral surfaces yellowish brown, dark pigment not forming distinct spots.

Secondary sex characters. — Two females containing enlarged ova measure 58,5 and 60,9 mm. Four males with nuptial pads similar to those of *Xenopus laevis* measure 48,9-60,1 mm.

Ecological notes. — Of the 14 frogs in this sample, 6 were caught in streams, 2 in marshes, and 1 each in a spring, a temporary pond, and a permanent pond. No information is available on 3. These aquatic situations were mainly in grass savanna (7 specimens), but also in gallery forest (2) and tree savanna (1).

Though *Xenopus tropicalis* is primarily a rain forest species, it has been reported from savannas at the edge of the rain forest province (SCHIOTZ, 1963).

Range. — From Portugese Guinea and Liberia to northeastern Congo and southward to the mouth of the Congo (PARKER, 1936A) and northeastern Angola (LAURENT, 1954B).

NOBLE (1924) reported *tropicalis* from Medje and Avakubi about 250 km from the Garamba, and DE WITTE (1930) reported it (rather, its synonym *calcaratus*) from Faradje at the boundary of the Garamba park. Unfortunately, neither author distinguished between *tropicalis* and *fraseri*, which PARKER (1936A) clearly demonstrated to be a distinct species.

Garamba localities and specimens : Cellule Biologique I (4), Cellule Biologique II (6), Dungu River at Nagero (1), Garamba River (1), Napokomweli (1), Wilibadi (1).

Xenopus fraseri BOULENGER.

Xenopus fraseri BOULENGER, 1905, Proc. Zool. Soc. London, **1905**, p. 250 — West Africa.

Descriptive notes. — Head moderately small, axilla to snout distance 3 1/2 to 4 times in snout-vent length, diameter of eye one-half or slightly more of interorbital width; lower eyelid covering two-thirds of eye; three inner toes and inner metatarsal tubercle with black, horny claws; throat, chest and abdomen brown without spots or yellow with black spots; ventral surfaces of limbs yellow with bold, black spots.

The two females making up this sample contain enlarged ova. Their snout-vent lengths are 46,4 and 51,4 mm.

Larvae. — Three tadpoles, two of them in metamorphic stages. The inner metatarsal tubercle has a black claw which immediately set these larvae apart from *Xenopus muelleri* and *X. laevis*. Larvae of *X. tropicalis* from the Ivory Coast, which is oustide the range of *X. fraseri*, have no lateral stripe on the tail and body. The present series has a light stripe on the side as in *X. muelleri*.

Ecological notes. — The adults were collected in a marsh formed by rains in the flood plain of a stream in a wooded part of the park. The larval series was taken in a marshy stream in the same general area. The species occurs generally in the rain forest belt.

Range. — Northeastern Congo westward to the Cameroons (PARKER, 1936A) and southwestwards to the mouth of the Congo (LAURENT, 1961).

Garamba locality and specimens : Bagbele-Moke (2), Napokomweli (3 larvae).

Bufo funereus funereus BOCAGE.

Bufo funereus BOCAGE, 1866, Jour. Sc. Lisbonne, **1**, p. 77 — Duque de Bragança, Angola.

T a x o n o m i c n o t e s . — With the large series from the Garamba at hand the subspecific status of *Bufo funereus upembae* from southeast Congo can be confirmed. The northern Congo population, like that of Angola, lacks a tarsal ridge though a few small, spinose tubercles may appear in that position. The tympanum in the Garamba toads, as in Angolan ones, is two-thirds to three-fourths the diameter of the eye instead of one-half the eye as in *funerus upembae* (SCHMIDT and INGER, 1959). The relative tympanum width, in terms of thousandths of snout-vent length, is 43-60 (median 48) in *f. upembae* (4 ♂♂, 4 ♀♀) as compared to 55-80 (median 71) in Garamba *f. funerus* (10 ♂♂, 10 ♀♀).

The dorsal skin in Garamba males does not become as smooth as it does in those of *funereus upembae*. The nuptial pad, which in *f. upembae* covers the entire inner surface of the forearm (SCHMIDT and INGER, 1959), is confined to the fingers in Garamba males.

Bufo gracilipes BOULENGER from the Cameroons-Gabon area was made a synonym of *funereus* by BOULENGER (1906). PERRET and MERTENS (1957) treat this population as a subspecies, *funereus gracilipes*. Thanks to Dr. PERRET, I have been able to examine a series from the Cameroons.

Besides being much smaller than typical *funereus*, the difference on which PERRET and MERTENS maintain *gracilipes* as a distinct form, *gracilipes* differs from *f. funereus* and *f. upembae* in having a vocal sac, in the ornamentation of the skin, and in the amount of webbing. Females of *gracilipes* have 4 or, less commonly 3 1/2 phalanges of the fourth toe free of webbing. At most 3 1/2 and usually only 3 phalanges of the fourth toe are free in female *f. funereus* and *f. upembae*. The other toes have correspondingly less webbing in *gracilipes* as compared to the larger forms. The sides of the body in *gracilipes* have isolated, long, conical warts that are twice as high as the dorsal ones. The lateral warts of *funereus* are higher than the dorsal ones, though not twice as high, and are closely grouped. The condition in *gracilipes* recalls *camerunensis*.

As the differences between *gracilipes* and *funereus* are of the magnitude associated with the graps between sympatric species of *Bufo*, *gracilipes* should be recognized as a distinct species.

D i a g n o s i s . — Size small to moderate, adults 36-65 mm; no cranial crests; parotoids long, low, separated from eyelid; tympanum 2/3 to 3/4 eye diameter; a series of separate, conical glands behind rictus; first finger longer than second; two round or oval metatarsal tubercles; no tarsal ridge.

Color (in alcohol) dark brown above; a broad yellowish interorbital bar usually with a short spur anteriorly on snout and a longer spur on occipital region; a few indistinct dark spots on back.

Secondary sex characters. — Males have the same nuptial pads and skin characters as males of *funereus* (SCHMIDT and INGER, op. cit.) exept for the differences noted above. Contrary to Witte's statement (1930, p. 242), males from the northern Congo do not have vocal sacs. In addition to the Garamba series, males from Niapu (AMNH 8520, 8523-4, 8527) and Niangara (AMNH 8551), northern Congo, have been examined.

The 42 Garamba males having nuptial pads measure 35.5-49.3 mm (mean 42.69 ± 0.49). The smallest female containing ova measures 45.9 mm, the largest 62.2 mm; the mean of 13 within that range is 54.15 ± 1.54 mm.

Ecological notes. — The distribution of *funereus* in various habitats is given in Table 14. Though occasionally living in grass savanna, it is more restricted to forest conditions than either *regularis* or *latifrons*. The preference for forest is more pronounced than the table shows, for 16 of the 24 *funereus* listed under « grassy seepage areas » were caught in a gap in a gallery forest.

The number of adults available is not sufficient to define reproductive cycles. Some males of *funereus upembae* having well-developed secondary sex characters are found in all months of the year (INGER and GREENBERG, 1956). Some males having nuptial pads on the first two or three fingers were collected in every month from March through September in the Garamba. But the ratio of sexually competent to incompetent each month cannot be determined on the basis of the small samples available. Garamba females containing mature ova were collected in May, July, and August.

Range. — Angola and southern and eastern Congo.

Garamba localities and specimens : Cellule Biologique I (11); Cellule Biologique II (30); source of Aka River (8); Bagbele (1); Biadimbi (1); Buluku (4); Dedegwa (5); source of Makpe River (1); Mobaba (14); Morubia (1); Naluguambala (1); Ndelele (1); Mount Uduku (1).

Bufo latifrons BOULENGER.

Bufo latifrons BOULENGER, 1900, Proc. Zool. Soc. London, **1900**, p. 435, pl. 27, fig. 1 — Benito River, Gaboon; PARKER, 1936, Proc. Zool. Soc. London, **1936**, p. 152.

Taxonomic notes. — One of the two most abundant toads in the savannas of the Garamba differs from *regularis* in being smaller and in having a less elevated parotoid, a longer eye-parotoid gap, and a longer and less deep snout (Table 7). In *regularis* the dorsal surface of the snout is horizontal immediately in front of the eyes and begins to slope downwards only near the tip. In the smaller species (*latifrons*) the profile of the snout slopes downward from the eyes. In *regularis* the parotoid overlies one-half of the tympanum; in *latifrons* the anterior margin of the parotoid is even with the rear edge of the tympanum. The call of *latifrons* is also different from that of *regularis* (Fig. 17).

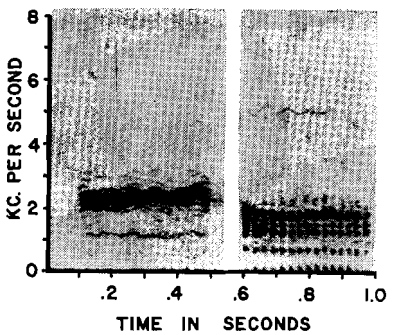


FIG. 17. — Comparison of calls of (left) *Bufo latifrons* (RFI-2313) and (right) *B. regularis* (RFI-2314) recorded within a few minutes of each other on the Dungu River, February 28, 1959.

The Garamba series agrees with *latifrons* BOULENGER (as redifined by PARKER, 1936) from Cameroons and Gaboon in the low, inconspicuous parotoid, in the separation of parotoid and eye, in the narrow, branching, black dorsal markings (see BOULENGER, 1900, pl. 27, fig. 1), and in the notched edge of the rictal gland. It is in these characters that *latifrons* of West Africa differs from *regularis*.

One of Parker's specimens and three others from the Cameroons (CNHM 19816-18) and two from Gaboon (CNHM 75043, 75048) were examined. They differ from the Garamba population in the lengths of foot, tibia, and fingers, in the width of the tympanum, and in the number of tubercles on the ventral surface of the foot (Table 8). The Garamba toad is therefore described as a new subspecies.

Table 7. — **Comparison of body proportions in males of** Bufo latifrons savannae **and** B. regularis **from the Parc National de la Garamba. Proportions given in terms of thousandths of snout-vent.**

	Number	Range	Median	U (1)	P
			Tibia length		
l. savannae	11	324–382	367	—	—
regularis	10	368–399	381	14,5	0,007
			Head with		
l. savannae	11	345–373	358	—	—
regularis	10	348–387	369	21,5	0,02
			Tympanum diameter		
l. savannae	11	61–73	67	—	—
regularis	10	61–79	71	26	0,05
			Eye-parotoid distance		
l. savannae	10	29–67	55	—	—
regularis	10	10–44	20	4	< 0,001
			Eye-nostril distance		
l. savannae	11	69–90	80	—	—
regularis	10	63–76	71	8	< 0,001
			Nostril-mouth distance		
l. savannae	11	71–80	76	—	—
regularis	13	75–88	83	12	< 0,001

(1) U of Mann-Whitney test.

Table 8. — **Comparison of** Bufo latifrons **from Cameroons and Gaboon with sample from the Parc National de la Garamba. Body proportions given in thousandths snout-vent length.**

Sample	Number (1)	Range	Median	U (2)	P
			Tibia length		
West Africa	5	375–438	394	—	—
Garamba	21	324–382	356	2	0,001
			Foot length		
West Africa	5	381–434	410	—	—
Garamba	10	354–406	382	7,5	0,05
			Fourth finger, length		
West Africa	4	135–169	140	—	—
Garamba	10	109–130	119	0	< 0,001
			Head width		
West Africa	5	335–369	361	—	—
Garamba	21	339–373	351	34,6	> 0,10
			Tympanum diameter		
West Africa	5	43–65	56	—	—
Garamba	21	54–75	67	10	0,008
			Eye-parotoid distance		
West Africa	5	59–86	67	—	—
Garamba	20	29–67	47	4,5	0,002
			Number of tubercles, fifth toe		
West Africa	5	5–6	—	—	—
Garamba	10	7–8	—	—	—

(1) Sexes lumped. West African sample : 2 ♂♂, 3 ♀♀. Garamba sample : 11 ♂♂, 10 ♀♀; or 10 ♂♂, 10 ♀♀; or 5 ♂♂, 5 ♀♀.

(2) U of Mann-Whitney test.

Bufo latifrons savannae n. subsp.

Holotype. — Field number RFI-3231. An adult male collected at the source of the Nabakoyo River, Parc National de la Garamba, Congo, at approximately 750 m, March 26, 1959, by ROBERT F. and MARY LEE INGER.

Paratypes. — Three hundred seventy two adults and subadults from the Parc National de la Garamba.

Diagnosis. — Size moderate, adults 45-75 mm; parotoid low; eye-nostril distance equal to or longer than nostril-mouth distance. Like the typical form but having 7 or 8 tubercles on the fifth toe between the outer metatarsal tubercle and the tip of the toe instead of 5 or 6; foot (measured from base of inner metatarsal tubercle to tip of fourth toe) less than two-fifths of snout-vent instead of more than two-fifths.

Description. — Body robust; head broad, obtusely pointed, without ridges; snout sloping downward from preorbital level, rounded in profile, projecting slightly beyond mandible; canthus distinct, lores sloping, not concave; prefrontal region concave; interorbital slightly greater than width of upper eyelid; eye not as long as snout; tympanum distinct, diameter equals three-fifths eye diameter; parotoids distinct, but low, oval, length subequal to parotoid-nostril distance; rictal gland a long serrated ridge.

First finger longer than second; subarticular tubercles and accessory tubercles of palm distinct, single. Toes with thick web; web leaving two phalanges of third and fifth toes and 3 1/2 of fourth toe free; subarticular tubercles conspicuous, single; numerous accessory tubercles on sole; an oval inner and a round outer metatarsal tubercle, both raised but not compressed; a smooth-edged tarsal ridge.

Dorsal warts heterogeneous, dense; lateral warts not larger than dorsals; ventral surface coarsely granular; interorbital and prefrontal areas with small melanin-tipped spinules.

Color (in alcohol) grayish brown above; a pair of small, black prefrontal spots; a pair of oblique, black bars on posterior halves of eyelids narrowly separated on mid-line; a pair of black spots middorsally bordering parotoids posteromedially; two additional pairs of black spots mid-dorsally; limbs with dark cross-bars; venter cream colored, immaculate; gular region black (see *secondary sex characters* below).

Measurements (mm) of holotype : snout-vent 62.7; tibia 23.4; head width 22.0; tympanum 4.1.

In general the dark dorsal markings form a thin network of small spots or bars except for the preorbital, interorbital, and scapular spots. An indication of this pattern is shown in Boulengers's illustration (1900, pl. 27, fig. 1)

Table 9. — **Sexual dimorphism in** Bufo latifrons savannae **from the Parc National de la Garamba. Body proportions given in thousandths of snout-vent.**

Sex	Number	Range	Median	U (1)	P
			Tibia length		
Males	11	324–382	367	—	—
Females	10	326–364	342	23	0,03
			Head width		
Males	11	345–373	358	—	—
Females	10	339–355	345	9,5	0,002
			Eye-parotoid distance		
Males	10	29–67	55	—	—
Females	10	30–58	40	16	0,013
			Tympanum diameter		
Males	11	61–73	67	—	—
Females	10	54–75	66	47	> 0,10

(1) U of Mann-Whitney test.

of the type of *l. latifrons*. The diameter of the tympanum varies from slightly smaller to slightly larger than half the eye diameter. The rictal gland may have from one to five or six notches with the result that it appears to consist of two long ridges or as many as five or six adjacent cones. An oblique lateral row of enlarged warts is usually present. Variation in body proportions is shown in Table 8.

Comparisons. — Differences between *l. savannae* on the one hand *l. latifrons* and *regularis* on the other have already been noted. The absence of long, conical, lateral warts distinguishes this form from *camerunensis* PARKER. The other toads in northeastern Congo, *steindachneri* and *funereus*, lack tarsal ridges.

Secondary sex characters. — Females are larger than males. The smallest female containing enlarged pigmented eggs measures 54.3 mm., snout to vent, and the next larger one 55.1 mm. The maximum size for females is 77.4 mm. The mean of 63 adult Garamba females (55.0 mm. and over) is 64.62 ± 0.58 mm. The smallest male having vocal sacs measures 40.9 and the largest 67.6 mm. The mean of 122 is 53.86 ± 0.47 mm. Males have slightly longer tibias, wider heads, and larger eye-parotoid gap (Tabel 9).

The vocal sac in males is median and subgular, extending across the entire width of the throat. The sac opens into the mouth by means of a single long slit that may be on either side of the tongue. In 35 Garamba males chosen at random, the vocal sac opening is on the right side in 16, on the left in 18, and bilateral in one. The vocal sac and its investing muscle are usually densely pigmented; in only one small adult male (47.5 mm.) are melanophores absent. The gular skin is usually black; seven Garamba males, however, have cream-colored throats.

Nuptial pads typical of *Bufo* (INGER and GREENBERG, 1956) occur on the first three fingers. On the first finger the pad covers the dorsal and medial surfaces from the distal third of the metacarpal to the base of the terminal phalanx, and a small patch of nuptial spinules on the medial part of the palmar tubercle. On the second finger the pad covers a small oval area on the dorsal surface near the base of the finger and extends along the medial edge of the finger to the center of the terminal phalanx. When present on the third finger, the pad is restricted to a narrow strip on the medial edge of the finger. Some males seen have nuptial pads on the first fingers only but most have them on the first and second fingers. The pads also vary in the development of melanin in association with the number of fingers occupied (Table 10).

Table 10. — **Frequency distribution of adults males of** Bufo latifrons savannae **with respect to pigmentation and extent of development of nuptial pads.**

Color of pad	Fingers covered by pad		
	First only	First two	First three
Yellow	4	2	—
Brown	6	19	—
Black	3	84	8
Total	13	105	8

The dorsal warts of both sexes are tipped by a cone usually surrounded by similar though smaller cones. In females and juvenile males the cones are whitish and flattened. In mature males they may resemble those of females (« female » type of Table 11), or be raised into sharp spinules tipped with melanin (« strong » type of Table 11). Variation in this character is correlated with the development of the nuptial pad. The contingency test applied to the frequencies of Table 11 yields a chi-square value of 33.9, which with 6 degrees of freedom is equivalent to a probability of less than 0.001; the hypothesis of random distribution within the table may be safely rejected.

Table 11. — **Frequency distribution showing relation of development of nuptial pad to that of dorsal spines in adult males of** Bufo latifrons savannae.

Dorsal spines (1)	Fingers covered by nuptial pads			
	None	First only	First two	First three
« Female » type	2	2	—	—
Intermediate	2	8	6	—
Strong	—	3	36	2
	4	13	42	2

(1) Definition of these categories given in text.

The deposition of melanin on the nuptial pads is part of the same process as the build up of melanin on the dorsal spines (Table 12). As the amount of melanin in the pads increases, so does the amount on the dorsal spines.

The vocal sacs apparently develop prior to the nuptial pads. Four of the of the males seen have vocal sacs but no nuptial pads. All males having nuptial pads also have vocal sacs.

L a r v a e . — On the night of March 22-23, 1959, a pair of adults (RFI 2496-7), caught in amplexus in shallow water in the Dungu River, were placed in a plastic bag with a small amount of water and left at the edge of the river. Between 01 : 00 and 07 : 00 hours, this pair laid many eggs some of which were transferred to pans and allowed to develop. Tadpoles hatching from these eggs were fed high protein Pablum (a dried prepared infants' food). The larvae were preserved 08 : 00 hours, March

Table 12. — **Frequency distribution showing relation of build up of dorsal spines, amount of melanin on nuptial pads, and extent of nuptial pads in adult males of** Bufo latifrons savannae.

Dorsal spines	Position of nuptial pads					
	First finger only			First two fingers		
	Color of pads			Color of pads		
	Yellow	Brown	Black	Yellow	Brown	Black
« Female » type	2	—	—	—	—	—
Intermediate	1	6	1	1	3	2
Strong	1	—	1	—	3	33

31, at which time they were in Stages I and II (TAYLOR *and* KOLLROS, 1946; Stages 26-28 of LIMBAUGH and VOLPE, 1957). The description that follows is based on these Stage II larvae.

Body oval, flattened above and below, width about half of length; eyes superior, one-third of distance from snout to end of body; interorbital slightly larger than internarial; eye-nostril distance about half of interorbital; nostril much closer to eye than to tip of snout; spiracle sinistral, non-tubular, opening in line between eye and root of limb bud and closer to limb bud than to eye; anus tubular, median.

Tail margins subparallel, tip broadly rounded; dorsal fin beginning at root of tail, rising slightly beyond level of anus, deeper than ventral fin; caudal muscle weak, not as deep as dorsal fin beyond proximal quarter or third of tail, not reaching end of fins.

Oral disk ventral, subterminal; width of disk half width of body; short, thick papillae in a single row at sides of oral disk; labial teeth I : 1-1/III (44 specimens) or I : 1-1/1-1 : II (17); gap in the inner anterior row much narrower than each half of the row; gap in the inner posterior row narrower than that of anterior row; three posterior rows subequal in length, shorter than outer anterior row; outer anterior and posterior rows forming margins of lips; beaks finely serrated, black at margins, anterior beak broadly U-shaped.

Color black above and on sides; below colorless or with a narrow transverse streak of melanophores at anterior margin of branchial chamber;

caudal muscle black, with a colorless band in ventral third running two-thirds of tail length; fins colorless or with a few melanophores on dorsal fin near root of tail.

Total length 9.0-10.5 mm.

Four specimens three days younger than the above had vestiges of suckers and had only two posterior tooth rows, both continuous. Total lengths of these four were 6.3-6.8 mm.

Seven additional lots of tadpoles, similar to those just described, were collected, six of them from the same place on the Dungu River. They are in various stages of development from early limb bud (Stage III) to the beginning of tail resorption (Stage XXII). Labial tooth counts are I : 1-1/III (13 specimens) and I : 1-1/1-1 : II (1). The dorsal fin in all but one (Stage III) has a thin network of melanophores. The ventral portion of the caudal muscle is colorless as in others described above, but the more dorsal portions of the muscle has colorless spots in the midst of the previously solid black area. The underside of the body has many more melanophores than do those of the younger larvae. Beginning at Stage XVII, the paired dorsal spots characteristic of adults of both *regularis* and *latifrons savannae* become apparent. The sizes at various stages are given in Table 13. Full larval size is reached near Stage XI, when all five toes are indicated by notches.

Table 13. — **Size, proportions, and stage of** Bufo **larvae** (regularis **or** latifrons savannae) **from the Parc National de la Garamba.**

Stage (1)	Number	Total length	Tail/Body
III	1	14,0	1,33
IX–X	3	16,5–20,0	1,35–1,60
XI	2	22,5–24,0	1,40–1,50
XII	3	18,5–24,0	1,31–1,52
XIII–XIV	3	17,5–27,5	1,33–1,75
XVII–XVIII	2	20,0–23,5	1,23–1,35
XIX	1	23,0	1,42
XX	1	24,5	1,45
XXI	1	21,5	1,26
XXII	1	17,5	0,84

(1) Stages according to scheme of TAYLOR and KOLLROS, 1946.

A pair of adult *B. regularis* were caught in amplexus at the same time and place as the pair of *latifrons* and treated in the same manner. Eggs and larvae from the *regularis* pair were reared and fed as were the *latifrons* larvae, and were preserved in the same hour. These *regularis* larvae, which reached the same stage of development as the *latifrons* larvae, are indistinguishable from them. The *latifrons* larvae have fewer melanophores on the ventral surface of head and body and a larger proportion of the series have completely developed labial tooth rows.

Because of this similarity, the seven lots of older tadpoles mentioned above cannot be identified to species with assurance. They do agree with descriptions of *regularis* larvae from Guinea (LAMOTTE and ZUBER-VOGELI, 1954), Tripolitania (SCORTECCI, 1936), and Bechuanaland (POWER, 1927).

Table 14. — **Frequency distribution with respect to habitats of** Bufo **species collected in the Parc National de la Garamba.**

Species	Non-aquatic habitats (1)			
	Grass savanna	Shrub savanna	Tree savanna	Gallery forest
regularis	222	2	8	—
latifrons.	88	5	25	6
funereus	2	—	10	11
	Aquatic habitats			
	Marsh	Pond	Grassy seepage area (2)	Stream (3)
regularis	14	9	—	18
latifrons.	48	30	6	51
funereus	3	1	24	26
steindachneri.	—	8	—	2

(1) Specimens listed in either aquatic or non-aquatic habitats, but not in both.

(2) With flowing water; usually drainage of small springs or marshes.

(3) Includes specimens caught on banks.

Ecological notes. — Of the specimens collected away from the immediate vicinity of water and for which detailed habitat notes are available, roughly 5 per cent were caught in gallery forest, 20 per cent in tree savanna, and the rest in grass savanna (Table 14). Thus, though this form of *latifrons* is primarily an animal of the grass savanna, it ranges into wooded habtats.

Bufo latifrons was found in rodent burrows and other holes in the savana as well as on the surface (Table 15). As a significantly larger proportion of those caught below the surface were taken during the dry season (November through March) than during the wet, *latifrons* probably uses burrows primarily to escape the low humidity of the dry season.

Table 15. — **Monthly frequency distribution with respect to capture above and below ground of** Bufo latifrons **and** B. regularis **in the Parc National de la Garamba.**

	Months												Seasons	
	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.	Dry	Wet
	latifrons													
On the surface (1) ...	2	2	8	14	22	19	19	2	1	—	—	1	13	77
In holes	9	7	13	2	2	2	—	—	—	—	—	5	30	6
	regularis													
On the surface (1) ...	7	—	—	15	47	54	18	10	—	1	1	4	12	145
In holes	38	12	41	—	10	3	4	—	—	—	—	1	92	17

(1) Does not include animals caught in aquatic situations.

Though many specimens were collected at a variety of aquatic habitats (Table 14), *latifrons* usually comes to such places only to breed. Oviposition occurs in standing or very slowly moving water. Many of the specimens listed in Table 14 under « stream » were caught in breeding aggregations at the Dungu River in an area of small, isolated pools left in holes in the bed rock as the water level fell towards the end of the dry season in 1959 (Fig. 9). Immediately downstream from the area shown in Fig. 9 the bed of the river dips downard forming a permanent deep pool in which the current was maintained even at the nadir of low water; very few males of *latifrons* called from this part of the river.

Photo: R. F. INGER.

FIG. 18. — Cut-off meander of Garamba River, Parc National de la Garamba.

Photo: R. F. INGER.

FIG. 19. — Dungu River in flood, Parc National de la Garamba.

Trees line the banks of the Dungu and males called from beneath their overhanging branches at the river's edge. They also called from seepage areas under trees adjacent to the river. A small breeding aggregation was seen at the edge of a marsh where small trees overhung the water.

An enormous breeding aggregation formed around a cut-off meander of the Garamba River (Fig. 18) in open grass savanna.

The time of day at which calling began was relatively constant during the period March through May, 1959. The first call was heard between 18 : 00 and 18 : 30 hours and calling continued to midnight but stopped sometime before 03 : 00 hours.

The breeding period begins toward the end of the dry season in early March and continues at least until June and possibly until July. Large choruses were heard in March, April, and May and the high proportion of adults in breeding condition in June and July (Table 16) indicates contiuation of activity until that time. Data are not available for the later months of the year.

Table 16. — **Monthly frequency distributions with respect to breeding competence of adult** Bufo latifrons savannae **from the Parc National de la Garamba.**

Month	Males		Females	
	Secondary sex characters		Ova	
	complete (1)	incomplete	mature	not mature
January	2	3	—	1
February	3	5	6	3
March	28	6	2	10
April	27	7	9	12
May	19	—	9	3
June	12	—	4	3
July	6	—	2	1
August	4	—	—	—
September	1	2	—	—

(1) Brown or black nuptial pads on at least the first and second fingers.

Eggs and larvae were found in the small pools of the Dungu River mentioned above (Fig. 9). Though all of the larvae cannot be assigned definitely to *latifrons* (see above p. 36), collection of clasping pairs of *latifrons* in these pools is strong circumstantial evidence that this species oviposits in this situation. Larvae developing in these pools, which at the time of my observations varied in area from 30 × 60 cm. to 1 × 3 m. and in depth from 3 to 30 cm., are exposed to radical fluctuations in the physical aspects of their environment. Those hatching in early March while the drought continues live in constantly shrinking water holes that may dry up if no light rains fall. During one day in March, a 60 cm. pool shrank 10 cm. in length. Larvae hatching after the middle of March are likely to be swept away by periodic floods. Figure 19 is a view of the same area shown in Figure 9 after heavy rains in the fourth week of March.

As these pools are only partially shaded, the water temperature has a large range. On two successive days in March water temperatures in a pool 60 × 30 × 10 cm. varied from 24°,6 to 34°,6 C.

Bufo latifrons is often found with *regularis*. On twelve occasions the De Saeger Mission caught these species together in rodent burrows. Both species bred along the part of the Dungu River described above, though *regularis* was more abundant away from the banks and, therefore, the trees. Thirty-five lots from the De Saeger Mission contain both *regularis* and *latifrons*. Apart from the 12 in burrows, 14 of those lots are from grass savanna, 4 in shrub or tree savanna, 2 along stream margins, and 3 from marshes.

An additional lot from tree savanna includes *latifrons*, *regularis*, and *B. funereus*. Lots including *latifrons* and *funereus* are from tree savanna (1), grass savanna (1), gallery forest (1), and marshy streams just below gallery forest (2). Two series including *latifrons* and *B. steindachneri* are from temporary flood-plain marshes.

R a n g e . — This subspecies is known at present only from the Parc National de la Garamba, Niangara (AMNH 8552), and Mauda, about 60 kilometers north of Niangara (MRCB 1799-1801).

Garamba localities and specimens : Cellule Biologique I (50); Cellule Biologique II (159); headwaters of Aka River (1); Anzeli (1); Bagisana (1); Bagunda (4); Biadimbi (4); Iso (1); Km. 17 from Bagbele (1); Mabanga (1); Haute Makpe (1); Mobaba (2); source of Moko (1); Nabakoyo (8); Nagero (38); Ndelele (6); Tikadje (1).

Bufo regularis REUSS.

Bufo regularis REUSS, 1834, Mus. Senckenb., **1**, p. 60 — Egypt.

Taxonomic notes. — All adult males from the Garamba have bilateral vocal sac openings and thus support the previously observed north-south dichotomy in this character (SCHMIDT and INGER, 1959). They, therefore, differ from males in the southern part of the Congo where a single opening is typical. The Garamba population also differs from the southern Congo population in reaching sexual maturity at a larger size. The average snoutvent length of 141 adult males from the Province of Katanga in the southern Congo is 58.49 ± 0.69 mm (ibid.); more than one-half of the Katanga males are less than 60 mm, the minimum of adult Garamba males. Seventy adult males from the Garamba have a mean of 71.61 ± 0.52 mm. The difference between the means is statistically significant ($P<0.001$). Corresponding data for females are : Katanga 70.22 ± 1.28 mm ($N=98$), Garamba 83.20 ± 0.86 mm ($N=44$); the difference between these two means is also statistically significant.

Descriptive notes. — Size large, adults 60-100 mm; no cranial crest; parotoids large, elevated, oval, narrowly separated from eyelid; tympanum 1/2 to 2/3 eye diameter; an elongate smooth-edged gland behind rictus; first finger longer than second; two oval metatarsal tubercles, a distinct tarsal ridge.

Color clay or olive brown above, with dark brown or black spots in pairs beginning on interorbital.

Secondary sex characters. — These have been described in detail elsewhere (INGER and GREENBERG, 1956).

Males with vocal sacs measure 60.0-82.6 mm (mean $=71.61 \pm 0.52$; $N=70$). Females containing enlarged, pigmented ova measure 67.3-98.3 mm (mean $=83.20 \pm 0.86$; $N=44$).

Ecological notes. — Of the specimens for which detailed habitat information is available, all but about 5 per cent were caught in grass savanna; none were caught in gallery forest (Table 14). An additional 41 were collected in aquatic situations : in or at the edge of streams, in ponds, and in marshes (Table 14). These aquatic sites are used for breeding.

Bufo regularis was collected in rodent burrows and other holes in the savanna as well as on the surface of the ground. As Table 15 shows, it is found below ground more often in the dry season (November through mid-March) than in the wet season. Aquatic captures are omitted from Table 15.

Breeding takes place in standing or slowly moving water. I observed *regularis* calling and clasping most often in small pools of the Dungu River.

By late February or early March, at the end of the dry season, the Dungu has dropped leaving many small pools isolated in the rocky bed (Fig. 9). Males call (Fig. 17B) more frequently out in the open away from the tree-lined banks (in contrast to *Bufo latifrons savannae*, see p. 39) and never in the marshy areas that occur at intervals under the trees along the river. Males were also calling from the edges of a cut off meander (Fig. 18) of the Garamba River. This, too, is a site without overhead vegetation cover.

Calling and oviposition occur at least from the end of February through May, the inteval of my observations, and may extend over a much longer period. Indirect information from the secondary sex characters of the males and the gonads of the females suggests a peak of reproductive activity in the first four months of the year (Table 17).

Ecological relations with *Bufo latifrons savannae* are discussed under that species.

Table 17. — **Monthly frequency distribution with respect to reproductive competence adult** Bufo regularis **from the Parc National de la Garamba.**

Month	Males		Females	
	Secondary sex characters		Ova	
	complete (1)	incomplete	mature	not mature
January	13	5	5	10
February	10	—	11	4
March	15	—	15	15
April	6	2	5	2
May	—	1	1	3
June	1	3	1	3
July	1	1	1	3
August	1	—	1	3
September	—	2	—	2
October	1	3	—	—
November	1	1	1	—
December	2	1	2	1

(1) Brown or black nuptial pads on first two fingers.

Range. — All of Africa south of the Shara.

Garamba specimens and localities : Cellule Biologique I (47); Cellule Biologique II (270); Mount Aka (2); Akam (1); Mount Bamangwa (2); Gangala na Bodio (4); Kalimvua (1); Km. 17 from Bagbele (5); Mabanga (2); Makpe (4); Mobaba (4); source of Moko River (1); Mount Moyo (1); Nagero (12); Ndelele (1); Mount Otro (4); Mount Tungu (4); Mount Uduku (2).

Bufo steindachneri PFEFFER.

Bufo steindachneri PFEFFER, 1893, Jahrb. Hamburg. Wiss. Anst., **10**, p. 35, pl. 2, fig. 8 — Kihengo, Tanganyika.

Taxonomic notes. — The Garamba series agress with the original description almost point for point. The sole difference lies in the dorsal surface of the head, which, according to Pfeffer, is flat in the type, but is concave above the snout in the Garamba toads. The tympanum in the type is slightly less than half the eye diameter but varies in the present series from that size to slightly larger than half the eye diameter.

The Garamba series has been compared with coastal Kenya specimens and are certainly conspecific with them. The distinctive characters of the species — long fingers, reduced webbing, obscure parotoid, dense dorsal warts, and absence of tarsal ridge — are present in both series. They differ from one another in size and ventral coloration. Adult males (those having vocal sacs) from Kenya have a snout-vent range of 39.6-52.5 mm (mean = 46.00 $\pm$ 1.26 mm; N = 10); the eight from the Garamba have a range of 29.0-40.2 mm (mean = 35.63 $\pm$ 1.14 mm). Eight of the 13 Garamba toads have small black spots on the pectoral and abdominal regions, none of the Kenya sample does. PFEFFER (1893) noted similar dark spots on the type.

Descriptive notes. — Size small, adults 30-40 mm; no cranial crests; parotoids obscure, elongate, separated from eyelids by half width of tympanum; tympanum distinct, about one-half eye diameter, 0.058-0.077 of snout-vent; rictal glands not spinose; dorsal warts small, conical or spinose, very close together; an oblique lateral row of slightly larger spinose warts; subarticular tubercles of fingers emarginate or not; first finger slightly shorter than second, fourth one and one-half times length of upper eyelid; both metatarsal tubercles conical; web usually leaving two phalanges of fifth and four of fourth toe free.

Color (in alcohol) dark clay brown or blackish above with paired oblique spots beginning at preorbital and continuing to sacral region; below yellowish brown, with or without small black spots on pectoral and abdominal regions.

Secondary sex characters. — The sexes are approximately the same size. Mature males of this sample average 35.63 mm; the two females containing enlarged ova both measure 35.2 mm. The means in the Kenya sample are : males -46.00 ± 1.26; females -45.24 ± 1.03 mm. No sex dimorphism in body proportions was observed.

The nuptial pad is typically bufonid, consisting of clusters of blackish spinules. On the first finger the pad covers dorsal and medial surfaces and extends from the base of the finger to the base of the terminal phalanx. In half the Garamba males the nuptial pad appears on the second finger as a dorsomedial oval patch at the base of the finger.

The vocal sac is single, subgular, and reaches across the entire width of the throat. The sac and its investing muscle are densely pigmented. The vocal sac usually has one opening, which may be on either side, or paired openings (1/8 of Garamba males, 3/10 of Kenya males).

The gular skin may or may not be pigmented in males. But since such pigment, when it appears, is similar to the abdominal and pectoral spotting and since similar gular spotting appears in females, this pigmentation is not a sexual character.

Ecological notes. — The type locality of *steindachneri* lies in an area of high grasses and scattered *Acacia*, the Ethiopian locality (BOULENGER, 1898) in woodlands of low deciduous trees and grasses, and the Kenya localities (LOVERIDGE, 1936) in an area of forest-savanna mosaic. The Garamba specimens were caught in the northwestern part of the park, one of the more heavily wooded areas. The vegetation of all of these areas falls into the physiognomic types; woodland, savanna woodland, and tree savanna (BOUGHEY, 1957).

LOVERIDGE (1936) collected his specimens in marshy places and rainfilled pools in which breeding toads had gathered. Eight of the 13 Garamba toads, including the only gravid females, were caught in temporary pools in the flood plains of small rivers in tree savanna. Two other Garamba toads were collected on the banks of such rivers and another on a granitic outcrop in tree savanna.

All Garamba specimens were collected between mid-May and mid-September — during the rainy season but well after its beginning. Collecting in the same temporary marshes early in May several years later, I did not find *steindachneri* nor did I hear an unidentifiable amphibian call that migth have been made by this species.

Range. — Northeastern Tanganyika and Kenya to southwestern Ethiopia and northeastern Congo.

Garamba localities : surroundings of Bagbele (13).

Phrynomerus microps (PETERS).

Phrynomantis microps PETERS, 1875, Monatsber. Akad. Wiss. Berlin, **1875**, p. 210, pl. 3, fig. 4 — Accra, Ghana.

Phrynomerus microps LOVERIDGE, 1930, Proc. Zool. Soc. London, **1930** : p. 15.

Phrynomerus bifasciatus microps DE WITTE and LAURENT, 1942, Rev. Zool. Bot. Afr., **36**, p. 102.

Taxonomic notes. — The five specimens from the Garamba are like topotypes of *microps* (MCZ 28176-79, CNHM 74855-6) in coloration. The coccygeal glandular mass is narrower (0.18-0.23 of snout-vent, mean 0.192) in the Garamba specimens than in the topotypes (0.20-0.29, mean 0.243). However, the gland is larger in the Garamba series than in 20 *bifasciatus* from Katanga (0.14-0.20, mean 0.168). The distinctions between *microps* and *bifasciatus* suggested earlier (SCHMIDT and INGER, 1959) appear to be confirmed.

Descriptive notes. — Habitus stocky, hind limb short; snout truncate, longer than eye; tympanum present, usually obscured by skin; tips of fingers (except first) dilated into broad, truncate disks; toes without webbing; except for last two phalanges, fifth toe tightly bound to fourth; a low, oval, inner metatarsal tubercle; no outer metatarsal tubercle.

Skin smooth or slightly wrinkled dorsally; rugose on sides; smooth or rugose ventrally; a large coccygeal glandular mass.

Color (in alcohol) reddish brown above; sides of head and body blackish brown; an anterodorsal extension of dark lateral color in groin; chest and belly dark brown with many small yellow spots.

Secondary sex characters. — Two females containing enlarged, pigmented ova measure 50.8-51.8 mm snout to vent. Three mature females (CNHM 74855, MCZ 28177, 28179) from Accra, Ghana, the type locality, measure 51.9-54.3 mm. Two Garamba males having vocal sacs have snout-vent lengths of 36.2 and 40.1 mm. Three adult males (CNHM 74856, MCZ 28176, 28178) from the type locality are 42.1-43.3 mm long.

The throats of females are brown, those of mature males black. The median subgular vocal sacs have long, slit-like openings on each side of the mouth. Males lack nuptial pards.

Ecological notes. — All of five Garamba frogs were collected in areas of grass savanna. Two females were dug out of the ground, one at a depth of 20 cm. An immature female (34.1 mm) was found in a crevice of a dead tree. Two males were caught on the surface of the ground during and after long, heavy rains. According to the collector, J. VERSCHUREN, the call is rather weak.

Range. — From West Africa (Ghana) to Sudan (WERNER, 1908) and northeastern Congo.

Garamba locality and specimens : Cellule Biologique II (5).

Rana ornata ornata (PETERS).

Pyxicephalus ornatus PETERS, 1878, Monatsber. Akad. Wiss. Berlin, **1878**, p. 207, pl. 2, fig. 7 — Teita, Kenya.

Rana ornatissima (nec BOCAGE) NOBLE, 1924, Bull. Amer. Mus. Nat. Hist., **49**, p. 227, pl. 53, fig. 2.

Taxonomic notes. — The Garamba specimens and two from Uganda (CNHM 68761-2) agree in coloration with Peters' (1878) figure. They differ sharply from the illustration of the type of *Rana ornata ornatissima* (BOCAGE, 1895). Noble's (1924) series, also from Garamba, were mistakenly referred to as *ornatissima*.

Descriptive notes. — Habitus stocky, limbs short; snout obtusely pointed; tympanum conspicuous, almost as large as eye; tips of fingers and toes blunt; fingers very short, first a little longer than second, toes about half webbed; fourth toe with 3 phalanges free, fifth toe with 1 1/2 — 2 free; inner metatarsal tubercle compressed, elevated, slightly shorter than first toe; tibia 0.38-0.46 of snout-vent, ratio smaller in larger specimens.

Skin of back with low warts, each set in a black spot; throat and chest smooth; abdomen rugose.

Color (in life) of head reddish brown, a black stripe from snout to eye just below canthus, a black stripe on upper eyelid; trunk with a narrow reddish brown vertebral stripe, a broad dorsolateral reddish brown stripe, and a broad oblique, lateral stripe from above tympanum to groin, all these stripes on body continuous with reddish brown of head; stripes separated by a narrow paravertebral row of black spots and a broad, lateral, black triangular band; a similar black band below lateral reddish stripe beginning at eye; limbs reddish brown with broad, black crossbars; throat and chest brownish, marked with small black spots and a pair of parallel cream-colored stripes; belly cream-colored, unmarked.

Secondary sex characters. — As described for *Rana ornata moeruensis* (SCMIDT and INGER, 1959). The only male harving nuptial pads measured 64.2 mm., the three mature females 54.8-59.6 mm.

Larvae. — Four series agree with the description of *R. ornata* larvae from southern Congo (SCHMIDT and INGER, 1959). They differ from Somalia larvae (BOULENGER, 1896) only in lacking teeth on the upper lip. The dental formula in all Garamba tadpoles (Stages from pre-limb bud to X) is 0/II.

One Stage III larva has a total length of 39.5 mm; two Stage X larvae measure 44,0 mm. The tail has a drawn out, filamentous tip.

Ecological notes. — Two specimens (Fig. 20) were caught in amplexus at night following a very heavy rain at a temporary pond (Fig. 16) in an area of grass savanna. This pair plus the only other female having mature ova were collected in April.

Photo: R. F. INGER.

FIG. 20. — *Rana ornata* in amplexus.

The larvae were collected in shallow, temporary bodies of water in grass savanna in April and May.

Range. — Kenya, Tanganyka, Uganda, and northern Congo.

Garamba localities and specimens : Cellule Biologique I (2 sets of larvae), Bagbele (1), Km 17 (1), Nagero (2), Ndelele (2).

Rana occipitalis GÜNTHER.

Rana occipitalis GÜNTHER, 1858, Cat. Batr. Sal. Brit. Mus., p. 130, pl. 11 — West Africa.

Descriptive notes. — Habitus stocky, legs thick; size large, to ca. 120 mm; lores sloping; tympanum visible; interorbital about half width of upper eyelid; skin of back with numerous, short, longitudinal ridges; digits not expanded at tips; toes fully webbed; a flap of skin along outer edge of fifth toe; inner metatarsal tubercle low, no outer metatarsal tubercle.

Table 18. — **Frequency distribution with respect to breeding condition of** Rana occipitalis **from Parc National de la Garamba.**

	Males (1)		Females (2)		
	Nuptial pads		Ova		
	absent	present	immature	intermediate	mature
February	—	3	1	—	1
March	—	15	3	1	5
April	2	20	—	1	7
May	1	11	1	1	2
June	—	4	—	3	2
July	—	2	—	2	—
August	—	3	—	—	2
September ...	—	1	—	—	—
October	—	—	1	—	—
November ...	—	1	—	—	—
	Snout-vent (mm)				
Range	60,3–89,6	61,5–111,0	66,7–106,7	100,8–120,7	90,9–130,0
Mean	77,87	89,92 ± 1,44	82,50	109,63 ± 2,60	108,92 ± 2,26

(1) With vocal sacs.

(2) With mature oviducts.

Color (in life) dark olive or bright grassy green above, usually dark spots visible; some individuals bright green on head becoming olive posteriorly; ventrally yellowish spotted with black; rear of thigh mottled with yellow.

Secondary sex characters. — Females are larger than males (Table 18), though both become mature at between 60 and 85 mm.

Males have subgular vocal sacs and conspicuously wrinkled outpocketing of the gular skin. The nuptial pad is a gray, velvety structure covering the dorsal and medial surfaces of the first finger from its base to the terminal phalanx.

Larvae and development. — Twenty-nine lots correspond to descriptions of *R. occipitalis* larvae (GUIBÉ and LAMOTTE, 1958A). These tadpoles have a subterminal oral disk and heavy beaks with one cusp in the upper and two in the lower. Labial tooth counts are given in Table 21. The ratio of tail to total lenght varies from 0,57 to 0,66 (15 specimens).

Metamorphosis begins when snout-vent length is about 20 mm. (Table 21). The smallest frog lacking a tail measured 22,2 mm.

Ecological notes. — Only one-tenth (40/419) of frogs for which data are available were caught at any distance from water : 21 were collected in grass savanna, 11 in shrub savanna, 7 in tree savanna, and 1 from gallery forest. The remainder were caught either in or at the edges of various types of aquatic environments, mainly streams and temporary ponds (Table 19). With the exception of a single specimen caught in a gallery forest stream, all of those listed in Table 19 were at aquatic sites in savanna.

Juveniles are over-represented in temporary ponds and under-represented in marshes and streams. A chi-square test of the frequencies in the lower half of Table 19 shows the difference between aldults and juveniles to be statistically significant (chi-square = 47,6; degress of freedom = 4; $P < 0,001$). These differences between the age groups are not simply differences in habitat selection, for many of the juveniles collected at temporary ponds were transforming young. Clearly, the young had not migrated to these ponds. Rather they had developed from eggs laid there by adults. Thus the differences in distributions may reflect selection of certain sites for oviposition by adults or greater ease of collecting juveniles at such places for purely mechanical reasons.

Most of the larval series were obtained in standing water in marshes (5), ponds (6), or marshy expansions of small streams (7). Ten were collected in temporary bodies of water such as ponds or marshes in flood plains.

Larvae in early stages of limb development were collected from March through September. In October only advanced larvae (Stages XIV and beyond) were found. Young in metamorphic stages were collected from March to October.

Table 19. — **Habitat-frequency distribution of** Rana occipitalis **from the Parc National de la Garamba.**

	Dry season	Wet season	Total
Marsh	31	14	45
Stream	26	121	147
Spring	1	4	5
Permanent pond	6	7	13
Temporary pond	22	147	169
Subtotal	86	293	379
	Juveniles (1)	Adults (2)	Total
Marsh	26	19	45
Stream	106	41	147
Spring	5	—	5
Permanent pond	1	12	13
Temporary pond	143	26	169
Subtotal	281	98	379

(1) As defined in Table 20.

(2) As defined in Table 18.

Juveniles comprise more than two-thirds of the collections in all months from June through January (Table 20). The high proportions in December and January should perhaps be discounted because of the small numbers involved.

The decrease in absolute and relative number of adults after May possibly results from two factors. Only during the three months (March-May) in which large numbers of adults were obtained was night collecting employed. Adults of *occipitalis* are wary and strong jumpers; they are particulary difficult to collect by day. Breeding activity frequently makes adult frogs more susceptible to capture. This factor may be a partial explanation of the greater importance of adults in March-May if a peak of breeding activity occurs in that period.

Table 20. — **Frequency distribution with respect to stage of development of** Rana occipitalis **from Parc National de la Garamba.**

Month	Juveniles (1)			Adults (2)
	under 40 mm	40–59 mm	60 mm and +	
January	—	2	—	—
February	—	5	4	5
March	1	5	21	24
April	1	1	7	30
May	24	—	4	16
June	86	1	2	9
July	11	13	—	4
August	28	5	2	6
September	66	4	1	1
October	12	5	—	1
November	17	2	—	1
December	4	1	1	—

(1) All having erupted fore limbs. Males lacking vocal sacs, females having straight, slender oviducts.

(2) Adults as defined in Table 18.

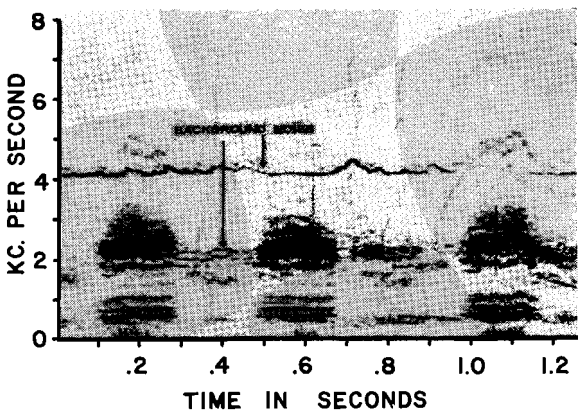


FIG. 21. — Analysis of call of *Rana occipitalis* collected in Dungu River, March 23, 1959.

Table 21. — **Variation in larvae of** Rana occipitalis **from Parc National de la Garamba.**

Stage	Total length	Head plus body	Labial teeth	
			upper	lower
I	—	7,7	II : 1–1	2–2 : II
II	21,4–24,5 (4)	8,0–9,4	II : 1–1	1–1 : II — 2–2 : II
III	—	—	II : 1–1	2–2 : II
VI	35,0	14,9	II : 1–1	2–2 : II
X	45,0	17,0	II : 2–2	2–2 : II
XI	42,0–46,0 (5)	16,6–17,3	II : 1–1 — II : 2–2	2–2 : II — 3–3 : II
XV	52,5	18,2	II : 2–2	2–3 : II
XVII	—	19,2	II : 2–2	2–2 : II
XVIII	63,0–64,5 (2)	22,1–23,7	II : 1–1 — II : 2–2	2–2 : II
XX–XXIII	—	19,0–23,4 (12)	—	—

The presence of larvae in most months suggests that breeding may take place throughout the year. The data in Table 18 do not negate that possibility.

A sonogram of the call is given in Fig. 21.

R a n g e . — From Senegal (MERTENS, 1938) and Liberia (PARKER, 1936B) to Kenya and Tanganyika (LOVERIDGE, 1942), south from Nigeria to coastal Angola (BOCAGE, 1895).

Garamba localities and specimens : Cellule Biologique I (99), Cellule Biologique II (117), Akam (3), Anzeli (1), Bagbele (4), Beredwa (3), Kassi (1), Km. 17 of Bagbele (10), Mabanga (84), Makpe (2), Moko River (4), Morubia (2), Nabakoyo (3), Nagbarama (8), Nagero (16), 1 km. N. of Nagero (3), 3 km. W. of Nagero (3), Napokomweli (46), Ndelele (18), Otro River (1), Pali (1).

Rana galamensis DUMÉRIL & BIBRON.

Rana galamensis DUMÉRIL & BIBRON, 1841, Erp. Gén., **8** : p. 367 — Galam, Senegal.

T a x o n o m i c n o t e s . — The single frog collected by the de Saeger Mission does not differ in any significant way from specimens from Senegal (CNHM 19346) and Mali (CNHM 19376).

Descriptive notes. — Snout-vent length of adult male 68,6 mm, body moderately stout, limbs moderate; snout obtusely pointed; tympanum conspicuous, almost as large as eye; tips of fingers and toes not expanded, without grooves; first finger longer than second; third and fourth metacarpals with supernumerary tubercles; no toes webbed to tips; third toe with 2 phalanges free on outer edge, fourth toe with 3 phalanges free and fifth toe with 1; a low, oval, inner metatarsal tubercle; no outer metatarsal tubercle.

A broad dorsolateral fold; a thick rictal gland followed by a narrow, lateral glandular fold.

Color (in alcohol) slaty brown above and laterally; upper lip, dorsolateral and lateral glandular folds light brown; throat and chest brown, belly yellow with light brown suffusion; limbs with same ground colors dorsally and ventrally as body; hind limb heavily spotted with black.

Secondary sex characters. — The vocal sac openings are round and located near the corners of the mouth. The slit-like openings of the gular pouches are parallel to the upper jaw. Each is approximately as long as the diameter of the eye and slightly shorter than the very large, flat humeral gland.

The yellowish, velvety nuptial pad is confined to the dorsal and median surfaces of the first finger. Dorsally the nuptial pad ends at the base of the proximal phalanx; medially it extends to the end of that phalanx.

Ecological notes. — The only specimen was caught near the head of a temporary stream in tree savanna.

Range. — In savanna country from Senegal and Guinea to Somalia and Kenya, south to Zambia and Mozambique (LOVERIDGE, 1957).

Garamba locality and specimen : Iso River (1).

Rana albolabris albolabris HALLOWELL.

Rana albolabris HALLOWELL, 1856, Proc. Acad. Nat. Sci. Philadelphia, **1856**, p. 153 — West Africa.

Rana albolabris albolabris LOVERIDGE, 1938, Proc. New England Zool. Club, **17**, p. 71.

Descriptive notes. — Habitus slender to moderately stocky; snout pointed, longer than eye; tympanum distinct, subequal to diameter of eye; tips of fingers and toes dilated into small disks, each with a circummarginal groove; all toes except fourth with at most one phalanx free of webbing, fourth with 2 1/3 — 2 3/4 phalanges free; a low, oval inner metatarsal tubercle and a smaller, round outer one.

Skin above granular; a continuous, narrow, dorsolateral ridge (Fig. 22).

Color in life olive above; in alcohol brownish gray above, whitish below; obscure dark crossbars on hind legs.

Secondary sex characters. — Adult males of this form have the same secondary sex characters as the southern race, *R. albolabris lemairei* (SCHMIDT and INGER, 1959). The Garamba females are considerably larger than the males, and have relatively longer legs and relatively narrower

Table 22. — **Sexual dimorphism of** Rana a. albolabris **from Parc National de la Garamba.**

	Males (1)	Females (2)
	Snout-vent (mm)	
Range	38,0-53,7	48,3-73,7
Number	44	22
Mean ± SE	44,84 ± 0,60	57,77 ± 1,64
	Tibia length (3)	
Range	486-518	489-526
Number	10	10
Median	498	512
	U = 22 (4)	P < 0,05
	Tympanum diameter (3)	
Range	99-125	74-99
Number	10	10
Median	108	91
	U = 1 (4)	P < 0,001

(1) Nuptial pads present.

(2) Oviducts mature.

(3) As thousandths of snout-vent length.

(4) Mann-Whitney U test.

tympana than males (Table 22). The dimorphism in tympanic diameter is common in species of the *Hylarana* group.

L a r v a e a n d d e v e l o p m e n t . — Twenty-one series of tadpoles ranging in development from pre-limb bud to metamorphic stages agree with descriptions of larval *Rana albolabris* (LAMOTTE, LAUWARIER, and PERRET, 1957; GUIBÉ and LAMOTTE, 1958). The dorsolateral folds and form of the appendages of transforming larvae are identical to the corresponding structures of adult *albolabris*.

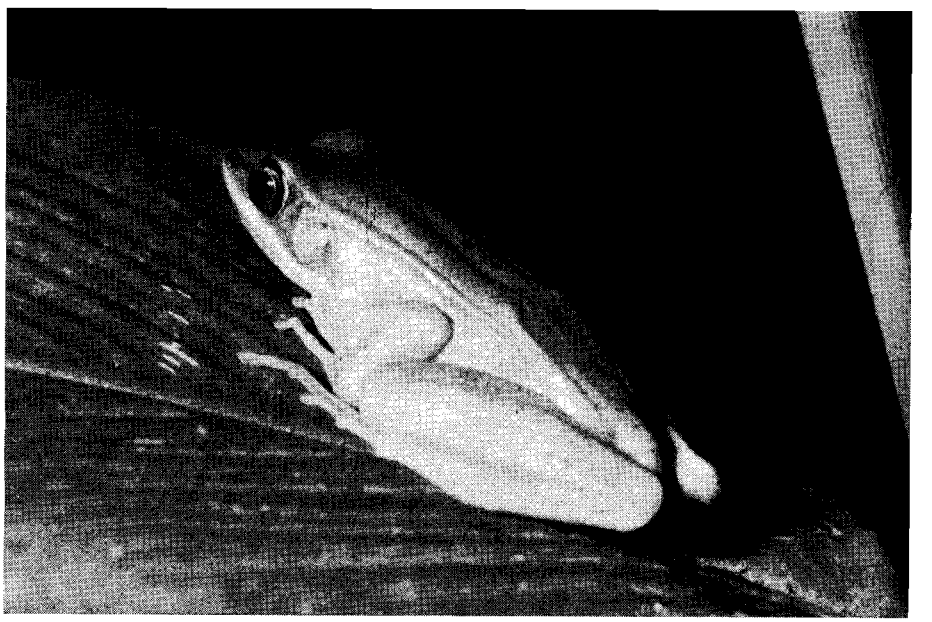


Photo: R. F. INGER.

FIG. 22. — *Rana albolabris*.

One character of these larvae that seems to have been overlooked is the presence of large clusters of glands dorsolaterally behind the head, ventrolaterally near the end of the body, and mid-dorsally. These clusters recall those found in larvae of *R. chalconota* (LIEM, 1961; INGER, 1966) and *R. signata* (INGER, 1966), though they differ in number and outline. The presence of these structures strengthens the relationship of these three species which have been placed in the subgenus (or genus of some authors) *Hylarana*.

The arrangement of the tooth rows on the lower lip is 1-1 : II in all Garamba larvae of *albolabris*. The arrangement on the upper lip varies as follows :

Formula	Number of larvae	Stage
I : 2-2	2	pre-limb bud
I : 3-3	7	VI-XVI
I : 3-4	4	II-XVII
I : 4-4	3	XVI-XX

The stages are according to the scheme of TAYLOR and KOLLROS (1946). More advanced larvae tend to have more tooth rows, a trend also observed by LAMOTTE *et al.* (1957).

The largest tadpole without evident limb buds had a total length of 29,5 mm. Two in which the fore limbs had just erupted measured 51-55 mm. The ratio of tail to total length in 9 tadpoles within this span of developmental stages varied from 0,58 to 0,64. Both the total lengths and tail ratios are comparable to values in West African *albolabris* (LAMOTTE *et al.*, 1957, fig. 12 and Table C).

Metamorphosis begins when the frogs are 17-25 mm long (Table 23). Correlation of degree of tail resorption and extent of gape is good, though correlation between either of these characters and snout-vent is not.

Table 23. — **Size frequency distribution with respect to development of metamorphosing** Rana a. albolabris **from Parc National de la Garamba. All individuals have erupted fore limbs.**

Extent of gape	Tail length (mm)					Snout-vent mean
	6 and +	3–6	1–3	1	absent	
Front border of eye	3 (19,1–26,0)	4 (17,6–19,3)	—	—	—	20,43
Center of eye ...	—	5 (17,6–26,5)	1 (17,0)	—	—	20,50
Rear border of eye	—	—	6 (19,1–24,3)	8 (18,4–23,4)	13 (19,4–25,1) (1)	21,53
Snout-vent mean ..	23,03	19,99	21,28	20,18	22,13	—

(1) No juveniles larger than 26,0 mm were included in this cell in order to restrict it to newly metamorphosed individuals.

Table 24. — **Monthly frequency of male** Rana a. albolabris **from Parc National de la Garamba with respect to development of secondary sex characters. Snout-vent (mm) in parentheses.**

	No humeral gland	Humeral gland present		
		No vocal sac	Vocal sac present	
		No nuptial pads		Nuptial pads
January	—	2 (36,0)	—	—
March	—	1 (35,1)	—	2 (38,7–45,3)
April	—	1 (35,7)	—	1 (47,3)
May	4 (34,6–38,0)	2 (36,5–39,9)	2 (39,0–40,0)	9 (40,2–53,7)
June	1 (35,2)	4 (37,0–38,1)	—	4 (38,0–48,0)
July	2 (35,4–37,1)	3 (35,4–37,7)	2 (38,2–42,0)	18 (39,0–46,9)
August	—	1 (38,0)	1 (38,6)	—
September	—	—	1 (44,2)	2 (43,6–46,5)
October	—	—	—	2 (43,5–44,7)
November	—	—	—	5 (45,6–52,4)
December	—	—	—	1 (50,6)
Range	34,6–38,0	35,1–39,9	38,2–44,2	38,0–53,7
Total number	7	14	6	44
Mean	36,19	36,91 ± 0,37	40,33	44,84 ± 0,60

Males become mature at about 38 mm and females at about 48 mm (Table 22). Of ten females in the size range 48-55 mm, four have straight or slightly kinked oviducts and six have strongly convoluted ones.

Unlike most African frogs, males of *R. a. albolabris* do not develop vocal sacs before all other secondary sex characters (see SCHMIDT and INGER, 1959, and other sections of this paper). Humeral glands are the first of these structures to appear (Table 24), followed by the vocal sacs, and then the nuptial pads. The differences in the lengths of frogs in the three last columns of Table 24 probably reflect differences in ages.

Ecological notes. — In the essentially savanna country of north-eastern Congo, *Rana albolabris* is largely confined to densely wooded areas.

The majority of the specimens listed in Table 25 from such seemingly open habitats as marshes were associated with gallery forest or tree cover. For example, 32 *albolabris* were caught in small, open marshes that interrupt gallery forests at Beredwa, Dedegwa, and Cellule Biologique II. Another 16 were collected in a wooded marsh at Mobaba. Twenty-one of the 59 listed from streams were taken along wooded banks.

Larvae were collected mainly in sluggish streams in gallery forest (12 lots). Five lots were obtained from streams that, though shaded by trees, were more open than gallery forest. Another three lots were found in a wide marshy depression with trees around its periphery.

Elsewhere in its range *Rana albolabris* is a forest species (NOBLE, 1924; PERRET, 1960B).

As males having nuptial pads are found virtually throughout the year (Table 24), *albolabris* seems to lack a distinct breeding season in the Garamba just as it does in the southern Congo (SCHMIDT and INGER, 1959). Only three Garamba females held ripe ova; one was collected in May and the others in December. Juveniles were taken every month except January, and larvae in seven months scattered from February to December.

Table 25. — **Habitat-frequency distribution of** Rana a. albolabris **in Parc National de la Garamba.**

	Dry season	Wet season	Total
Aquatic :			
Marsh	2	67	69
Grassy seepage	11	37	48
Stream side	12	47	59
Subtotal	25	151	176
Non-aquatic :			
Grass savanna	4	1	5
Tree savanna	—	4	4
Gallery forest	20	117	137
Subtotal	24	122	146

Range. — From Liberia (LOVERIDGE, 1938) and Angola (BOCAGE, 1895) to Uganda (NIEDEN, 1915) and southern Congo (SCHMIDT and INGER, 1959).

Garamba localities and specimens : Cellule Biologique I (38), Cellule Biologique II (73), Aka (28), Akawa (1), Anzeli (2), Bagbele (1), Bamangwa (3), Beredwa (4), Biadimbi (4), Buluku (22), Dedegwa (32), Inimvua (6), Kalikimvua (1), Lamu (1), Makako (1), Makpe (12), Mobaba (85), Morubia (8), Nabakoyo (1), Nagbarama (4), Nagero (6), Napokomweli (1), Ndelele (2), PFS/Km 21 (2), Km 22 (1), Pidigala (9), Zungumbia (2).

Rana huguettae sp. nov. [1].

(Fig. 23.)

Holotype. — Field number RFI 3317. An adult female collected at Ndelele, Parc National de la Garamba, Congo at 900 m, April 2, 1959 by MARY LEE and ROBERT F. INGER.

Paratypes. — Forty-two specimens from the Parc National de la Garamba (34 Institut Royal des Sciences Naturelles; 8 CNHM).

Diagnosis. — A moderate-sized member of the *Ptychadena* group having an immaculate brown or orange brown dorsum (in life); short, weak longitudinal ridges on the back; vomerine teeth in transverse groups; a large, compressed, inner metatarsal tubercle; no supernumerary metatarsal tubercles.

Description. — Body moderately stocky, limbs slender; head width 0.30-0.37 (median 0.337; N=10) of snouth-vent; snout obtusely pointed, projecting beyond mandible a distance equal to two-thirds diameter of tympanum; nostril equidistant between eye and tip of snout or slightly nearer the latter; internarial distance equal to eye-nostril distance but much greater than width of interorbital or upper eyelid; interorbital and upper eyelid subequal; canthus rostralis rounded; lores sloping, weakly concave; tympanum distinct, about two-thirds diameter of eye; vomerine teeth in transverse groups touching anteromedian corners of choanae, groups widely separated.

Fingers and toes bluntly rounded; first finger equal to or slightly longer than second; second and fourth subequal; metacarpals with distinct supernumerary tubercles. Toes almost fully webbed; first and second toes with 1/2 to 1 phalanx free; third toe usually with 2 (sometimes 2 1/2) phalanges free on inner edge and 1/2 free on outer edge; fourth toe with two phalanges free; fifth with less than one phalanx free; inner metatarsal tubercle

[1] This species is named for Mme HUGUETTE ORY, wife of M. ORY, Conservateur of Parc National de la Garamba, and herself a keen naturalist. It is a pleasure to acknowledge the many kindnesses shown my wife and myself by Mme ORY.

elevated and slightly compressed, its length equal to 0,48-0,68 (median 0,590; N = 10) of length of first toe; outer metatarsal tubercle elongate, continuous with a weak tarsal ridge; no supernumerary tubercles on metatarsals; no tarsal tubercle; tibia 0,54-0,65 (median 0,612; N = 19) of snout-vent.

Back with numerous short, low ridges of skin; none running entire length of torso; no continuous dorsolateral fold; no folds on snout; skin between ridges shagreened; a weak supratympanic fold present or absent; a thick glandular ridge at rictus; skin smooth ventrally; posteroventral aspect of thigh coarsely granular.

Photo: R. F. INGER.

FIG. 23. — *Rana huguettae*, new species.

Color in life above and laterally tan to reddish brown; a blackish brown stripe below canthus beginning at tip of snout, expanding behind eye, and running at least half distance to groin; a similar dark line on pre-axial edge of thigh; rear of thigh dark brown with yellowish green spots, stripes, or network; ventral surface white with yellowish green wash posteriorly on abdomen and at groin; underside of feet dark brown, without light areas.

Measurements (mm) of holotype : snout-vent 47,1; head width 15,3, tibia 29,7.

Secondary sex characters. — Fifteen adult females measure 39,1-48,9 mm (mean 44,80±0,76 mm). Twenty-three mature males measure 34,4-42,2 mm (mean 38,52±0,42 mm). The difference between means is statistically significant.

The vocal apparatus is typical of males of *Rana* (*Ptychadena*) (INGER, 1956). The gular pouch openings are at an angle to the lower jaw and end near the ventral borders of the axillae. The skin of the pouches is black and gray.

The grayish nuptial pad is confined to the first three fingers. It covers the entire dorsomedial surface of the first finger except for the terminal phalanx, and the entire dorsal surface of the second finger except for the terminal phalanx. On the third finger the pad forms an oval area limited to the dorsal surface of the metacarpal. These three areas of nuptial pad are separated from one another by undifferentiated epidermis.

Most males have feebly developed, inconspicuous, colorless asperities on the throat and chest.

Comparisons. — The absence of spots and stripes from the back distinguishes this uniform series from most species of *Rana* (*Ptychadena*). The species having a similar coloration are: *longirostris* PETERS (type locality — Keta, Chana), *newtoni* BOCAGE (type locality — St Thomas Island), *retropunctata* ANGEL (type locality — Mt. Nimba, Guinea), and *obscura* SCHMIDT and INGER (type locality — Upemba, Congo).

The first appears most similar to *huguettae* yet differs in several characters. The vomerine teeth of *longirostris* are set in oblique groups, those of *huguettae* are in transverse groups. The inner metatarsal tubercle is less than half the length of the first toe in *longirostris* (0,34-0,38 in two measured), but usually much more than half the first toe in *huguettae* (0,48-0,68 in 10; only 2 less than 0,56). *Rana longirostris* has longer legs, the ratio of tibia to snout-vent in 3 *longirostris* being 0,67-0,72 and in 19 *huguettae* 0,54-0,65 The head of *longirostris* (0,29-0,32 in 3; median 0,294) is narrower than that of *huguettae* (0,30-0,37 in 19; median 0,337). The webbing is slightly more extensive in *longirostris* usually leaving only 1 to 1 1/2 phalanges of the fourth toe free (GUIBÉ and LAMOTTE, 1957), whereas in *huguettae* 2 phalanges of the fourth are free.

Rana retropunctata agrees with *huguettae* and *longirostris* in lacking long ridges or folds of skin on the back. The short ridges illustrated and described by GUIBÉ and LAMOTTE (1957) seem higher than those of *longirostris* and *huguettae*. The inner metatarsal tubercle of *retropunctata* appears not to be raised at it is in *huguettae*, and the outer metatarsal tubercle is round in contrast to the elongate one of *huguettae*. The third and fourth metatarsals of *retropuncta* have rows of small supernumerary tubercles, which are absent in *huguettae*. The webbing of the latter is slightly more extensive; in *retropunctata* the third toe has 3 phalanges free on the inner edge and 1 on the outer (GUIBÉ and LAMOTTE, 1957), whereas in *huguettae* the corres-

ponding numbers are 2, 2 1/2 and 1/2, respectively. The first toe of *retropunctata* has 2 phalanges free, that of *huguettae* only 1. The pattern of the rear of the thigh consists of small light spots on a dark background in *retropunctata;* in *huguettae* the light areas may be in the form of large spots, stripes, or a network. The largest male and female of *retropunctata* available to GUIBÉ and LAMOTTE measured 31,5 and 41 mm, respectively (ibid.), and are smaller than the means of *huguettae* (see above, *Secondary sex characters*).

Although *Rana newtoni* BOCAGE is only poorly known, the original description (BOCAGE, 1886) stated that the species has oblique groups of vomerine teeth, a gular pouch ending near the upper border of the axilla, small dark spots on the throat, and a dark stripe on the side of the head that ended above the axilla. Besides differing from *huguettae* in these characters, *newtoni* is a much larger frog, the adult male measured 57 mm and the female 68 mm (ibid.), dimensions that exceed the maxima of *huguettae* significantly.

The fourth of these dorsally uniform species, *obscura*, has regular, continuous dorsal skin folds and thus differs sharply from *huguettae*. *Rana obscura* also differs from *huguettae* in having rows of supernumerary metatarsal tubercles and in having a shorter inner metatarsal tubercle (i.e., less than half the length of the first toe).

Rana christyi BOULENGER (type locality — Medje, Congo) resembles *huguettae* in having a dark band on the side of the head. But *christyi* has strong, continuous, dorsolateral folds but no median dorsal ridges. *Rana christyi* also differs from *huguettae* in having a shorter inner metatarsal tubercle (0,30-0,38 of length of first toe in 10 topotypes) and greater snout-vent length (47,3-51,7 mm in 11 males, 55,2-58,7 mm in 4 females).

Ecological notes. — The majority (31 of 43) of the frogs caught were in breeding aggregations at a shallow (less than 15 cm deep), temporary pool in grass savanna early in April (Fig. 16). The first calling males were heard April 12, though the species was seen at this site April 2. Nine of ten females caught here contained enlarged ova.

Eight additional specimens were collected in grass savanna and four along the banks of streams. Two of the last were in gallery forest.

Besides the females referred to above, the other five mature ones in the collection were obtained in the interval February-April. Three contained mature ova.

Range. — Known only from the Parc National de la Garamba, but probably occurring in the savanna across northern Congo, southern Sudan, and the Central African Republic.

Garamba localities and specimens : Cellule Biologique II (9), Beredwa (1), Km 17 south of Bagbele (1), Morubia (1), Ndelele (31).

Rana maccarthyensis ANDERSSON.

(Fig. 24.)

Rana maccarthyensis ANDERSSON, 1937, Ark. Zool., **29A**, no. 16, p. 9, figs. 3-4 — MacCarthy Island, Gambia; GUIBÉ and LAMOTTE, 1957, Bull. Inst. Franc. Afr. Noire, **19**, p. 954, figs. 11-13.

Rana mascareniensis (part) NOBLE, 1924, Bull. Amer. Mus. Nat. Hist., **49**, p. 218.

Taxonomic notes. — GUIBÉ and LAMOTTE (1957) suggest that *R. maccarthyensis* is confined to West Africa and is replaced in Central Africa by *R. grandisonae* LAURENT. *Rana grandisonae* has less extensive webbing than *maccarthyensis* and median skin folds that begin between the eyes rather than behind the eyes as in *maccarthyensis* (GUIBÉ and LAMOTTE, 1957). SCHMIDT and INGER (1959) observe that *maccarthyensis* males have the nuptial pad extending up the arm whereas it is confined to the fingers in male *grandisonae*, that the gular pouch of the latter is black and white whereas that of *maccarthyensis* is black or black and dark gray, and that *maccarthyensis* has a short median pair of skin folds extending forward only as far as the sacrum, whereas the median pair in *grandisonae* extend from the coccyx to the interorbital (1).

The Garamba series, because it is somewhat intermediate geographically between the ranges of *grandisonae* and *maccarthyensis*, was compared with both (Table 26). These specimens agree with West African *maccarthyensis* and differ from *grandisonae* in most characters, and are intermediate between *maccarthyensis* and *grandisonae* in webbing. The hind limb is shorter in the Garamba specimens than in either of the other samples. As the resemblance with *maccarthyensis* is strong in those characters (dorsal skin folds, secondary sex characters) that show little intraspecific variation in the subgenus *Ptychadena*, I am assigning the Garamba specimens to that species.

WAKE and KLUGE (1961) record *maccarthyensis* from southeastern Tchad. Their color description suggests they may have had the closely related species *perreti*, for their specimens were spotted ventrally (see below, p. 78).

Descriptive notes. — Body moderately stocky, limbs relatively short; snout long, obtusely pointed; vomerine teeth in short transverse groups touching anterior rims of choanae; back with 8 longitudinal ridges or folds of skin beginning behind eyes, median pair interrupted over sacrum forming a short posterior pair; supernumerary metacarpal tubercles present;

(1) The diagram of the dorsal skin folds of *maccarthyensis* given by GUIBÉ and LAMOTTE (1957 : fig. 13 top) is incorrect. It fails to show the short median folds mentioned in the original description (ANDERSSON, 1937) and clearly visible in their photograph of *maccarthyenss* (GUIBÉ and LAMOTTE, 1958 : pl. 5, fig. 6).

toes extensively webbed; fourth toe usually with 2 1/2 phalanges free on lateral border, a few specimens with 3 phalanges free; fifth toe with 1/2 to 1 phalanx free; inner metatarsal tubercle oval, not compressed; a round outer metatarsal tubercle; rows of small supernumerary tubercles on third and fourth metatarsals; tibia 0,50-0,59 of snouth-vent (Table 26).

Photo: R. F. INGER.

FIG. 24. — *Rana maccarthyensis.*

Color in life olive brown above with dark olive spots; vertebral band golden brown; canthi olive; upper half of lores black; lower half of lores and lip olive; upper half of iris gold; ground color of limbs same as back, crossbars not interrupted; rear of thigh dark olive with yellowish-green light stripes, which are irregular in some individuals; lower lip grayish olive; rest of venter immaculate white except posterior half of abdomen which may be pale yellowish white.

Secondary sex characters. — Females having mature ova are, on the average, about 6 mm larger than males having fully developed nuptial pads (Table 26).

Gular pouch openings run at an angle to the lower jaw and end near the ventral border of the axilla. The pouches are uniformly black (10 specimens), black and gray (14), uniform gray (3), or black and white (6).

Table 26. — **Comparison of Garamba** Rana maccarthyensis **with Liberian** maccarthyensis **and** Rana grandisonae **from the Upemba, Congo.**

	West Africa *maccarthyensis*	Garamba *maccarthyensis*	Upemba *grandisonae*
Phalanges free :			
fourth toe	2	2 1/2–3	3
fifth toe	1/2	1/2–1	1
Anterior extent of skin folds ..	Behind eyes	Behind eyes	Between eyes
Short, median skin folds (1) ...	Present	Present	Absent
Nuptial pad	Arm and fingers	Arm and fingers	Fingers only
Gular pouch (2)	B, B & G	B, B & G, B & W	B & W
Snout-vent (3) :			
males	41,8–47,0 (44,26)	42,3–50,8 (46,15)	33,6–43,5 (38,63)
females	48,1	48,0–56,8 (52,71)	37,5–49,4 (42,10)
Tibia ratio (4)	558–616 (593)	499–588 (526)	495–567 (538)
Foot ratio (4)	484–541 (524)	445–523 (492)	478–529 (511)

(1) In posterior half of back.

(2) B=black; B & G=black and gray; B & W=black and white.

(3) Mean in parentheses.

(4) As thousandths of snout-vent; median in parentheses.

The nuptial pad is usually yellowish. Its distributions is as given in SCHMIDT and INGER (1959 : 71, fig. 37). Small colorless asperities are distributed over the throat and chest but are absent dorsally.

L a r v a e . — Five sets of tadpoles agree with the description (LAMOTTE and PERRET, 1961B) of larval *maccarthyensis*. The distinctive characters are : the shape of the upper beak — with a distinct median convexity; and the dental formula — I/II. Larvae of *R. tournieri* (LAMOTTE *et al.*, 1958) share these characteristics with larval *maccarthyensis*, but lack the large dark spots that appear on the caudal muscle of *maccarthyensis* (see LAMOTTE and PERRET, 1961B, fig. 13).

The papillae of the present samples are in a staggered, continuous row across the margin of the lower lip. The dorsal fin arises near the end of

the body behind the level of the spiracle. Eye diameter is slightly greater than the eye-nostril distance. Tadpoles in Stages XIV-XVI have total lengths of 31-32 mm.

Ecological notes. — In the Garamba this species is much more abundant in grass savanna than in other habitats. Though most of the specimens were caught in aquatic habitats, 30 of those listed in Table 27 from temporary ponds were in ponds formed in grass savanna (Fig. 25). Apparently *R. maccarthyensis* is inactive and secretive except during the rains as less than 15 per cent of those collected were obtained in the dry season. During the rainy season the call of this species is one of the characteristic night sounds of the savanna. In 1959 the first calls we could attribute to this species were heard on May 2. We had collected *maccarthyensis* previously only on April 22. GUIBÉ and LAMOTTE (1958) report *maccarthyensis* from savanna of the Mt. Nimba Reserve, Guinea.

Table 27. — **Habitat-frequency distribution of** Rana maccarthyensis **from Parc National de la Garamba.**

	Wet season	Dry season	Total
Non-aquatic :			
Grass savanna	32	3	35
Tree savanna	5	—	5
Gallery forest	—	4	4
Subtotal	37	7	44
Aquatic :			
Marsh	2	3	5
Stream	7	—	7
Temporary pond	37	—	37
Permanent pond	1	—	1
Subtotal	47	3	50

The larval series were collected in marshes or in marshy expansions of small streams in savanna.

Eleven females collected in May contained mature ova. No more than 2 females were caught in any other month making it impossible to delimit a breeding season. Ripe females were taken April through August.

The only male adult in size (49,6 mm) but lacking nuptial pads was caught in October. This single frog does not constitute enough evidence to support a hypothesis of regression during the dry season; males from all other months (except February and June when no males were collected) had well-developed nuptial pads.

A sonogram of the call is given in Fig. 30A.

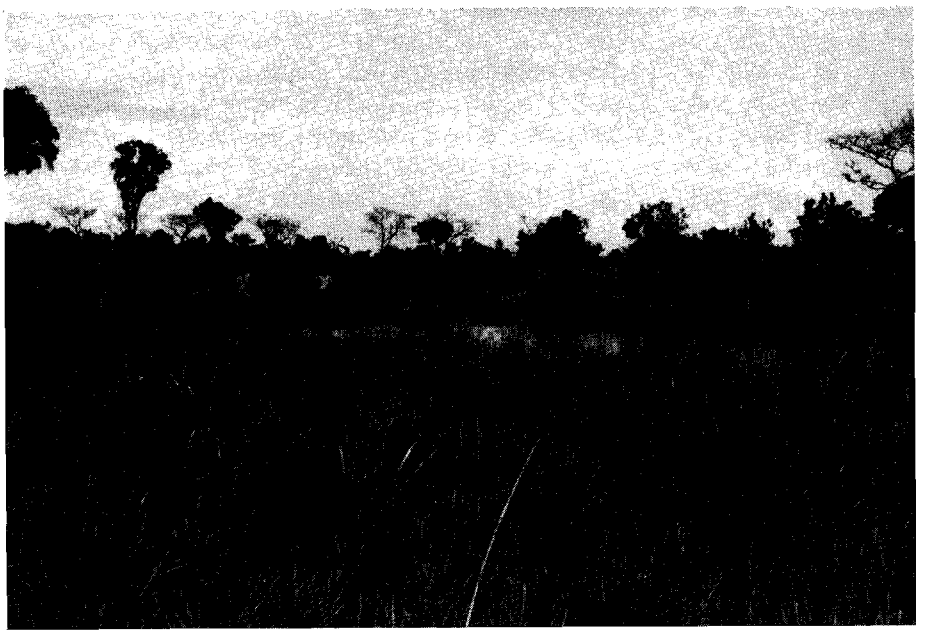


Photo: R. F. INGER.

FIG. 25. — Temporary pond, habitat of *Rana maccarthyensis*, Bagbele, Parc National de la Garamba.

Range. — From Gambia and other parts of West Africa (GUIBÉ and LAMOTTE, 1957) to northeastern Congo.

Garamba localities and specimens : Cellule Biologique I (9), Cellule Biologique II (27), Km 17 south of Bagbele (7), Morubia (1), Nagbarama (2), Nagero (4), 1 km north of Nagero (16), Ndelele (18), Tikadje (1), Zungumbia (1).

Rana mascareniensis hylaea SCHMIDT and INGER.

Rana mascareniensis hylaea SCHMIDT and INGER, 1959, Expl. Parc. Nat. Upemba, Fasc. 56, p. 83, fig. 39.

Taxonomic notes. — The Garamba sample agrees with the western subspecies in the characters said to distinguish it from the eastern subspecies (SCHMIDT and INGER, 1959). Adults from the Garamba are distinctly larger than frogs from southeastern Congo. Average snout-vent length of males from the Garamba is 45,44 ± 0,40 mm, females 53,19 ±0,99 mm; the corresponding means from the southern populations are 41,73±0,22 and 47,80±0,52 mm. The webbing of Garamba frogs is dark brown and not bicolored as in the typical subspecies (ibid.). Males from the Garamba have colorless spinules on the chest and abdomen in contrast to those of the typical, eastern form. Finally, the leg is longer in the Garamba frogs than in those from southeastern Congo. The ratio of tibia to snout-vent is 0,53-0,61 (median 0,558) in 10 males from the Garamba. In 13 males from Upemba the ratio is 0,49-0,57 (median 0,542). Applying the Mann-Whitney U test gives these results : U=22, P=0,01, showing that the two samples are drawn from different statistical populations.

Description. — Body slender (males) to moderately stocky (females); limbs long, slender; snout obtusely pointed; vomerine teeth in short, transverse groups touching anterior rims of choanae; back with 8 longitudinal ridges, median pair beginning on occiput and continuous to end of body; no supernumerary metacarpal tubercles; toes extensively webbed; fourth toe with 1 1/2 to 3 phalanges free of broad webbing on inner margin, fifth toe with one free; inner metatarsal tubercle oval, not compressed; no outer metatarsal tubercle; no row of small tubercles on any metatarsal; tibia 0,53-0,61 of snout-vent.

Color in life brown above with rows of squarish black spots; a yellow or cream-colored vertebral band or line usually present (85 % of those examined); rear of thigh black with two yellowish green stripes; tibia with broadly interrupted black crossbars, resulting in two marginal rows of black spots; tibia with fine yellow line dorsally in 45 of 47 specimens larger than 25 mm; ventral surfaces white anteriorly, yellowish posteriorly and under legs; webbing dark brown; in small specimens light area at base of membrane between first and second and between second and third toes.

Secondary sex characters. — Females are distinctly larger than males (Table 30).

Male secondary sex characters are identical to those of *R. m. mascareniensis* (SCHMIDT and INGER, 1959 : 81) except that ventral spinules are present in males of *R. m. hylaea* (see above).

There is evidence in this subspecies as in the cases of *R. taenioscelis* (p. 86), *R. tournieri* (p. 91) and *R. perreti* (Table 28) that the gular pouch begins development before the vocal sac. Fifteen males of *R. m. hylaea*, snout-vent 34,1-47,6 mm, have distinct creases in the gular skin at the ultimate site of the gular pouch opening but have no vocal sac openings. Six males, snout-vent 37,3-47,1 mm, having deep folds on the throat have vocal sac openings.

L a r v a e . — Twenty-two lots varying in development from prelimb bud to metamorphic stages agree with descriptions of larval *Rana mascareniensis* (Mertens, 1938B; Lamotte and Perret, 1961B).

The body is ovoid, the labial tooth formula is I : 1-1/II, the dorsal fin begins near the end of the body well behind the level of the spiracle, and the tail is spotted. The two rows of teeth on the lower lip are long and subequal. The upper beak is a smooth, concave arc without a median convexity. Head plus body lengths vary from 7,9-8,1 at Stages II to IV to 14,0-15,0 at Stages XIV and XV. The ratio of eye diameter to eye-nostril distance is 0,68-0,91 (median 0,77; N=8).

In life the ventral surface is bronzy green anteriorly changing to bronze-orange posteriorly.

These tadpoles differ from those of *R. maccarthyensis* (see p. 65) in dental formula and in shape of the upper beak, and from those of *R. perreti* (p. 78) in the origin of the dorsal fin and in relative size of the eye.

Table 28. — **Habitat distribution of** Rana mascareniensis hylaea **in Parc National de la Garamba.**

	Wet season	Dry season	Total
Aquatic :			
Marsh	91	45	136
Stream	125	48	173
Spring	17	1	18
Pond	86	43	129
Subtotal	319	137	456
Non-aquatic :			
Savanna	16	9	25
Gallery forest	8	7	15
Subtotal	24	16	40

Ecological notes. — In the Garamba park *R. mascareniensis* is far more abundant around aquatic sites than elsewhere, and roughly equally numerous along streams, ponds, and marshes (Table 28). Most of the aquatic sites from which frogs were collected are in savanna (Fig. 10). Only 93 of these frogs were obtained at wooded aquatic situations, either in entrenched gallery forest or at streams having a dense fringe of trees (Fig. 8).

Twenty larval series were obtained from standing water in marshes or temporary ponds in savanna. Two lots were obtained in pools formed in pot holes in the rocky bed of the Dungu River. As these pools (0,6-1,0 m in diameter, 0,1 m deep) were not under trees, water temperature varied as much as 10 °C in a day (24,6°-34,2° on Mar 31). Evaporation was rapid and one pool shrank 10 cm in a seven-hour period.

The frequencies of juveniles and adults collected month by month are complementary, relative abundance of juveniles being high from May through January (Table 29). Adults in breeding condition were obtained in numbers only from February through June (Table 30). The data of these two tables suggest that breeding takes place in the interval February-June, or in the last part of the dry season and early part of the rainy season.

Table 29. — **Monthly frequency distribution with respect to stage of development of** Rana mascareniensis **hylaea from Parc National de la Garamba.**

	Larvae (1)	Juveniles (2)	Adults
January	—	23	10
February	—	9	27
March	9	6	83
April	8	6	63
May	4	51	9
June	—	75	9
July	1	85	1
August	1	22	2
September	—	11	1
October	—	9	1
November	—	1	—
December	—	54	1

(1) Number of series.

(2) Males with no sign of developing or mature gular pouches. Females with straight oviducts.

R a n g e . — From the Garamba southwards and westwards in the rain forest provinces to the west coast of Africa.

Garamba localities and specimens : Cellule Biologique I (32), Cellule Biologique II (299); Akam River (1); Bagbele (3); Bagunda (2); Bamangwa (2); Biadimbi (1); Buluku (1); Dedegwa (2); Garamba River (7); Kalikimvua (1); Kassi (8); Makako (1); Makpe (22); Mobaba (9); Morubia (50); Nabakoyo (2); Nagero (8); Napokomweli (2); Ndelele (12); Otro River (1); Pali (3); PFS Km 21 (1); Pp Km 10 (4); Tikadzi (1); Mount Tungu (1); Utukuru (9).

Table 30. — **Frequency distribution with respect to breeding condition of** Rana mascareniensis hylaea **from Parc National de la Garamba.**

	Males (1)		Females (3)		
	Nuptial pads		Ova		
	incomplete (2)	complete	immature	intermediate	mature
January	1	3	3	2	1
February	—	17	2	5	3
March	3	25	5	11	6
April	—	50	6	3	4
May	—	—	3	2	4
June	—	4	—	2	3
July	—	1	—	—	—
August	—	—	—	—	2
September	—	—	—	1	—
October	—	—	1	—	—
December	—	1	—	—	—
	Snout-vent (mm)				
Range	36,9–42,4	39,0–52,7	45,2–59,3	43,6–60,6	44,5–64,8
Mean	40,88	45,44 ± 0,40	53,23 ± 0,84	53,31 ± 1,00	53,19 ± 0,99

(1) With fully developed gular pouch.
(2) Nuptial pads not present on third finger.
(3) With mature oviducts.

Rana oxyrhyncha SMITH.

(Fig. 26.)

Rana oxyrhynchus SMITH, 1849, Ill. Zool. South Africa, pl. 77, fig. 2 — Natal.

Descriptive notes. — Body moderately stocky, limbs long; snout long, obtusely pointed; vomerine teeth in transverse groups touching anteromedian borders of choanae; back with 6 or 8 longitudinal ridges,

Photo: R. F. INGER.

FIG. 26. — *Rana oxyrhyncha.*

median pair beginning behind the eyes and continuous to end of body; usually no supernumerary metacarpal tubercles, in a small proportion of individuals weak tubercles are present on third or fourth metacarpal; all toes except fourth webbed to tips on lateral borders; fourth toe usually with 1/2 to 1 1/2 phalanges free; no outer metatarsal tubercle; no row of small tubercles on any metatarsal; tibia 0,65-0,80 of snout-vent (median 0,713; N=20).

Color in life yellowish brown above or center of dorsum blackish brown with sides of body and top of head reddish; back with longitudinal rows of

black spots centered on ridges of skin; a black stripe below canthus, a broader black stripe behind eye ending short distance behind axilla; dorsal surface of limbs brown with blackish crossbars; rear of thigh with a dark network, light spots greenish yellow; underside of hind limbs greenish yellow; rest of venter cream-colored; lower lip blackish brown with narrow cream-colored bars.

Secondary sex characters. — The characters of the males are as described previously (SCHMIDT and INGER, 1959).

Photo: R. F. INGER.

FIG. 27. — Swale in flood plain of Garamba River, site of calling aggregation of *Rana oxyrhyncha*.

The 15 females containing enlarged ova measure 58,2-69,8 mm (mean $65,97 \pm 0,86$). They are significantly larger than adult males, which measure 49,8-63,0 mm (mean $55,81 \pm 0,55$; $N=26$).

Ecology. — Only 12 adults and subadults were collected away from water; 9 of the 12 were caught in grass savanna, 2 in tree savanna, and 1 in shrub savanna. Those caught in or near water were mostly in grass savanna (33), though a few were found in galleries along streams (3), in tree savanna (3), or in bush savanna (1). Thirteen were taken at the edges of streams, 27 at temporary ponds, and one in a papyrus marsh.

In the Garamba this long-legged *Rana* is clearly more abundant in grass savanna than elsewhere. Occasionally *R. oxyrhyncha* does breed in streams as we caught one pair (RFI 2451-2) in amplexus at the edge of the Dungu River. We heard many calling in temporarily flooded grass (Fig. 27), but none at extensive permanent marshes or along stream banks.

Some of these small, grassy pools are very short-lived. The one (Fig. 16) around which we saw most specimens of *oxyrhyncha* was on a flat-topped hill. The history of this temporary pool is detailed on p. 174.

Rana oxyrhyncha begins to breed shortly after the start of rains in March in the Garamba. Ten of 12 adult females collected in April held enlarged, pigmented ova. All 22 adult males (i.e., those having vocal sacs) caught in April had nuptial pads. The pair in amplexus mentioned above was caught the night of March 18. The extent of the breeding season in the Garamba cannot be determined because too few specimens are available.

The call of this species is analysed in Fig. 28.

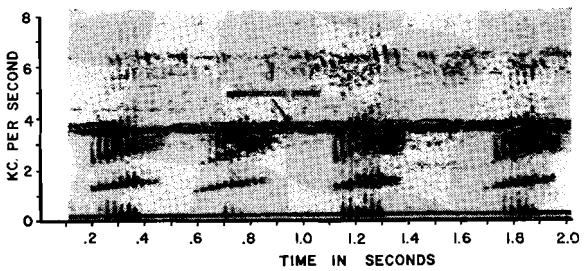


FIG. 28. — Call of *Rana oxyrhyncha* (RFI-3684) recorded April 24, 1959.

R a n g e . — According to GUIBÉ and LAMOTTE (1961), *Rana oxyrhyncha* occurs from Senegal and Sierra Leone in the west to Uganda in the east and southwards to Cape Province on the east and to Angola on the west. The species has a typical circum-forest, savanna distribution.

Garamba localities and specimens : Cellule Biologique I (5), Cellule Biologique II (13), Bagbele (1), Morubia (2), Nagero (1), Ndelele (28), PFS/Km 22 (1), Tikadje (1), Wilibadi River (1).

Rana perreti (GUIBÉ and LAMOTTE).

(Fig. 29.)

Ptychadena perreti GUIBÉ and LAMOTTE, 1958, Bull. Inst. Franc. Afr. Noire, **20**, p. 1456, figs. 3, 5 — Foulassi, Sangmelina, Cameroon.

Taxonomic notes. — When this species was described, it was not known to be sympatric with *R. maccarthyensis*. Hence GUIBÉ and LAMOTTE (1958B) did not compare it with the latter.

Photo: R. F. INGER.

FIG. 29. — *Rana perreti.*

These two species are superficially very similar when preserved. Both have supernumerary tubercles on the metatarsals, both have a short median pair of skin folds on the rear of the back, both have irregular yellowish green stripes behind the thighs, both have complete bars on the legs, and males of both have nuptial pads on the wrist (see fig. 37 in SCHMIDT and INGER, 1959).

Two species are clearly recognizable in the large Garamba sample, one being identical to *maccarthyensis* (see p. 63) and the other agreeing with

the original description of *perreti* and with specimen (CNHM 59155, 59164-6, 59167, 75060) from Cameroon and Gaboon. The two differ in a number of ways.

GUIBÉ and LAMOTTE (ibid.) state that often the throat, chest and knees of *perreti* have dark spots. In the Garamba series of *perreti* 19 of 23 adults have dark spots on the chest and 21 of 23 have spots on the ventral surface of the knee. Only 4 adults of *maccarthyensis* are spotted ventrally, and those have only a series of dots on the throat. In life the ventral surface of *maccarthyensis* is white, with some individuals having a pale yellowish wash posteriorly. The ventral surface of live *perreti* has a bright lemon-yellow or yellowish-green wash.

The leg of *perreti* is distinctly longer than that of *maccarthyensis*. When the leg is brought forward, the tibiotarsal joint extends beyond the snout in *perreti* by at least a distance equal to the diameter of the eye, whereas in *maccarthyensis* that joint just reaches the tip of the snout or not quite so far. The ratio of tibia to snout-vent is correspondingly longer in *perreti* (Table 31).

Table 31. — **Comparison of adults of** Rana maccarthyensis **and** R. perreti **from the Parc National de la Garamba.**

	Snout-vent (mm)			
	Males (1)		Females (2)	
	maccarthyensis	*perreti*	*maccarthyensis*	*perreti*
Range	42,3–50,8	34,9–48,9	48,0–56,8	45,7–57,0
Number.	40	29	15	26
Mean	46,15 ± 0,33	42,54 ± 0,60	52,71 ± 0,70	53,35 ± 0,57
	Tibia (3)			
Range	513–562	605–693	496–588	552–671
Number	10	12	6	9
Median	530	639	522	648

(1) Males having fully developed nuptial pads.

(2) Females having mature ova.

(3) In thousandths of snout-vent.

The web of *maccarthyensis* is slightly more extensive than in *perreti*. The latter invariably has the entire terminal phalanx of the fifth toe free of web, whereas many Garamba *maccarthyensis* have only half of that phalanx free. The difference in webbing is more evident if the toes are spread. Then the edge of the membrane between the fourth and fifth toes appears concave in *perreti* and straight in *maccarthyensis*. This difference is evident only in adults.

The nuptial pad of *maccarthyensis* covers the entire dorsal surface of the proximal segment of the third finger. In males of *perreti* the pad at its maximum development covers about one-third of the proximal segment of the third finger.

The calls of these species, while similar, are readily distinguished (Fig. 30).

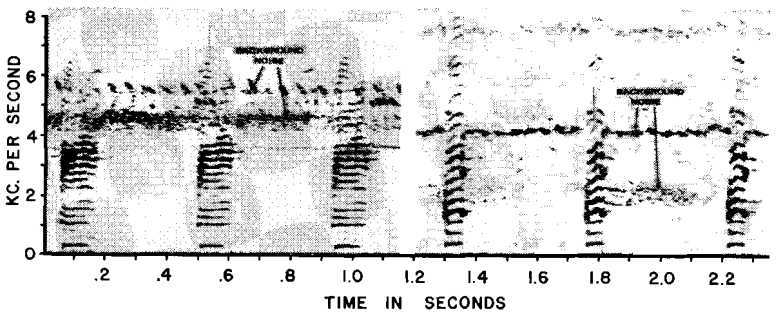


FIG. 30. — Comparisons of calls of *Rana maccarthyensis* (left) and *R. perreti* (right).

Differences in snout-vent length are minor (Table 31).

The Garamba record for *perreti* represents a range extension of about 1800 kilometers.

Descriptive notes. — Body moderately stocky in females, slender in males; limbs long, slender; snout long, pointed; vomerine teeth in short transverse groups touching anterior rims of choanae; back with 8 to 10 longitudinal ridges or folds of skin beginning behind eye, a short median pair of folds beginning over sacrum and running to end of body; supernumerary metacarpal tubercles present; toes extensively webbed; fourth toe with 2 1/2 — 3 (usually 2 3/4 — 3) phalanges free on outer edge; fifth toe with 1 — 1 1/3 phalanges free; inner metatarsal tubercle oval, not compressed; a round outer metatarsal tubercle; rows of small supernumerary tubercles on third and fourth metatarsals; tibia 0,55-0,69 of snout-vent (Table 31).

Color in life clay brown above with rectangular black spots; vertebral band golden brown; canthi clay brown; upper half of lores black; lower half of lores pale brown; upper half of iris golden brown; sides and dorsal

surfaces of limbs pale brown; crossbars of limbs not interrupted; rear of thigh black with irregular yellowish green stripes; lower lip barred with dark brown; venter whitish with bright lemon-yellow or yellowish green wash; dark brown or black spots usually present on chest and ventral surfaces of hind limbs.

Secondary sex characters. — Adult females are larger than adult males (Table 31).

Males have grayish nuptial pads similar to those of *R. maccarthyensis* (SCHMIDT and INGER, 1959 : fig. 37) except that the pad is not as well developed on the third finger. Of 38 males having the pad developed on the wrist, the pad of the third finger is absent in 9, it occupies between one-fifth and one-third of the dorsal surface of the basal segment in 27, and it covers more than one-third of that segment in 2. The males lacking nuptial pads on the third finger are not simply younger; they do not differ significantly in size from males having pads on that finger (Table 33).

The gular pouch openings run at an angle to the lower jaw and end near the ventral border of the axilla. The pouches are uniformly black (10 specimens), black and gray (12), or uniformly gray (4).

Ventral asperities are absent.

Larvae and development. — The dorsal fin of these tadpoles rises sharply anterior to or at the perpendicular through the spiracle. It is more or less horizontal thereafter except near the tip. The ventral fin is one-half the depth of the dorsal. The labial teeth have the formula I : 1-1/II, though in a few individuals the inner lower row is divided. Eye diameter is equal to or longer than the eye-nostril distance. Body and tail are heavily pigmented, the dorsal fin with large black spots throughout its length and the ventral fin only in its distal half.

These larvae agree in the above characters with the description of larval *R. perreti* (LAMOTTE and PERRET, 1961B). They differ from tadpoles of *mascareniensis* in the origin and shape of the dorsal fin and relative eye size and from those of *maccarthyensis* in the origin of the dorsal fin and in labial tooth counts.

Females reach sexual maturity, i.e., the oviducts become highly convoluted, between 45 and 50 mm (Table 32). Males acquire their secondary sex characters when they reach a size of 35-40 mm (Table 33).

Ecological notes. — *Rana perreti* was originally collected in forest in the Cameroons (GUIBÉ and LAMOTTE, 1958B). In the largely savanna Parc National de la Garamba, *R. perreti* is usually found at or in bodies of water and those often under cover of trees. Only 15 of the 258 for which habitat notes are available were collected away from water. Eleven of the 15 were in grass savanna, 2 in tree savanna, and 2 in gallery forest.

Table 32. — **Monthy frequency of female** Rana perreti **with respect to developmental stages. Snout-vent lengths in parenthese.**

	Oviduct immature	Oviduct mature		
		Ova immature	Ova intermediate	Ova mature
January	1 (45,4)	—	1 (50,6)	—
February	2 (36,4–47,3)	3 (45,7–55,6)	—	2 (50,5–54,6)
March	—	1 (51,6)	2 (49,2–50,0)	3 (51,9–56,0)
May	3 (34,8–45,2)	2 (45,9–53,0)	2 (56,3–57,5)	12 (45,7–56,8)
June	5 (39,1–47,6)	3 (46,9–52,4)	3 (49,5–53,5)	4 (50,8–55,5)
July	11 (34,2–49,4)	1 (53,7)	—	4 (51,1–47,0)
August	3 (38,4–41,4)	—	—	1 (53,8)
September	2 (34,0–47,6)	—	—	—
October	2 (37,6–45,8)	1 (53,5)	—	—
November	1 (47,3)	2 (50,6–53,4)	—	—
December	—	1 (59,6)	—	—
Range	34,0–49,4	45,7–59,6	49,2–57,5	45,7–57,0
Total number	30	14	8	26
Mean	—	51,29 ± 1,08	52,33 ± 1,12	53,35 ± 0,57

Almost half of the frogs collected at aquatic sites were found along streams of various sizes (Table 34). In the Garamba rivers commonly have wooded banks (see DE SAEGER, 1954 : pl. 36, fig. 2; pl. 47, fig. 1). Small streams are often entrenched in ravines supporting gallery forest (ibid.; pl. 50, fig. 1). Thus the importance of streams as habitats of *perreti* tends to associate it with tree cover.

Marshes and ponds, on the other hand, are commonly in open savanna in the Garamba. But even some marshes are close to and even a part of gallery forest systems. The Nabakoyo, an insignificant tributary of the Dungu River, arises as a spring in a deep, forested ravine (crown of gallery forest shown in fig. 7), then after 500 m spreads out into an open marsh of Cyperaceae that has a fringe of trees and shrubs (Fig. 13), before wandering across the grass savanna. *Rana perreti* was caught in this marsh.

Table 33. — **Monthly frequency of male** Rana perreti **with respect to development of secondary sex characters. Snout-vent lengths in parentheses.**

Gular pouch	Absent	Incomplete	Complete	Complete	Complete	Complete
Vocal sac openings	Absent	Absent	Present	Present	Present	Present
Nuptial pad, wrist	Absent	Absent	Absent	Present	Present	Present
Nuptial pad, third finger	Absent	Absent	Absent	Absent	< 1/3 (1)	> 1/3 (1)
January	—	—	—	1 (42,1)	1 (40,2)	—
February	—	—	1 (41,8)	1 (41,8)	1 (37,6)	—
March	—	—	—	1 (41,0)	3 (34,9–44,1)	—
April	—	—	—	—	1 (45,9)	—
May	—	1 (40,6)	2 (42,0–43,5)	4 (37,1–43,1)	8 (38,0–48,9)	1 (40,8)
June	—	—	—	1 (45,0)	2 (40,2–47,4)	—
July	—	—	—	1 (43,6)	7 (40,2–46,1)	1 (46,7)
August	1 (35,9)	—	—	—	3 (39,8–41,3)	—
September	1 (41,8)	—	—	—	1 (45,4)	—
October	1 (33,2)	—	—	—	—	—
Range	33,2–41,8	40,6	41,8–43,5	37,1–45,0	34,9–48,9	40,8–46,7
Total number	3	1	3	9	27	2
Mean	—	—	42,43	41,77 ± 0,74	42,54 ± 0,60	43,75

(1) These categories are explained in the text (p. 78).

Further description of the aquatic sites from which *R. perreti* was obtained also suggest the importance of tree cover to this species (Table 34).

Table 34. — **Frequency distribution of** Rana perreti **in aquatic environments** (1) **in the Parc National de la Garamba.**

	Wet season	Dry season	Total
Aquatic habitats :			
Marsh	57	12	69
Spring	52	6	58
Stream	104	12	116
Subtotal	213	30	243
Location of aquatic site :			
Grass savanna	—	1	1
Degraded gallery forest (2)	11	9	20
Dense gallery forest (2)	24	12	36
Opening in gallery forest	28	—	28
Wooded river bank (2)	22	4	26
Uncertain	128	4	132
Subtotal	213	30	243

(1) Only 15 were collected away from bodies of water (see p. 78).

(2) Descriptions of these environments are given by De Saeger (1954).

The localities at which the three series of larvae were collected do not support the preceding suggestion. Two of the larval series were caught in temporary ponds in open savanna and only one in a temporary pond shaded by trees.

Only a tentative idea of the breeding cycle can be obtained from these specimens. The first calling males were heard on March 23, 1959, and a pair was caught in amplexus on the following night. Adult females lacking enlarged ova are relatively most frequent during the period October-February

(Table 32). Though these numbers are by themselves too small to be reliable, they receive some support from the monthly frequency of juveniles (i.e., snout-vent less than 30 mm).

Month	Total	% juvenile	Month	Total	% juvenile
January ...	3	—	July	88	45
February ...	11	9	August	22	14
March	15	7	September .	10	—
April	1	—	October ...	3	—
May	52	31	November ...	3	—
June	51	35	December ...	1	—

The most active period of breeding seems to be from the second half of March to the first half of August.

Range. — From Cameroons to northeastern Congo.

Garamba localities and specimens : Cellule Biologique I (9), Cellule Biologique II (132), Aka (2), Bamangwa (3), Buluku River (3), Dedegwa (3), Dungu River (1), Inimvua (4), Km. 17 south of Bagbele (1), Makpe (14), Mobaba (19), Morubia (45), Nabakoyo (7), Nagero (1), Ndelele (1), PFS Km 21 (2), Pp Km 10 (5), Pp Km 56 (3), Pp Km 62 (1), Tayele (1), Wilibadi (2).

Rana straeleni sp. nov. [1].

Holotype. — Field number RFI 4351. An adult male collected one km north of Nagero, Parc National de la Garamba, Congo, on May 11, 1959 by MARY LEE and ROBERT F. INGER.

Paratypes. — Nine specimens from the Parc National de la Garamba (6 Institut Royal des Sciences Naturelles; 3 CNHM).

Diagnosis. — A moderately small member of the *Ptychadena* group having the median skin folds continuous from the end of the body forward on to the snout; dark crossbars of the tibia interrupted; adult males with nuptial pad on the arm at the wrist as well as on the fingers.

Description. — Body and limbs slender; head width 0,30-0,34 (median 0,320) of snout-vent; snout pointed, projecting beyond mandibile a distance equal to three-fourths of tympanum diameter; nostril equidistant between eye and tip of snout or closer to latter; internarial distance subequal to eye-nostril but greater than interorbital width; interorbital subequal to

[1] Named in honor of the late Dr. V. VAN STRAELEN in recognition of his great services to the cause of conservation in Africa.

width of upper eyelid; canthus rostralis rounded; lores sloping, concave; tympanum distinct, two-thirds to three-fourths diameter of eye; vomerine teeth in short, transverse groups touching anteromedian corners of choanae, distance between groups greater than length of one group.

Fingers and toes bluntly rounded; first finger equal to second; second and fourth subequal; metacarpals with distinct supernumerary tubercles. Toes not fully webbed; first and second toes with 1 1/2 phalanges free, third toe with 1 to 1 1/2 phalanges free, fourth with 3 free, and fifth with 1 free; inner metatarsal tubercle oval, weakly compressed; outer metatarsal round; a row of small tubercles on fourth metatarsal and another usually on third metatarsal; no tarsal tubercle; tibia 0,57-0,62 (median 0,595; N=8).

Back with 8 long ridges of skin, the median pair continuous from end of body forward on to snout; a moderate glandular ridge at rictus; ventrally skin smooth except for narrow rugose area at end of abdomen.

Color (in alcohol) dark brown above with large, squarish black spots that tend to run together in transverse rows; a black stripe on side of snout ending at eye; a narrow light vertebral stripe; rear of thigh blackish with light stripes; dark crossbars of tibia interrupted; ventral surfaces cream-colored, immaculate; underside of feet dark brown.

In life posterior third of belly and ventral surfaces of legs lemon yellow.

Measurements (mm) of holotype : snout-vent 36,0; head width 11,8; tibia 22,2.

The eight adult males (including the holotype) measure 35,0-37,6 mm (mean $36{,}28 \pm 0{,}40$). An additional male having gular pouches but no nuptial pads measures 35,0 mm, and an unsexed juvenile 20,8 mm.

Secondary sex characters. — The males composing this series have black and white gular pouches. The openings of these pouches end at the ventral border of the arm insertion. Yellowish nuptial pads cover the dorsal surfaces of the first two fingers except for the terminal phalanx. On the third finger the pad occupies an oval area on the dorsal surface of the metacarpal. A large, irregular patch of the lower arm is also covered by nuptial pad material. In several males very weak, colorless asperities appear on the ventral surfaces of head and body. There are no dorsal asperities.

Comparisons. — Only three species of the subgenus *Ptychadena* have median skin folds extending forward on to the snout : *straeleni*, *uzungwensis*, and *taenioscelis* (at least southern populations). *Rana straeleni* differs from *uzungwensis* in coloration of the rear of the thigh (spotted in *uzungwensis*), coloration of the tibia (dark bars uninterrupted in *uzungwensis*), webbing (third toe with two phalanges free in *uzungwensis*), and male secondary sex characters (*uzungwensis* with dorsal and ventral asperities, but no nuptial pad on wrist).

Rana taenioscelis differs from *straeleni* in the position of the gular pouch (ending near center of arm insertion in *taenioscelis*); in lacking nuptial pad on the wrist; in having the dark bars on the tibia uninterrupted; and in lacking an outer metatarsal tubercle, a row of small tubercles on the fourth metatarsal, and supernumerary metacarpal tubercles.

Nuptial pad appears on the wrist only in males of *maccarthyensis* ANDERSSON, *perreti* GUIBÉ and LAMOTTE, and *straeleni*. *Rana straeleni* differs from *maccarthyensis* and *perreti* in lacking a pair of short, median skin folds over the sacrum, in having skin folds on the snout, and in having interrupted crossbars on the tibia.

Rana straeleni differs from all other species of *Rana* (*Ptychadena*) at least in the extension of the skin folds forward on to the snout and in the development of nuptial pad on the arm.

Ecological notes. — With two exceptions, the entire series was caught May 11, 1959 at a shallow temporary pond (Fig. 14) formed by heavy rains in April. A large mixed aggregation of species was in full chorus at the time. The exceptional specimens were caught in tree savanna, one in March and the other in September.

Range. — Known only from the Parc National de la Garamba.

Garamba localities and specimens : Cellule Biologique I (1), Nagero (1), 1 Km north of Nagero (8).

Rana taenioscelis (LAURENT).

(Fig. 31.)

Ptychadena taenioscelis LAURENT, 1954, Ann. Mus. Roy. Congo Belge, **34**, p. 25, pl. 4, fig. 6, pl. 5, fig. 1 — Lukula, Katanga, Congo.

Taxonomic notes. — This large series agrees with the description of specimens from Cameroon (GUIBÉ and LAMOTTE, 1958B). These frogs have the opening of the gular pouch ending near the middle of the arm insertion, no supernumerary metacarpal tubercles, a distincly bicolored foot, the rear of the thigh regularly striped, and the nuptial pad of the third finger restricted to an oval dorsomedian area of the metacarpal. In these characters they agree with *taenioscelis* from southeastern Congo (LAURENT, 1954; SCHMIDT and INGER, 1959), which we may call typical *taenioscelis*.

In several respects they differ from the latter population. The median skin folds do not run forward of the eyes except in a very few individuals. The webbing is more extensive, leaving 2 1/3 — 2 2/3 phalanges of the fourth toe free, instaed of 3 as in Katanga specimens. The males usually have fine asperities on the dorsal surfaces; these are absent in Katanga frogs.

Finnaly, the ratio of tibia to snout-vent is larger; the ratios are 0,58-0,65 (median 0,603; N=9) in Garamba males and 0,49-0,56 (median 0,520; N = 7) in males from Katanga.

Description. — Body moderately stout; limbs long, slender; snout pointed; vomerine teeth in short, transverse groups touching anterior rims of choanae; back with 8 longitudinal ridges, median pair continuous from end of body to occiput or, more rarely, interorbital and prefrontal region;

Photo: R. F. INGER.

FIG. 31. — *Rana taenioscelis*.

no supernumerary metacarpal tubercles; webbing moderate, fourth toe with 2 1/3 — 2 2/3 phalanges free of webbing, fifth toe with one phalanx free; a small oval, inner metatarsal tubercle; no outer metatarsal tubercle; no row of tubercles on any metatarsal; tibia 0,58-0,65 of snout-vent.

Color in life very similar to that of *R. mascareniensis* (see p. 68) except : crossbars of tibia not interrupted; light longitudinal line on tibia in only 60 % of individuals; males often with black gular spots; membrane between first and second toes and between second and third toes yellow to margin.

Secondary sex characters. — Females are slightly larger than males, the former reaching sexual maturity at about 33-35 mm and

the latter at 30-32 mm (Table 35). Male secondary sex characters of Garamba frogs are identical to those of Katanga frogs (SCHMIDT and INGER, 1959 : 111), except for the presence of dorsal asperities (see above).

Table 35. — **Frequency distribution with respect to breeding condition of** Rana taenioscelis **from Parc National de la Garamba.**

	Males (1)		Females (3)		
	Nuptial pads		Ova		
	incomplete (2)	complete	immature	intermediate	mature
January	1	—	2	—	—
February	3	1	5	—	1
March	3	14	6	2	9
April	1	13	6	2	7
May	1	24	1	2	22
June	—	15	—	1	8
July	—	10	—	—	12
August	1	14	—	1	5
September	—	4	—	2	1
October	—	—	1	—	—
December	1	—	—	—	—
	Snout-vent (mm)				
Range	32,2–36,0	30,4–39,4	33,3–43,1	34,6–41,2	35,2–43,1
Mean	34,43 ± 0,41	34,40 ± 0,16	38,74 ± 0,54	38,46 ± 0,72	39,41 ± 0,24

(1) With fully developed gular pouch.
(2) Nuptial pads not present on third finger.
(3) With mature oviducts.

Four males of this sample measuring 29,4-32,5 mm have very shallow gular folds but no vocal sac openings. Fourteen males (30,2-34,2 mm) with deep gular folds but no pouches have vocal sacs.

Males have « fast » and « slow » calls (Fig. 32).

Table 36. — **Habitat-frequency distribution of** Rana taenioscelis **in Parc National de la Garamba.**

	Wet season	Dry season	Total
Aquatic :			
Marsh	144	74	218
Stream	38	31	69
Spring	10	3	13
Pond	16	22	38
Subtotal	208	130	338
Non-aquatic :			
Savanna	37	1	38
Gallery forest	6	9	15
Subtotal	43	10	53

Ecological notes. — Only about one-seventh of these were caught at non-aquatic sites (Table 36). About two-thirds of those collected at aquatic sites were found in and at the edges of marshes. Most of the aquatic habitats were in savanna formations; only 39 of the 338 were caught at wooded springs, gallery forest streams, or marshy openings in gallery forest (Fig. 13).

Juveniles are relatively more abundant in the collections from September, which is near the end of the rainy season, until February near the end of

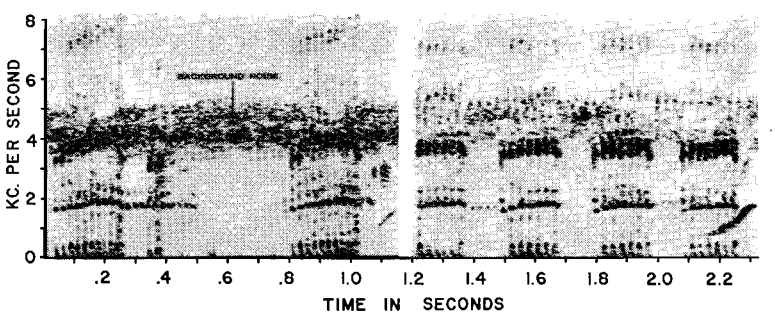


FIG. 32. — « Slow » (left) and « fast » (right) calls of *Rana taenioscelis* (RFI-4333) recorded at Nagero on May 8, 1959. End of last call has note of *Kassina* superimposed on it.

the dry season (Table 37). Adults in breeding condition are relatively and absolutely more abundant from the end of the dry season (March) until about two months before the end of the wet season (Table 35). The first calling males were heard the night of March 25, 1959, though we had collected at that site (Nabakoyo) beginning March 19. These facts suggest breeding activity from the end of the dry season until just past the middle of the wet season.

Table 37. — **Monthly frequency distribution with respect to stage of development of** Rana taenioscelis **from Parc National de la Garamba.**

	Juveniles (1)	Adults
January	7	3
February	29	12
March	24	49
April	16	32
May	4	105
June	7	25
July	15	22
August	8	21
September	14	7
October	10	1
December	15	1

(1) Males with no sign of developing or mature gular pouches. Females with straight oviducts.

The virtual disappearance of adults from the collections after August may reflect either an annual life cycle, which does not seem likely because of the size of these frogs, or secretive behavior in response to the approach of the dry season.

Range. — Known from Nigeria (GUIBÉ and LAMOTTE, 1958B; SCHIØTZ, 1963), and northeastern and southeastern Congo. Probably the species occurs throughout the savanna bordering the rain forest on the east and the north

Garamba localities and specimens : Cellule Biologique I (65); Cellule Biologique II (111); Bagunda (1); Bamangwa (1); Beredwa (1); Garamba River (16); Kalikimvua (1); Km 17 south of Bagbele (23); Mabanga (4); Morubia (14); Nabakoyo (6); Nagero (89); Nambia near Nagero (7); Napokomweli (24); Nawaroko (3); Ndelele (51); Otro River (1); Pali (2); Tori (1); Mount Tungu (1).

Rana tournieri GUIBÉ and LAMOTTE.

(Fig. 33.)

Rana (*Ptychadena*) *tournieri* GUIBÉ and LAMOTTE, 1955, Bull. Mus. Nat. Hist. Nat. Paris, (2), **27**, p. 442, 1 fig. — Guinéa, Sierra Leone, Liberia, and Gambia.

Taxonomic notes. — The present sample represents a range extension of almost 4.000 kilometers. Despite this wide distribution, the Garamba frogs differ from descriptions of West African ones (GUIBÉ and LAMOTTE, 1955, 1957) in only two minor details. According to the descriptions of GUIBÉ and LAMOTTE, the West African frogs have 1 to 1 1/2 phalanges of the fifth toe and 1 1/2 to 2 phalanges of the third toe free of webbing. The Garamba frogs invariably have 2 phalanges of both toes free. The rows of metatarsal tubercles are apparently weaker than those of West African specimens.

Descriptive notes. — Body slender; snout long, about twice diameter of eye, pointed; vomerine teeth in transverse groups touching anteromedian borders of choanae; back with 8 longitudinal ridges, median pair beginning over sacrum and extending to end of body, next pair laterad beginning between eyes and extending to end of body; longitudinal ridges of skin on tibia; supernumerary metacarpal tubercles usually present; third and fifth toes with two phalanges free of web, fourth with 3 — 3 1/3 free; outer metatarsal tubercle present; rows of small tubercles on fourth and (less often) third metatarsals, usually present but not conspicuous; tibia 0,57-0,68 of snout-vent (median 0,615; N=20).

Color in life of back light brown with jet black spots; mid-dorsal band golden brown; dorsolateral ridge gold; supracanthal stripes dark brown; lores black, bordered below by gold; upper edge of iris gold; upper lip dark gray; ground color of legs olive brown, tibia with two rows of black spots widely separated in mid-line; rear of thigh with two narrow, light olive brown stripes; lower lip dark gray, without light bars or spots; throat white or gray; anterior two-thirds of abdomen irridescent golden white, posterior third bright yellow.

Secondary sex characters. — Females having mature oviducts measure 35,9-43,4 mm. Six having enlarged, pigmented ova are 38,1-

43,4 mm (mean 39,85 ± 0,76 mm). Adult males having nuptial pads measure 31,2-35,9 mm (mean 33,58 ± 0,10 mm N = 13).

The gular pouch openings run at an angle to the lower jaw and end near the ventral border of the axilla. The pouches themselves are black or black anteriorly and gray posteriorly. The small, round vocal sac opening lie near the commisure of the jaws.

Photo: R. F. INGER.

FIG. 33. — *Rana tournieri.*

The yellowish gray nuptial pads are confined to the first three fingers. The pad covers the entire dorsal and median surfaces of the first finger to the beginning of the terminal phalanx, the entire dorsal surface of the second finger to the beginning of the terminal phalanx, and an oval area on the dorsal surface of the third metacarpal.

Inconspicuous, small, colorless asperities appear on the ventral surface of the snout and on the throat and abdomen in males.

Development. — None of the nine juveniles shorter than 20 mm (13,5-18,6 mm) has even a vestige of a tail. Metamorphosis probably occurs when the frogs are about 10 mm snout to vent.

Females become sexually mature at about 35 mm. Five measuring 34,0-40,9 mm have immature, feebly kinked oviducts. Six measuring 36,0-41,8 mm have enlarged, convoluted oviducts though the ova are small.

Three males (26,8 29,6 33,3 mm) lack vocal sac openings. The two smallest have no sign of developing gular pouches, but the largest has a weak indentation in the gular skin near each mandible. This male does not fit the developmental pattern described for *Rana* (*Ptychadena*) *porosissima* (INGER, 1956). A fourth male (30,4 mm) has vocal sac openings and incompletely developed gular pouches. None of these four males has nuptial pads or ventral asperities.

Ecological notes. — Most specimens were collected near or in aquatic situations. Sixty-six were caught in marshes, 8 along stream banks, and 1 at a small temporary pond. Six were caught away from water, 5 in grass savanna and 1 in tree savanna. The marshes, some of which were permanent (« ndiwilis ») were all located in grass and shrub savanna. The first calling males we encountered in 1959 were in a small marsh on April 27.

Range. — Known from West Africa and northeastern Congo. Presumably the species has a more or less continuous distribution in the Sudanese and Guinean savannas.

Garamba localities and specimens : Cellule Biologique I (6), Cellule Biologique II (63), Biadimbi (1), Km 17 south of Bagbele (1), Morubia (1), Nagero (7), Nambia River (1), Napokomweli (1), Ndelele (2), Tikadje (1).

Rana trinodis BOETTGER.

Rana trinodis BOETTGER, 1881, Abh. Senck. Naturf. Ges., **12**, p. 414, pl. 1, fig. 2 — Senegal.

Taxonomic notes. — Three frogs are identical to a specimen (CNHM 19333) from Bambako, Mali and agree with published descriptions of *trinodis* (BOETTGER, 1881; GUIBÉ and LAMOTTE, 1957). They differ from West African *trinodis* in only one minor respect : the tarsal tubercle is about half the size found in western examples.

Descriptive notes. — Body stocky; limbs heavy, rather short; snout long, obtusely pointed; vomerine teeth in transverse groups touching anterior rims of choanae; back with 8 longitudinal ridges, the median pair beginning behind eyes and either continuous to end of body or interrupted in sacral region; supernumerary metacarpal tubercles present; toes extensively webbed; fourth toe with 2 to 2 1/2 phalanges free on lateral border; fifth toe webbed to tip or with about 2/3 of terminal phalanx projecting; a

distinct yellow tubercle at proximal end of tarsus; a compressed inner metatarsal tubercle, 0,6-0,7 length of first toe; an oval outer metatarsal tubercle, not raised as high as inner one; no row of small tubercles on any metatarsal; tibia 0,53 of snout-vent (one specimen).

Color in alcohol blackish brown above; a yellow vertebral line; dorsolateral skin ridge yellow; top and side of head dark; back with rows of squarish black spots; dorsal surface of limbs brown with black crossbars; lower lip barred yellow and black; rest of venter yellow; throat with or without black spots.

Secondary sex characters. — All three specimens are adult males (snout-vent 58,6-60,4 mm) having black gular pouches. The openings of the pouches end near the ventral border of the axilla. The largest male lacks nuptial pads. The other two have yellowish nuptial pads covering the entire dorsal and median surfaces of the first finger, the entire dorsal surface of the second finger, and the median half of the dorsal surface of the third finger; the terminal phalanx of each finger is free of these sexual excrescences. The surface of the head and torso bears distinct yellowish asperities except in the male lacking nuptial pads.

Ecological notes. — These three frogs were caught at a granite outcrop (Fig. 44) near water in mixed grass and bush savanna. The species has been reported from non-forest regions of West Africa (GUIBÉ and LMAOTTE, 1957).

Range. — Previously known from West Africa (ibid.) and the Tchad (WAKE and KLUGE, 1961). These specimens thus extend the range almost 1.000 km southeastward.

Garamba locality and specimens : Km 17 south of Bagbele (3).

Phrynobatrachus natalensis (SMITH).

(Fig. 34.)

Stenorhynchus natalensis SMITH, 1849, Ill. S. Afr. Rept., App., p. 23 — Natal.

Phrynobatrachus natalensis GÜNTHER, 1862, Proc. Zool. Soc. London, **1862**, p. 190.

Taxonomic notes. — The specimen (AMNH 9047) on which NOBLE (1924) based a Garamba locality for *Arthroleptis bottegi* BOULENGER is a typical *P. natalensis*.

Descriptive notes. — A medium-sized species, adults 25-40 mm; tympanum present, hidden under skin; tips of digits not dilated, without horizontal grooves; third and fifth toes webbed to distal subarticular tuber-

cles; short, round warts on back between fore limbs; gular pigmentation of males confined to skin; males without femoral glands.

Color in life grayish brown above, with small black spots usually centered on dorsal warts; belly white; throat of males black, of females spotted with brown; rear of thigh without stripes.

Photo: R. F. INGER.

FIG. 34. — *Phrynobatrachus natalensis*.

Secondary sex characters. — These structures have been described by SCHMIDT and INGER (1959).

Garamba females are about 4 mm larger than males (Table 38). The call is analysed in Figure 35.

Ecological notes. — In the Parc de la Garamba adults of *P. natalensis* are fairly even distributed among a wide variety of habitats (Table 39). Juveniles show approximately the same relative concentration in aquatic versus non-aquatic environments as the adults in both seasons.

Table 38. — **Monthly frequency with respect to breeding condition of adult** Phrynobatrachus natalensis **from Parc National de la Garamba. Snout-vent lengths in parentheses.**

	Females (1)			Males (2)	
	Ova			Nuptial pads	
	immature	intermediate	mature	absent	present
January	2 (23,4–28,1)	—	1 (26,2)	3 (23,0–24,8)	—
February	8 (21,4–25,1)	5 (23,8–27,4)	10 (25,8–28,0)	3 (22,3–23,6)	14 (22,1–25,5)
March	7 (21,3–28,7)	3 (24,2–27,9)	7 (25,7–29,7)	1 (21,3)	23 (20,6–25,5)
April	5 (21,0–29,1)	2 (23,8–23,9)	18 (23,7–31,0)	—	25 (19,0–28,4)
May	1 (27,0)	3 (28,0–30,7)	17 (26,7–31,4)	—	20 (22,5–28,3)
June	—	—	7 (24,9–32,6)	—	7 (25,3–28,8)
July	—	—	5 (24,2–32,5)	1 (23,3)	11 (22,1–28,2)
August	3 (22,3–27,4)	—	4 (27,8–32,4)	—	10 (22,8-27,7)
September	1 (27,0)	—	5 (26,7–31,3)	—	16 (21,6-27,0)
October	—	—	1 (28,8)	—	—
December	—	—	—	1 (22,7)	—
Total number	27	13	75	9	126
Range (mm)	21,0–29,1	23,8–30,0	23,7–32,6	21,3–24,8	19,0–28,8
Mean (mm)	24,61 ± 0,58	26,50 ± 0,64	28,20 ± 0,34	23,08 ± 0,34	24,88 ± 0,25

(1) All with mature oviducts.
(2) All with vocal sacs.

The relative abundance of adults in the several aquatic and terrestrial habitats varies significantly from wet to dry season (chi-square=70,8; df=8; P<0,001); they are more numerous in the savanna and ponds in the wet season, when the savannas are more humid and ponds more widespread. Juveniles show comparable seasonal changes in distribution (chi-square= 84,8; P<0,001).

The frequency of gravid females is moderately high (Table 38), though the percentage is higher in the wet season (79 %) than in the dry (42 %).

Adult males without nuptial pads and, hence, not in breeding condition are most common in the dry season; all of these males are rather small and may be newly maturing, young adults rather than old males in a quiet state. The monthly distribution of adults in reproductive condition (Table 38) suggests the possibility of breeding activity from February to September. We observed calling males for the first time on March 20, 1959, though similar environments had been investigated as early as March 2. Juveniles are abundant (i.e. 25 % of the sample) in all months except March, April, and June (Fig. 36); this pattern supports the suggestion of breeding except from October through January.

Table 39. — **Habitat frequency distribution of juvenile and adult** Phrynobatrachus natalensis **in Parc National de la Garamba.**

	Adults		Juveniles	
	Wet season	Dry season	Wet season	Dry season
Marshes	13	26	24	8
Springs	46	29	4	15
Temporary ponds	31	—	—	1
Permanent ponds	13	1	6	—
Streams	50	33	18	40
Subtotal aquatic	153	89	52	64
Grass savanna	22	2	12	—
Shrub savanna	28	—	2	—
Tree savanna	17	2	10	—
Gallery forest	21	18	—	32
Subtotal non-aquatic ...	88	22	24	32

Range. — Most of sub-Saharan Africa outside of the rain forest.

Garamba localities and specimens : Cellule Biologique I (189), Cellule Biologique II (171), Aka (17), Akam (2), Akawa (6), Baganola (35), Bamangula (24), Beredwa (3), Biadimibi (2), Dedegwa (1), Garamba (7), Kalikimvua (3), Kassi (1), Km 17 S. of Bagbele (18), Mabanga (1), Makpe (5), Mobaba (4), Morubia (16), Nabakoyo (16), Nagero (5), Namolobia (15), Nawaroko (5), Ndelele (52), Pidigala (10), Pp Km 10 (4), Sudan River (4), Tori (2), Wilibadi (2).

Phrynobatrachus parkeri WITTE.

(Fig. 37.)

Phrynobatrachus parkeri WITTE, 1933, Rev. Zool. Bot. Afr., **24**, p. 97 — Kunungu, Congo.

Taxonomic notes. — The original description was based on two sets of specimens, one from Kunungu, west-central Congo, and the other from Mauda, Upper Uele, northeastern Congo. Both series were examined and compared with another from Monga, Lower Uele (CNHM 109283-6). The three series agree in webbing, form of the digits, coloration, dermal ornamentation of the back, and male secondary sex characters. In this combination of characters, these frogs agree with a large series from the Garamba and I have no hesitation in assigning the last to this species.

Phrynobatrachus acridoides (COPE), three cotypes (MCZ 15026, 15027, 15030) of which were examined, is similar to this species; it has small disks at the tips of the toes, males lack femoral glands, and it has a pair of concave ridges on the anterior part of the back. But *acridoides* has more extensive webbing than *parkeri*. In the former, the web extends as a broad sheet beyond the distal subarticular tubercle of the fifth toe, which has a ridge of skin on its outer edge. In *parkeri* the web usually reaches the distal tubercle of the fifth toe, but never extends beyond it except as a very narrow strip; the outer edge of the fifth toe does not have a ridge of skin.

Descriptive notes. — A medium-sized species, adults 19-25 mm; tympanum present, visible or obscured by skin; tips of toes only dilated into small but distinct, round disks having circummarginal grooves; third and fifth webbed beyond basal tubercles, usually to distal subarticular tubercles; back with a pair of long narrow ridges beginning behind eyes (see below for variation); gular pigmentation of males confined to skin; males without femoral glands.

Coloration in life takes three patterns. In one the back and sides are dark grayish brown usually with black areas overlying the dermal ridges. Some individuals have a narrow yellow or orange vertebral stripe superimposed on the previous pattern. The third type of coloration consists of a reddish brown dorsum edged with a black line and grayish brown sides. Individuals of all three types usually have a narrow oblique stripe on the rear of the thigh. All frogs have whitish bellies. Males may or may or may not have gray or black throats.

The dermal ridges may be parallel and confined to the dorso-lateral line; or they may converge above the shoulders and then diverge forming concave curves. Parallel, dorsolateral ridges are always associated with a reddish brown back. The curved ridges are always associated with the other two patterns.

Thus this species is locally polymorphic. Each form appears in both sexes. As no other characters show segregation of states in the same way, only one species is involved.

Secondary sex characters. — Females reach maturity when about 19 mm, snout to vent; those with mature ova average 22,75 mm (Table 40). Males acquire vocal sacs at about 18 mm; the average size of those with fully developed vocal sacs is 21,26 mm (Table 41).

Table 40. — **Monthly frequency with respect to sexual development of female** Phrynobatrachus parkeri Witte **from Parc National de la Garamba. Snout-vent lengths in parentheses.**

	Oviduct immature	Oviduct mature		
		Ova immature	Ova intermediate	Ova mature
January	15 (17,4–25,3)	3 (21,2–22,5)	—	—
February	19 (17,5–25,8)	17 (20,4–25,2)	1 (19,8)	2 (20,3–21,6)
March	2 (17,6–18,4)	13 (19,6–22,5)	5 (20,7–21,9)	5 (20,3–23,0)
April	—	4 (18,6–20,7)	3 (21,4–23,6)	18 (19,5–23,5)
May	—	4 (18,9–23,4)	1 (20,5)	20 (20,1–24,6)
June	—	—	—	25 (20,3–24,8)
July	2 (18,2–18,6)	5 (19,6–23,3)	3 (20,4–22,6)	15 (19,2–23,7)
August	—	—	2 (21,1–22,6)	9 (21,5–24,5)
September	—	1 (23,3)	1 (24,6)	4 (22,4–24,5)
October	—	1 (23,5)	—	—
November	8 (19,5–22,5)	1 (23,8)	—	—
December	9 (18,0–20,4)	—	—	—
Total number	55	49	16	98
Range	17,4–25,8	18,6–25,2	19,8–24,6	19,2–24,8
Mean	19,99 ± 0,40	21,39 ± 0,27	21,59 ± 0,31	22,75 ± 0,17

Adult males have subgular vocal sacs, gray nuptial pads on the first finger, numerous minute spinules on the throat and chest, and lineae masculinae at dorsal and ventral borders of the obliquus muscle. They do not have dorsal asperities or femoral glands. The musculature investing the vocal

sac lacks pigment, but the gular skin, which in some males has longitudinal folds, usually has varying amounts of dark pigment.

The sequence of development of the secondary sex characters suggested by the data in Table 41 is vocal sacs, nuptial pads, and lastly the ventral spines. There is no evidence of seasonal regression of nuptial pad or ventral spines. The males without these structures (second and third data columns of Table 41) are smaller and, therefore, probably younger than those having them.

A sonogram of the call is presented in Figure 35.

Table 41. — **Monthly frequency with respect to secondary characters of male** Phrynobatrachus parkeri **from Parc National de la Garamba. Snout-vent lengths in parentheses.**

	Vocal sac absent	Vocal sac present		
	Nuptial pads absent		Nuptial pads present	
	Ventral spines absent			Ventral spines present
January	4 (18,2–25,2)	2 (18,7–21,2)	1 (21,5)	—
February	10 (18,0–20,5)	7 (18,6–22,6)	1 (20,3)	4 (19,2–21,4)
March	2 (18,5–18,8)	2 (19,9)	3 (19,4–20,1)	18 (17,8–21,7)
April	—	1 (18,2)	—	23 (19,1–21,6)
May	—	—	—	25 (19,4–22,4)
June	—	—	—	25 (20,2–23,4)
July	—	—	—	25 (19,4–23,1)
August	—	—	—	12 (20,8–23,5)
September	—	—	—	25 (19,7–23,4)
October	—	—	—	3 (21,2–22,4)
November	4 (17,3–20,2)	—	—	1 (21,2)
December	4 (18,4–23,0)	—	—	1 (20,7)
Total number. ...	24	12	5	162
Range	17,3–25,2	18,2–22,6	19,4–21,5	17,8–23,5
Mean	19,31 ± 0,36	20,03 ± 0,36	20,16	21,26 ± 0,11

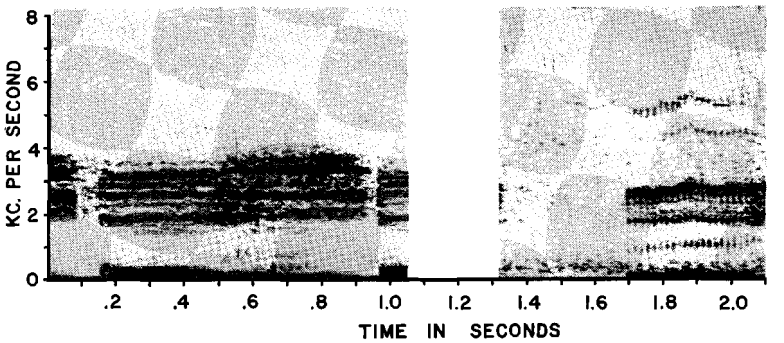


FIG. 35. — Comparison of calls of (left) *Phrynobatrachus parkeri* (RFI-3889) and (right) *P. natalensis* (RFI-3162).

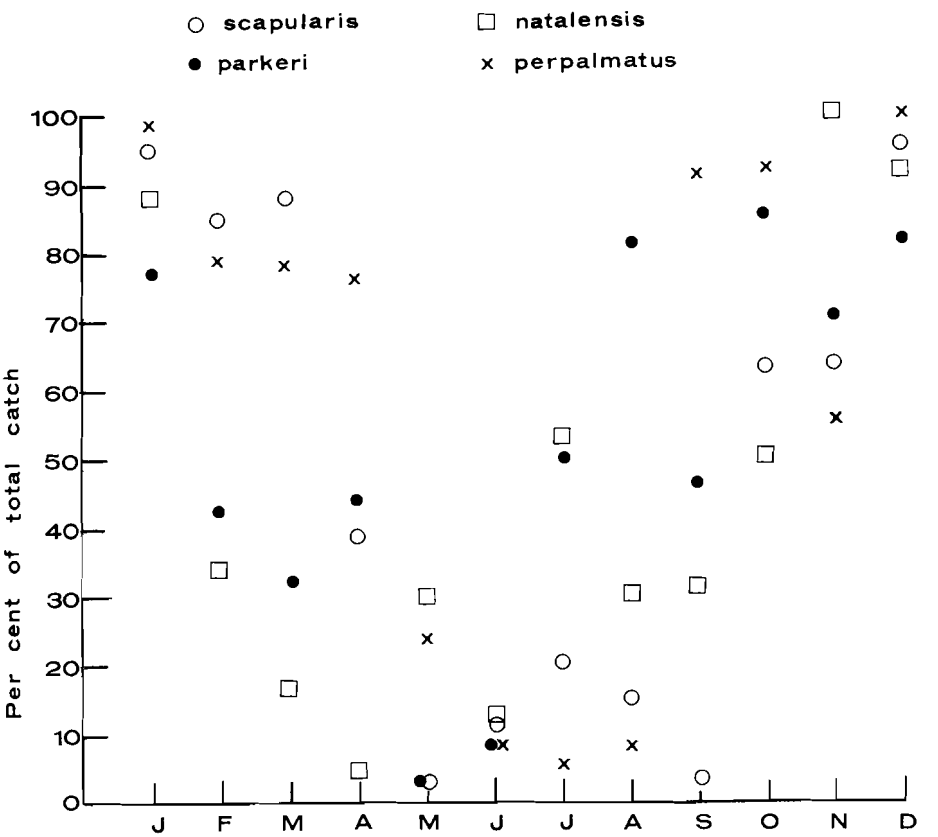


FIG. 36. — Monthly frequency of juveniles of four species of *Phrynobatrachus* collected in the Parc National de la Garamba.

Ecological notes. — This species lives in a variety of environments in the Parc de la Garamba (Table 42), though only 29 % of the adults were caught away from aquatic sites. The distribution of adults among these habitats varies from wet to dry season (test of homogeneity of aquatic sites : chi square=16,5, P<0,01); seasonal differences in the non-aquatic environments are obvious (Table 42). Juveniles also show seasonal differences in occupancy of the various environments.

Table 42. — **Habitat frequency distribution of juvenile and adult** Phrynobatrachus parkeri **in Parc National de la Garamba.**

	Adults		Juveniles	
	Wet season	Dry season	Wet season	Dry season
Marshes.	85	57	113	120
Springs..	39	63	31	102
Temporary ponds	91	73	—	9
Permanent ponds	49	66	82	43
Streams.	201	208	89	161
Subtotal aquatic	465	467	315	435
Grass savanna	99	4	20	86
Shrub savanna	80	—	12	—
Tree savanna	1	—	2	—
Gallery forest	48	167	7	61
Subtotal non-aquatic ...	228	171	41	147

Juveniles and adults have differing distributions, the former being more abundant in marshes and the latter proportionately more numerous in temporary ponds.

The proportion of adult females containing enlarged eggs is very low (0,15) during the dry season. The increase in gravid females from March, at the end of the dry season, to April is striking (Tale 40). The proportion remains high until September. Thus the breeding season probably extends over most of the rainy season. In 1959 we first noticed this species calling in numbers on March 19. Males call during the day as well as at night, often from very small pools (Fig. 38) in marshy savanna. Juveniles become abundant in July (Fig. 36) as expected if breeding commences in April.

Photo: R. F. INGER.

FIG. 37. — *Phrynobatrachus parkeri.*

R a n g e . — Reported only from the type locality in west-central Congo and northeastern Congo.

Garamba localities and specimens : Cellule Biologique I (1291), Cellule Biologique II (2141), Akam (1), Anzeli (11), Bagbele moke (8), Bagunda (42), Bamangwa (96), Biadimbi (8), Dedegwa (1), Garamba (25), Kalikimvua (4), Kassi (65), Km 17 S. of Bagbele (19), Kpayika River (17), Makpe (32), Mobaba (2), Morubia (9), Mount Moyo (19), Nabokoyo (14), Nagero (136), Nambia River (14), Namologbia (14), Naworoko (22), Ndelele (110), Ngorobongo (496), Otro River (2), Pali (3), Pp Km 10 (1), Pp Km 55 (7), Pp Km 56 (28), Pp Km 62 (1) Wilibadi (24).

Phrynobatrachus scapularis (WITTE).

Arthroleptis scapularis WITTE, 1933, Rev. Zool. Bot. Afr., **24**, p. 100 — Buta, Uele, Congo.

Taxonomic notes. — A very large series of a small *Phrynobatrachus* is tentatively assigned this name. De Witte's descriptions (1933, 1934) refer to one tarsal and two metatarsal tubercles; we may therefore safely assign *scapularis* to the genus *Phrynobatrachus*.

The following characters of *scapularis* are found in the present series : extremely reduced webbing, a pair of oval, interscapular glands, a median papilla on the tongue, a light longitudinal stripe on the rear of the thigh, and a black throat in the male. De Witte's descriptions state that the tips of the digits are very slightly dilated. The Garamba specimens agree with de Witte's illustrations (1934, pl. 11, figs. 1-2) in having non-dilated digits. The male holotype measured 18 mm, which is several millimeters longer than the largest male (15,9 mm) in the Garamba series.

Other small species of *Phrynobatrachus*, such as *minutus*, *anotis*, *keniensis*, and *parvulus*, have oval, interscapular glands and rudimentary webbing But none of these have black pigment on the subhyoideus muscle in males. In addition the males of these species have small whitish spinules on the throat or back or on both; spinules are absent in Garamba males. *Phrynobatrachus minutus* apparently lacks a light stripe on the thigh and *anotis* lacks a tympanum.

Other differences separate the Garamba series from other small species. Males of *Phrynobatrachus cryptotis*, which also occurs in the Garamba, have lineae masculinae and spinules dorsally on the head or back; these structures are absent in the Garamba *scapularis*. *Phrynobatrachus guttu-rosus* and *P. feae* have distinct grooves around expanded tips of toes, dorsal asperities, and linae masculinae.

Assigning the Garamba series to *scapularis* on the basis of comparison with literature descriptions leaves the issue uncertain. The two points on which I have the most doubt are the nature of the tips of the toes (illustrations and text at odds in original description) and the pigmentaton of the throat (on the gular skin or muscle). One of the attractions of this tentative identification is that the type locality of *scapularis* is only 450 km from the Parc de la Garamba. Another is that it obviates describing still another species in this poorly known genus.

The specimens from Faradje (AMNH 9037-46) listed by NOBLE (1924 : 201) as *Arthroleptis feae* are conspecific with the present series. The Stanley-ville specimens (AMNH 8979-80) were correctly assigned to *feae* by NOBLE.

Descriptive notes. — A small species, adults 13-20 mm; tympanum present, usually obscured by skin; tips of digits not dilated, without

horizontal grooves; third and fifth toes webbed to distal edges of basal subarticular tubercles; a pair of converging, large, oval warts on back between forelimbs; smaller round and oval warts scattered on dorsum; gular pigmentation of adult males always on subhyoideus muscle and sometimes on gular skin; males with femoral glands.

Color in alcohol dark brown above; black spots dorsally, usually coincident with warts; a small proportion of individuals with a light vertebral line; chin and, less commonly, throat with small brown spots; abdomen usually immaculate white; dorsal surface of limbs with dark crossbars; rear of thigh with a distinct light stripe.

Table 43. — **Monthly frequencies with respect to sexual development of female** Phrynobatrachus scapularis (Witte) **from Parc National de la Garamba. Snout-vent lengths in parentheses.**

	Oviduct immature	Oviduct mature		
		Ova immature	Ova intermediate	Ova mature
January	5 (12,5–15,9)	2 (15,5–15,6)	—	2 (16,4–17,7)
February	2 (12,6–14,1)	7 (14,1–16,1)	—	—
March	3 (12,8–13,1)	4 (12,5–15,5)	1 (15,4)	1 (12,8)
April	11 (12,8–14,0)	11 (12,8–15,2)	2 (14,3–15,5)	1 (14,4)
May	—	5 (13,7–15,9)	4 (14,2–17,2)	15 (13,5–17,4)
June	—	1 (15,5)	2 (16,2–16,5)	21 (13,1–19,6)
July	1 (12,9)	—	1 (17,4)	23 (14,7–16,6)
August	2 (14,0–14,6)	2 (15,5–15,8)	5 (14,6–19,0)	17 (15,1–17,4)
September	—	—	—	4 (16,2–18,4)
October	—	—	—	6 (14,8–17,0)
November	1 (13,2)	1 (15,0)	—	—
December	3 (12,1–14,2)	—	1 (16,2)	—
Total number. ...	28	33	16	90
Range	12,1–15,9	12,6–16,1	14,2–19,0	12,8–19,6
Mean	13,36 ± 0,14	15,17 ± 0,24	15,82 ± 0,31	16,12 ± 0,17

Secondary sex characters. — Females containing ripe ova vary from 12,8 to 19,6 snout to vent (mean 16,12±0,17 mm; N=90). The smallest having convoluted oviducts measures 12,6 mm, the largest having immature oviducts 15,9 mm (Table 43). Males having fully developed secondary sex characters are slightly smaller, 12,3-15,9 mm (Table 44).

Adult males have vocal sacs and densely pigmented subhyoideus muscles. The gular skin is usually not pigmented, except near the chin. A large oval gland is present on the rear of the thigh in all but two males having vocal sacs. Presumably the femoral glands develop very shortly after the vocal sacs. A gray nuptial pad covers the dorsal and medial surfaces of the first finger from the wrist to the base of the terminal phalanx.

Table 44. — **Monthly frequency with respect to secondary sex characters of male** Phrynobatrachus scapularis **from Parc National de la Garamba. Snout-vent lengths in parentheses.**

	Vocal sac absent	Vocal sac present		
	Femoral glands absent		Femoral glands present	
	Nuptial pads absent			Nuptial pads present
January	1 (13,8)	—	6 (12,6–14,9)	2 (14,5–14,7)
February	1 (13,1)	—	1 (14,2)	1 (14,9)
March	2 (12,7)–12,8	—	5 (12,8–14,8)	2 (13,1–14,1)
April	2 (11,8–12,2)	2 (12,8–12,9)	4 (12,4–13,9)	8 (13,5–14,5)
May	—	—	—	25 (12,5–14,4)
June	—	—	2 (12,5)	25 (12,3–15,8)
July	—	—	—	25 (12,8–14,7)
August	—	—	1 (13,2)	24 (13,2–15,9)
September	—	—	—	25 (12,5–15,3)
October	—	—	—	18 (12,6–15,2)
November	—	—	—	3 (13,7–14,5)
December	2 (11,6–12,6)	—	1 (13,1)	9 (13,9–15,2)
Total number	8	2	20	167
Range	11,6–13,8	12,8–12,9	12,4–14,9	12,3–15,9
Mean	12,58 ± 0,25	12,85	13,47 ± 0,17	14,00 ± 0,10

Males do not have asperities on the ventral or dorsal surfaces of the head or body.

The rather large number of adult males lacking nuptial pads in the months January to April (third data column in Table 44) suggests that these structures may be sloughed during the dry season (November to March).

Tabel 45. — **Ecological distribution of** Phrynobatrachus scapularis **in Parc National de la Garamba.**

	Adults		Juveniles	
	Wet season	Dry season	Wet season	Dry season
Marshes.	345	14	73	188
Springs..	83	4	26	8
Temporary ponds	20	13	1	450
Permanent ponds	39	5	4	19
Streams.	234	2	30	63
Subtotal aquatic	721	38	135	728
Grass savanna	24	—	11	—
Shrub savanna	44	—	4	3
Tree savanna	9	1	—	—
Gallery forest	11	1	3	34
Subtotal non-aquatic ...	88	2	18	37

Ecological notes. — Although this species was caught in a wide variety of habitats, it was much more abundant in aquatic environments (Table 45). Many of the adults listed oppositie « streams » were collected in the marshy borders of a small stream, the Nambirima (Fig. 10), so that the proportion from marsh-like environments is even greater than indicated in the table. The distributions of juveniles and adults in aquatic environments during the wet season do not differ (chi-square test of homogeneity $=6{,}48$; $df=4$, $P>0{,}10$). However, during the dry season their distributions differ significantly (chi-square $=34{,}18$; $df=4$; $P<0{,}001$).

Adults were more abundant away from aquatic sites in the wet season.

Roughly three-fourths (73 %) of the adult females collected during the rainy season (April-October) contained mature ova, the proportion being

highest in June and July (Table 43) (1). The proportion of gravid females in the five months of the dry season is 0,16. Slightly more than half (57 %) of the adult males caught in the dry season had nuptial pads; virtually all males had nuptial pads in the wet season (Table 44) and hence were in breeding condition. In 1959 we first encountered calling aggregations on May 2, though we had collected the species as early as March 27.

From these data it appears that breeding begins in May and continues until the end of the rainy season. If larval development requires about two months, juveniles should appear in numbers in August or September. The proportion of juveniles actually increases in October (Fig. 36).

Range. — Recorded only from northeastern Congo.

Garamba localities and specimens : Cellule Biologique I (444), Cellule Biologique II (2050), Aka (2), Akam (6), Bagunda (3), Biadimbi (3), Garamba (3), Iso River (5), Kalikimvua (1), Kassi (34), Km 17 S. of Bagbele (3), Mabanga (4), Makpe (4), Mobaba (7), Moko (2), Mount Tungu (3), Nabokoyo (1), Nagero (49), Nambia River (1), Napokomweli (2), Ndelele (54), Ngorobongo (14), Otro River (28), Pali (37), Pp Km 55 (2), Pp Km 62 (1), Sudan River (6), Tori (1), Utukuru (8), Wilibadi (3).

Phrynobatrachus perpalmatus BOULENGER.

Phrynobatrachus perpalmatus BOULENGER, 1898, Proc. Zool. Soc. London, **1898**, p. 479, pl. 38, fig. 1 — Lake Mweru.

Descriptive notes. — A medium-sized species, adults 19-26 mm; tympanum present, usually visible through skin; tips of fingers not dilated; toes with small disks having weak circummarginal grooves; toes except fourth broadly webbed to disks; usually with small, round warts scattered over back; gular skin of males whitish; males without femoral glands.

Color in alcohol brown above and on sides; a broad, oblique light band from eye to groin; ventrum yellowish, throat of females and juveniles usually with brown spots; rear of thigh with horizontal stripes of brown and yellow.

Secondary sex characters. — Females are slightly but significantly larger than males (Table 46).

Secondary sex characters of males have been described (SCHMIDT and INGER, 1959).

Ecological notes. — *Phrynobatrachus perpalmatus* is more restricted to aquatic sites than the other species of *Phrynobatrachus* occurring

(1) The samples in September and October are too small to give reliable population estimates.

Table 46. — **Monthly frequency distribution with respect to breeding condition in adult** Phrynobatrachus perpalmatus **from Parc National de la Garamba. Snout-vent length in parentheses.**

	Females (1)			Males (2)	
	Ova			Nuptial pads	
	immature	intermediate	mature	absent	present
January	—	1 (21,9)	—	—	—
February	5 (20,5–22,2)	1 (22,9)	1 (20,5)	3 (19,2–20,4)	—
March	14 (19,4–25,3)	—	1 (20,5)	8 (19,2–22,0)	—
April	3 (18,6–23,2)	—	1 (23,4)	6 (18,8–20,7)	—
May	4 (18,4–22,1)	9 (19,1–23,0)	10 (18,8–24,3)	6 (18,4–20,2)	9 (19,3–23,5)
June	2 (19,9–21,6)	3 (20,5–23,1)	20 (20,5–25,8)	1 (21,6)	24 (20,2–24,4)
July	1 (22,0)	3 (20,9–25,3)	14 (22,1–25,4)	—	10 (20,3–22,8)
August	—	1 (24,3)	6 (21,8–25,5)	—	4 (21,6–23,0)
September	—	—	5 (21,3–22,9)	1 (20,6)	—
October	—	—	1 (23,3)	—	3 (20,4–21,7)
November	1 (24,2)	3 (22,1–24,5)	—	—	—
Total number	30	21	59	25	48
Range	18,4–25,3	19,1–25,3	18,8–25,8	18,4–22,0	19,3–24,4
Mean	21,23 ± 0,41	22,25 ± 0,14	22,73 ± 0,25	20,08 ± 0,30	21,51 ± 0,21

(1) All with mature oviducts.

(2) All with vocal sacs.

in the Garamba (cf. Table 47 with Tables 39, 42, and 45). It also tends to avoid temporary bodies of water in contrast to its congeners; only 2 % of the specimens came from temporary ponds (Table 47).

Adults in full breeding condition (i.e., females with pigmented ova, males with nuptial pads) were abundant only from May to August (Table 46), suggesting that this is the period of maximum breeding activity. In 1959 we did not encounter any breeding choruses; we left the Garamba late in May.

Table 47. — **Habitat frequency distribution of** Phrynobatrachus perpalmatus **in Parc National de la Garamba.**

	Adults		Juveniles	
	Wet season	Dry season	Wet season	Dry season
Marsh	100	12	16	36
Spring	34	10	6	20
Temporary pond	—	—	—	13
Permanent pond	5	1	3	19
Stream	147	23	61	146
Subtotal aquatic	286	46	86	234
Grassy savanna	2	3	—	8
Gallery forest	—	—	2	—
Subtotal non-aquatic ...	2	3	2	8

Juveniles form large proportions of the monthly sample from September to April (Fig. 36). Metamorphosing young were collected in September and October. If breeding began in June and if two months were required for larval development, one would expect large numbers of young to appear in September.

Range. — From Liberia (BARBOUR and LOVERIDGE, 1930) and the Cameroons (PERRET, 1957) to central Sudan (ANDERSON, 1904), southwards to Mozambique (LOVERIDGE, 1953).

Garamba localities and specimens : Cellule Biologique I (4), Cellule Biologique II (688), Bamangwa (1), Biadimbi (9), Garamba (2), Kassi (4), Kpayika River (20), Mount Moyo (1), Namologbia (38), Pp Km 55 (4), Pp Km 56 (16), Pp Km 62 (5).

Phrynobatrachus cryptotis SCHMIDT and INGER.

Phrynobatrachus cryptotis SCHMIDT and INGER, 1959, Explor. Parc. Nat. Upemba, fasc. 55, p. 143, figs. 58, 60 — Bwalo River, Parc Nat. Upemba, Prov. Katanga, Congo.

Taxonomic notes. — The present series has been compared with paratypes.

Descriptive notes. — A small species, adults 16-22 mm; tympanum hidden under skin; tips of digits not dilated, without grooves; broad webbing midway between subarticular tubercles of third and fifth toes; a pair of converging oval warts on back between forelimbs; smaller round warts scattered over back; gular pigmentation in males on subhyoideus muscle and on gular skin; males with femoral glands.

Color in alcohol dark brown above with scattered black spots; ventrally whitish with brown spots on throat and chest, denser on chin and throat of males; rear of thigh brown, usually with a narrow, light, horizontal stripe.

Secondary sex characters. — The smallest male with vocal sacs measured 15,8 mm; this specimen did not have nuptial pads. Males with nuptial pads varied from 16,3 to 19,5 mm (mean $17,35 \pm 0,23$; $N=15$). Females with mature oviducts ranged from 18,3 to 21,1 mm (mean $19,42 \pm 0,26$; $N=11$); the smallest contained enlarged ova.

Other secondary sex characters are as given by SCHMIDT and INGER (1959).

Ecological notes. — The few specimens were obtained mainly at aquatic sites : 6 at marshes, 3 at springs, 4 at temporary ponds, and 26 in streams. Two juveniles were caught in grass savanna. Five of those listed above were found in streams in gallery forest.

Range. — Reported from southeastern Congo (the type locality) and Southern Rhodesia (INGER, 1959). The present record, therefore, constitutes a significant northward extension of the known range.

Garamba localities and specimens : Cellule Biologique I (8), Cellule Biologique II (21), Buluku (1), Km 17 S. of Bagbele (2), Morubia (7), PFS Km 21 (2).

Phrynobatrachus sp.

Four small ranid tadpoles resemble the larvae of *Phrynobatrachus francisci* (LAMOTTE and DZIEDUSZYCKA, 1958). The anus is dextral and tubular, opening at the margin of the ventral fin; the spiracle sinistral; and the papillae are continuous across the lower lip. These characteristics determine the family identification.

The tadpoles have two rows of papillae, an outer row of very long ones (ca. 1/10 of the body length) and an inner row of short ones. The dental formula is I : 1-1/II or I : 1-1/III. The outer-most lower row is short and irregular when three rows are present. The beaks are weak and narrowly edged with black. As larval *P. francisci* have similar character states, these larvae are assigned to *Phrynobatrachus* but not to *P. francisci* which is not known from the Garamba.

Other feature of these larvae are : head and body oval; eyes dorsal, eye diameter equal to eye-nostril distance; oral disk ventral, subterminal; tail

lanceolate, dorsal fin beginning near end of body; fins deeper than caudal muscle; head and body mottled with dark brown; caudal muscle dark brown with light area distally and usually a mid-lateral light streak proximally; fins usually mottled.

Head plus body 5,5-7,0 mm; total lengths 13,0-15,0 mm.

This series was collected in a marsh in grass savanna.

Photo: R. F. INGER.

FIG. 38. — Small pool in marshy grass savanna at Ndelele. Typical of calling sites of *Phrynobatrachus parkeri*.

Arthroleptis poecilonotus PETERS.

Arthroleptis poecilonotus PETERS, 1863, Monatsber. Akad. Wiss. Berlin, **1863**, p. 446 — Boutry, Ghana.

Taxonomic notes. — According to some authors (e.g., DE WITTE, 1921; LOVERIDGE, 1955) this species has slightly dilated digit tips. The original description, however, clearly states that the tips of the fingers and toes are « cylindrisch » and hence not dilated. The Garamba specimens agree with the original description.

Descriptive notes. — Habitus stocky; head broad; tympanum visible, about half diameter of eye; maxillary teeth present; tongue with

a papilla; tips of fingers and toes not dilated; first finger equal to or slightly longer than second; toes without webbing, 4 1/2 phalanges of fourth toe free; small supernumerary tubercles on second, third, and fourth metatarsals; inner metatarsal tubercle compressed, blade-like, subequal to length of first toe; no outer metatarsal tubercle.

Skin above with scattered, small round tubercles; throat and chest smooth; posterior half of abdomen coarsely granular.

Color (in alcohol) dark grayish brown above, uniform, spotted, or with diamond pattern mid-dorsally; throat brown spotted with white, chest whitish, densely spotted with brown; posterior part of abdomen whitish.

Secondary sex characters. — The two males (23,5, 24,7 mm) have small round vocal sac openings. The skin of their throats is not modified in any way. Their third fingers are 0,20-0,21 of snout-vent. In the one female (28,7 mm) containing enlarged, non-pigmented ova the third finger is 0,18 of snout-vent. Head width in the female (0,40 of snout-vent) is greater than in the two males (0,36-0,37). Relative tibia length is greater in the males (0,48-0,49) than in the female (0,38).

Ecological notes. — Five of the seven specimens were caught in wooded savanna. Another was collected in a village, and the seventh at the edge of a stream issuing from a gallery forest.

Range. — From Ghana to northeastern Congo.

Garamba localities and specimens : Cellule Biologique I (2), Aka (1), Bagunda (1), Nagero (2), Tikadje (1).

Arthroleptis sp.

Taxonomic notes. — A single specimen from the Garamba differs from original descriptions of species of *Arthroleptis* (*sensu lato*). It is a medium-sized adult male (IPN no. 1617), having a conspicuously elongated third finger, maxillary teeth, a shovel-like inner metatarsal tubercle, short legs (heels not overlapping), and cylindrical, non-dilated digit tips. It differs from the Garamba frogs identified here as *A. poecilonotus* in having a narrower head, smooth dorsal skin, and shorter legs (heels overlapping in *poecilonotus*), and in lacking a papilla on the tongue.

Given the extensive intraspecific variation already known in this genus and the many names already avalaible in the literature, it does not seem wise to describe a new species based on a single specimen.

Description. — A medium-sized *Arthroleptis*, adult male 24,0 mm snout to vent; body stocky; head narrower than body, width 0,33 of snout-vent; snout pointed, longer than diameter of eye; nostril closer to tip of

snout than to eye; canthus distinct, lores almost vertical; interorbital wider than upper eyelid; tympanum visible, half diameter of eye; maxillary teeth present; tongue without papilla.

Tips of fingers and toes not dilated; first finger shorter than second; metacarpals with conspicuous tubercles. Toes without web; small supernumerary tubercles on second, third, and fourth metatarsals; inner metatarsal tubercle compressed, blade-like, as long as first toe; no outer metatarsal tubercle; tibia 0,37 of snout-vent, foot measured from proximal edge of metatarsal tubercle 0,38 of snout-vent; heels not meeting when legs are flexed, tibio-tarsal articulation reaching tympanum.

Skin of back and center of abdomen smooth; sides and edges of abdomen granular.

Color (in alcohol) brown above with a double hour-glass, dark marking middorsally; a dark rhomboidal spot from eye over upper part of tympanum to axilla; lips with whitish spots; limbs with narrow dark crossbars; throat with dark suffusion (probably a male secondary sex character); remainder of ventral surfaces cream-colored, immaculate.

Secondary sex characters. — The gular skin is finely shagreened and stretched. Round vocal sac openings are located far back in the mouth. The third finger is elongated to more than twice the length of the second finger. Both second and third fingers have spinules on their dorsomedial edges, the third finger on three phalanges and the second on two.

Ecological notes. — This frog was caught under a termite nest in grass savanna.

Garamba locality : Moyenne Aka (1).

Hemisus marmoratus (PETERS).

Engystoma marmoratum PETERS, 1854, Monatsber. Akad. Wiss. Berlin, **1854**, p. 628 — Cabaceira, Mozambique.

Hemisus marmoratus PETERS, 1882, Reise Mozam., Zool., **3**, p. 173, pl. 25, fig. 1, pl. 26, fig. 10.

Taxonomic notes. — LAURENT (1963) has suggested that *H. marmoratus* (PETERS) and *H. guineensis* COPE are not subspecies, as they have often been considered (e.g., LOVERIDGE, 1957). The evidence from the Garamba collections confirms Laurent's opinion. Two sharply distinct forms were collected at each of four localities within the Parc de la Garamba.

These forms differ in size, in coloration, and in some body proportions. The smaller one, which is clearly *H. marmoratus*, is olive or olive brown above with dark markings. The two females with ripe ova measure 32,5

and 33,4 mm and the three adult males range from 25,2 to 26,4 mm. The inner metatarsal tubercle is shorter than the eye nostril distance. The large form, which agrees with descriptions of *H. guineensis*, is black above with small yellow or orange dots. Females with mature ova range from 37,6 to 52,9 mm and adult males from 30,5 to 36,9 mm. The inner metatarsal tubercle is longer than the eye-nostril distance in 85 % of the individuals.

Descriptive notes. — Body stout, legs short; snout acutely pointed and hard; nostrils directed obliquely upward and outward; tips of digits not dilated; toes without webbing; inner metatarsal tubercle larger than first toe, compressed, shorter than eye-nostril distance.

Color in alcohol olive or olive-brown above with black marbling.

Secondary sex characters. — Adult females are about 7 mm larger than males (see above). Males have vocal sacs, black throats, and glandular areas on the dorsal surface of the hand.

Ecological notes. — This fossorial species is almost completely confined to savannas in the Parc de la Garamba. Only one specimen out of 20 was collected in gallery forest. Nine were caught in tree savanna, and 3 in shurb savanna. Of these 7 were taken along small streams, 1 at a marsh, 1 at a permanent pond, and 3 at a temporary pond; only the last 3 were adults.

Range. — Transvaal and Mozambique north to Kenya (LAURENT, 1963) and northeastern Congo. The Garamba localities apparently represent the northestern corner of the range.

Garamba localities and specimens : Cellule Biologique I (14), Cellule Biologique II (4), Nagero (1), Ndelele (2), Pali (1).

Hemisus guineensis COPE.

(Fig. 39.)

Hemisus guineensis COPE, 1865, Nat. Hist. Rev., **5**, p. 100 footnote — Guinea.

Taxonomic notes. — See under *Hemisus marmoratus* above.

Descriptive notes. — Body stout, legs short, snout acutely pointed and hard; nostrils directed outward; tips of digits not dilated; toes without webbing; inner metatarsal tubercle larger than first toe, compressed, usually longer than eye-nostril distance.

Color in life black above with small yellow or orange dots.

Secondary sex characters. — Females with ripe ova measure 37,6-52,9 mm (mean 44,12 $\pm$ 1,04; N = 15). Males with nuptial glands range from 30,5 to 36,9 mm (mean 34,12 $\pm$ 0,51; N = 15).

Photo: R. F. INGER.

FIG. 39. — *Hemisus guineensis.*

In addition to the glandular area on the dorsal surface of the hand (NOBLE, 1924 : 282), the adult males have black throats.

The call is illustrated in Figure 40.

Ecological notes. — This fossorial species was obtained in grass (27 specimens), shrub (19), and tree savanna (8). Two were found in rodent burrows in grass savanna. Four were dug out of the earth at depths of 6 to 10 cm. During the rainy season, this species emerges from the ground at

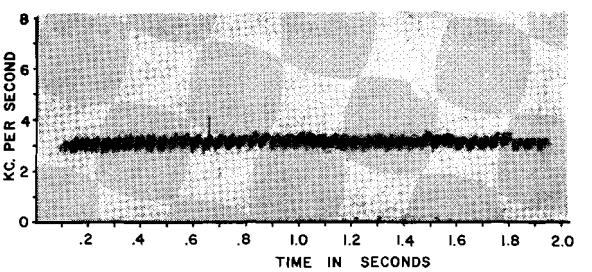


FIG. 40. — Sonogram of call of *Hemisus guineensis* (RFI-3308) recorded at Ndelele, April 3, 1959.

night and calls in the vicinity of water. In 1959 we heard calling males beginning April 2; on April 7 we first observed clasping pairs. Nine were collected along the edge of streams, two at marshes, and eight at temporary ponds.

Range. — This species occurs from Senegal and Sierra Leone to western Tanganyika and Angola (LOVERIDGE, 1957).

Garamba localities and specimens : Cellule Biologique I (14), Cellule Biologique II (29), Nagero (1), Ndelele (14).

Hemisus larvae.

Numerous samples of tadpoles having the two types of papillae characteristic of *Hemisus* larvae (WAGER, 1929) were collected at various points in the park. Only one species seems to be represented. The tadpoles show little variation in labial tooth counts : I : 4-4/1-1 : III (17), I : 4-5/1-1 : III (1), I : 3-3/1-1 : III (1).

These dental formulae agree with those of *Hemisus* tadpoles from Guinea (GUIBÉ and LAMOTTE, 1958A), where only the species *H. guineensis* is known. According to WAGER (1929) mature tadpoles of *Hemisus* from northern Transvaal, where only the species *marmoratus* occurs, have counts of II : 3-3/1-1 : III. Agreement with the West African larvae suggests that the Garamba larvae belong to *H. guineensis*. However, none of the older tadpoles (Stages XV-XX, TAYLOR and KOLLROS, 1946) have the light dorsal spots typical of transformed *guineensis*. Instead a number of them have large, obscure, dark markings of the sort found on the backs of adult *marmoratus*. It does not seem reasonable they should all be larvae of *marmoratus*, for adults of that species were only half as numerous as adults of *guineensis* in the Garamba collection.

The Garamba larvae agree in habitus and coloration with the descriptions of WAGER (1929), GUIBÉ and LAMOTTE (1958A), and SCHMIDT and INGER (1959). The ventral flap mentioned by the last authors covers the developing hind limbs until all toes are distinct (Stage X).

Head-plus-body lengths of larvae show the following variation : pre-limb bud 7,8-14,5 mm, Stage II 11,0-14,9, Stage VI 10,0-15, Stage X 15,5-17,0, Stage XVII 19,7, Stage XX 19,0. Head-plus-body is 0,46-0,50 of tail length (4 specimens). Tail depth is 0,31-0,33 of tail length.

One clutch of eggs was reared in an aquarium. After 65 days the only larva left had a total length of 26 mm, head-plus-body 10 mm. The larvae that WAGER (1926) reared reached total lengths of 35 mm in three months. These rates of development may differ widely from those of free tadpoles.

Ecological notes. — Most of the 35 lots were collected in marshes or in marshy expansions of small streams. One lot was obtained in a temporary pond. Eight of the lots were from temporary marshes formed in the flood plains of rivers.

Tadpoles were collected from May through October. Thus breeding of *Hemisus* in the Garamba begins a short time after the onset of rains and continues to the end of the rainy season.

Garamba localities : Cellule Biologique I (18 lots), Cellule Biologique II (4), Nagero (2), Napokomweli (7), Ndelele (3), Ngorobongo (1).

Leptopelis flavomaculatus (GÜNTHER).

(Fig. 41.)

Hyperolius flavomaculatus GÜNTHER, 1864, Proc. Zool. Soc. London, **1864**, p. 310, pl. 27, fig. 1 — Rovuma Bay, Tanganyika.

Leptopelis flavomaculatus LAURENT, 1947, Ann. Mag. Nat. Hist., (11), **14**, p. 293.

Hylambates johnstoni BOULENGER, 1897, Proc. Zool. Soc. London, **1897**, p. 803, pl. 46, fig. 4 — Kandowe-Karonga and Nyika Plateau, Nyasaland.

Taxonomic notes. — This small series agrees with the original description of *Hylambates johnstoni* BOULENGER (1897) in all details. Two of them have the light dorsal dots BOULENGER noted in some, but not all, of the syntypes. I am following LAURENT (1947) and LOVERIDGE (1953) in considering *johnstoni* BOULENGER a synonym of *flavomaculatus*.

Descriptive notes. — Head broad, body slender; snout rounded, as long as diameter of eye; interorbital as wide as upper eyelid; tympanum distinct, more than half diameter of eye, equal to eye nostril distance, 0,08-0,09 of snout-vent; tips of fingers and toes dilated into distinct disks, those of outer fingers slightly wider than those of toes; disks of third and fourth fingers about half diameter of tympanum; outer fingers webbed to level of basal subarticular tubercles; fifth toe webbed to distal subarticular tubercle (i.e., two phalanges free), fourth toe to central subarticular tubercle (i.e., three phalanges free); inner metatarsal tubercle weakly compressed, between one-half and three-fifths length of first toe, 0,057-0,059 of snout-vent; tibia 0,43-0,47 of snout-vent.

Skin above smooth or weakly shagreened; entire ventral surface coarsely granular.

Color in life rich clay brown above and laterally; in two frogs a darker brown line just below canthus, continued as a supratympanic curve; a dark brown triangular blotch occupying most of back, apex pointed forwards; limbs with dark brown crossbars; blackish brown mottling low on side; ventrally cream-colored, usually with a brown wash on throat; cream-colored lines on outer edge of lower arm, tarsus, and fifth toe.

Photo: R. F. INGER.

FIG. 41. — *Leptopelis flavomaculatus.*

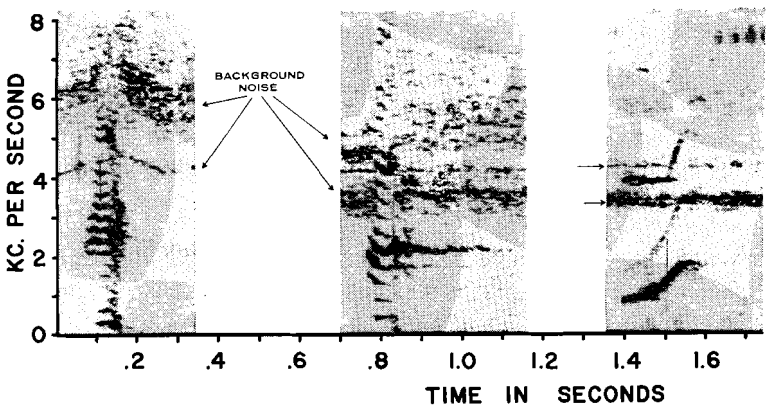


FIG. 42. — Sonograms of calls :
Left : *Leptopelis oryi* (RFI-2477) recorded at Nabokoyo on March 20, 1959; Center : *Leptopelis flavomaculatus* (RFI-3364) recorded at Pidigala on April 8, 1959; Right : *Kassina senegalensis* (RFI-3676) recorded at Nagero on April 23, 1959.

Secondary sex characters. — All five specimens are adult males having vocal sac openings, pink lineae masculinae, and distinct pectoral glands. Snout-vent lengths vary from 36,3 to 44,2 mm (mean 41,56 mm).

The call is analysed in Figure 42.

Ecological notes. — All five were caught at night, April 8, 1959, while calling from vegetation 1-2 m above groud in a well-developed gallery forest. Most records of this species, under the name *johnstoni*, are from forested areas of East Africa (LOVERIDGE, 1936, 1942). DE WITTE (1934) listed the locality Dika, in the Upper Uele, where gallery forests project into the savanna as in the Garamba. FITZSIMONS (1939) reported eight specimens from the Chirinda Forest, Southern Rhodesia. An unrecorded specimen (AMNH 68547) was caught in the Makondara Forest, Kenya.

Range. — This species is known from northeastern Congo to Kenya, Tanganyika, Nyasaland, Southern Rhodesia, and, possibly, Transvaal (HEWITT, 1911). It undoubtedly occurs also in southern Sudan just across the border from the Parc National de la Garamba.

Garamba locality and specimens : Pidigala (5).

Leptopelis oryi sp. nov. [1].

(Fig. 43.)

Holotype. — Field number RFI 3198. An adult male collected at the source of the Nabakoyo River, Parc National de la Garamba, Congo, at approximately 750 m., March 25, 1959 by ROBERT F. and MARY LEE INGER.

Paratypes. — One hundred seventy three specimens from the Parc National de la Garamba (148 Institut Royal des Sciences Naturelles, 25 CNHM).

Five specimens identified as *Leptopelis anchietae* by NOBLE (1924) : AMNH 8668 from Yakuluku, AMNH 8670 from Garamba, AMNH 8675-6 from Faradje, AMNH 8677 from Niangara.

Diagnosis. — A moderately small species of *Leptopelis* having slightly dilated finger tips, no webbing between the fingers, a large, compressed inner metatarsal tubercle, three narrow dark stripes on the back, a dark lateral band, and no pectoral glands in adult males.

Description. — Habitus stout, body as wide as or wider than head; snout rounded, as long as or slightly longer than diameter of eye; inter-

[1] It is an honor to dedicate this new species to M. ALBERT ORY, Conservateur of Parc National de la Garamba, in recognition of his great services to that park.

orbital as wide as upper eyelid; tympanum distinct, about half diameter of eye, equal to or slightly less than eye-nostril distance, 0,06-0,08 of snout-vent; vomerine teeth in two small patches between the choanae.

Tips of fingers and toes dilated into distinct disks, those of outer fingers wider than those of toes; disk of third finger about diameter of tympanum;

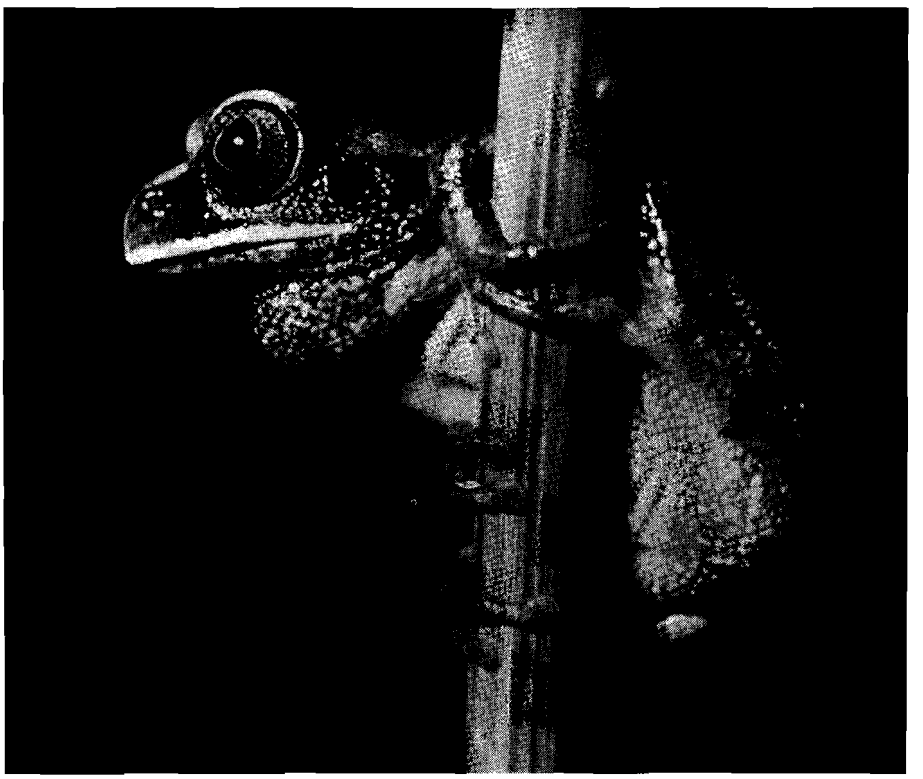


Photo: R. F. INGER.

FIG. 43. — *Leptopelis oryi*, new species.

fingers without webbing; toes with reduced webbing; web reaching distal subarticular tubercle on outer side of third toe, not reaching distal tubercle of fifth toe, reaching between basal and middle tubercle of fourth toe (i.e., 3 1/2 phalanges free); inner metatarsal tubercle compressed, elevated, between 2/3 to 1 times length of first toe, 0,071-0,081 of snout-vent; length of tibia usually less than width of head, 0,36-0,44 of snout-vent.

Skin above shagreened, without coarse granules; below coarsely granular.

Color in life clay brown above; back with three narrow, dark brown stripes, one middorsally and one dorsolaterally on each sise; side of head

same color as back; side of body with broad dark brown band beginning immediately behind eye; lateral band usually bordered dorsally by a thin light line; band merges gradually with ventral coloration; ventrally whitish, immaculate except on throat which usually is suffused with brown.

Secondary sex characters. — Females having enlarged ova measure 42,4-57,5 mm, snout to vent (mean = 48,39 ± 1,98; n = 8). Adult males measure 29,0-40,3 mm (mean = 36,14 ± 0,30; n = 53).

Adult males have round openings to vocal sacs and pink linae masculinae. They do not have pectoral glands. A sonogram of the call is shown in Figure 42.

Larvae. — These tadpoles resemble those of other *Leptopelis* (LAMOTTE and PERRET, 1961) in shape of body and tail and in the general aspect of the oral disk. Advanced larvae have distinct disks on the toes and a large inner metatarsal tubercle. They are assigned to *L. oryi* for the following reasons. (1) They were collected at widely scattered parts of the savanna where adult *L. oryi* were numerous. The other species of *Leptopelis* found in the Garamba were either confined to gallery forest (*L. flavomaculatus*) or to a restricted edaphic situation (*L. viridis*). (2) They differ from the larvae of *L. viridis* described by LAMOTTE and PERRET (1961) in the usual labial formula (I : 2-2/III in *viridis*) and in the heavily pigmented underside of the head. (3) Metamorphic stages have the dark lateral band of adult *L. oryi*. The descriptive notes that follow are composite.

Body oval, tapered towards the snout; eyes dorsolateral, not visible from below; spiracle sinistral, mid-way between eye and root of hind limb; oral disk ventral, subterminal; papillae in a continuous double row at margin of lower lip; beaks finely serrated, lower beak V-shaped, both beaks black along margins; labial teeth I : 2-2/1-1 : II (24 specimens), I : 2-2/III (4) or I : 3-3/1-1 : II (3), rows of lower lip subequal in length; tail long, tapering gradually; fins beginning at end of body, margins not rising; depth of tail 0,20-0,25 of tail length; head plus body 0,40-0,48 of tail length; head and body dark brown above and on sides; head with numerous melanophores below, remainder of body without chromatophores ventrally; tail muscle and dorsal fin brown, spotted with black; ventral fin without pigment in proximal half.

Total length of 6 larvae in Stages IX-XI 35-47 mm, of 3 larvae in Stages XVI-XVIII 39-49 mm.

Comparisons. — The slightly dilated finger tips, the lack of webbing between the fingers, and the large, compressed inner metatarsal tubercle ally *oryi* with *Leptopelis gramineus* (BOULENGER), *L. anchietae* (BOCAGE), *L. bocagei* (GÜNTHER), and *L. argenteus* (PFEFFER).

Leptopelis anchietae has a distinct narrow, dark stripe that curves upward from the tip of the snout, runs backward below the edge of the canthus, and resumes behind the eye, passing above the tympanum and curving down into the dark side. A short spur from the dark lateral coloration extends upward and forward from the groin. *L. anchietae* lacks clear dorsal markings. The pattern of *anchietae* thus differs sharply from that of *L. oryi* (see above). The fingers of *anchietae* are longer than those of *oryi*. In the latter the third finger equals the distance from the nostril to the rear of the eye; in *anchietae* the finger equals the distance from the tip of the snout to the rear of the eye. The inner metatarsal tubercle does not exceed half the length of the first toe in *anchietae*, whereas in *oryi* it exceeds two-thirds the length of the toe.

Leptopelis argenteus also differs from *oryi* in pattern, having two dark stripes, one dorsolaterally and one on the side (PFEFFER, 1893; LOVERIDGE,

Table 48. — **Comparison of body proportions in** Leptopelis oryi, L. gramineus, **and** L. bocagei (1). **Proportions are given in terms of thousandths of snout-vent.**

	Males			Females		
	Number	Range	Median	Number	Range	Median
			Tibia			
oryi	11	374–411	396	9	358–441	384
gramineus	3	330–348	334	1	366	—
bocagei.	9	320–392	343	10	343–385	362
			Head width			
oryi	10	377–415	408	9	385–422	412
gramineus	3	363–405	380	1	402	—
bocagei.	10	362–435	416	12	392–430	417
			Metatarsal tubercle			
oryi	10	71–81	79	6	73–81	77
gramineus	3	73–77	75	1	68	—
bocagei.	8	66–85	73	11	66–84	73

(1) Specimens of *bocagei* from Ethiopia (8), Tanganyika (4), Katanga (4), Angola (4).

1951). According to PFEFFR, the tibiotarsal joint of *argenteus* reaches the front of the eye; in *oryi* it reaches the tympanum.

Leptopelis gramineus, which may be a synonym of *anchietae*, differs from *oryi* in coloration. Ethiopian specimens of *gramineus* from the British Museum collections (BM 1947.2.10.20 — syntype, 76.1.17.4, 1902.12.13.1964, 1927.7.5.36-38) have a stripe or row of dark spots on the side, the stripe or spots widely separated from the ventrum by an area having the same hue as the back. The dorsum lacks a distinct pattern. The three males of *gramineus* (1927.7.5.36-38) have pectoral glands and thus differ from males of *L. oryi.*

These two species also differ in body proportions. *Leptopelis gramineus* has a shorter leg and a narrower head than *L. oryi* (Table 48).

Leptopelis bocagei, though its dorsal pattern varies (PARKER, 1936 B), never has three dark lines on the back or dark sides as does *oryi.* These two species also differ in size and relative length of the tibia (Table 48). Adult males of *bocagei* range from 37 to 56 mm (N = 31), those of *oryi* from 29 to 40 mm (N = 53). Adult females of *bocagei* measure 47-68 mm (N = 23), those of *oryi* 42-58 (N = 8). In contrast to *oryi*, males of *bocagei* have distinct pectoral glands.

Ecological notes. — This species is found in all types of savanna in the Parc National de la Garamba. The De Saeger Mission collected adults in grass savanna (11), tree savanna (7), shrub savanna (1), in marshes (2), and along marshy banks of streams (5). Juveniles (14-29 mm) were caught by the de Saeger Mission in the same types of habitats as the adults. Our field party got adults at a savanna-forest ecotone (5), along the bank of a small stream, but mostly in grass savanna around the edges of marshes (43). Most of those we caught were males calling from tall grass stems, usually

Table 49. — **Seasonal distribution of adult females of** Leptopelis oryi **collected in the Parc National de la Garamba.**

Months	Ova immature	Ova intermediate	Ova mature
February	—	3	—
March	—	2	1
April	1	2	6
May	2	—	1
June	2	—	—
August	3	—	—

1 to 2 meters above ground. Larvae were found in small ponds and in marshes either isolated in savanna or in the flood plains of small streams.

Ten specimens were caught by the De Saeger Mission in rodent burrows or under rocks; all 10 were taken during the dry season (December-March).

Males were first heard calling March 20. Thereafter we heard males calling nightly until our deparature May 20. Females with mature ova were found between March 19 and May (Table 49). Larvae were collected from May through early September. Breeding thus seems to begin near the end of the dry season and to extend at least to the middle of the rainy season. The seasonal abundance of juveniles (Table 50) supports that hypothesis.

Range. — The upper Uele region of northeastern Congo.

Garamba localities and specimens : Cellule Biologique I (26), Cellule Biologique II (93), Mabanga (3), Mobaba (5), Moko River (5), Morubia (1), Mabakoyo (24), Napokomweli (1), Ndelele (10), PFS km 22 (1), Pidigala (5).

Table 50. — **Seasonal distribution of juveniles and adults of** Leptopelis oryi **collected in the Parc National de la Garamba.**

	De Saeger Mission		Inger Mission (1)
	Juvenile	Adult	Adult
January	4	—	—
February	2	4	—
March	1	4	—
April	—	7	24
May	3	5	21
June	10	2	7
July	47	—	—
August	26	4	—
September	2	—	—
October	4	—	—
November	4	1	—
December	5	—	—
Total	108	27	52

(1) Party in the field only three months.

Leptopelis viridis (GÜNTHER).

Hylambates viridis GÜNTHER, 1868, Proc. Zool. Soc. London, **1868**, p. 487 — West Africa.
Leptopelis viridis PARKER, 1936, Zool. Meded., **19**, p. 95.

Taxonomic notes. — These frogs from Garamba agree in habitus, size (Table 51), webbing, coloration (as in LAMOTTE and PERRET, 1961 : fig. 6), and secondary sex characters with nine *L. viridis* from Ghana and Liberia (CNHM 57666-8, 57765, 57904-5, 74853-4).

The Garamba frogs are also similar to descriptions of *L. concolor* (AHL, 1929), but differ from that form in several diagnostic characters. In *concolor* the finger disks are two-thirds the width of the tympanum, the skin is smooth (AHL, 1929), and the side of the snout is as light as its dorsal surface except for a dark stripe along the canthus (AHL, 1929; LOVERIDGE, 1942 : pl. 2, fig. 5). In *viridis* from West Africa (the type « locality ») and in the Garamba specimens, the tympanum is twice the width of the finger tips, which are swollen into distinct disks, the dorsal skin is coarsely granular, and the entire side of the snout is dark except for a small area.

Although the Garamba frogs differ slightly from West African *viridis* in several body proportions (Table 51), they are clearly conspecific with *viridis*. The relationship of *concolor* to the West African and Garamba frogs cannot be determined on the basis of material at hand.

Descriptive notes. — Habitus stout, body as wide as head; snout rounded, as long as or slightly longer than diameter of eye; interorbital narrower than upper eyelid; tympanum distinct, one-half diameter of eye, equal to eye-nostril distance, 0,07-0,10 of snout-vent; tips of fingers and toes dilated into distinct disks, those of outer fingers wider than those of toes; disks of outer fingers about half diameter of tympanum; fingers without webbing; fifth toe webbed to base of distal subarticular tubercle; fourth toe to between basal and central subarticular tubercles (i.e., 3 1/2 phalanges free); inner metatarsal tubercle compressed, shovel-like, between 3/4 to 1 times length of first toe, 0,070-0,085 of snout-vent; length of tibia less than width of head, 0,37-0,41 of snout-vent.

Skin coarsely granular dorsally, laterally, and ventrally.

Color in alcohol reddish-brown above, a large, black blotch middorsally beginning as an interorbital triangle; dorsal blotch fenestrated with irregular islands of ground color; a dark stripe below canthus and several dark spots on side of snout and cheek; a black arc from eye above tympanum to insertion of arm; in some specimens a row of black spots laterally; limbs with dark crossbars; ventral surface cream colored; usually a suffusion of brown on throat and chest.

Secondary sex characters. — Adult females are distinctly larger than males (Table 51). The sexes also differ in the ratio of tibia length, head width, and tympanum diameter (Table 51). Though the absolute differences are small, they are statistically significant ($P<0,05$; Mann-Whitney U test).

All the males seen have vocal sac openings, pink lineae masculinae, and distinct pectoral glands.

Photo: H. DE SAEGER.

FIG. 44. — Xerophytic association at Km. 17 south of Bagbele, habitat of *Leptopelis viridis* and *Rana trinodis*.

Ecological notes. — These frogs were collected in April, May, and July. Three of eight females (April and May) have enlarged, nearly mature ova; the other five have moderately enlarged, but distinctly immature ova.

All specimens except one were caught at an outcrop of rocks supporting a xerophytic association of savanna plants (Fig. 44). No ecological data

Table 51. — **Comparison of** Leptopelis viridis **from West Africa (WA)** (1) **and the Parc National de la Garamba (G). Snout-vent in mm. Other dimensions in thousandths of snout-vent.**

	Snout-vent		Tibia		Head width		Tympanum		Metatarsal tubercle	
	G	WA	G	WA	G	WA	G	WA	G	WA
					Males (2)					
Range	28,8–34,2	31,8–35,4	386–410	383–442	411–443	386–429	81–105	62–74	73–83	67–73
Mean	31,13 ± 0,64	33,03 ± 0,51	—	—	—	—	—	—	—	—
Median	—	—	403	418	430	403	87	69	78	70
					Females (3)					
Range	39,9–49,6	44,8	369–406	392	401–429	406	71–85	66	70–85	80
Mean	46,02 ± 1,16	—	—	—	—	—	—	—	—	—
Median	—	—	382	—	413	—	74	—	80	—

(1) Two from Ghana, six from Liberia. One juvenile from Liberia not included.

(2) Ten males from the Garamba, seven from West Africa.

(3) Eight females from the Garamba, one from West Africa.

accompanied the exceptional specimen. LAMOTTE and PERRET (1961) state that *L. viridis* is widespread in savanna in West Africa.

Range. — Sierra Leone to northeastern Congo.

Garamba localities and specimens : Bagbele (1), Km 17 (17).

Kassina maculosa (STERNFELD).

Megixalus maculosus STERNFELD, 1917, Erg. Zweiten Deutschen Zentral Afrika Expedition, **1**, p. 501, pl. 24, fig. 11 — Duma, Ubangi.
Kassina maculosa LAURENT, 1952, Rev. Zool. Bot. Afr., **46**, p. 274.

Taxonomic notes. — A single female specimen having a dorsal pattern of narrowly separated, dark spots agrees with Sternfeld's description (1917); it has the coarsely granular skin and the dark mottling on the belly noted by STERNFELD. The dorsal spots are arranged in pairs mid-dorsally and the foot is distinctly longer than the tibia, both characteristics of *masculosa* according to LAURENT (1952B).

The ratio of tibia to foot (measured from the inner metatarsal tubercle to the tip of the fourth toe) varies from 0,88 to 1,03 (median 0,96) in 21 *K. senegalensis* from the Garamba. In the female of *maculosa* it is 0,87; in two males of *K. maculosa decorata* from Cameroons (CNHM 120154-5) the ratio is 0,81 and 0,84. Relative to snout-vent the foot is 0,38-0,40 in the three *maculosa* and 0,30-0,38 (median 0,33) in the 21 *senegalensis*. The snout is longer than the diameter of the eye in the 21 Garamba *senegalensis* (snout : eye 0,95-1,34, median 1,17), whereas in the three *maculosa* specimens the snout and eye are about the same length (snout : eye 0,89-1,03).

Descriptive notes. — Habitus stocky; snout obtusely pointed, same length as eye; interorbital slightly wider than upper eyelid, tympanum faintly visible through skin, about one-third diameter of eye; tips of fingers only slightly wider than basal phalanges; subarticular and supernumerary metacarpal tubercles prominent; tips of toes about as wide as those of fingers; toes webbed at bases only; two phalanges of fifth toe and three of fourth toe free; outer metatarsals united; a low, oval inner and a smaller indistinct outer metatarsal tubercle; weak supernumerary metatarsal tubercles; vent of female at ventral edge of thighs, surrounded by fringed pads; ventral surface coarsely granular except on throat.

Color (in alcohol) grayish brown dorsally and laterally; dorsally with black spots, each smaller than upper eyelid; spots in 7 to 9 slightly diverging rows; vertebral area with two rows of spots; ventrally cream color with faint dark network. The dorsal pattern is similar to that figured by PERRET (1958, figs. 2-4) for *K. m. decorata*.

The single Garamba female has enlarged, convoluted oviducts but immature ova. It is 29,2 mm, snout to vent.

Ecological notes. — The Garamba specimen was found under a heap of dead grass in grass savanna.

Range. — The species range extends from the Cameroons (*K. m. decorata* ANGEL) to northeastern Congo.

Garamba locality : Cellule Biologique II (1).

Kassina senegalensis uelensis LAURENT.

(Fig. 45.)

Kassina argyreivittis uelensis LAURENT, 1956, Folia Sci. Afr. Cent., **2**, No. 2, p. 17 [not seen] — Uele; LAURENT, 1957, Rev. Zool. Bot. Afr., **56**, p. 279.

Taxonomic notes. — The call of *K. senegalensis* in the Garamba consists of a single distinct whistle (Fig. 42). CURRY-LINDAHL (1956) referred to the call in Kivu and Ruanda as a « whistling sound ». The call of *senegalensis* in southern Africa, if these populations are conspecific with the northern ones, is like the the sound of a cork being pulled out of a bottle or like a bubble bursting according to POWER (1926).

Descriptive notes. — Habitus stocky, limbs short; snout-vent 25-40 mm; snout obtusely pointed, slightly longer than diameter of eye (snout : eye 0,95-1,34); tympanum faintly visible, about one third diameter of eye; tips of fingers not expanded; subarticular and supernumerary metacarpal tubercles prominent; tips of toes not expanded; toes webbed at bases only; about two phalanges of fifth and 3-3 1/3 of fourth toe free of web; outer metatarsals united; a low oval inner and a smaller, round outer metatarsal tubercle; no supernumerary metatarsal tubercles.

Color (in alcohol) grayish brown or gray above; a black mid-dorsal stripe, usually continuous from interorbital to sacrum; one or two rows of large black spots on each side; no dark spots on upper eyelid, though in a few specimens a dark stripe on the side of the head includes the corners of the eyelid; ventral surfaces cream color, immaculate, except for throat in adult male (see below).

Secondary sex characters. — Females are slightly larger than males. The snout-vent lengths of 56 adult males are 25,8-39,5 mm, those for 16 females containing ova 34,8-38,6. Corresponding means are 35,18 $\pm$ 0,40 and 36,95 $\pm$ 0,41; the difference between the means is statistically significant ($P<0,01$).

Adult males have median vocal sacs with a short oval opening on each side of the mouth. Other sex characters of the males are as described elsewhere (SCHMIDT and INGER, 1959).

Larvae and development. — Thirty-one lots were obtained. All tadpoles have the high dorsal fin originating far forward on the body, the large, black lower beak, and the small horny plates parallel to the lower beak all of which are diagnostic of *Kassina* larvae. The smallest tatpoles (total length 10 mm) are pale with a dense black vertebral stripe and on each side a lighter stripe from the snout through the eye.

Photo: R. F. INGER.

FIG. 45. — *Kassina senegalensis.*

The anal fringes typical of adult females appear only after the oviduct has become enlarged and convoluted. In two small females (26,2 and 29,2 mm), the oviduct is coiled but not enlarged. The vent in these females has the same high position and form as the vent in males. Two other females (27,8 and 29,3 mm) have enlarged oviducts and the anus as in adult females, that is, low on the rear of the thighs and surrounded by fringed pads.

The vocal sac probably develops before the other male secondary sex characters. No males lacking vocal sacs have any of the other structures. On the other hand, ten males (22,0-26,9 mm) having fully developed vocal sacs have weakly developed glands on the forearms (see SCHMIDT and INGER, 1959, for a description), incompletely formed gular pouches, and lightly

pigmented throats. Adult males have black gular pouches. Eight of the ten subadult males have no sign of linae masculinae; the other two have faint, clear strips of tissue that lack the deep pink hue characteristic of the structure in adult males.

Ecological notes. — *Kassina senegalensis* is an inhabitant of the savanna country from Senegal (DUMÉRIL and BIBRON, 1841), and Cameroons (MERTENS, 1940) to northern Kenya (BATTERSBY, 1954), thence southward through eastern Congo (SCHMIDT and INGER, 1959) to at least Mozambique, the type locality of *argyreivittis* PETERS.

In the Garamba *senegalensis* is most abundant in grass or shrub savanna (Table 52). The temporary ponds listed in the table were formed in the midst of grass savanna.

Table 52. — **Habitat frequency distribution of adult** Kassina senegalensis uelensis **in Parc National de la Garamba.**

	Wet season	Dry season	Total
Aquatic :			
Marsh	4	—	4
Temporary pond	42	2	44
Stream side	2	—	2
Grassy seepage	1	—	1
Subtotal	49	2	51
Non-aquatic :			
Grass savanna	41	4	45
Shrub savanna	59	—	59
Tree savanna	2	—	2
Gallery forest	1	—	1
Subtotal	103	4	107

After heavy rains filled grassy depressions in the savanna of the Garamba in April, 1959, *K. senegalensis* males began to call from the bases of clumped grass stems and debris (Fig. 45) at the edge of shallow temporary ponds and marshes (Fig. 14). *Kassina senegalensis* has been reported to breed in small temporary ponds in Gambia (ANDERSSON, 1937) and in the Parc National Albert in eastern Congo (CURRY-LINDAHL, 1961).

The Garamba larvae were collected in temporary pools and marshes (12 lots), marshy borders of streams (8 lots), and permanent marshes (2).

The de Saeger Mission collected only 6 of these frogs during the dry season. Our party caught none until April 22, about four weeks after the rains began. A day later we heard the first calls. The only small pre-limb bud larvae (ca. 10 mm) were collected in May. No other larvae were less than 30 mm total length. Tadpoles in various stages of development from early limb bud to metamorphosis were found from May to October. The scarcity of adults in the dry season and the distribution of larvae indicate that breeding is confined to the wet season.

Range. — Senegal to Kenya, south to Cape Province.

Garamba localities and specimens : Cellule Biologique I (54); Cellule Biologique II (86), Km 17 south of Bagbele (34), Mabanga (1), Nagero (11), Ndelele (2), Pp Km 10 (1).

Afrixalus fulvovittatus leptosomus (PETERS).

Hyperolius leptosomus PETERS, 1877, Monatsber. Akad. Wiss. Berlin, **1877**, p. 619, fig. 5 — Chinchoxo, Cabinda, Angola.
Afrixalus fulvovittatus leptosomus LAURENT, 1950, Explor. Parc Nat. Albert, fasc. 64, p. 18.

Descriptive notes. — A small frog, adults to 27 mm; habitus slender, limbs short; snout obtusely pointed; tympanum present but obscured by skin; outer fingers distinctly webbed at bases; fourth toe with 2 phalanges free of web; skin smooth above except in mature males; skin coarsely granular below.

Color in alcohol grayish brown with four dark brown or blackish stripes, two on back and one on each side; immaculate cream-colored below. In life gular pouch of males bright yellow.

Secondary sex characters. — Males have pink lineae masculinae at the dorsal and ventral edges of the obliquus muscles, slit-like vocal sac opening, a thick-walled gular pouch, fine black spinules dorsally and ventrally, and a gland on the wrist. The spinules are especially numerous on the back and chin, and less dense or even absent on the abdomen. The arm gland consists of an oval patch of glandules in the colorless postero-median aspect of the wrist.

Females having enlarged oviducts measured 23,5-26,2 mm (mean 24,73 $\pm$ 0,25; N = 13) and males having vocal sacs 20,4-24,5 mm (mean 22,38 $\pm$ 0,11; N = 68). The difference between the means is statistically significant.

Table 53. — **Size-frequency distribution of metamorphosing and juvenile** Afrixalus fulvovittatus leptosomus **from the Parc National de la Garamba.**

Snout-vent	Vestige of tail (1)	Without tail	Male (2)	Female (3)
10,0–10,4	1	—	—	—
10,5–10,9	4	1	—	—
11,0–11,4	3	—	—	—
11,5–11,9	5	—	—	—
12,0–12,4	6	—	—	—
12,5–12,9	5	2	—	—
13,0–13,4	4	9	—	—
13,5–13,9	2	10	—	—
14,0–14,4	2	23	—	—
14,5–14,9	—	12	—	—
15,0–15,4	—	16	—	—
15,5–15,9	—	15	—	—
16,0–16,4	—	8	—	—
16,5–16,9	—	5	—	—
17,0–17,4	—	9	—	—
17,5–17,9	—	11	—	—
18,0–18,4	—	—	4	1
18,5–18,9	—	—	5	7
19,0–19,4	—	—	4	2
19,5–19,9	—	—	2	4
20,0–20,4	—	—	—	1
20,5–20,9	—	—	—	2
21,0–21,4	—	—	1	3
21,5–21,9	—	—	—	1
Size range	10,0–14,2	10,9–17,9	18,3–21,4	18,3–21,8

(1) All have erupted fore limbs.
(2) None with vocal sacs.
(3) None with mature oviducts.

Larvae and development. — Sixteen lots of tadpoles agree in body form, coloration, and general structure of the oral disk with descriptions of larval *A. fulvovittatus* (GUIBÉ and LAMOTTE, 1958; SCHIØTZ, 1963). Tadpoles in pre-metamorphic and metamorphic stages have the dorsal pattern of adult *A. fulvovittatus*.

Two larvae in stages XVII and XVIII have no labial teeth. Fourteen others in Stages II to XVII have a short, continuous row of teeth on the lower lip. This population thus agrees with the Nigerian larvae reported by SCHIØTZ (1963) and differs from the Mount Nimba series described by GUIBÉ and LAMOTTE (1958).

Metamorphosis begins when the larvae have attained a snout-vent length of about 10-12 mm. (Table 53). Metamorphosis is completed usually by the time the young are 13 mm long. Females do not reach sexual maturity, as judged by enlargement and convolution of oviducts, until they are more than 22 mm long (Table 53). Males achieve sexual maturity at about 20 mm; the smallest having vocal sacs measured 20,4 mm.

Male secondary sex characters follow the usual sequence of development, that is vocal sacs develop before any of the other structures. No male lacking vocal sac openings has any sign of gular pouch or asperities. One male (21,9 mm) having vocal sac openings has an incomplete gular pouch but no arm gland or asperities.

Ecological notes. — Adults of *A. f. leptosomus* were found at all types of aquatic habitats but were most numerous where the current was slow or non-existent (Table 54). Most of those listed in the table from « stream side » were caught in marshy vegetation beside small, slowly flowing streams. Larvae were collected at similar locations : 5 lots from marshes, and 3 from ponds. PERRET (1960A) reports that this frog appears in almost every wet place in Cameroon savanna.

Evidently this species rarely leaves the immediate vicinity of water. Like other riparian species in the Garamba (e.g., *Hyperolius schoutedeni*, *H. cinnamomeoventris*), *A. f. leptosomus* moves away from water mainly during the wet season (April-October). It is primarily a savanna inhabitant. Most of the aquatic habitats at which it was caught are in savanna. Only 8 individuals were collected in gallery forests.

The loud call (Fig. 46) of this species was one of the characteristic night sounds of the savanna once the rains began. Males vocalize while perched on vegetation 30-60 cm above the groud or water. We first heard calling males in 1959 on March 20. Adult females were caught only in the interval April-July; in each of those months the majority of adult females contained mature ova. Two pairs were found in amplexus the night of April 22, 1959. Both females laid white eggs lacking dark hemispheres.

Metamorphosing larvae were found in March, June through October, and December indicating an extensive breeding season.

Table 54. — **Habitat-frequency distribution of** Afrixalus fulvovittatus leptosomus **caught in the Parc National de la Garamba.**

	Dry season	Wet season	Total
Aquatic :			
Marsh	17	93	110
Permanent pond	6	5	11
Temporary pond	44	18	62
Grassy seepage	6	65	71
Stream side	11	46	57
Subtotal	84	227	311
Non-aquatic :			
Grass savanna	—	25	25
Shrub savanna	—	4	4
Tree savanna	3	2	5
Gallery forest	—	6	6
Subtotal	3	37	40

Range. — This subspecies has been reported from Cameroons (LAURENT, 1951; PERRET, 1960A) to western Kenya and Tanganyika (LOVERIDGE, 1957). In southern Congo this subspecies is replaced by *Afrixalus fulvovittatus upembae* (LAURENT). The boundary between these two froms has not been determined.

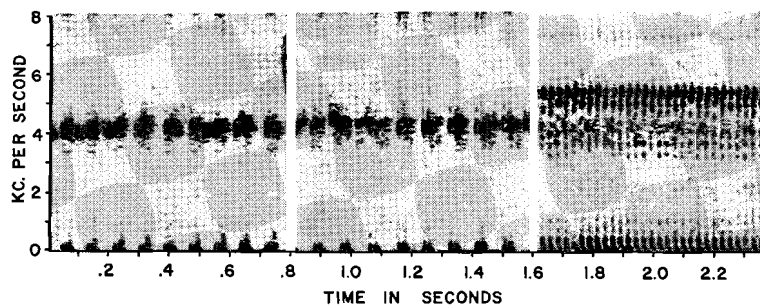


FIG. 46. — Sonograms of the calls :
Left : *Afrixalus fulvovittatus leptosomus* (RFI-3147); Center : *A. f. leptosomus* (RFI-2478), and Right : *A. weidholzi* (RFI-4203).

Garamba localities and specimens : Cellule Biologique I (75), Cellule Biologique II (173), Beredwa (8), tributary of Dungu River (5), Iso River (5), Km 17 S. of Bagbele (1), Makpe (3), Mobaba (3), Nabakoyo (13), Nagero (8), 3 Km W. of Nagero (21), Naluguambala (2), Ndelele (18), PFS (1), Pp Km 10 (6).

Afrixalus weidholzi (MERTENS).

(Fig. 47.)

Megixalus weidholzi MERTENS, 1938, Zool. Anz., **123**, p. 244, fig. 2 — Dienoundialla, Senegal.

Afrixalus weidholzi LAURENT, 1951, Ann. Soc. Roy. Zool. Belg., **82**, p. 28.

Descriptive notes. — A small frog, adults to about 22 mm; habitus slender, limbs short; snout obtusely pointed or truncate; tympanum present, hidden under skin; outer fingers with narrow web at base; fourth toe with about 2 1/2 phalanges free of web; skin smooth above in both sexes; skin coarsely granular below; outer metatarsal tubercle present.

Color in life lemon yellow to yellowish brown above; a narrow brown vertebral stripe; a brown lateral stripe from snout to groin; below white; males with lemon yellow throat; no red flash colors on legs.

Secondary sex characters. — Males have the same assemblage of secondary sex characters as appear in *Afrixalus fulvovittatus leptosomus* (p. 131), except that no spinose asperities occur on the skin of *A. weidholzi.*

Females having enlarged oviducts measured 17,2-21,1 mm (mean 19,66 ± 0,47; N = 9) and males having vocal sacs 17,2-19,3 mm (mean 18,24 ± 0,10; N = 25). The difference between the means is statistically significant ($t>3,0$; $P<0,01$).

The call is analysed in Figure 46.

Larvae and development. — A single tadpole (Stage XVII) is tentatively assigned to this species. The terminal position of the oral disk, the non-angular beaks, and the absence of anterior labial teeth recall larvae of other species of *Afrixalus* (GUIBÉ and LAMOTTE, 1958). Only *A. fulvovittatus* and *A. weidholzi* are known from the Garamba.

This tadpole differs from those assigned to *A. fulvovittatus* (see above) in the following ways :

— no teeth on lower lip
— no spots or stripes under the head
— papillae in a single staggered row, instead of in two well separated rows
— sides of body and tail with large spots instead of stripes or short lines

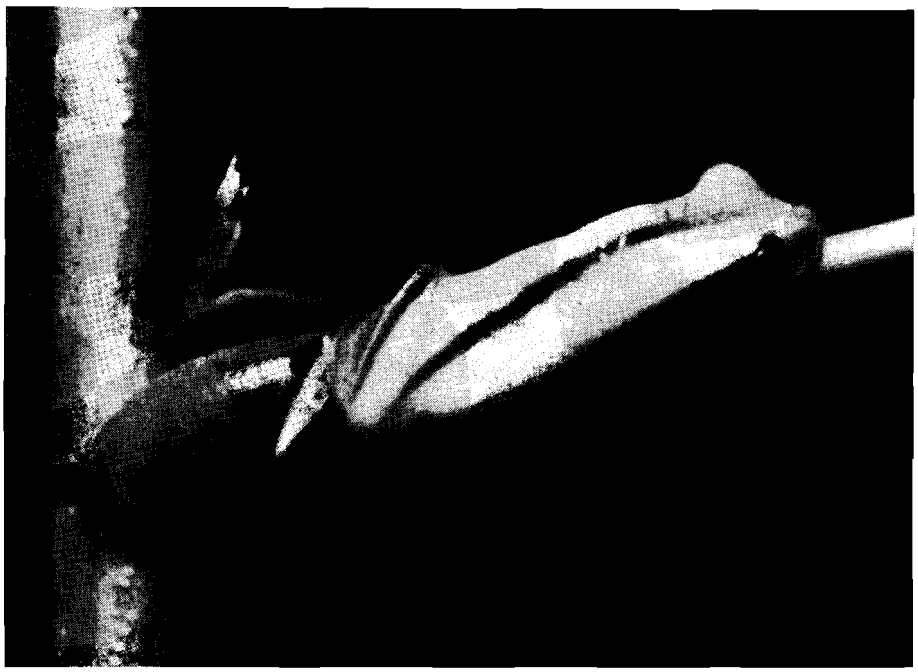


Photo: R. F. INGER.

FIG. 47. — *Afrixalus weidholzi.*

Head and body are oval, slightly depressed; eyes lateral; beaks finely serrate, without cusps or notches, non-angular, about three-fourths black; spiracle sinistral, much closer to root of hind limb than to eye; fins beginning at end of body, weakly convex; tail tapering gradually; head plus body 9,4 mm, total length 27,0 mm.

Young retaining vestiges of the tail measured 10,3-14,9 mm snout to vent (N = 5). Nine juveniles that had completely resorbed tails measured 9,5-13,0 mm.

Ecological notes. — Forty-eight adults were collected in shallow temporary ponds in grass savanna. The remaining adults were caught in marshes (6), permanent ponds (2), grass savanna (1), and tree savanna (1). Males were observed calling at night from grass and low shrubs mainly from 30 to 45 cm above the surface, though as low as 10 and as high as 60 cm.

One pair was caught in amplexus May 3, 1959 at 20 : 30 hours. The female (19,2 mm) laid non-pigmented ova. Thirty-one mature ova (1,2-1,5 mm) were removed from the left ovary of one female (20,6 mm).

Although we had worked suitable habitats as early as April 23, 1959, we did not hear males calling until May 3.

Range. — Known from Senegal (Mertens, 1938) and Sierra Leone (LOVERIDGE, 1956) to northeastern Congo.

Garamba localities and specimens : Cellule Biologique I (27), Cellule Biologique II (20), Mobaba (1), Moko (1), Nagero (3), Naluguambala (1), Ndelele (20), Pp Km 10 (1).

Hyperolius nasutus GÜNTHER.

(Fig. 48.)

Hyperolius nasutus GÜNTHER, 1864, Proc. Zool. Soc. London, **1864**, p. 483, pl. 33, fig. 3 — Duque de Bragança, Angola.

Hyperolius sagitta LAURENT, 1943, Ann. Mus. Congo Belge, Zool., Ser. 1, **4**, p. 72, figs. 5 and 6 — Kambo, Katanga Province, Congo.

LAURENT (1957) notes variability of *nasutus* and refers *adspersus* PETERS and *sagitta* LAURENT to this species with the recommendation that they be considered subspecies. However, the reasons for maintaining these as subspecies — more slender body, pigmentation — are not substantiated by comparison of specimens allocated by LAURENT to the forms *sagitta* (MCB 23567-8) and *nasutus* (CNHM 119563-648).

Males from Katanga Province (CNHM 109389, 109391-2, 109600) have the same secondary sex characters as those described below for the Garamba population.

Descriptive notes. — Adults less than 25 mm; habitus slender; snout acute, projecting; upper eyelid much narrower than interorbital space; tympanum present, obscured by skin; fingers webbed at base, web reaching basal subarticular tubercles of two outer fingers; fourth toe with two phalanges free of web, fifth with about 1-1/2; outer metatarsal tubercle present; skin almost transparent, lineae masculinae visible through it; skin of temporal region coarsely granular.

Color in life translucent green; in alcohol, pale straw color with numerous small melanophores on dorsal surface.

Secondary sex characters. — The dorsal surfaces of body and legs are covered with minute whitish asperities in males. Pink lineae masculinae are present along dorsal and ventral borders of the *M. obliquus externus* and are visible through the skin. Anteriorly the ventral linea is obscured by fibers of the *pars abdominis* of the *M. pectoralis*. In its posterior third the ventral linea is not superficially visible, being overlain by the *M. rectus abdominis*, which is very narrow transversely but thick dorso-ventrally.

Table 55. — **Monthly frequency of male** Hyperolius nasutus **with respect to development of secondary sex characters. Snout-vent lengths in parentheses.**

	Vocal sac absent	Vocal sac present				
	Gular pouch absent		Gular pouch intermediate	Gular pouch complete		
	Lineae masculinae absent			Lineae masculinae present		
	Dorsal asperities absent					Dorsal asperities present
January	3 (14,4–17,2)	—	2 (18,5)	—	—	—
February	1 (16,2)	—	1 (18,0)	—	—	—
April	1 (17,2)	2 (16,3–16,9)	4 (18,0–18,9)	1 (19,8)	—	4 (18,2–21,5)
May	1 (15,9)	6 (15,6–19,2)	2 (17,5–18,1)	5 (18,9–20,9)	4 (19,9–21,0)	15 (19,5–22,8)
June	—	—	—	—	—	25 (18,8–21,9)
July	—	—	—	—	3 (20,0–21,1)	19 (19,1–23,5)
August	—	—	—	—	5 (20,9–22,3)	20 (20,2–22,3)
September	—	—	—	—	—	25 (18,5–22,7)
October	1 (16,2)	—	—	—	2 (19,6)	6 (19,9–20,8)
November	—	—	—	—	—	2 (17,5–19,0)
December	3 (14,5–15,2)	—	—	—	—	—
Range	14,4–17,2	15,6–19,2	17,5–18,9	18,9–20,9	19,6–22,3	17,5–23,5
Mean	15,69 ± 0,33	17,41 ± 0,51	18,29 ± 0,14	19,72 ± 0,33	20,68 ± 0,23	20,85 ± 0,96

The gular pouch is thick and usually extends entirely across the intermandibular space. The slit-like vocal sac openings parallel the mandible and begin just behind the attachment of the tongue. The vocal sac develops before any of the secondary sex characters and is followed by the gular pouch, lineae masculinae, and dorsal asperities in that order (Table 55). The differences between mean snout-vent lengths of successive columns in Table 55 are statistically significant except for the differences between columns two and three and between five and six. The gradual increase in size from column to column suggests progression through successive ontogenetic stages and thus corresponds to the increasing development of the secondary sex characters. The difference between the snout-vent means of the last two columns is so slight that probably no difference in age is represented.

Table 56. — **Monthly frequency of female** Hyperolius nasutus **in various stages of development. Snout-vent lengths in parentheses.**

	Oviduct immature	Oviduct mature		
		Ova immature	Ova intermediate	Ova mature
January	4 (16,0–20,2)	3 (20,4–21,4)	—	—
February.	3 (15,3–19,3)	—	—	—
April	3 (15,9–17,7)	6 (18,6–20,1)	5 (20,0–22,4)	2 (19,7–22,0)
May	8 (15,3–18,6)	11 (18,9–22,2)	10 (19,6–22,7)	9 (20,4–22,3)
June	1 (18,1)	3 (20,4–20,9)	—	9 (20,8–22,4)
July	—	5 (20,4–23,2)	2 (21,2–22,4)	3 (21,2–22,3)
August	—	6 (20,0–22,0)	—	19 (20,2–23,2)
September	—	1 (18,8)	1 (21,6)	4 (20,1–22,0)
October	—	—	2 (21,4–22,3)	1 (22,1)
December	—	—	—	2 (18,0–21,4)
Range	15,3–20,2	18,6–23,2	19,6–22,7	18,0–23,2
Mean	16,98 ± 0,32	20,33 ± 0,17	21,15 ± 0,21	21,65 ± 0,13

The oviduct acquires the enlarged, convoluted form in females about 18,0 mm long, the size of the smallest female having enlarged, pigmented ova (Table 56). As there is slight but statistically significant increase in

size in each successive column of Table 56, the second column probably includes a larger proportion of newly matured females than the last two columns. Eleven of the females in the second column, one of those in the third column, and two of those in the last column are less than 20 mm long. If the individuals of the last columns in Tables 55 and 56 represent mature frogs, females are slightly but significantly larger than males (differences between means = 0,80 mm; $t = 4{,}938$; $P < 0{,}001$).

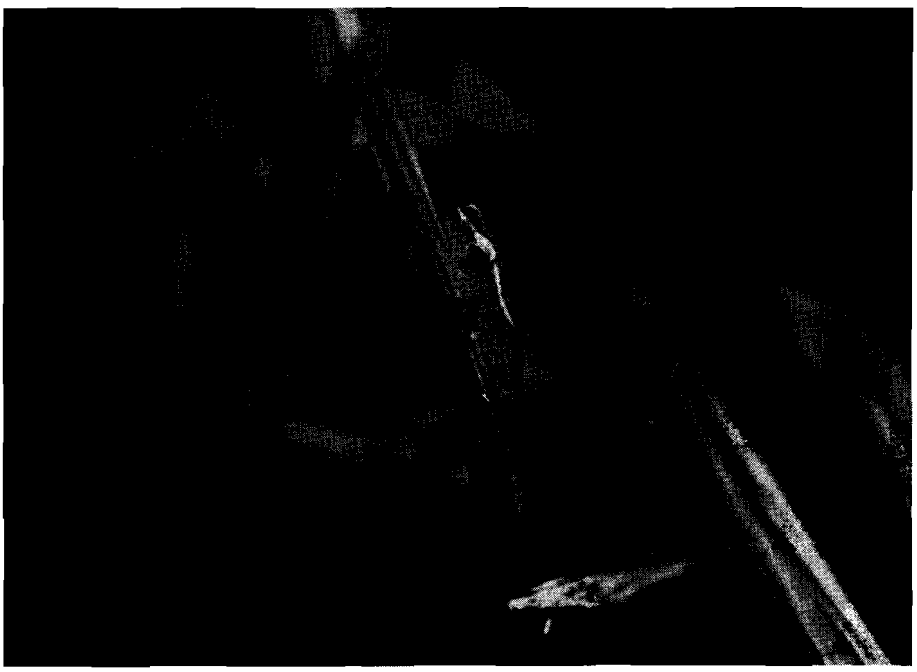


Photo: R. F. INGER.

FIG. 48. — *Hyperolius nasutus* in characteristic diurnal resting position.

Development. — Metamorphosis begins when the larvae have reached snout-vent lengths of about 9 mm. Eighteen metamorphosing juveniles (i.e., fore limbs erupted, larval oral appendages absent, at least a vestige of tail present) had snout-vent lengths of 8,8-11,0 mm. By the time a length of 9 to 11 is reached, metamorphosis is complete (Table 57). Males become sexually mature around 15.5 mm (Table 55) and females around 18,0 mm (Table 56).

Ecological notes. — *Hyperolius nasutus* lives in a variety of situations in the Parc de la Garamba but is most often found along small streams (Fig. 10) and grassy seepage areas in grass or shrub savanna

Table 57. — **Monthly size-frequency distribution of juveniles** (1) **of** Hyperolius nasutus **in the Parc National de la Garamba.**

	Number	Mm		Number	Mm
January	202	12,1–14,9	July	4	9,2–10,9
February	17	11,2–14,9	September	4	9,2–10,2
March	7	13,1–14,5	October	9	9,4–14,1
April	14	12,6–14,9	November	1	14,5
May	19	11,6–14,7	December	65	9,6–14,9
June	1	9,9			

(1) Males without vocal sacs; females without enlarged, convoluted oviducts; no vestige of tail.

Table 58. — **Habitat frequency distribution of** Hyperolius nasutus **in Parc National de la Garamba.**

	Dry season	Wet season	Total
Aquatic :			
Marsh	29	96	125
Pond	37	34	71
Grassy seepage	177	12	189
Stream side	93	218	311
Subtotal	336	360	696
Non-aquatic :			
Grass savanna	22	182	204
Shrub savanna	—	123	123
Tree savanna	—	19	19
Gallery forest	—	9	9
Subtotal	22	333	355

Photo: R. F. INGER.

FIG. 49. — *Hyperolius viridiflavus pachydermus.*

(Table 58). It seems to be much more rigidly confined to aquatic habitats during the dry season than during the wet season (April-October). It apparently does not utilize burrows for refuges during the dry season.

This frog by day usually perches on a blade of grass or the stalk of a Cyperacaea about 30 cm above ground (Fig. 48). Its translucent green color makes it difficult to find.

Judging by the condition of secondary sex characters in males and the development of ova in females (Table 59), the breeding period at this locality extends at least from May to September. Metamorphosing young were found in January (1), July (2), and September (15). The presence of one in January suggests breeding continues beyond September. The same impression is conveyed by the presence of juveniles smaller than 13 mm in almost every month of the year (Table 57).

Range. — The name *nasutus* has been applied to frogs from Cameroons (MERTENS, 1940) to Ethopia (PARKER, 1930) and south to Southern Rhodesia (FITZSIMONS, 1958). However, in view of the uncertainties of

Table 59. — **Monthly frequency distribution with respect to breeding competence of adult** Hyperolius nasutus **from the Parc National de la Garamba.**

	Males (1)		Females (2)		
	Dorsal asperities		Ova		
	present	absent	mature	intermediate	immature
January	—	—	—	—	3
April	4	—	2	5	6
May	15	4	9	10	11
June	25	—	9	—	3
July	19	3	3	3	5
August	20	5	19	—	6
September	25	—	4	1	1
October	6	2	1	2	—
November	2	—	—	—	—
December	—	—	2	—	—

(1) Males having completely developed gular pouches and lineae masculinae.

(2) Females having mature oviducts.

identifying species of *Hyperolius* from cryptic literature description, it is probably wiser to give a range based on specimens reported by LAURENT (1943b, 1950a, 1950b, 1957). The present specimens were compared with some identified by LAURENT as *nasutus*.

Northern Angola, Northern Rhodesia, and southern and eastern Congo.

Garamba localities and specimens : Cellule Biologique I (337); Cellule Biologique II (580); Bagbele-moke (31); Iso River (10); Moko (10); Morubia (5); Nambia near Nagero (11); Napokomweli (38); Ndelele (5); Otro River (6); Pp Km 62 (1).

Hyperolius concolor balfouri (WERNER).

Rappia balfouri WERNER, 1908, Sitzber. Akad. Wiss. Wien, **116** : p. 1904, pl. 4, fig. 15 — Gondokoro, Sudan.

Hyperolius concolor balfouri LAURENT, 1950, Explor. Parc Nat. Albert, Fasc. 64, p. 57, figs. 65-66.

Taxonomic notes. — The Garamba sample is identical to a series of 4 (CNHM 109262-5) from the Parc National Albert and identified by LAURENT (1950A). The species has been reported from Gangala na Bodio (LAURENT, 1946) on the southwestern edge of the Parc National de la Garamba and on its southcentral border at Faradje (NOBLE, 1924, as *H. nasutus* nec GÜNTHER) and on the Garamba River (NOBLE, *ibid.*).

The distinctive features of the pattern are narrow, dark dorsolateral stripes and the absence of light dorsolateral stripes in adults.

Descriptive notes. — Adults 23-37 mm; habitus moderate to stocky for the genus; snout obtusely pointed, projecting; upper eyelid about half of interorbital width; tympanum present, obscured by skin; fingers webbed at base, web reaching subarticular tubercles of outer fingers; fourth toe usually with two phalanges free of web, rarely more, fifth toe with one phalanx free; outer metatarsal tubercle present; ventral skin translucent, dorsal skin opaque; skin of temporal region scarcely, if at all, more granular than elsewhere dorsally; dorsum feebly granular.

Color in life sandy brown or olive above, usually with a dark dorsolateral stripe beginning behind eye, occasionally indicated on canthus by black spots; dorsum sometimes with a few small dark spots, never with red spots; venter usually white or pale yellow; anterior face of thigh, distal half of posterior face of thigh, inner face of lower leg, feet, and hands orange-red; vocal pouch pale cream. In alcohol brownish above, white below; dorsolateral dark stripe visible.

Secondary sex characters. — The dorsal surfaces of head, trunk, and limbs are covered with minute asperities in males. Pink lineae masculinae are present at dorsal and ventral borders of the obliquus muscle; the ventral band is overlain by the *p. abdominis* of the *M. pectoralis*.

The gular pouch is thick and does not occupy the entire intermandibular space. The slit-like vocal sac openings, beginning just behind the root of the tongue, run parallel to the mandible and are about one-half the length of the gape. The vocal sac begins its development before the other secondary sex characters and is followed by the gular pouch and lineae masculinae, and, finally, by the dorsal asperities (Table 60). The difference in snout-vent lengths of the frogs listed in the first and fourth columns is strong evidence of age difference between these two groups. The absence of vocal sacs in the smaller group is probably explained by age rather than by regression.

Table 60. — **Monthly frequency with respect to development of secondary sex characters of male** Hyperolius concolor balfouri **from the Parc National de la Garamba. Snout-vent lengths in parentheses.**

	Vocal sac absent	Vocal sac present		
	Gular pouch absent		Gular pouch present	
	Lineae masculinae absent		Lineae masculinae present	
	Dorsal asperities absent			Dorsal asperities present
January	5 (18,9–21,2)	—	—	—
February	—	—	1 (28,9)	1 (24,4)
March	6 (18,9–23,0)	—	—	—
April	2 (20,9–22,5)	2 (22,1–24,3)	—	25 (26,0–29,6)
May	—	—	—	25 (24,8–29,4)
June	—	—	—	11 (26,4–29,4)
July	—	—	—	1 (24,3)
August	—	—	—	2 (28,5–29,6)
September	—	—	1 (23,7)	2 (23,5–24,2)
November	5 (20,3–23,3)	—	—	—
December	3 (21,7–23,1)	—	—	—
Range	18,9–23,3	22,1–24,3	23,7–28,9	23,5–29,6
Mean	21,15 ± 0,29	23,2	26,3	26,29 ± 0,16

Oviducts achieve the enlarged, convoluted, adult form in females of about 26-29 mm (column two of Table 61). The difference in snout-vent lengths of the females in the second and fourth columns of Table 61 probably results from a greater proportion of newly mature females in the second column.

Adult females (i.e., those of last three columns ot Table 61) are distinctly larger than adult males (last three columns of Table 60).

Ecological notes. — Though *Hyperolius concolor balfouri* occurs in a variety of situations in the Parc National de la Garamba (Table 62), it

Table 61. — **Monthly frequency with respect to stage of development of female** Hyperolius concolor balfouri **from the Parc National de la Garamba.**

	Oviduct immature	Oviduct mature		
		Ova immature	Ova intermediate	Ova mature
January	5 (21,1–24,8)	—	—	—
February	1 (26,7)	2 (31,2–36,1)	1 (37,7)	2 (34,3–37,4)
March	3 (22,2–29,3)	9 (28,6–34,2)	—	—
April	1 (27,2)	12 (26,1–36,1)	—	6 (31,6–36,2)
May	—	3 (29,5–34,7)	—	4 (29,6–35,7)
June	—	—	1 (34,0)	1 (33,8)
July	3 (29,8–31,4)	1 (30,4)	1 (31,6)	4 (31,2–33,8)
August	—	—	—	1 (33,2)
September	—	1 (36,9)	—	—
October	2 (23,6–28,4)	—	—	—
November	3 (23,3–24,8)	—	—	—
December	3 (21,7–24,7)	—	—	—
Range	21,1–31,4	26,1–36,9	31,6–37,7	29,6–37,4
Mean	25,37 ± 0,68	32,38 ± 0,49	34,4	34,08 ± 0,38

clearly avoids shallow trickles of water (grassy seepages), in contrast to *H. nasutus*, and rarely enters gallery forests. One specimen was caught while hopping across a large camp clearing in midday; several were caught in houses and one was found under the hood of an automobile.

In the Parc National de la Garamba, *balfouri* is distinctly a savanna form. LAURENT (1950A) notes that it penetrates the rain forest belt but is more characteristics of the savanna; some of the localities LAURENT (1943A) cites are deep in the forest zone. Considering the association of *balfouri* with human habitation (see above), its occurrence in the forest zone may indicate that it, like *Bufo regularis*, follows man as he destroys the forest.

Males call from the water's surface or while perching on grass or small shrubs at the water's edge and as high as 45 cm above the ground. Six were observed between 10 and 45 cm above ground and 23 between the water's surface and 10 cm above ground.

Table 62. — **Habitat-frequency distribution of** Hyperolius concolor balfouri **in Parc National de la Garamba.**

	Dry season	Wet season	Total
Aquatic :			
Marsh	2	64	66
Pond	1	18	19
Grassy seepage	1	—	1
Stream side	24	29	53
Subtotal	28	111	139
Non-aquatic :			
Grass savanna	2	8	10
Shrub savanna	—	3	3
Tree savanna	5	6	11
Gallery forest	—	—	—
Subtotal	7	17	24

In 1959 males were first seen calling on April 15. Virtually all adult males collected April through September have completely developed secondary sex characters (Table 60). The proportion of adult females with ripe ova appears somewhat higher in the period May-July than in April (Table 61), but the numbers available are too small for reliance. A female caught April 15 and kept with two males in a plastic bag deposited ova having a darkly pigmented hemisphere.

Range. — The Sudan, Ubangi-Shari, Kasai, and northeastern Congo.

Garamba localities and specimens : Cellule Biologique I (80); Cellule Biologique II (29); Akam (1); Beredwà (22); Buluku (7); Inimvua (1); Iso River (1); Km 17 S. of Bagbele (10); Mabanga (1); Makpe (5); Morubia (1); Nagero (9); Ndelele (3); Pp. Km 10 (1); Pp Km 55 (3).

Hyperolius viridiflavus pachydermus (WERNER).

(Fig. 49.)

Rappia pachyderma WERNER, 1908, Sitzber. Akad. Wiss. Wien, **116** : p. 1903 — Gondokoro, Sudan.

Hyperolius viridiflavus pachydermus LAURENT, 1951, Ann. Soc. Roy. Zool. Belg., **82** : p. 392.

Rappia burgeoni WITTE, 1921, Rev. Zool. Afr., **9** : p. 19, pl. 5, fig. 2 — Medje, Congo.

Taxonomic notes. — Juveniles (e.g., IPN 1932A) identical to the types of *pachydermus* and *burgeoni* in color patterns are included in the Garamba collections. Some of the juveniles have the mid-dorsal dark stripe figured by DE WITTE (1921) and others lack it, as in the type of *pachydermus* (WERNER, 1908). A few males retain the latter type of juvenile pattern, a characteristic noted by LAURENT (1946). Despite the extensive variation in pigmentation (see below), the Garamba specimens all have thick skin (mentioned by WERNER, op. cit.); small, but conspicuous, scattered, dorsal tubercles; outer fingers webbed to the subarticular tubercles; no outer metatarsal tubercle; and usually red spots on the back and on the venter when alive. The thigh, referred to as colorless by WERNER, is purplish red in life.

The ventral skin is almost opaque, presumably because of a layer of guanophores, and as a result the deep red lineae masculinae are not visible through the skin as they are in males of other Garamba species (e.g., *balfouri*, *schoutedeni*, etc.).

The green dorsal coloration, noted by LAURENT (op. cit.) as a characteristic of adults of this form, was not observed in any of the numerous specimens I saw in the field.

Descriptive notes. — Adults 22-31 mm; habitus stocky; snout obtusely pointed to truncate, projecting in profile; upper eyelid about two-thirds of interorbital width; tympanum present, obscured by skin; inner fingers webbed at base, web between two outer fingers reaching subarticular tubercles (i.e., about half webbed); fourth toe with two phalanges free of web; fifth toe with one phalanx free; usually no outer metatarsal tubercle; skin usually opaque; skin of temporal region not conspicuously granulate; small but distinct tubercles scattered over back, all ages and sexes have a transverse gular fold, which in adult males is incorporated into the gular pouch.

Color in life brownish gray or dark brown above with red dots on the dorsal tubercles; a broad blackish band on side from eye to groin, present or absent; ventral surfaces white or lemon yellow, usually with red dots; gular pouch of males often with black dusting; hidden surfaces of legs, hands, and feet purplish red.

Table 63. — **Monthly frequency of male** Hyperolius viridiflavus pachydermus **with respect to development of secondary sex characters. Snout-vent lengths in parentheses.**

	Vocal sac absent	Vocal sac present			
	Gular pouch absent		Gular pouch incomplete	Gular pouch complete	
	Lineae masculinae absent				Lineae masculinae present
January	4 (16,5–17,6)	—	—	—	1 (24,0)
March	—	—	1 (23,2)	—	22 (23,7–27,5)
April	1 (19,2)	—	3 (20,0–23,9)	—	25 (23,6–27,5)
May	—	3 (20,0–22,6)	3 (21,7–25,2)	—	25 (22,2–28,8)
June	—	—	1 (23,9)	—	25 (22,9–29,2)
July	—	2 (19,5–23,1)	1 (26,4)	—	25 (24,8–29,2)
August	—	—	—	1 (23,6)	24 (23,1–29,6)
September	—	—	—	—	19 (22,3–29,9)
October	—	—	—	1 (23,3)	11 (20,8–25,9)
November	—	—	—	—	25 (22,3–28,0)
December	5 (15,7–20,4)	1 (21,6)	1 (21,8)	1 (23,3)	3 (23,0–25,0)
Total number	10	6	10	3	205
Range	15,7–20,4	19,5–23,1	20,0–26,4	23,3–23,6	20,8–29,9
Mean	18,01	21,53 ± 0,60	23,11 ± 0,64	23,40	25,92 ± 0,33

In alcohol color faded but red dots on dorsum and venter usually visible; hidden surfaces of legs pale pinkish brown; often a dark network enclosing large pale brown spots on back; juveniles often with a broad, dark, mid-dorsal band.

In both adults and juveniles the dorsal pigmentation covers the exposed surfaces of the legs and extends on the fourth and fifth toes. The three inner toes are completely free of melanophores.

Secondary sex characters. — Deep red lineae masculinae are present along dorsal and ventral edges of the *M. obliquus externus*. Anter-

Table 64. — **Monthly frequency of female** Hyperolius viridiflavus pachydermus **with respect to developmental stages. Snout-vent lengths in parentheses.**

	Oviduct immature	Oviduct mature		
		Ova immature	Ova intermediate	Ova mature
January	1 (18,1)	3 (26,1–27,1)	1 (27,2)	—
February	1 (22,3)	—	—	—
March	6 (19,2–24,7)	—	2 (27,4–28,6)	2 (26,2–29,8)
April	7 (16,2–25,6)	4 (26,5–30,8)	1 (24,2)	14 (25,3–28,8)
May	4 (19,9–25,4)	8 (25,1–28,4)	6 (22,8–29,3)	12 (22,0–31,2)
June	1 (23,2)	1 (23,0)	3 (25,3–28,9)	2 (27,0–28,4)
July	4 (20,6–22,5)	1 (26,1)	3 (26,2–26,8)	7 (27,4–29,6)
August	1 (17,5)	2 (27,6–29,0)	2 (25,8–26,9)	4 (28,2–31,4)
September	—	2 (24,2–29,0)	1 (28,2)	3 (27,9–29,4)
October	2 (19,6–21,8)	—	—	2 (27,3–29,9)
November	1 (18,5)	1 (25,6)	—	1 (25,9)
December	8 (16,0–21,5)	—	—	1 (24,0)
Total number. ...	36	22	19	48
Range	16,0–25,6	23,0–30,8	22,8–29,3	22,0–31,4
Mean	20,72 ± 0,43	26,69 ± 0,36	26,50 ± 0,38	27,77 ± 0,24

iorly the ventral lineae is overlain by fibers of the *pars abdominis* of *M. pectoralis* as in *H. concolor balfouri.*

The gular pouch is broad, filling the space between the mandibles. The transverse, posterior fold is very deep, and the reflected inner margin reaches forward to the level of the center of the pupil. In none of the other Garamba *Hyperolius* does the reflected posterior margin of the pouch extend forward beyond the level of the posterior margin of the eye.

The slit-like vocal sac openings parallel the mandibles and begin just behind the attachment of the tongue. As Table 63 shows, the vocal sacs develop first, then the gular pouch, and finally, the lineae masculinae. The mean snout-vent length of males in the last column of Table 63 is signifi-

Table 65. — **Size-frequency distribution with respect to development of metamorphosing** Hyperolius viridiflavus pachydermus **from the Parc National de la Garamba.**

Extent of gape	Tail length (mm)					Number	Snout-vent	
	10,1 and +	5,1–10,0	2,1–5,0	0,5–2,0	Absent		Range	Mean
Between nostril and eye	2 (12,7–13,0)	1 (13,2)	—	—	—	3	12,7–13,2	12,96
To front border of eye	1 (12,8)	—	1 (12,2)	—	—	2	12,2–12,8	12,50
To below pupil ...	1 (15,2)	2 (13,6–16,2)	11 (11,9–15,3)	1 (13,0)	—	15	11,9–16,2	13,69
To rear border of eye	—	—	3 (13,3–14,3)	3 (11,6–14,4)	9 (11,9–15,6)	15	11,6–15,6	13,96
Number	4	3	15	4	9	—	—	—
Snout-vent range ...	12,7–15,2	13,2–16,2	11,9–15,3	11,6–14,4	11,9–15,6	—	—	—
Mean	13,56	14,33	13,30	12,77	14,45	—	—	—

cantly larger ($t>3,0$; $P<0,01$) than the means of the other columns suggesting that the difference in condition of the secondary sex characters between the last column and the others is a product of ontogenetic change rather than the result of seasonal regression of these structures.

The oviduct assumes the enlarged, convoluted shape of maturity when females are about 23-25 mm long (Table 64). The proportion of newly matured females is probably larger in the second and third columns than in the fourth as the mean snout-vent length of females in the last column is significantly larger ($t>2,5$; $P<0,02$) than those of the other columns. Letting the frogs of the last columns of Tables 63 and 64 represent fully mature individuals, females are slightly but statistically significantly larger than males ($t=4,5$; $P<0,001$).

Larvae and development. — Numerous series agreeing with the description of larval *viridiflavus* (LAMOTTE and PERRET, 1963) were collected at various places in the park. These tadpoles have one row of teeth on the upper lip and three rows on the lower. The outermost lower row is very short; all rows of teeth are continuous except for the inner-most lower row in some individuals. The beaks have a narrow black margin. Both body and tail are spotted.

Characters of the oral disk are shared by other species of *Hyperolius* (for examples, see LAMOTTE and PERRET, 1963). Identification of these tadpoles as *viridiflavus* is based mainly on coloration and size. Tadpoles of two smaller species of *Hyperolius*, *H. nasutus* and *H. schoutedeni*, are smaller having head plus body lengths of less than 12 mm as compared to 11,5-16 mm in *viridiflavus* (Table 65). According to SCHIØTZ (1963), tadpoles of *H. concolor* have a dark stripe on the tail, a character absent in the present series.

Metamorphosis begins when the frogs are about 11-15 mm long (Table 65). Correlation between the degree of tail resorption and growth of the mouth is close though correlation of either character with snout-vent length is not. Males become sexually mature at about 22 mm (Table 63), females at about 24 mm (Table 64).

Ecological notes. — *Hyperolius viridiflavus pachydermus* occupies many types of habitats (Table 66) but is most often found on vegetation in marshes (Fig. 14) and along small, slowly-moving streams (Fig. 10). The proportion found away from the vicinity of water did not change from wet season to dry season. Calling males perch on grass or shrubs emerging from water or at the water's edge 30 to 150 cm above the surface. Most larval series were collected in marshes (6 lots) or marshy borders of small streams (6). Two lots were obtained in small permanent ponds.

Table 66. — **Habitat-frequency distribution of** Hyperolius viridiflavus pachydermus **in the Parc National de la Garamba.**

	Dry season	Wet season	Total
Aquatic (1) :			
Marsh	35	113	148
Pond	23	36	59
Grassy seepage	5	45	50
Stream side	42	174	216
Subtotal	105	368	473
Non-aquatic :			
Grass savanna	19	63	82
Shrub savanna	1	19	20
Tree savanna	5	3	8
Gallery forest	2	—	2
Subtotal	27	85	112

(1) None were recorded as actually having been found in water. Rather they were found on emergent or riparian vegetation.

The proportion of adult females containing mature or nearly mature ova remains high from April through September (Table 64), suggesting a breeding season roughly coincident with the wet season (April through October). Choruses of males were heard in March, April, and May, 1959. Larvae were collected in all months except January, April, and June.

If breeding starts in March just before the heavy rains begin and continues well into the wet season, one should expect many metamorphosing and juvenile individuals in the monthly samples at least in June and subsequent months. However, this expectation is not satisfied (Table 67). Perhaps collecting bias, introduced because the small size of juveniles makes them difficult to find, is responsible for the low proportions of juveniles in April-November. This explanation does not seem reasonable as both the absolute and relative numbers of juveniles in January and December are higher than in any of the rainy months. On the other hand, sixty per cent (14) of the larval series were obtained July-September, which is to be expected if breeding starts in April or May.

Table 67. — **Monthly age-frequency distribution of** Hyperolius viridiflavus pachydermus **in the Parc National de la Garamba.**

Month	Metamorphants (1)	Juveniles (2)	Adults	Total
January	0,38	0,34	0,28	32
February	0,92	0,08	—	11
March	0,03	0,18	0,79	39
April	0,03	0,08	0,89	112
May	—	0,03	0,97	122
June	0,02	0,02	0,96	42
July	0,12	0,05	0,83	102
August	—	0,03	0,97	40
September	0,07	—	0,93	28
October	—	0,06	0,94	31
November	—	0,03	0,97	31
December	0,04	0,65	0,31	23

(1) Forelimbs erupted, at least a vestige of tail remaining.

(2) Individuals without vestige of tails; males without vocal sacs, females without mature oviducts.

Range. — The distribution of *H. viridiflavus pachydermus* as given by LAURENT (1961) is southeastern Sudan, northern Congo, northern Uganda, and western Kenya.

Garamba localities and specimens : Cellule Biologique I (108); Cellule Biologique II (337); Bamangwa (1); Beredwa (13); Gangala na Bodio (1); Iso River (1); Km 17 S. of Bagbele (5); Mabanga (1); Makpe (2); Mobaba (24); Moko River (13); Morubia (6); Nabakoyo (13); 3 km west of Nagero (18); Napukumwali (12); Ndelele (40); Pp Km 10 (1); Pp Km 55 (1); Tori (1); Utukuru (15).

Hyperolius cinnamomeoventris cinnamomeoventris BOCAGE.

(Fig. 50.)

Hyperolius cinnamomeoventris BOCAGE, 1866 Jour. Acad. Sci. Lisbonne, **1** : pp. 55, 75 — Duque de Bragança, Angola.

Hyperolius cinnamomeoventris cinnamomeoventris LAURENT, 1943 Ann. Mus. Congo Belge, Zool., **4** : p. 78.

Taxonomic notes. — The coloration of the Garamba sample agrees with that of the typical form (LAURENT, 1943A), but differs from those of *c. olivaceus* BUCHHOLZ and PETERS (LAURENT, 1943A) and *c. wittei* LAURENT (1967).

Descriptive notes. — Adult males less than 25 mm, females 19-27 mm; habitus moderately slender; snout obtusely pointed, projecting slightly in profile; upper eyelid about two-thirds of interorbital width; tympanum present, obscured by skin; fingers without webbing; fourth toe with two phalanges free of web, fifth toe with one phalanx free; outer metatarsal tubercle feebly developed or not visible; skin translucent; skin of temporal region smooth dorsally, granulate ventrally; skin of back smooth or with low rounded tubercles; females and juveniles without transverse gular fold.

Color in life of males green, yellow-green, olive, or reddish brown above; a golden dorsolateral stripe from nostrils to groin, obscured on snout of some individuals; dorsolateral stripe bordered with narrow dark brown streak; no ventrolateral stripe; venter whitish; gular pouch usually lemon yellow; anterior face of thigh orange-red, rear of thigh with orange-red spot; no red on hands or feet.

Females bright green above and laterally; no dorsolateral stripe; a black line on snout below canthus; a wavy black ventrolateral stripe beginning at rictus and extending to groin; venter whitish; red on thigh as in male; no red on hands or feet.

Juveniles colored as males except for throats, which are white.

In alcohol both sexes brown or gray above; males often with obscure dark spots dorsally; dorsolateral stripes of males and juveniles remain visible; ventrolateral stripes of females visible; dorsal surfaces of all toes with a dusting of chromatophores.

Secondary sex characters. — Pink lineae masculinae are present along dorsal and ventral borders of the *M. obliquus externus*. Anteriorly the line is overlaid by fibers of the *M. pectoralis* as in *Hyperolius concolor* and *H. viridiflavus*.

The thickened portion of the male's gular pouch is narrower than the space between the mandibles. The transverse posterior fold of the pouch is relatively shallow. The vocal sac openings are slit-like as in other species of *Hyperolius*.

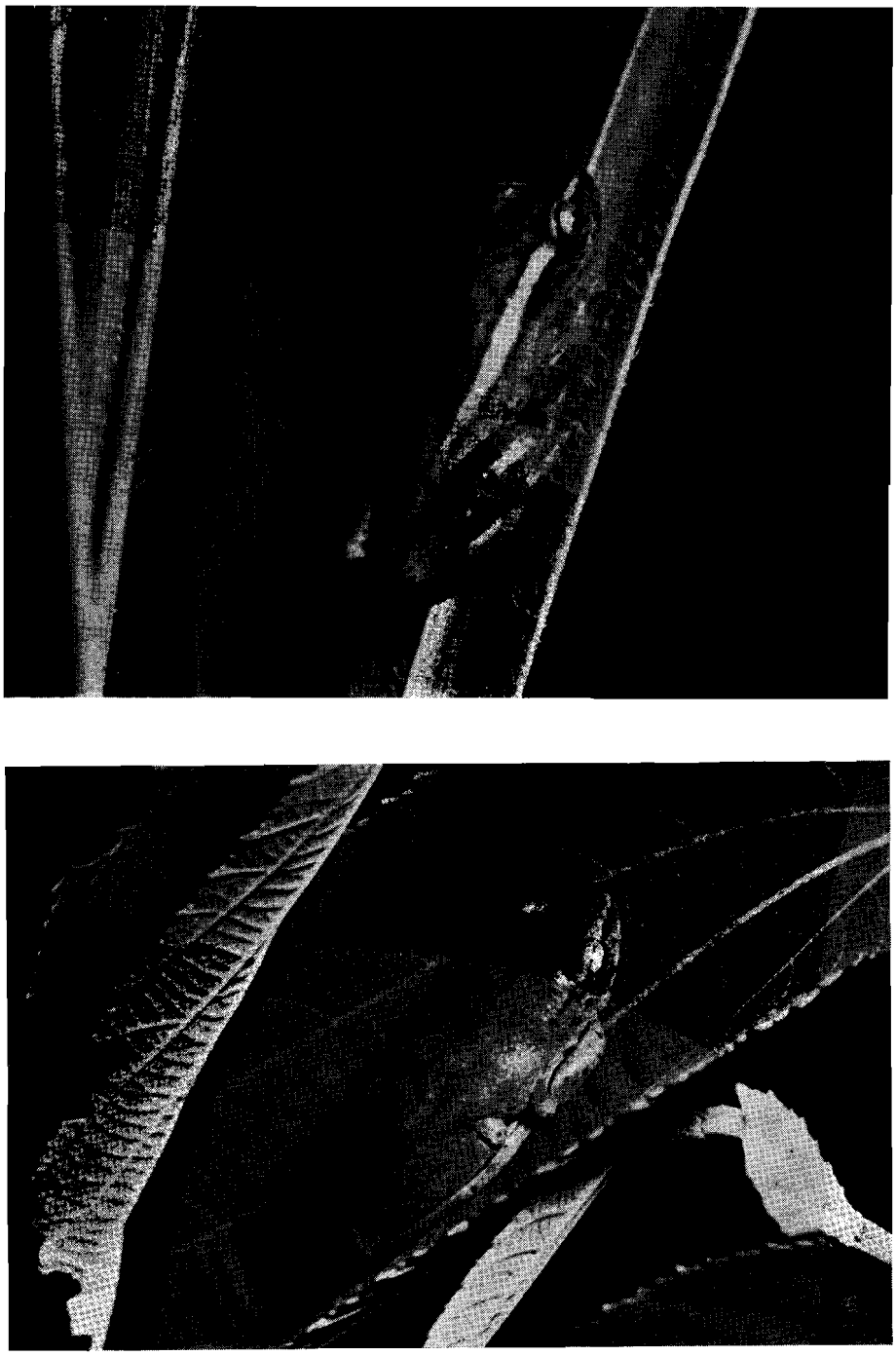


Photo: R. F. INGER.

FIG. 50. — Sex dimorphism in *Hyperolius c. cinnamomeoventris*.
Top : Male; Bottom : Female.

Table 68. — **Monthly frequency with respect to snout-vent lengths (mm.) of adult** Hyperolius cinnamomeoventris **from the Parc National de la Garamba.**

	Males (1)			Females (2)	
	Number	Snout-vent		Number	Snout-vent
		Range	Mean		Mean
January	24	15,7–19,4	17,53 ± 0,20	—	—
March	25	15,4–20,5	17,38 ± 0,23	14	22,90 ± 0,32
April	25	16,0–19,1	17,73 ± 0,18	2	21,60
May	25	15,5–19,3	17,27 ± 0,18	15	22,94 ± 0,27
June	25	16,5–21,5	19,23 ± 0,23	6	22,33 ± 0,41
July	25	19,5–22,3	20,65 ± 0,13	13	25,20 ± 0,23
August	25	18,0–22,2	19,17 ± 0,21	7	24,38 ± 0,60
September	25	16,9–21,9	18,78 ± 0,22	11	23,71 ± 0,48
October	11	17,2–23,0	18,90 ± 0,48	3	23,03
November	25	16,9–20,5	18,59 ± 0,23	1	23,20
December	7	17,4–20,2	18,94 ± 0,39	3	22,27
Total ...	242	15,4–23,0	18,52 ± 0,09	75	23,47 ± 0,19

	Analysis of variance ♂♂			Analysis of variance ♀♀		
	Sum of squares	Number	Mean of squares	Sum of squares	Number	Mean of squares
Within months	250,27	231	1,08	115,27	65	1,77
Between months ...	251,18	10	25,12	73,79	9	8,19
	F=23,26	P<0,001		F=4,62	P<0,001	

(1) All have vocal sacs, completely developed gular pouches, and lineae masculinae.

(2) All have enlarged ova.

The vocal sac openings develop before the gular pouch and lineae masculinae. Four males having vocal sacs and gular pouches lack lineae masculinae.

Besides the dimorphism in coloration (see description above), the sexes differ in size (Table 68). Although the ranges of snout-vent lengths overlap, the mean of adult females is significantly larger than that of adult males.

Development. — Metamorphosis is complete when the frogs are about 12 mm snout to vent. At that time both sexes have light dorsolateral stripes. In females these stripes disappear as the oviducts acquire the convoluted, swollen condition associated with maturity; maturation of the oviduct occurs when females reach the size range 18-20 mm (Table 69). Disappearance of the stripes begins posteriorly. Simultaneously or slightly

Table 69. — **Monthly frequency of female** Hyperolius cinnamomeoventris **with respect to developmental stages. Snout-vent lengths in parentheses.**

	Oviduct immature	Oviduct mature		
		Ova immature	Ova intermediate	Ova mature
January	1 (16,6)	5 (19,7–23,0)	1 (24,7)	—
March	—	9 (19,0–23,7)	2 (21,5–22,4)	14 (21,2–24,6)
April	10 (14,9–19,6)	20 (18,3–21,4)	3 (19,6–22,0)	2 (20,0–23,2)
May	—	4 (20,5–23,8)	6 (20,6–24,2)	15 (21,8–24,9)
June	—	14 (20,1–24,5)	5 (21,5–24,9)	6 (21,0–23,8)
July	—	7 (21,5–26,1)	5 (23,8–26,4)	13 (23,7–26,6)
August	—	11 (22,2–25,4)	7 (21,7–24,9)	7 (22,9–26,8)
September	—	4 (20,1–25,2)	3 (20,1–24,6)	11 (21,6–24,9)
October	1 (19,4)	2 (22,7–25,8)	2 (23,4–25,1)	3 (19,3–25,3)
November	2 (16,8–18,7)	3 (20,9–24,5)	2 (22,1–25,1)	1 (23,2)
December	3 (15,2–18,8)	—	1 (23,4)	3 (21,8–22,6)
Total number	17	79	37	75
Range	14,9–19,6	18,3–26,1	19,6–26,4	19,3–27,3
Mean	17,43 ± 0,38	21,79 ± 0,21	23,12 ± 0,28	23,47 ± 0,19

earlier the dark ventrolateral stripe develops. The color changes usually occur when the females are between 16 and 20 mm, though the transformation of pattern was still going on in a few larger ones (Table 70). The remaining 191 mature females examined (Table 69) had the modified coloration described above (p. 155).

Males become mature, that is, have completely developed secondary sex characters when about 15,5 mm long (Table 68).

Table 70. — **Transformation of color pattern in maturing females of** Hyperolius cinnamomeoventris **from the Parc National de la Garamba.**

Snout-vent	Oviduct	Dorsolateral stripe	Ventrolateral stripe
14,9	Immature	Complete	Absent
15,2	Immature	Complete	Absent
15,4	Immature	Complete	Absent
16,4	Immature	Complete	Absent
16,5	Immature	Complete	Absent
16,6	Immature	Complete	Absent
16,8	Immature	Complete	Absent
16,8	Immature	Complete	Absent
17,0	Immature	Complete	Faint
17,5	Immature	Complete	Faint
17,8	Immature	Complete	Faint
18,7	Immature	Complete	Absent
18,8	Immature	Complete	Faint
19,4	Immature	Complete	Absent
19,5	Immature	Complete	Absent
19,6	Immature	Complete	Absent
16,8	Mature	Anteriorly	Complete
18,3	Mature	Anteriorly	Complete
19,4	Mature	Faint	Complete
22,5	Mature	Anteriorly	Complete
22,6	Mature	Anteriorly	Complete

Snout-vent lengths of both sexes vary slightly but significantly from month to month. As within each sex the monthly means prescribe a more or less regular progression with coinciding peaks, the data suggest an age progression in the adult population based on a one-year life span. This explanation of the pattern requires that reproduction be limited to a relatively narrow interval, a condition not fulfilled by the distribution of gravid females (Table 68).

Ecological notes. — This species, though found in a variety of situations (Table 71), is clearly most abundant in marshes and along small streams. As 6,322 of the 9,152 listed from « stream side » were caught in the marshy ground that borders many small savanna streams (e.g., Fig. 10) in the Garamba park, it would be fair to say that *cinnamomeoventris* characteristically occurs in marshy terrain. Less than 6 per cent of the total collection were caught at any distance from water.

Table 71. — **Habitat-frequency distribution of** Hyperolius cinnamomeoventris **in the Parc National de la Garamba.**

	Dry season	Wet season	Total
Aquatic :			
Marsh	193	1.309	1.502
Pond	216	63	279
Grassy seepage	402	900	1.302
Stream side	740	8.412	9.152
Subtotal	1.551	10.684	12.235
Non-aquatic :			
Grass savanna	6	601	607
Shrub savanna	—	7	7
Gallery forest	8	2	10
Subtotal	14	610	624

Usually *cinnamomeoventris* was seen low (within 45 cm ot the surface) on grass or other vegetation emerging from water or at the edge of small bodies of water.

The proportion of adult females containing enlarged ova fluctuates almost regularly from month (Table 69). None were found in January or February, which are dry months; after that the monthly sequence of percentages with

enlarged ova is 56, 8, 60, 24, 52, 28, 61, 43, 17, 75. This alternation between high and low percentages suggests bimonthly pulses of breeding activity beginning in March (or at the end of March) and almost every other month thereafter.

Males having fully developed secondary sex characters were found in every month except February. However, as these sex characetrs — vocal sacs, gular pouches, lineae masculinae — are not known to undergo cyclic regression, they are not indicators of testicular activity, or of breeding activity.

Range. — The nominate form is now known from northern Angola (BOCAGE, 1866) and throughout the Congo except for Katanga Province (LAURENT, 1943A, 1950A).

Garamba localities and specimens : Cellule Biologique I (72); Cellule Biologique II (12,018); Beredwa (35); Biadimbi (11); Buluku (28); tributary of Dungu River (3): Duru (2); Inimvua (14); Iso River (23); Kalikimvua (19); Makpe (94); Mobaba (110); Moko (1); Morubia (22); Mount Moyo (5); Nabakoyo (21); 3 km west of Nagero (18); Naluguambala (3); Namologbia (1); Napokomweli (2); Ndelele (53); Pali (23); PFS Km 21 (7); Pidigala (1); Pp Km 10 (3); Pp Km 55 (61); Pp Km 56 (1); Utukuru (192).

Hyperolius schoutedeni LAURENT.

Hyperolius schoutedeni LAURENT, 1943, Ann. Mus. Congo Belge, Zool., Ser. 1, **4** : p. 86, fig. 10 — Kunungu, Congo.

Taxonomic notes. — Though originally described from a specimen taken along the middle Congo, the species has since been taken in the Uele district of Province Orientale (LAURENT, 1946). Specimens (CNHM 109287-90) of the latter collection are at hand to confirm the identification of the Garamba sample.

Two species of *Hyperolius* from the Garamba have dorsolateral light stripes as adults. Only one, *schoutedeni* of, the two retains the stripes in adults of both sexes. Females of the other (*cinnamomeoventris*) lose the dorsolateral light stripe and acquire a ventrolateral dark one when they reach 20 mm. Adult females of *schoutedeni* often exceed 25 mm and are usually larger than females of *cinnamomeoventris;* males of the two species show analogous size differences.

The pattern on the dorsal surface of the tibia of *schoutedeni* (males and females) consists of two dark longitudinal lines that may be interrupted; frequently the space between these lines is also dark, forming a broad stripe. In *cinnamomeoventris* this surface may bear small black spots or not; in a small proportion of individuals the spots are arranged in rows but they never form stripes. Both species have red pigment (in life) on the anterior

Table 72. — **Monthly frequency of male** Hyperolius schoutedeni **with respect to development of secondary sex characters. Snout-vent lengths (mm.) in parentheses.**

	Vocal sac absent	Vocal sac present				
	Gular pouch absent		Gular pouch intermediate		Gular pouch complete	
	Lineae masculinae absent			Lineae masculinae present		
	Dorsal asperities absent					Dorsal asperities present
January	1 (17,0)	—	—	1 (19,9)	—	—
February	1 (16,4)	—	—	—	—	—
March	5 (16,0–17,7)	—	—	3 (19,0–21,0)	2 (20,9–22,1)	6 (18,8–22,0)
April	9 (16,9–19,4)	—	20 (16,9–21,1)	1 (20,3)	6 (18,5–20,4)	4 (18,7–21,6)
May	1 (16,0)	2 (15,0–17,6)	8 (16,2–20,0)	2 (18,8)	5 (19,5–22,4)	20 (18,4–23,4)
June	—	—	—	—	4 (18,6–21,4)	21 (18,2–22,0)
July	—	—	—	—	5 (19,1–21,9)	20 (17,9–21,5)
August	—	—	—	—	1 (21,8)	9 (18,0–23,8)
September	—	—	—	—	1 (19,8)	24 (18,9–21,6)
October	—	—	—	—	6 (18,9–21,9)	13 (18,6–21,6)
November	—	—	—	—	1 (20,0)	2 (20,3–20,6)
December	2 (16,4–16,7)	—	—	—	—	—
Range	16,0–19,4	15,0–17,6	16,2–21,1	18,8–21,0	18,5–22,4	17,9–23,8
Total number ...	19	2	28	7	31	120
Mean	17,19 ± 0,23	16,3	18,78 ± 0,23	19,70 ± 0,33	20,32 ± 0,20	20,27 ± 0,11

face of the thigh; the same pigment often forms a large round spot on the dorsal surface of the foot only in *schoutedeni*.

Descriptive notes. — Adult males less than 25 mm, females 21-28 mm; habitus slender to moderate; snout pointed, projecting; upper eyelid about half the width of interorbital space; tympanum present, hidden beneath skin; fingers with very narrow webbing at bases; fourth toe with 2 1/4 — 2 1/3 phalanges free of broad web, fifth with 1 free; outer metatarsal tubercle present or absent; dorsal skin opaque, ventral skin weakly translucent; skin of temporal region weakly granular; dorsal skin smooth except for paravertebral rows of weak tubercles; ventral skin coarsely granular.

Color in alcohol grayish brown or purplish brown above with a broad, dark-edged, light dorsolateral stripe from snout to groin; often a pale vertebral stripe bordered by a row of black spots covering row of low tubercles; tibia with a pair of dark longitudinal lines or a broad, dark, longitudinal stripe; ventral surfaces of body and limbs whitish, usually densely punctate with dark pigment, posterior face of thigh and dorsal surfaces of all toes densely spotted with black; anterior face of thigh pink, many individuals with a circular spot of pink on posterior face of thigh and on dorsal surface of metatarsal.

Secondary sex characters. — Males have pink lineae masculinae at dorsal and ventral borders of the oblique muscle. The dorsal surfaces of head and trunk are covered with minute, white asperities in males.

The gular pouch is thick and occupies the entire intermandibular space. The slit-like vocal sacs are about half the length of the gape. As in other species of *Hyperolius*, the vocal sacs develop before the other secondary sex characters, to be followed by the gular pouch, lineae masculinae, and the dorsal asperities (Table 72).

Oviducts acquire the enlarged, convoluted adult form in females around 19,5 mm (second column of Table 73).

Adult females (last three columns of Table 73) are distinctly larger than adult males (last two columns of Table 72).

Larvae and development. — A complete developmental series of tadpoles from early limb bud stages to metamorphosis is assignable to *H. schoutedeni*. All individuals have numerous, thin, dark stripes on the side of the body. In addition a larva with the fore limbs about to erupt has the dorsolateral and vertebral light stripes typical of adults of this species (see above).

Head and body oval; eyes dorsolateral, not visible from below; diameter of eye subequal to eye-nostril distance; oral disk ventral, subterminal; beaks narrowly edged with black, finely serrated; upper beak a smooth, broad

Table 73. — **Monthy frequency of female** Hyperolius schoutedeni **in various stages of development. Snout-vent lengths in parentheses.**

	Oviduct immature	Oviduct mature		
		Ova immature	Ova intermediate	Ova mature
January	2 (16,7–18,7)	—	—	—
February	2 (16,4–18,9)	—	—	—
March	5 (17,8–20,2)	1 (21,7)	—	1 (24,7)
April	12 (17,4–21,5)	16 (19,5–25,8)	7 (20,7–23,6)	6 (20,7–26,1)
May	5 (14,3–17,8)	4 (21,4–25,7)	4 (22,4–24,6)	17 (20,8–26,2)
June	—	11 (22,2–25,9)	1 (23,4)	5 (21,4–26,8)
July	—	7 (21,2–23,6)	9 (20,8–26,7)	14 (21,2–28,3)
August	—	8 (24,0–27,9)	4 (21,4–25,1)	13 (21,5–27,1)
September	—	3 (24,2–25,9)	—	2 (24,3–24,6)
October	1 (18,9)	—	—	—
December	6 (16,8–17,9)	—	—	—
Total number	33	50	25	58
Range	14,3–21,5	19,5–27,9	20,7–26,7	20,8–28,3
Mean	18,33 ± 0,28	23,61 ± 0,28	23,48 ± 0,33	23,64 ± 0,22

arc; lower beak V-shaped; labial teeth I/III, the outermost lower row much shorter than the others; papillae in a continuous, staggered row along margin of lower lip; spiracle sinistral, slightly closer to eye than to root of hind limb.

Tail lanceolate, deepest near center, tapering gradually; dorsal fin beginning at end of body, deeper than ventral fin.

Head and body brown, spotted dorsally until about Stage XVII when adult pattern appears; sides of body and, in some individuals, base of caudal muscle with numerous thin dark stripes; usually underside of head, posterior half of caudal muscle, and fins with dark spots.

Head plus body lengths 8,9-9,5 mm in four larvae in stages VII to XX.

The ten young frogs still having vestiges of the tail measured 10,4-12,2 mm. The mouth in each case was adult in form.

Males develop vocal sacs at about 16,5 mm and the gular pouch when between 18 and 20 mm (Table 72). Females become mature when about 20 mm (Table 73).

Ecological notes. — *Hyperolius schoutedeni* is largely confined confined to marshes, ponds, springs, and marshy vegetation along small streams. Less than 10 % of the total collection of *schoutedeni* was caught away from the immediate vicinity of water (Table 74). Tadpoles were caught in the marshy edges of small streams (3 lots) and in a small, thinly wooded stream (1 lot).

Table 74. — **Habitat-frequency distribution of** Hyperolius schoutedeni **from the Parc National de la Garamba.**

	Dry season	Wet season	Total
Aquatic (1) :			
Marsh	58	385	443
Pond	72	9	81
Grassy seepage	53	44	97
Stream side	111	928	1.039
Subtotal	294	1.366	1.660
Terrestrial :			
Grass savanna	10	104	114

(1) All were caught on emergent or riparian vegetation.

The proportion of adult females containing enlarged ova is high from April through September (Table 73), indicating an extensive breeding season roughly coincident with the rainy season. Adult males, apparently in breeding condition, were relatively abundant from March to October (Table 72). All four series of tadpoles were collected in September.

The almost complete absence of adults from the collections of December to February (Table 75) suggests that the adults estivate or become less active during the dry season, or that adults live only one season and are replaced each rainy season by the young of the preceding wet season.

As the ratio of adult males to females is much larger in the March collections than in those of the next six months, males probably either mature earlier or resume activity earlier than females.

Table 75. — **Monthly proportions of juveniles and adults of** Hyperolius schoutedeni **caught in Parc National de la Garamba.**

	Juveniles	Adult		Total number
		Males	Females	
January	0,98	0,02	—	66
February	1,00	—	—	13
March	0,84	0,13	0,02	83
April	0,80	0,10	0,10	687
May	0,24	0,49	0,26	370
June	0,02	0,73	0,25	110
July	—	0,76	0,24	188
August	0,04	0,20	0,76	49
September	0,52	0,42	0,06	83
October.	0,63	0,37	—	52
November	0,80	0,20	—	15
December	0,99	0,01	—	138

Range. — *H. schoutedeni* is now known from the northern part of Province Oriental and adjacent western parts of Provinces Equateur and Leopoldville (LAURENT, 1943A, 1946, 1952). The Garamba localities extend the range eastward.

Garamba localities and specimens : Cellule Biologique I (8); Cellule Biologique II (1,739); Morubia (6); Napokomweli (4); Ndelele (10); Ngorobongo (27); Pali (2); Pp Km 62 (8); Torí (2).

Hyperolius sp.

One series of larvae cannot be assigned to any adults with reasonable certainly. They have the dental formula characteristic of many larval forms of *Hyperolius* : I/1-1 : II. The innermost lower row is narrowly divided and the outermost row is much shorter than the other two. These small larvae (head plus body 8,5 mm in Stage XX) were collected with transforming and metamorphosed *H. cinnamomeoventris* and *H. nasutus*, which

at this stage are very similar. The tadpoles almost certainly belong to one of these species, the only small *Hyperolius* in the Garamba whose larvae are unknown.

Head and body oval; eyes dorsal, not visible from below; oral disk ventral, subterminal; beaks and papillae as in larvae of *H. schoutedeni* (p. 163); dental formula I/1-1 : II; spiracle sinistral, closer to eye than to base of hind limb.

Tail lanceolate, tapering gradually in distal half; dorsal fin beginning at end of body, deeper than ventral fin.

Head and body light brown dorsally; underside of head with dark mottling; sides of body without stripes; caudal muscle with mid-dorsal dark streak and a mid-lateral stripe separated by a clear area; distal half or third of tail intense black, the pigment usually covering both fins except for clear spots near margins.

One series (IPN 1979) collected in September in a small pond formed by flood waters in a dense gallery forest in Cellule Biologique II.

ECOLOGICAL AND BIOGEOGRAPHIC CONCLUSIONS

SEASONAL VARIATION IN HABITAT DISTRIBUTION.

The relative frequency of observation of frogs at aquatic and nonaquatic sites remains unchanged from season, if we consider the total assemblages of species (1). During the rainy season, 87,6 % of the 18,595 frogs collected were caught at aquatic environments. In the dry season the percentage was 86,5 % of 5,547 individuals. Genera that were highly concentrated at aquatic sites during the wet season remained so during the dry season; the same generalization applies to species (Table 76). The genera and species that were less closely associated with aquatic environments during the wet season show more variation between seasons (Table 77). The most striking changes, in terms of magnitude and statistical significance among samples of reasonable size, are evident in *Bufo latifrons* ($P < 0{,}001$), *Leptopelis oryi* ($P < 0{,}001$), *Hyperolius nasutus* ($P < 0{,}001$), *H. viridiflavus* ($P < 0{,}001$), and *Phrynobatrachus natalensis* ($P < 0{,}001$) (2).

Seasonal variation in frequency of juveniles (see for examples, pp. 70, 108, 154) has no significant effect on the patterns in Tables 76 and 77. The distribution of juveniles in aquatic environments was the same in both seasons in *Hyperolius viridiflavus* and *Rana mascareniensis*. In *Phrynobatrachus scapularis* and *P. perpalmatus* the dry season samples are mainly composed of juveniles (83-95 %) and those of the wet season of adults (77-95 %). In both species juveniles and adults have the same relative

(1) Here we will consider only the specimens obtained by the De Saeger Mission; these may be viewed as constituting an unbiased sample. As our own collecting was concentrated at breeding sites, our sample was biased with respect to habitats.

(2) Tests of the hypothesis that the proportion in the dry season does not differ from that in the wet. The proportions at aquatic and non-aquatic environments during the wet season are taken as the exepected proportions p and q. The tests take the form diff./S.E. diff. where

$$\text{S.E. diff.} = \sqrt{\frac{\overline{pq}}{N}} \qquad N = \text{number in dry season sample.}$$

Table 76. — **Seasonal frequency of collection at aquatic sites of genera and species of Garamba frogs highly concentrated (i.e., > 80 %) at aquatic environments. All species samples larger than 25 in each season.**

	Wet season		Dry season	
	Number	% (1)	Number	% (1)
Xenopus	298	89,5	69	95,8
Rana	1.078	82,9	355	84,1
Afrixalus	169	81,2	72	96,0
Hyperolius	12.682	91,7	2.289	96,6
Phrynobatrachus	1.863	80,9	1.973	82,7
Xenopus muelleri	277	89,6	65	95,6
Rana occipitalis	264	100,0	61	100,0
Rana mascareniensis	288	92,6	132	89,2
Rana perreti	213	94,2	23	92,0
Rana taenioscelis	94	94,0	102	91,9
Afrixalus fulvovittatus.	161	81,3	71	96,0
Hyperolius cinnamomeoventris	10.684	94,6	1.551	99,1
Hyperolius schoutedeni	1.366	92,9	294	96,7
Phrynobatrachus scapularis	741	90,7	752	95,4
Phrynobatrachus perpalmatus	372	98,9	280	96,2

(1) Percentage of seasonal total.

abundance in aquatic and non-aquatic habitats in both seasons (Tables 45 and 47). Consequently the percentages shown in Table 76 for these species are not affected by seasonal disproportionality in age groups.

The dry season sample of *Hyperolius nasutus* contains 292 juveniles and 66 adults. If we eliminate the juveniles from the dry season sample, the percentage of frogs caught at aquatic sites is 89,3. Again seasonal differences in frequency of age groups is without signficant effect.

All of the species of Table 77 use aquatic environments for breeding purposes. We observed all except *B. funereus* calling at such places. Since between 30 and 90 % of the specimens of the species in Table 77 were

Table 77. — **Seasonal frequency of collection at aquatic sites of genera and species of Garamba frogs moderately concentrated (i.e., < 70 %) or uncommon at aquatic environments during the rainy season.**

	Wet season		Dry season	
	Number	%	Number	%
Bufo	116	34,2	31	16,7
Hemisus	19	35,2	1	14,3
Leptopelis	61	56,0	4	16,7
Kassina.	6	5,5	2	33,3
Bufo funereus	47	67,1	7	100,0
Bufo latifrons	46	38,7	11	17,7
Bufo regularis	13	9,3	13	11,1
Hemisus guineensis	10	26,3	1	25,0
Leptopelis oryi	61	66,3	4	16,7
Kassina senegalensis	6	5,6	2	33,3
Rana maccarthyensis	10	21,7	3	30,0
Hyperolius nasutus	360	51,9	325	93,7
Hyperolius concolor	46	65,7	27	79,4
Hyperolius viridiflavus	272	60,0	92	77,3
Phrynobatrachus parkeri	570	69,3	803	71,8
Phrynobatrachus natalensis	149	58,7	130	71,8

caught away from water, a significant amount of the resting and feeding activities of these frogs occurs at non-aquatic sites during the wet season. The distributions of these frogs during the dry season suggest that we are dealing with two physiological and behavioral groups. On the one hand are those species that are able to disperse through the savannas even when the general humidity is very low. No more than 35 % of the dry season observations of these forms were made at aquatic environments. This group includes *B. latifrons*, *B. regularis*, *L. oryi*, *H. guineensis* and probably *K. senegalensis* and *R. maccarthyensis*, though dry season data are weak for the last three. The other group consists of species that seemingly are not as capable of withstanding the low humidities of the savanna during the

dry season. At least 70 % of the dry season observations of these forms were made at aquatic environments. They include species, such as *P. parkeri*, that maintain the same relative distribution in both seasons as well as some (species of *Hyperolius* in Table 77 and *P. natalensis*) that show a marked increase in concentration at aquatic sites during the dry season.

The species listed in Table 76 apparently do not carry out any important portion of their activities away from water in either season. They certainly do not show significant ability to maintain themselves away from water during the dry season.

In summary, the species of these two tables form three groups in terms of their relations of water. Those of Table 76 use aquatic sites at all times for most activities, and are rarely found away from water. Some of the species of Table 77 (*B. regularis*, *B. latifrons*, *L. oryi*, *Hemisus guineensis*, *K. senegalensis* and *R. maccarthyensis*) use aquatic environments only for breeding and conduct other activities mainly in other situations. The remaining species of Table 77 carry out most activities at aquatic sites, and wander from water primarily in wet season.

BREEDING ACTIVITY.

As the individual accounts of species indicate, the Garamba amphibians breed mainly during the rainy season. All species, however, do not begin breeding at the same time. Although yearly variation is to be expected, the sequence of reproductive activities observed by us in 1959 (Table 78) may stand as representative. The relation of these dates to rainfall and relative humidity at 18 hrs. is shown in Fig. 51. The breeding sites were not in any one part of the park. But as the weather was essentially identical at Ndelele and Nagero (Fig. 51), which are at widely separated corners (72 km) of the park, we can ignore local climate as a significant factor in Table 78.

The actual sequence cannot be taken directly from the table and Fig. 51. The remarks in Table 78 emphasize the weakness of some of the evidence. Our field work began on February 28. Hence species observed breeding that night, i.e., *B. latifrons* and *B. regularis*, may have started breeding earlier. In other cases, the first observation of breeding activity coincided with our first work at a suitable habitat for the species, but some time after our work began in the Garamba. This was true for *Leptopelis flavomaculatus*, *Afrixalus fulvovittatus*, and *Rana perreti*. Perhaps had we collected at appropriate environments sooner we might have recorded reproductive activity earlier.

We collected larvae of two species, *Rana ornata* and *R. occipitalis*, before we observed calling or clasping. Obviously these species began to breed earlier than Table 78 indicates.

Table 78. — **Observed sequence of initiation of breeding activity of frogs in Parc National de la Garamba in 1959.**

Number in figure 51	First call	First amplexus	Remarks
2. *Bufo latifrons*	II–28	II–28	First night in the field
3. *Bufo regularis*	II–28	II–28	First night in the field
5. *Rana occipitalis*	III–13	III–13	Larvae found at this site III-1
8. *Rana oxyrhyncha*	—	III–18	First work at this site on II-28
13. *Phrynobatrachus natalensis* ..	III–20	—	First collection at similar habitat III-2; first work at this site III-19
14. *Phrynobatrachus parkeri* ...	III–19	—	First collection at similar habitat III-2
18. *Leptopelis oryi*	III–20	—	Similar habitat searched III-5
20. *Afrixalus fulvovittatus*	III–20	—	First work at suitable habitat III-20
9. *Rana perreti*	III–23	III–24	First work at this site on III-20
11. *Rana taenioscelis*	III–25	—	First work at this site on III-20
23. *Hyperolius viridiflavus*	III–26	—	Collecting at this site began III-20
16. *Hemisus guineensis*	IV–2	IV–7	Site visited III-5
17. *Leptopelis flavomaculatus* ...	IV–8	—	Only collection; first night of work in gallery forest IV-8.
1. *Xenopus muelleri*	—	IV–12	Only observation
4. *Rana ornata*	IV–12	IV–12	Larvae found at this site on IV-6
6. *Rana huguettae*	IV–12	IV–12	Males caught at this site IV-2
22. *Hyperolius concolor*	IV–15	—	Similar habitat searched III-20-25
19. *Kassina senegalensis*	IV–23	—	Similar habitats searched III-5, III-20-25
12. *Rana tournieri*	IV–27	—	Similar habitat searched IV-23; first collection of species IV-27
7. *Rana maccarthyensis*	V–2	—	Only one specimen collected earlier IV-22
15. *Phrynobatrachus scapularis* ..	V–2	—	First collection at similar habitat III-27
21. *Afrixalus weidholzi*	V–3	—	Similar habitat searched IV-23
10. *Rana straeleni*	V–11	—	This site worked first on IV-23; first collection of species V-11

The remaining species had been collected previously or suitable environments had been searched prior to the dates given in Table 78. Consequently, those dates are reasonable approximations of the initiation of breeding activity. There is no correlation between position of a species in this sequence and its geographic distribution (see p. 178).

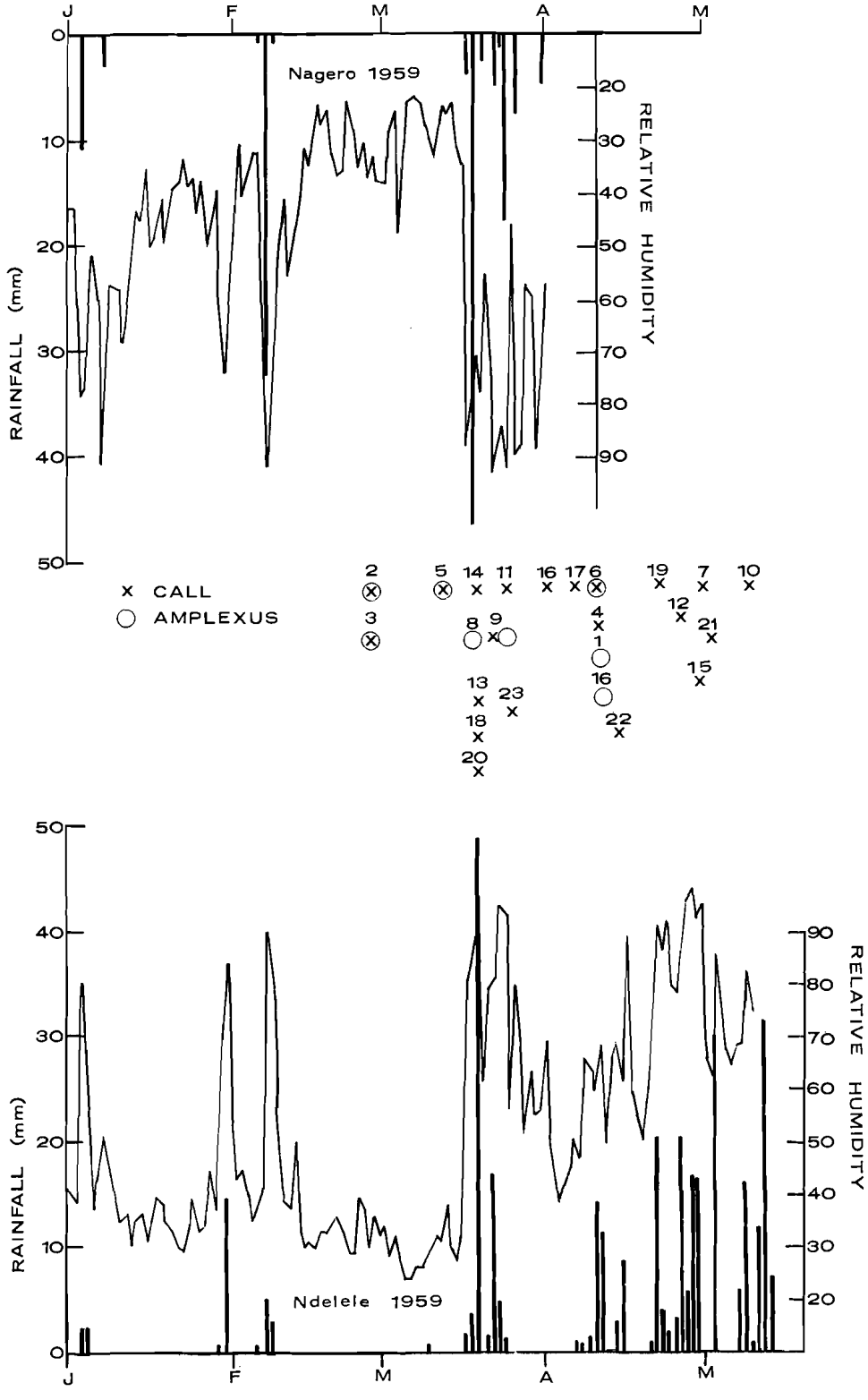
Except for *B. latifrons*, *B. regularis*, and *R. occipitalis*, none of these species begins to breed until the rains begin and the general relative humidity rises (Fig. 51). It seems likely that one or both of these environmental factors provide the stimulus to breeding activity. It is not clear what initiates breeding in the two species of *Bufo* and *R. occipitalis*.

The stimulating effect of rainfall early in the wet season was clearly demonstrated by a series of observations we made Ndelele in April, 1959. Between April 6 and April 12 we heard no frogs calling except *Hemisus guineensis* on the hill top. Rainfall between April 1 and 12 was 3,6 mm and the site of the temporary pool (see below) was dry. It began to rain at 22 : 40 hrs. on April 12 and 11,8 mm fell in the next 30 minutes. By 23 : 30 the small pool was forming from the run-off and frogs were extremely abundant and active. Between 22 : 30 and 00 : 30 hrs. we heard numerous calling males of *Rana occipitalis*, *R. oxyrhyncha*, *R. huguettae*, and *Hemisus guineensis* and a few of *R. ornata*. We saw clasping pairs of *Xenopus muelleri*, *H. guineensis*, *R. huguettae*, and *R. ornata*. On the morning of April 13, the surface of the pool, then 4 × 5 m, was covered with frog eggs. No rain fell on April 13. We worked around the pool that night for one and one-half hours and saw only six frogs — one *R. huguettae*, one *R. occipitalis*, and four *H. guineensis*.

In a tropical area having sharply defined seasons, an amphibian that breeds early in the rainy season has a better chance of producing several broods. Hence, there should be a selective advantage to early reponse to rains or even to a moderate anticipation of the rains. But certain hazards to which early broods are exposed may counteract the advantage.

Short term fluctuations in some environments early in the rainy season affect the survival of larvae of some species. The small pools that form in the rocky bed of the Dungu River (Fig. 9) have been described earlier (p. 9). Larval toads which live in these small pools not only must be able to tolerate high temperatures (34 °C), but are also subject to two serious hazards. If no rain falls for two weeks, the smaller of these pools will dry up completely. On the other hand, if too much rain falls, the river will rise (Fig. 18) and scour out these small habitats.

Other temporary ponds are likely to be death traps for tadpoles at the beginning of the wet season. The pool on the hill at Ndelele (Fig. 16) formed following rains beginning March 18, 1959 and totalling 79 mm by March 24. No rain fell between March 24 and April 8. On April 2 the pool measured 4 × 5 m and was crowded with tadpoles of *Rana ornata* and *Rana* (*Ptychadena*) species. The pool dried completely on April 6 destroying the tadpoles that remained.


J
F
M
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Nagero 1959
RAINFALL (mm)
RELATIVE HUMIDITY
0
10
20
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50
20
30
40
50
60
70
80
90
X CALL
○ AMPLEXUS
2 ⊗
3 ⊗
5 ⊗
14 X
11 X
8 ○
9 X ○
13 X
23 X
18 X
20 X
16 X
17 X
6 ⊗
4 X
1 ○
16 ○
22 X
19 X
12 X
7 X
21 X
15 X
10 X
Ndelele 1959

FIG. 51.

Since the climate is approximately the same in the Guinean savanna from the Garamba to the western coast of Africa, loss of tadpoles by early breeding frogs must be a common phenomenon. BENTLEY (1966) has suggested that a short larval period in species of frogs living under arid conditions may be a facultative response to some environmental factor such as temperature or to a stimulus resulting from shrinkage of the home pool. The mass death of tadpoles in the two kinds small pools in the Garamba indicates that the early breeding species do not have a facultative ability to shorten the larval period.

ECOLOGICAL DIFFERENTIATION.

Intrageneric ecological differentiation is best illustrated by the three types revealed by Tables 76 and 77. *Phrynobatrachus* and *Hyperolius* are both divisible into two groups of species, one group closely bound to water at all times and a second moving freely through savanna during the wet season.

Differentiation with respect to particular types of environments is not common in this assemblage of species. *Rana albolabris* is clearly different from its Garamba congeners in its almost complete restriction (94 %) to gallery forests or other heavily wooded habitats. All other species of *Rana* in the park are common in open savanna or at aquatic habitats in such situations.

Leptopelis flavomaculatus, unlike *L. oryi* and *L. viridis*, was found only in gallery forest. But since only 5 individuals of *flavomaculatus* were collected, the significance of the difference is questionable.

The species of *Bufo* differ in habitat frequency distributions (Table 14). But there is considerable overlap and *B. latifrons* was caught with each of the other three species (p. 40).

The species of *Phrynobatrachus* and *Hyperolius*, aside from the major dichotomy of aquatic versus non-aquatic mentioned above, show some intrageneric differentiation with respect to types of aquatic environments (Table 79). However, as intraspecific seasonal variation is large and statistically significant in both genera, no confidence can be placed in the interspecific differences. Species of *Rana* show less seasonal variation, permitting greater reliance on the interspecific differences in habitat distributions (Table 79). Neither *R. perreti* nor *R. albolabris* occur at ponds;

EXPLANATION OF FIG. 51.

FIG. 51. — Initiation of breeding activity of species of amphibians related to rainfall (vertical bars) and relative humidity at 18 hrs (continuous curve) in the Parc National de la Garamba in 1959. Climatic data for Ndelele below (Jan. 1 to May 14) and for Nagero above (Jan. 1 to March 31).

Table 79. — **Intrageneric variation in relative frequency distributions with respect to types of aquatic environments in frogs from Parc National de la Garamba.**

Species	Season	Marsh	Stream	Spring	Pond	Total
Phrynobatrachus natalensis	Wet	0,18	0,33	0,24	0,24	205
	Dry	0,22	0,48	0,29	0,02	153
Phrynobatrachus parkeri	Wet	0,25	0,37	0,09	0,29	780
	Dry	0,20	0,41	0,18	0,21	902
Phrynobatrachus scapularis	Wet	0,49	0,31	0,13	0,07	855
	Dry	0,26	0,08	0,02	0,63	766
Phrynobatrachus perpalmatus	Wet	0,31	0,56	0,11	0,02	372
	Dry	0,17	0,60	0,11	0,12	280
Hyperolius nasutus	Wet	0,27	0,61	0,03	0,09	360
	Dry	0,08	0,28	0,53	0,11	336
Hyperolius concolor	Wet	0,58	0,26	—	0,16	111
	Dry	0,07	0,86	0,04	0,04	28
Hyperolius viridiflavus	Wet	0,31	0,47	0,12	0,10	368
	Dry	0,33	0,40	0,05	0,22	105
Hyperolius cinnamomeoventris ...	Wet	0,12	0,79	0,08	0,01	10.684
	Dry	0,12	0,48	0,26	0,14	1.551
Hyperolius schoutedeni	Wet	0,28	0,68	0,03	0,01	1.366
	Dry	0,20	0,38	0,18	0,24	294
Rana occipitalis	Wet	0,05	0,42	0,01	0,52	290
	Dry	0,36	0,30	0,01	0,33	86
Rana albolabris	Wet	0,44	0,31	0,25	—	151
	Dry	0,08	0,48	0,44	—	25
Rana mascareniensis	Wet	0,29	0,39	0,05	0,27	319
	Dry	0,33	0,35	0,01	0,31	137
Rana perreti	Wet	0,27	0,49	0,24	—	213
	Dry	0,40	0,40	0,20	—	30
Rana taenioscelis	Wet	0,69	0,18	0,05	0,08	208
	Dry	0,57	0,24	0,02	0,17	130

Table 80. — **Relative frequency of** Rana (Ptychadena) **species at temporary bodies of water in the Parc National de la Garamba during the wet season.**

	At temporary bodies of water	Total at aquatic sites
Rana huguettae	97 %	32
Rana maccarthyensis	79 %	47
Rana oxyrhyncha	68 %	38
Rana straeleni	100 %	8
Rana taenioscelis	39 %	208
Rana tournieri	11 %	64
Rana mascareniensis	—	319
Rana perreti	—	213

R. occipitalis, *R. mascareniensis*, and *R. taenioscelis* are scare at the outflow of springs. Species of *Rana* also differ in their association with temporary bodies of water (Table 80).

These are rather crude differences. Observations on the spot reveal more subtle interspecific differences within environments. For example, though both *Bufo latifrons* and *B. regularis* bred along the Dungu River, the latter was consistently seen farther from the banks and hence more in the open. In the marsh at Nabakoyo (Fig. 13), *Hyperolius cinnamomeoventris* called from perches 10-45 cm above the surface of the water and *H. viridiflavus from* 30-60 cm above the water. At small permanent ponds, we saw *H. viridiflavus* calling from perches 45 to 100 cm above the water and *H. concolor balfouri* 10-45 cm above the water.

The entire assemblage of 14 species caught at the Nabakoyo marsh (Fig. 13) has a moderately complex distribution vertically and horizontally. *Rana occipitalis* and *Xenopus muelleri* were found only in open pools of various sizes. We caught *Bufo latifrons*, *R. mascareniensis*, *R. taenioscelis*, *R. perreti*, *Phrynobatrachus natalensis*, *P. parkeri*, and *P. scapularis* in small pools or on the ground. As already noted *H. cinnamomeoventris* perched on grass and sedges 10-45 cm, *H. viridiflavus* and *Afrixalus fulvovittatus* at 30-60 cm and *Leptopelis oryi* at 1-2 m above the surface. Except for *B. latifrons* and *R. albolabris* which were confined to the tree-lined edges, all of these species occurred across the entire width of the marsh. *Phrynobatrachus natalensis* and *P. parkeri* called during the day as well as at night. The other actively vocalizing species called only after dark.

GEOGRAPHIC RELATIONS OF THE GARAMBA AMPHIBIANS.

In terms of geographic distribution, the 43 species of Garamba amphibians may be divided into the following groups :

A. — **Guinean** (West Africa from the Nigeria-Liberia area to eastern Sudan or northeastern Congo) :

Bufo latifrons.
Phrynomerus microps.
Rana maccarthyensis (Fig. 52.).
R. tournieri.
R. trinodis.
Leptopelis viridis.
Kassina maculosa.
Afrixalus weidholzi.

B. — **Guinean — East African** (Ethiopia to Mozambique) :

Rana galamensis.
Phrynobatrachus perpalmatus.
Afrixalus fulvovittatus.
Hyperolius viridiflavus.

C. — **Guinean — East African — Angolan** (southern Congo, Angola, Zambia, and northern parts of Southern Rhodesia, Bechuanaland, and Southwest Africa) :

Xenopus muelleri.
Rana ornata (Fig. 53).
Rana occipitalis.
Rana oxyrhyncha.
Hemisus guineensis.

D. — **Guinean — Central African** (Cameroons, Gaboon, Congo) :

Xenopus tropicalis (Fig. 54).
Rana albolabris.
Arthroleptis poecilonotus.
Hyperolius concolor.
H. cinnamomeoventris.

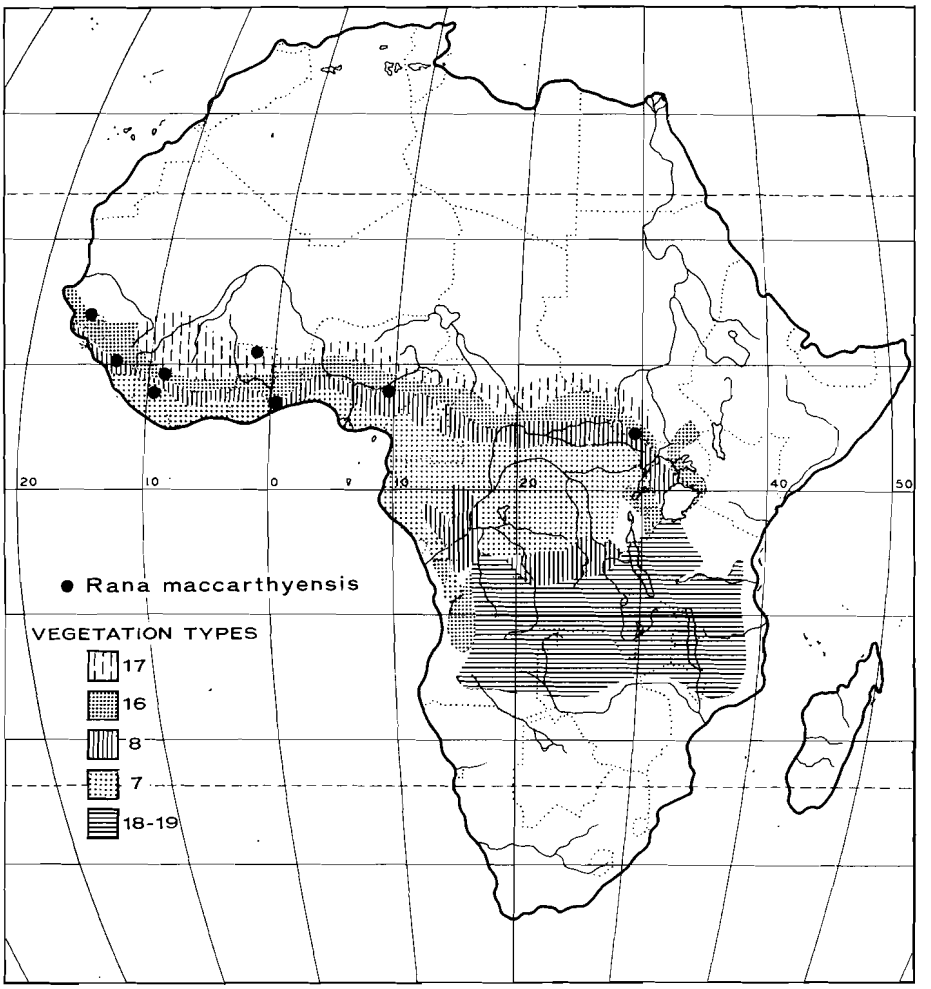

FIG. 52. — Distribution of *Rana maccarthyensis*.

Sources : ANDERSSON (1937), GUIBÉ and LAMOTTE (1957), and SCHIØTZ (1963, 1964). Vegetation zones simplified from *Vegetation Map of Africa*. Vegetation types : 7 : Moist forest at low altitudes; 8 : Forest-savanna mosaic; 16 : Relatively moist, undifferentiated open woodands and savannas; 17 : Northern open woodland, with *Isoberlinia*; 18-19 : Southern open woodland and savannas, with abundant *Brachystegia*. Base map with permission from Goode Base Map Series, Department of Geography, University of Chicago.

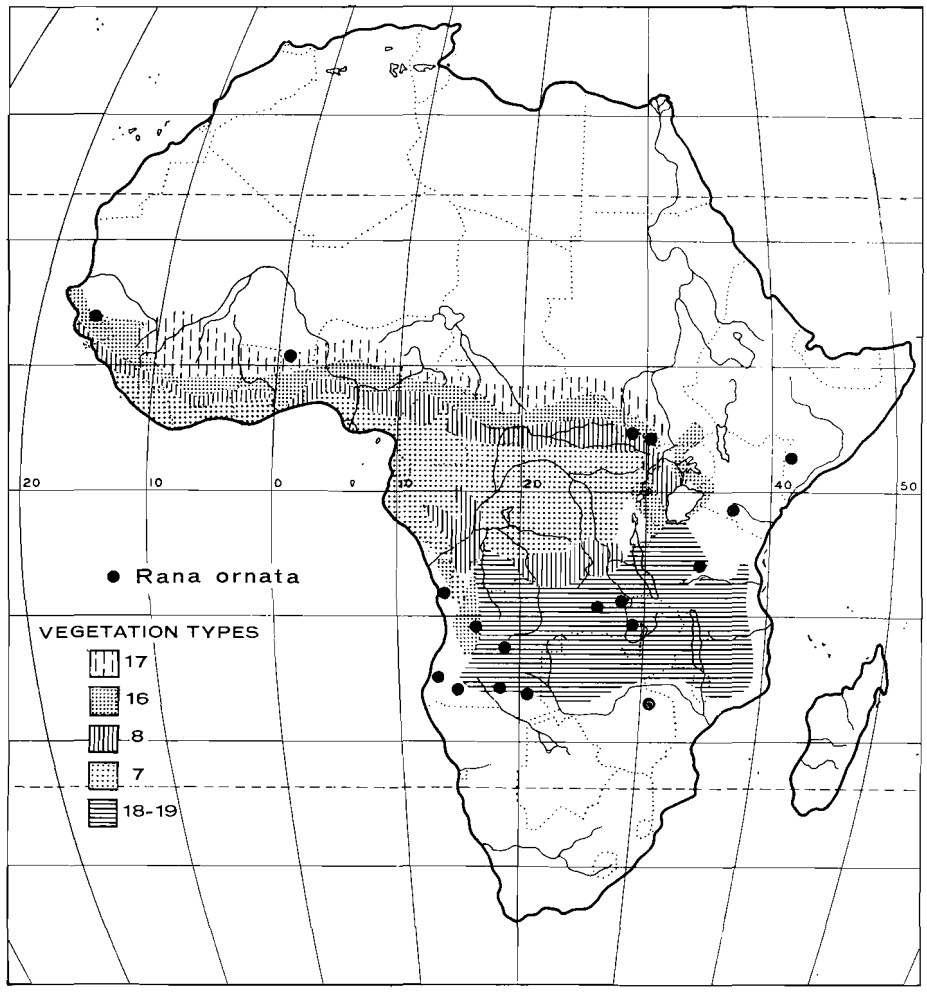

FIG. 53. — Distribution of *Rana ornata*. Source : SCHMIDT and INGER (1959). Vegetation zones simplified from *Vegetation Map of Africa*. Vegetation types : 7 : Moist forest at low altitudes; 8 : Forest-savanna mosaic; 16 : Relatively moist, undifferentiated open woodlands and savannas; 17 : Northern open woodland, with *Isoberlinia*; 18-19 : Southern open woodland and savannas, with abundant *Brachystegia*. Base map with permission from Goode Base Map Series, Departement of Geography, University of Chicago.

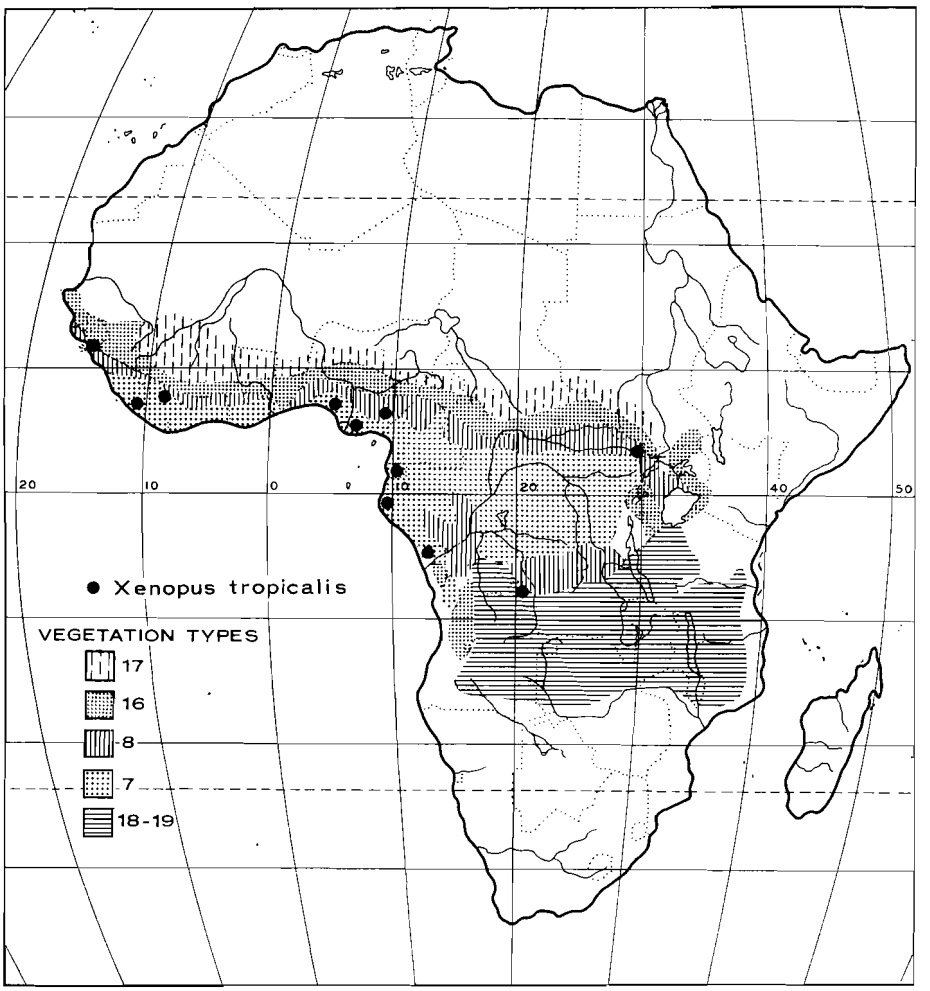

FIG. 54. — Distribution of *Xenopus tropicalis*.

Sources : LAURENT (1954*b*), PARKER (1936*a*), and SCHIØTZ (1963).
Vegetation zones simplified from *Vegetation Map of Africa*. Vegetation types : 7 : Moist forest at low altitudes; 8 : Forest-savanna mosaic; 16 : Relatively moist, undifferentiated open woodlands and savannas; 17 : Northern open woodland, with *Isoberlinia*; 18-19 : Southern open woodland and savannas, with abundant *Brachystegia*. Base map with permission from Goode Base Map Series, Department of Geography, University of Chicago.

E. — **Central African :**

Xenopus fraseri.
Rana perreti.
Phrynobatrachus parkeri.
Hyperolius schoutedeni.

F. — **East African :**

Bufo steindachneri.
Leptopelis flavomaculatus.
Hemisus marmoratus.

G. — **East African — Angolan :**

Xenopus laevis.
Bufo funereus.
Hyperolius nasutus.

H. — **Pan-African** (area under « C » above plus South Africa) :

Bufo regularis.
Rana mascareniensis.
Phrynobatrachus natalensis.
Kassina senegalensis.

I. — **Uncertain :**

Rana taenioscelis (Nigeria, eastern half of Congo).
Phrynobatrachus cryptotis (eastern half of Congo).
P. scapularis (northeastern Congo).
Rana huguettae (known only from the Garamba).
R. straeleni (known only from the Garamba).
Leptopelis oryi (known only from the Garamba).
Arthroleptis sp.

Clearly a good number of these distributions are incompletely known. Almost certainly *Rana huguettae*, which was found in some of the driest grass savannas in the Garamba, and *R. straeleni*, which was caught in rain filled depressions in grass savanna, have extensive distributions as yet undiscovererd. Their habitats are common throughout the Guinean savanna. The same is true of *Leptopelis oryi*. *Rana taenioscelis* was so abundant in the Garamba that its spotty distribution must be a reflection of our lack of knowledge.

Species listed under categories, A, F, G have one extreme of their known ranges in the Garamba (Fig. 52). As with few exceptions (*Bufo funereus*, *Leptopelis flavomaculatus*) these are savanna species, I expect that additional collecting and study will show that their distributions are more extensive. The Garamba may actually be the limit of distribution for some species. The northeastern corner of the Congo is near the eastern edge of the *Isoberlinia* woodland (vegetation type 17 of the *Vegetation Map of Africa*) and also near a gap in the moist savanna (vegetation type 16).

The recording of *Rana maccarthyensis*, *R. perreti*, *R. tournieri*, and *Leptopelis viridis* from the Garamba extends their ranges 2.000 km. Previously these species were known only the Cameroons or westward. These novelties demonstrate how little we know as yet concerning the distribution of amphibians in the northern savannas.

A few species — *Rana albolabris*, *Xenopus tropicalis*, and *X. fraseri* — are essentially humid forest species. They probably do not penetrate the moist savanna country much farther than the Garamba.

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Published January 31, 1968.