

Family RANIDAE.

Genus **RANA** LINNAEUS.8. — **Rana tuberculosa** BOULENGER.

(Pl. IV, 4.)

Pyxicephalus rugosus GÜNTHER, 1864, Proc. Zool. Soc. London, **1864**, p. 479, pl. 33, fig. 1 — Pungo Adongo, Angola.

Rana tuberculosa BOULENGER, 1882, Cat. Batr. Sal. Brit. Mus., p. 30 (new name).

Rana pulchra BOULENGER, 1896, Ann. Mag. Nat. Hist., (6), **18**, p. 468 — Lake Tanganyika.

Taxonomic notes. — The small Upemba series and two British Museum specimens (1940.1.20 5-6) from Ulengule, Tanganyika, bridge the gap between *tuberculosa* and *pulchra* and extend the range of variation. By a manuscript note in the British Museum catalogue, BOULENGER indicated that he, too, thought *pulchra* was conspecific with *tuberculosa*. The original description of *pulchra* notes a light V on the rear of the head (actually between the shoulders) and a similar mark is shown in the plate accompanying the original description of *rugosus*. The principal difference between the two descriptions lies in the absence of a vertebral light line in the type of *rugosus* (= *tuberculosa*).

In one Upemba frog the interscapular light mark is reduced to a squarish area and is followed by a series of square dark spots each of which encloses a large square wart. A complete transition to the V illustrated by GÜNTHER is formed by other specimens in our sample.

The Upemba series also demonstrates that the tuberculation of the back is subject to variation that differences in preservation will not account for. The large warts may be uniformly square or square and elongate (apparently as a result of fusion of adjacent warts). The interscapular light mark usually encloses a pair of oblique, elongate ridges but these may be broken into several small ones and a large square wart. In most of these frogs the pattern of tuberculation is symmetrical about the vertebral line, but there are exceptions to this rule also. One feature of tuberculation, however, seems invariable, i.e., the ring of small, low tubercles surrounding the large dorsal warts.

Diagnosis. — Habitus stocky; head obtusely pointed, deep; snout projecting slightly; vomerine teeth in small, oblique groups widely separated from each other and the choanae; tympanum below and behind eye, usually without prominent rim, half diameter of eye, less than distance between eye and nostril; mid-dorsum with two rows of warts beginning on snout

and continuing to anal region; warts small and roundish on head, becoming subequal to tympanum and squarish or elongate on trunk; sides with large squarish and elongate warts; all of larger warts surrounded by small, low tubercles.

Tips of fingers and toes bluntly rounded; first finger equal to or slightly longer than second; each metacarpal with a least one round supernumerary

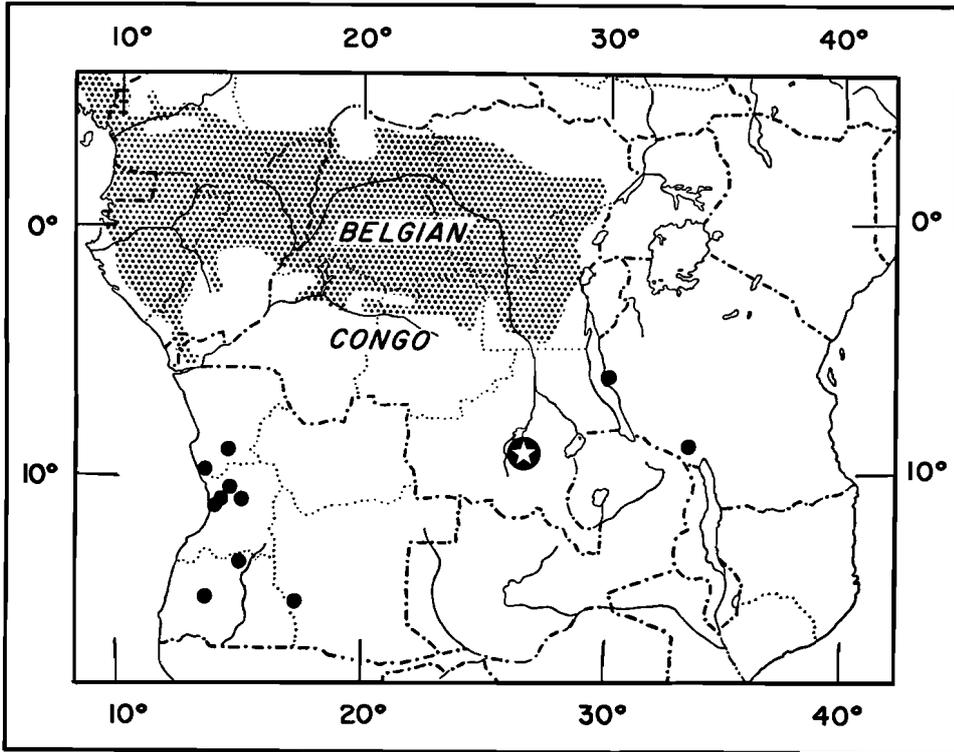


FIG. 15. — Distribution of *Rana tuberculosa*.

Parc National de l'Upemba indicated by symbol with open star.

tubercle. Toes webbed at bases; fourth toe with three and one-half to four phalanges free of web; fifth toe with two and one-half free; inner metatarsal tubercle compressed, blade-like, a little shorter than first toe; a small, round outer metatarsal tubercle usually visible.

Color (in alcohol) light brown above with a double row of dark brown squarish or oval spots; an interscapular light mark; dorsal surface of limbs boldly crossbarred; underside (at least in females) cream-colored, immaculate except at rear of lower jaw.

Secondary sex characters. — No males were available for intensive examination but one in the British Museum (1940.1.20.5) l.c. Has black pigment on the chin and anterior gular region. If this pigment is a secondary sex character, the specimen, which measures 32.5 mm, is probably mature. Two Upemba females with pigmented ova are 39.7 and 41.3 mm, snout to vent.

Ecological notes. — The known localities of *tuberculosa* all lie in the savanna provinces south of the rain forest belt (Fig. 15) and, with the exception of one specimen from Novo Redondo on the coast of Angola (FERREIRA, 1904), at elevations above 500 m. The six Upemba frogs were caught between 1,630 and 1,810 m above sea level.

The two females with pigmented ova were collected between November and February.

Range. — From the central highlands of Angola (BOCAGE, 1895) to Tanganyika (BOULENGER, 1896). The present specimens are the first recorded from the Belgian Congo (Fig. 15).

Upemba localities and specimens :

Lufwa (1); Lusinga (2); Mubale (2); Muye (1).

9. — *Rana ornata moeruensis* BOULENGER.

(Pl. IV, 5.)

Rana moeruensis BOULENGER, 1901, Ann. Congo Mus., Zool., (1), 2, p. 2, pl. 1, fig. 2 — Pweto, Belgian Congo.

Taxonomic notes. — The frogs of the subgenus *Hildebrandtia* NIEDEN, as outlined in BOULENGER's synopsis (1919), constitute a chain of closely related forms whose interrelationships are best expressed in trinomials. Restricted to the savanna provinces (Fig. 18), they include *budgetti* BOULENGER (Senegal), *togoensis* BOULENGER (Togo), *ornata* PETERS (Somaliland to Portuguese East Africa), *moeruensis* BOULENGER (south-eastern Belgian Congo), and *ornatissima* BOCAGE (Angola and South West Africa). On the basis of the individual variation seen in the Upemba series, we tentatively suggest that *ruddi* BOULENGER (type locality Portuguese East Africa) is a strict synonym of *ornata ornata* and that *miotympanum* BOULENGER (Angola) is a synonym of *ornata ornatissima*. *Rana macrotympanum* BOULENGER (Gallaland) may not be conspecific with the *ornata* series.

The pair of longitudinal light gular stripes or V-shaped marks that characterize the entire complex are invaded by dark pigment and even completely obscured in the Upemba sample of *moeruensis*.

Larvae from the Upemba differ from those of Somaliland (*ornata ornata*) in the number of labial tooth rows. Somaliland larvae have one upper

and two lower rows (BOULENGER, 1896), whereas Upemba specimens have two lower rows but no upper ones.

Diagnosis. — Habitus stocky, limbs relatively short; head bluntly pointed, snout projecting; vomerine teeth in two widely separated transverse groups in contact with antero-median corners of choanae; tympanum distinct, two-thirds to five-sixths horizontal diameter of eye, diameter equal to or greater than distance between eye and nostril; a dorsolateral glandular ridge continuous from above tympanum to sacral region; mid-dorsum usually with irregular elongate or round warts arranged in two rows; sides with round or elongate warts.

Tips of fingers and toes bluntly pointed; first and second fingers subequal, fourth shorter; no supernumerary metacarpal tubercles. Toes moderately webbed; fourth toe with three or three and one-half phalanges free of web; fifth toe with one to one and two-thirds phalanges free; an outer metatarsal tubercle feebly indicated.

Color (in alcohol) brownish above, a narrow light brown vertebral stripe flanked by two broad dark areas that may be broken into spots; a dark temporal mask; an oblique lateral light band; underside whitish; gular and pectoral regions with varying amounts of dark pigment.

Secondary sex characters. — Females are apparently slightly larger than males though the sample is too small for statistical treatment. The three females with pigmented ova vary from 65.4 to 69.4 mm, snout to vent, and the three males with developed secondary sex characters 62.2 to 63.9 mm.

The vocal sac apparatus consists of paired subgular vocal sacs, communicating with the mouth through round openings near the jaw commissures, and gular pouches that are everted during vocalization. The pouches are oblique to the mandible, begin below the front edge of the tympanum, and end near the ventral border of the insertion of the arm.

When fully developed the nuptial pads (Fig. 16) consist of a light brown velvety cluster of spinules on the forearm just above the bases of the three inner fingers and on the same three fingers. The pad is continuous from the forearm on to the first finger, which is completely covered dorsally and medially except for the terminal phalanx. The entire dorsal surface of the second finger and the dorso-median surface of the third finger are also covered by the pad except for the last phalanx of each, but these areas are not continuous with that of the forearm. Though based on the specimens of *moeruensis* at hand, the above description also applies to the nuptial pad of *ornatissima* (BOULENGER, 1905) but not to *budgetti*. Three adult males (CNHM 20836) of the last, while having the same distribution of pad material on the first three fingers, have no nuptial callosities on the forearm.

Larvae. — Forty-six larvae and transforming young were collected between the months of November and January. Most of the larvae have the hind limbs almost fully developed and others form a graded series from this stage to transformed juveniles. The latter have diagnostic characters of the adults, e.g., the rows of tubercles and color pattern, so that identification of the larvae is certain.

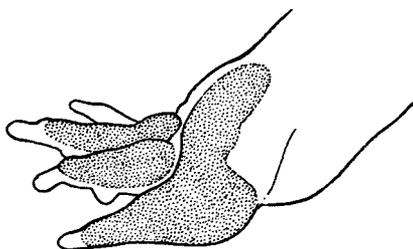


FIG. 16. — Nuptial pads of *Rana ornata moeruensis* ($\times 3$).

The larvae (Fig. 17) have sub-spherical bodies, terminal mouths, spiracle low on the left side and midway between eye and vent, fins subequal to tail muscle and the upper beginning high on body, vent median and opening at the edge of the fin. A tadpole (snout-vent 11.6 mm) with hind limbs in the paddle stage has two rows of labial teeth on the lower or



FIG. 17. — Oral disk of larva of *Rana ornata moeruensis* ($\times 18$).

posterior lip but no teeth on the upper lip. Since labial teeth usually reach their maximum development at this stage (INGER, 1956, p. 411), the tooth count of this larva can be considered typical for this population. Eleven of the twelve older larvae, those with fully or nearly fully developed hind limbs (snout-vent 16.5-21.2), have the same labial tooth formula; the twelfth has only a single row on the lower lip.

The beaks are very large, black, and finely serrated. Papillae form a continuous single row along the lower lip, reaching the extreme lateral corners of the upper lip. Those at the corners of the oral disk are conspicuously larger than the others.

None of the larvae having erupted fore limbs (16.3-23.9 mm) retain the horny beaks or labial teeth although the lateral papillae may still be present. One larva (18.2 mm) without erupted fore limbs has lost the labial teeth and the lower beak.

BOULENGER's brief description (1896) of larvae from Somaliland differs from the above only in noting that his material had one anterior tooth row.

Ecological notes. — As indicated above (p. 38), *ornata* and its related forms are confined to the savanna provinces (Fig. 18). The occurrence of *ornatissima* in the dry forest of upland central Angola (BOCAGE, 1895; BOULENGER, 1905) does not alter this generalization since this forest is of limited extent. The altitudinal distribution of *ornata* (*sensu lato*) derived from literature records runs from sea level at the coasts of Tanganyika (LOVERIDGE, 1951), Angola (MONARD, 1937), and Mozambique (BOULENGER, 1907) to 1,700 m in central Angola (BOCAGE, 1895), and is more extensive than shown by the Upemba records, which lie between 585 m (the lowest elevation in the park) and 960 m.

Range. — From Senegal and Gambia in the west to Somaliland in the northeast and to South West Africa and Mozambique (Fig. 18) in the south (BOULENGER, 1919).

Upemba localities and specimens :

Kanonga (4); Kaswabilenga (1); Kateke (1); Mabwe (87).

10. — *Rana albolabris lemairei* WITTE.

Rana lemairei WITTE, 1921, Rev. Zool. Bot. Afr., **9**, p. 1, pl. 1, figs. 1-4 — Lofoi, Katanga, Belgian Congo.

Taxonomic notes. — Specimens of the present series agree with the type, which we have examined, and differ from West African *albolabris* in having smaller finger disks. In addition to this difference between the two forms, WITTE (1921) states that *lemairei* has a smaller eye, a wider dorsolateral fold, and a darker ventral coloration. Our examination of 26 frogs from the Cameroons (CNHM 19967-74, 19986-93, 59084-93) and 21 from Liberia (CNHM 57797-805, 57907, 57932), which is presumed to be the type locality of *albolabris*, indicates WITTE to be correct only in the matter of size of disks and in coloration. In the last character, however, the difference is not sharp. The larger frogs (55 mm and over) from the Cameroons are usually brown on the throat and chest as are Upemba adults.

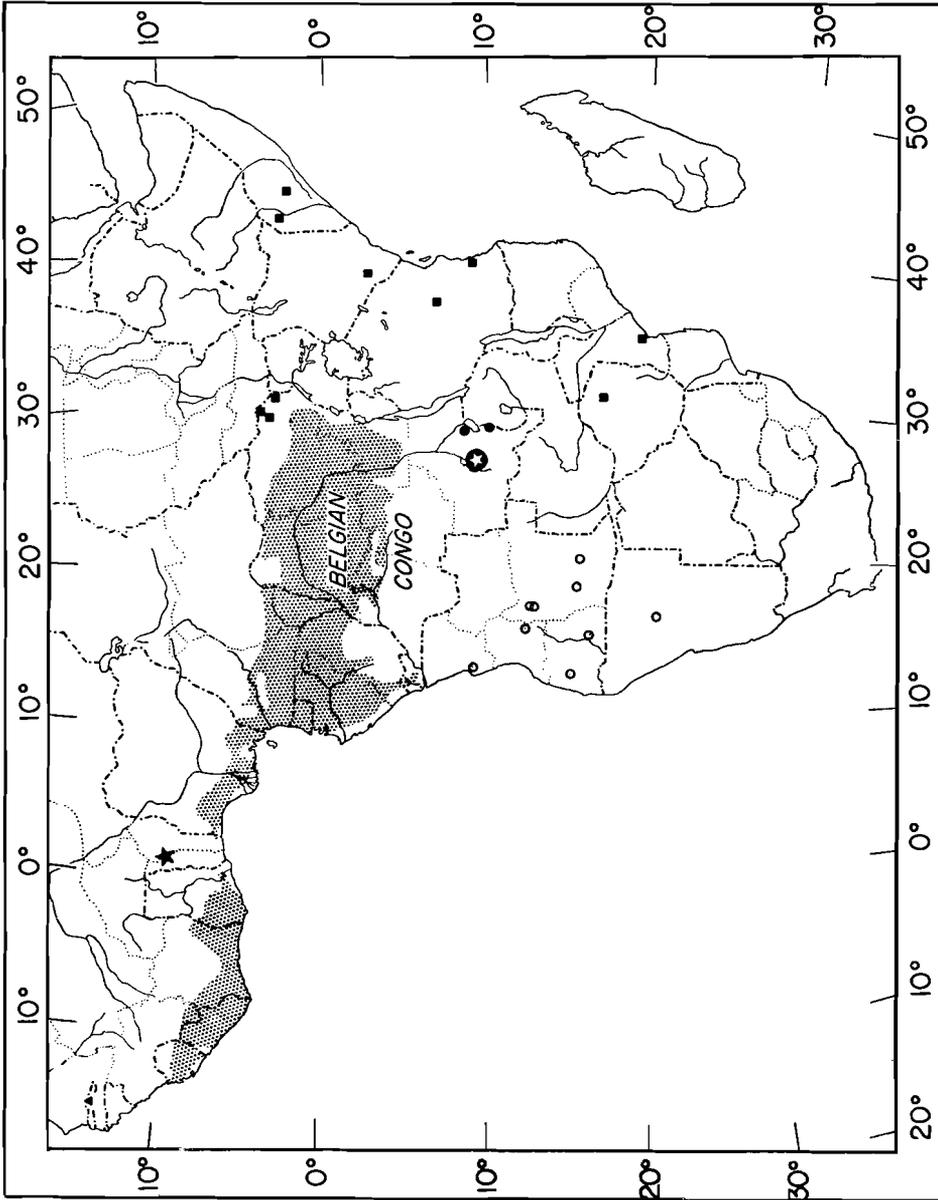


FIG. 18. — Distribution of *Rana ornata*.

R. o. ornata, solid squares; *R. o. moerueensis*, solid circles; *R. o. ornatissima*, hollow circles; *R. o. togensis*, solid star; *R. o. budgetti*, solid triangle.
Parc National de l'Upemba indicated by symbol with open star.

The greatest disparity in the two samples involves smaller frogs (below 50 mm), those from the Upemba being darker as a rule.

The Upemba frogs have slightly more extensive webbing (Fig. 19). The difference is most evident along the median edge of the second toe, which is webbed to the distal edge of the subarticular tubercle in *lemairei* but usually only to the base of the tubercle in our West African specimens.

In view of the slight differences between *lemairei* and West African *albolabris*, we prefer to regard the former as a subspecies.

Five Angolan frogs previously referred to *albolabris* (SCHMIDT, 1936) differ from the preceding forms and from *albolabris acutirostris* PARKER (= *a. parkeriana* MERTENS), also from Angola, in the absence of digital disks, in the absence of circummarginal grooves on the tips of the toes, in the reduced webbing, and in the relatively longer foot. *Rana a. parkeriana*, collected in the forested country of western Angola, resembles *a. albolabris* and *a. lemairei* in the extent of the web between the outer toes. In all three the web usually reaches the bases of the disks of the third and fifth toes, which means that only half of the respective terminal phalanges extend beyond the web ⁽¹⁾. In our Angolan frogs, which are from Chitau in the open country of central Angola, two phalanges of the third toe and 1 ½ to two phalanges of the fifth toe are free of web (Fig. 19, left).

The possession of distinctly dilated disks at the tips of fingers and toes characterizes *a. parkeriana* as well as the typical form and *a. lemairei*. The circummarginal horizontal grooves usually accompanying the development of disks are present at least on the toes and outer fingers of these three subspecies. On the other hand both grooves and dilated disks are absent in the Chitau series.

Differences in the relative lengths of the foot, though based on relatively few specimens, seem great enough to expect that additional material would substantiate the trend. In the four measurable Chitau frogs, the foot, measured from the base of the inner metatarsal tubercle to the tip of the fourth toe, varies from 0.52 to 0.59 of the snout-vent length. This proportion in four chosen at random from the Cameroons series (*a. albolabris*) ranges from 0.39 to 0.51 and in four Upemba frogs (*a. lemairei*) from 0.47 to 0.49.

The Chitau series is sufficiently distinct to warrant recognition as a subspecies and is described below as *Rana albolabris adiscifera*.

Diagnosis. — Habitus moderately stocky; head pointed; vomerine teeth in two oblique groups equidistant from each other and the choanae; tympanum distinct, two-thirds to four-fifths eye diameter, usually equal to distance between eye and nostril; dorsal skin granular; a continuous, narrow glandular dorsolateral ridge; tips of fingers and toes very slightly

⁽¹⁾ We are indebted to Miss GRANDISON of the British Museum for precise information on this and other characters of the types of *R. a. acutirostris* PARKER.

dilated, those of outer fingers and of all toes with circummarginal horizontal grooves; first finger longer than second; a supernumerary tubercle usually visible on each metacarpal; all toes except fourth usually webbed to base of disks; two terminal phalanges of fourth toe with a narrow fringe of web only; a round outer metatarsal tubercle usually visible.

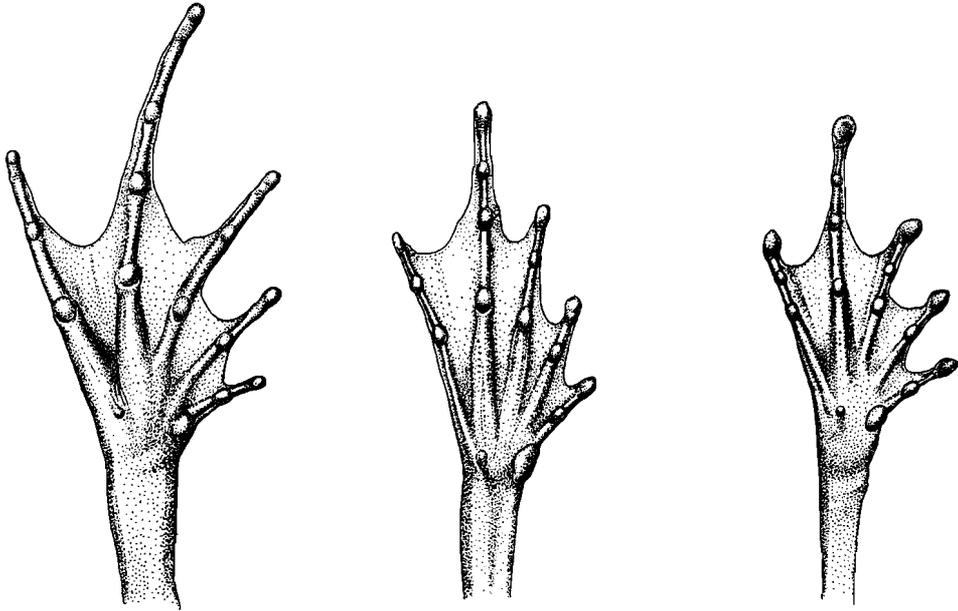


FIG. 19. — Extent of webbing in *Rana albolabris*.
Left, *R. albolabris adiscifera*. Center, *R. a. lemairei*. Right, *R. a. albolabris*.

Color (in alcohol) above slate gray with or without small, irregular dark spots; sides almost black; underside whitish, uniform in small frogs (ca. 30 mm) usually becoming increasingly darker with increase in size, especially on throat and chest; upper lip with a white streak extending to groin in small specimens but ending near axilla in adults; some adults with stripe completely obscured.

Secondary sex characters. — Females average about 10 mm larger than adult males. The smallest female containing well-developed pigmented ova measures 50.8 mm snout to vent, the largest 75.5 mm; the mean of 87 specimens equals 63.69 ± 0.71 mm. The size range of 119 males having vocal sacs is 38.2-66.3 with a mean of 53.22 ± 0.56 mm.

The vocal sacs of male *albolabris* are subgular, paired, and open through the floor of the mouth farther back in the throat than is usual for *Rana*. Male *albolabris* also have a large, flat, oval gland on the upper arm and a grayish, velvety nuptial pad on the first finger. On the dorsal surface of the finger the pad extends only to the end of the metacarpal but on the median edge it reaches the end of the basal phalanx or slightly beyond.

As in other species of *Rana* (p. 99), the nuptial pad of *albolabris* develops after the vocal sac. Apparently the pad undergoes seasonal regression since nine large males (55-63 mm) with vocal sacs and humeral glands have no pads. The humeral gland also develops later than the vocal sacs. In the smallest male with vocal sacs (38.2 mm), the gland is not evident; in eight other males (41.4-57.6 mm) vocal sacs and glands are present but the glands have only about half the depth achieved at maximum development.

Both males and females may have numerous white spinules scattered over dorsal and lateral surfaces of head and body. Though there is much individual variation within sexes, males generally have more numerous and stronger spinules.

Larvae. — Six nearly transformed young and one tadpole without erupted fore limbs are available. The hands and feet are identical to those of the adults whose disks, full webbing, and supernumerary metacarpal tubercles are not matched by any other Upemba species.

The tadpole (snout-vent 22.0 mm; tail 37.0 mm) has a subspherical body, sinistral spiracle a little closer to the eye than to the vent, and upper tail fin somewhat deeper than the muscle. The hind limbs are almost fully developed and have two metatarsal tubercles, fully webbed toes, and small disks. The body and tail are pale brown in preservative and spotted with dark brown. Spotting on the tail is almost confined to the muscle. The oral disk is subterminal and has a labial tooth formula of I:4+4/1+1:II. Papillae are arranged in a staggered, uninterrupted double row across the posterior lip and extend over the lateral quarters of the upper lip. At the corners of the oral disk the papillae are in two rows. The beaks are weak and feebly serrated. They are creamy white basally and brownish near the edges. Only the anterior beak has a black edge.

The partially resorbed tails of the transforming young have the bold brown spotting of the tadpole, and one (22.6 mm) has enough vestiges of the oral disk (teeth, papillae) to confirm the identification of the tadpole.

Ecological notes. — Most of the known localities for *albolabris* are in the rain forest belt though it has also been collected in the surrounding savanna country. NOBLE (1924) reports frogs on the ground in a coffee plantation, in grassy swamp, and in water holes. MERTENS' specimens (1938) from the Cameroons were seen on low vegetation.

Rana albolabris has been collected primarily at elevations below 1,000 m although LOVERIDGE (1942) reports a locality at approximately 2,000 m. The altitudinal distribution for the Upemba sample is as follows (maximum 1,480 m) :

Meters.	Specimens.
585- 750	179
751-1,000	191
1,001-1,250	34
1,251-1,500	156

A distinct breeding season does not emerge from examination of the Upemba sample. As Table 7 shows, only at the end of the wet season and beginning of the dry season does a large proportion of adult females have

TABLE 7. — Monthly frequency of adult *Rana albolabris lemairei* in various stages of sexual competence.

	Females (*)			Males (**)	
	Ova			Nuptial pad	
	pigmented	intermediate	immature	present	absent
February	0	1	1	1	0
April	12	1	0	12	2
May	12	3	8	11	7
June	13	6	0	22	0
July	1	2	4	5	2
August	4	1	4	12	10
September	0	0	4	8	2
October	0	0	3	3	0
November	0	0	6	10	4
December	0	0	1	8	0
Summary :					
Dry season	30	12	20	58	21
Wet season	12	2	11	34	6

(*) All females over 50.8 mm, the smallest with developed ova.

(**) All males with vocal sacs.

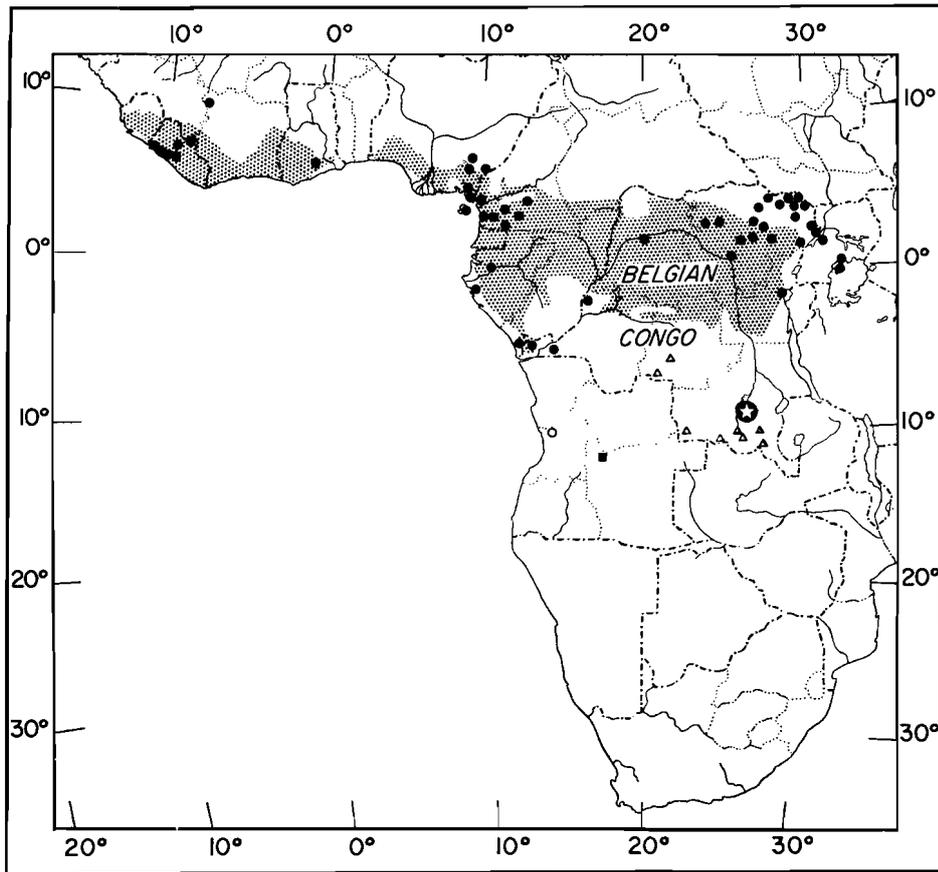


FIG. 20. — Distribution of *Rana albolabris*.

R. a. albolabris, solid circles; *R. a. lemairei*, hollow triangles;
R. a. parkeriana, hollow circle; *R. a. adiscifera*, solid square.
 Parc National de l'Upemba indicated by symbol with open star.

well-developed ova. Males with nuptial pads have approximately the same proportional frequency in wet and dry seasons. The collection of one tadpole and five transforming young in mid-September at the end of the dry season and one transforming juvenile in May during the dry season is consistent with the lack of a sharply defined breeding period.

Range. — *Rana albolabris* ranges across the central forest belt of Africa from Liberia (LOVERIDGE, 1938) and Angola (BOCAGE, 1895) on the west to Uganda (NIEDEN, 1915) and southeastern Belgian Congo on the east. The subspecies *lemairei* is confined to southeastern Belgian Congo (Fig. 20).

Upemba localities and specimens :

Kabwe (96); Kalala (2); Kalungwe (12); Kande (18); Kankunda (7); Kanonga (50); Kaswabilenga (47); Kateke (24); Kilwezi (72); Kipondo (16); Lukawe (28); Lupiala (36); Mokey (1); Munoi (64); Munte-Mubale (53); Pelenge (34).

11. — *Rana albolabris adiscifera* n. subsp.

Holotype. — Chicago Natural History Museum number 24171, an adult male from Chitau, Angola. Collected January 12-16, 1931.

Description of holotype. — Like the type form except in the following characters. Tips of digits not dilated, without horizontal circum-marginal grooves; toes half webbed; first toe with 1 ½ phalanges free, second toe with one, third toe with two, fourth toe with three, and fifth toe with 1 ½ phalanges free of web. Ventral surfaces without dark pigment.

Snout to vent 61.5 mm, length of foot 35.0 mm.

Paratypes. — CNHM 24170, CM 6754, 6756, 6788. All are from the type locality. CM 6754 is an adult female, 72.1 mm. The others are sub-adults varying from 42.8 to 45.7 mm. Variation among these is negligible and all agree with the holotype in the diagnostic characters.

Comparisons. — Differences between *adiscifera* and the other forms are discussed above (p. 43).

Remarks. — The holotype has well-developed secondary sex characters agreeing with the description given on p. 45.

Range. — Known only from the type locality in central Angola.

12. — *Rana fuscigula* DUMÉRIL and BIBRON.

(Pl. IV, 6.)

Rana fuscigula DUMÉRIL and BIBRON, 1841, *Erp. Gén.*, **8**, p. 386 — Cape of Good Hope, South Africa.

Rana angolensis BOCAGE, 1866, *Jour. Sci. Lisboa*, **1**, p. 73 — Duque de Bragança, Angola.

Rana chapini NOBLE, 1924, *Bull. Amer. Mus. Nat. Hist.*, **49**, p. 214, fig. 6 — Batama, Belgian Congo.

Taxonomic notes. — The relationship of the forms assigned to this species are poorly understood. The primary question still requiring an answer is : What is the nature of the variation observed in *fuscigula*? Is the variation geographic, ecological, or merely individual?

Division into subspecies was first suggested by HEWITT (1927), presumably based on his earlier work (1911). In the latter publication HEWITT distinguished between *fuscigula* DUMÉRIL and BIBRON and *angolensis*

BOCAGE on the basis of extent of web, rugosity of dorsal skin, length of leg, and color. But HEWITT noted that certain series of « *fuscigula* » resembled « *angolensis* » and certain series of the latter resembled the former. Furthermore, his two forms did not occupy separate regions of South Africa. It now appears that HEWITT's forms were typological in conception rather than « biological ».

This impression is strengthened by examination of the characters HEWITT used. The toes of *angolensis* were said by HEWITT to be « ... two thirds webbed or a little more », while those of *fuscigula* were « ... nearly entirely webbed ». If a difference in webbing does exist, it requires sharper definition especially when, as HEWITT indicates, the difference is not great. Again the dorsal skin in *angolensis* had « ... narrow interrupted lines » whereas in *fuscigula* the skin was « ... smooth or with elongate warts ». The distinction between an elongate wart and narrow interrupted lines is a fine one. HEWITT determined the difference in leg length by the customary but unreliable method of adpressing the limb against the body. Analysis of HEWITT's color distinction shows a gradation from one extreme to the other.

The Upemba series exhibits all the color variations of both forms as defined by HEWITT. Also included in this large sample are frogs with the area between the dorsolateral folds smooth and others with short glandular ridges in that region. The amount of webbing, however, varies less in the Upemba frogs than in HEWITT's material.

A similar typological approach seems to have prevailed in subsequent literature. LOVERIDGE (1933) presents a key to the forms of *fuscigula*, including *chapini* NOBLE. However, plotting the East African localities given by LOVERIDGE (1933, 1942, 1953) for the three forms shows them all to occur within a distance of 200 kilometers. If we add HEWITT's localities (1911), which LOVERIDGE seems to accept, the area of overlap for *angolensis* and *fuscigula* extends from Uganda to the Cape of Good Hope and half the east-west width of Africa.

LOVERIDGE (1933) expresses the opinion that *chapini* is a forest form and, by implication, that the others are open country forms. PARKER (1936 A), MERTENS (1940 A, 1955), and other authors have followed LOVERIDGE. The fact that « *chapini* » and « *angolensis* » have been collected at the same localities in Kenya (LOVERIDGE, 1936) and Tanganyika (MERTENS, 1940 a) has been explained away by assuming that specimens of the former were from local forests and the latter from surrounding savanna. Yet LOVERIDGE (1942) relates catching *angolensis* in forest and (1936 A) identified a large series (CNHM 12195-202, 12210-23) from the forests of Ruwenzori as *angolensis*.

The distribution records in the literature are sufficient evidence that the variation subsumed by the trinomials is not geographic. The facts

that several authors have found so-called forest and savanna forms in one locality and that the « savanna » frog has been collected in forest country demonstrate that the variation is not ecological. We are left then with the conclusion that what is involved is individual variation, that these subspecies are no more than morphological types.

Comparison of the Upemba sample with 22 from Ruwenzori, 28 from the Transvaal, and 31 from Angola exposes some geographic variation in extent of web. If the number of phalanges of the first toe distal to the maximum excision of the membrane between the first two toes is counted, the Upemba frogs have somewhat more extensive webbing (see Table 8). Similarly, the Upemba series has more web along the fifth toe. The Ruwenzori frogs have the least extensive web.

TABLE 8. — **Extent of web in *Rana fuscigula*.**

Locality	Number of phalanges of first toe beyond the excision of web						Number of phalanges of fifth toe free of web	
	1	1 1/4	1 1/3	1 1/2	1 2/3	2	1/2	1
	Number of individuals							
Upemba	3	3	2	5	1	0	14	0
Ruwenzori	0	0	0	0	6	4	0	10
Transvaal	0	0	1	7	3	0	6	5
Angola	0	0	2	4	3	0	3	1

Males of *fuscigula* during the breeding season have spinules (described in detail below) on the chin and, usually, across the rear of the abdomen. Males from Ruwenzori lack the abdominal spines though the abundance of these structures elsewhere on the body and the nuptial pads indicate that secondary sex characters were at the height of their development. As will be shown below in the section on secondary sex characters, very large males (over 60 mm) of all samples lack abdominal spines, but the Ruwenzori males are all in the size range (under 55 mm) in which these spines are developed in other populations.

Because no other geographic variation is evident in samples available to us and because the forms in the literature are not true geographic races, we do not recognize any subspecies of *fuscigula*.

Diagnosis. — Habitus moderately stocky; head obtusely pointed; vomerine teeth in oblique groups usually in contact with antero-median corners of choanae; tympanum distinct, about two-thirds eye diameter, slightly less than distance between eye and nostril; back and sides set with highly variable glandular ridges, usually a dorsolateral ridge; tips of fingers and toes bluntly rounded; first finger equal to or shorter than second; no supernumerary metacarpal tubercles; toes almost fully webbed; fourth toe (in Upemba sample) with one phalanx free of web on lateral border; fifth toe (Upemba sample) usually with half of terminal phalanx free of web; lateral border of fifth toe with a distinct flap or ridge of skin; no external metatarsal tubercle.

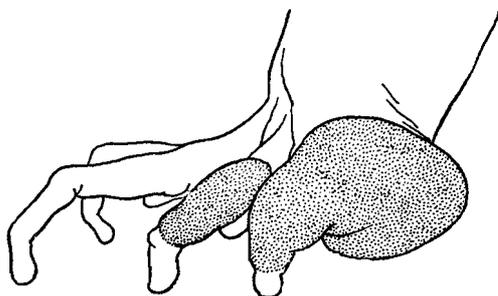


FIG. 21. — Nuptial pad of *Rana fuscigula* from the Parc National de l'Upemba ($\times 3$).

An obscure dark interorbital bar; back and dorsal surfaces of legs with irregular black spots that may be obscure in preserved material; underside of head with faint brown suffusion, a dark network, or solid brownish black; a distinct bar across front of arm insertion; chest, abdomen, and undersides of legs cream-colored.

Secondary sex characters. — Although the size ranges of the two sexes overlap very broadly, the females are distinctly larger, the means of snout-vent being 63.65 ± 0.96 mm (162 specimens) for Upemba females and 50.52 ± 0.65 mm (236 specimens) for Upemba males. The smallest female containing pigmented ova measures 48.8 mm, snout to vent, and the largest female 103.8 mm. This compares with the males' range of 41.4 mm (the smallest with developed nuptial pads) to 88.6 mm.

The nuptial pads at the height of their development (Fig. 21) cover the dorsal and median surfaces of the first finger, from its base to the beginning of the terminal phalanx, and the dorso-median surface of the second finger over the basal phalanx. At this stage the pads consist of brownish or yellowish clusters of spinules. The male prepollex is enlarged

and, though it does not pierce the skin, gives the inner finger a swollen appearance. As is usual in frogs, the pad develops first on the inner finger, and then on the second.

The dorsal surfaces of males are covered with whitish spinules. Some females have similar structures on the hind limbs but their visibility in preserved material depends on the quality of preservation. In males these spinules are uniformly dense except on the dorsal surface of the upper arm where they are less numerous. The development of the dorsal spinules is independent of seasonal changes, but similar asperities on the lower jaw and abdomen are not so constant. A male that, judging by the nuptial pad, is in breeding condition has a band of spinules under the lower jaw and, depending on the size of the frog, has the posterior half or third of the abdomen covered with them. At the height of development, the abdominal and lower lateral spinules are larger than those elsewhere on the body.

Male *fuscigula* also have subgular vocal sacs. The round openings are located on both sides of the floor of the mouth. The development of the vocal sacs relative to the other sex characters is the same as observed in Upemba *Rana (Ptychadena)*, i.e., the vocal sacs appear before the other structures and never regress. Of 158 adult-sized males, fourteen with vocal sacs lack the other secondary sex characters. Three have neither vocal sacs nor any other secondaries. All males having nuptial pads or ventral asperities in any stage of development also have vocal sacs.

Certain variations in the ventral spinules seem to be associated with age. The size frequency distribution of Upemba males, presented in Table 11, shows a distinct bimodality. It is a reasonable assumption that the larger group centering around 75 mm consists of older individuals. Not all males having well-developed nuptial pads have abdominal spinules. However, as the data of Table 9 show, abdominal spinules are characteristic of the younger group only. The use in Table 9 of the double criterion of nuptial pads and spinules on the lower jaw confines the query to sexually

TABLE 9. — **Distribution of Upemba male *Rana fuscigula* having abdominal spinules with respect to snout-vent lengths. All males have nuptial pads and asperities on the lower jaw and were collected March-June.**

Snout-vent (mm)	Abdominal spinules	
	present	absent
40-60	56	2
61-90	0	18

competent males and the restriction of the samples to the period March through June (the interval in which all the larger males were collected) eliminates seasonal variation as a factor. We have already (p. 50) noted the absence of abdominal spinules in even small males from Ruwenzori.

Ecological notes. — LOVERIDGE (1933, 1936, 1942, 1953) reports *fuscigula* from swift streams in forest or open country in East Africa. CURRY-LINDAHL (1956) found *fuscigula* to be abundant at the edges of both ponds and streams in forested country around Lake Kivu and in Ruanda. South African (HEWITT, 1911) and Angolan localities (PARKER, 1936 A) place this species in scrub savanna and grassland, while NOBLE's record (1924) is in the lowland rain forest.

Rana fuscigula has been recorded from near sea level in South Africa (HEWITT, 1911) to 2,200 m in East Africa (LOVERIDGE, 1933). The large Upemba series has the following altitudinal distribution.

Meters.	Specimens.
585- 750	51
751-1,000	45
1,001-1,250	491
1,251-1,500	59
1,501-1,750	233
1,751-1,860	474

Sexual activity of Upemba *fuscigula* does not have the same seasonal cycle as that observed in the *Rana (Ptychadena)* of this collection (see p. 101). As shown in Table 10, during the dry season (May through September), all of the adult-sized males have fully developed secondary sex characters whereas only three-fourths of the wet season males are in that stage. This pattern is radically different from that of Upemba *Rana porosissima* (p. 101) in which fully developed secondary sex characters appear only in males collected during the wet season.

Similarly, from the monthly distribution of female *fuscigula* having pigmented ova (Table 10), a picture emerges of acyclic sexual competence. The reproductive physiology of both sexes of *fuscigula* are different from those of, for examples, *Rana oxyrhyncha* (p. 95), a species more abundant below 1,000 m in the Upemba, and *Rana porosissima* (p. 100), which is more common above 1,500 m.

Rana fuscigula is known to have an extensive size range (LOVERIDGE, 1933) and this is borne out by the present series. But, as shown in Table 11, large individuals are only rarely encountered above 1,500 m though other authors e.g. (LOVERIDGE, 1936, 1953), have reported a few large (over 80 mm) specimens from such heights. An explanation of this differential distribution is not immediately evident. It is unreasonable to say that elevations above 1,500 m do not provide a suitable habitat because most of our material comes from those heights.

TABLE 10. — Monthly frequency of adult *Rana fuscigula* from the Upemba in various stages of sexual competence.

	Males (*)			Females (**)		
	Development of secondary sex characters			Stage of ova		
	Complete	In-complete	Absent	Pigmented	Intermediate	Immature
January	3	0	0	0	0	0
February	0	0	4	0	1	4
March	17	3	8	24	2	2
April	23	7	0	19	1	7
May	17	0	0	21	0	0
June	17	0	0	26	5	1
July	14	0	0	19	1	3
September	0	0	0	0	0	3
October	19	6	4	11	1	2
November	15	0	1	9	0	1
Summary :						
Dry season (May-September) ..	48	0	0	66	6	7
Wet season (October-April) ...	77	16	17	63	5	16

(*) All males exceeding 41.4 mm, the smallest with fully developed sex characters.

(**) All females exceeding 48.8 mm, the smallest containing fully developed ova.

The other phenomenon illustrated in Table 11 is a distinct bimodality in the frequency distributions of both sexes. We have already referred (p. 52) to the groups as representing different ages though we do not assume that the large frogs compose a single age class. However, the small frogs may; presumably they are young adults in their first breeding year. Bimodal size frequency distributions are characteristic of populations having a restricted breeding period and sampled over a narrow time range. But, as Table 10 shows, our series of *fuscigula* satisfies neither requirement. Differential susceptibility of the various size classes to predation does not provide a reasonable explanation of bimodality because the infrequent class of males is the same size (56-65 mm) as the most abundant females. A solution to this problem is clearly not available in the laboratory.

TABLE II. — Size frequency distribution by altitude of adult *Rana fuscigula* from the Upemba.

Snout-vent (mm)	Males				Females				Total
	Below 1,000 m	1,000-1,500 m	Above 1,500 m	Total	Snout-vent (mm)	Below 1,000 m	1,000-1,500 m	Above 1,500 m	
41-45	7	14	43	64	55	7	9	23	39
46-50	1	75	42	118	56-60	3	10	30	43
51-55	2	21	1	24	61-65	2	24	16	42
56-60	0	1	0	1	66-70	2	7	3	12
61-65	0	3	0	3	71-75	2	3	0	5
66-70	2	3	0	5	76-80	3	1	0	4
71-75	3	3	1	7	81-85	1	1	0	2
76-80	1	6	0	7	86-90	0	1	0	1
81-85	0	5	0	5	91-95	3	2	0	5
86-90	1	1	0	2	96-100	1	6	0	7
					101-105	0	2	0	2
Totals	17	132	87	236		24	66	72	162
Means	57.41 ± 3.67	52.85 ± 0.94	45.79 ± 0.40	50.52 ± 0.65		68.63 ± 3.02	68.08 ± 1.76	57.50 ± 1.59	63.65 ± 0.96
	Minimum = 41.4			Maximum = 88.6		Minimum = 48.8			Maximum = 103.8

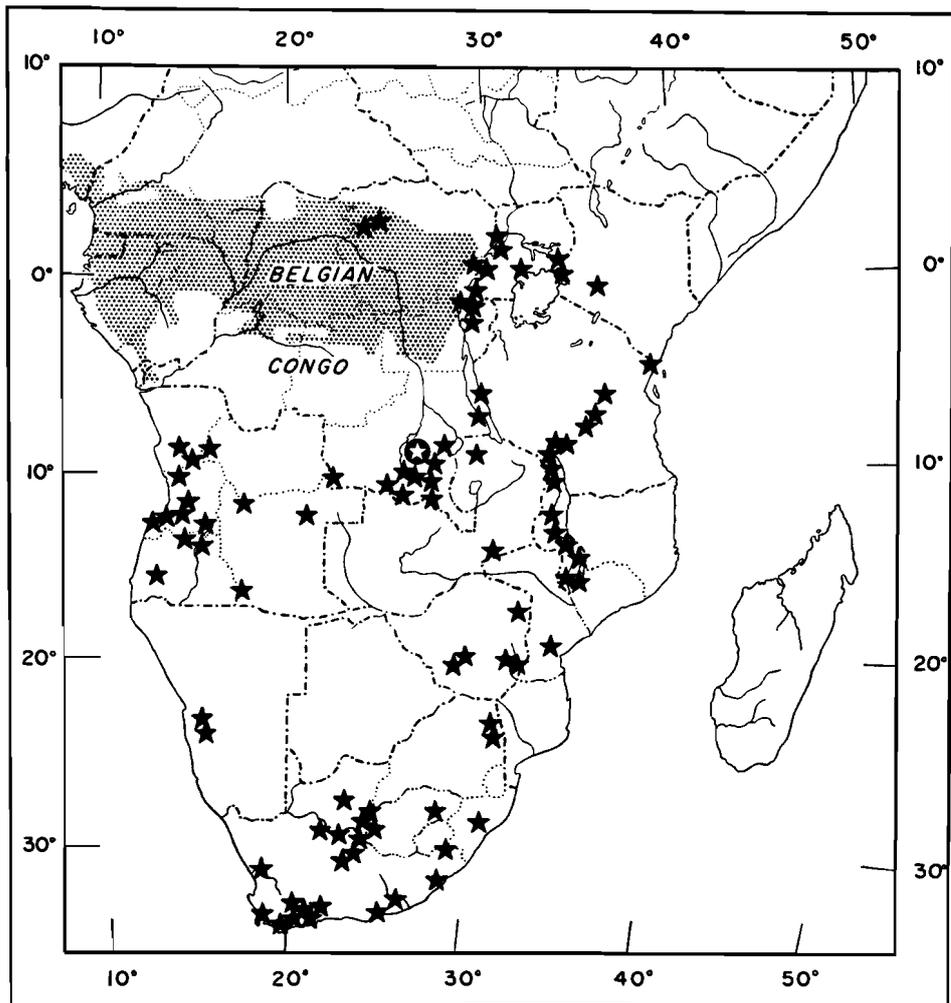


FIG. 22. — Distribution of *Rana fuscigula*.
Parc National de l'Upemba indicated by symbol with open star.

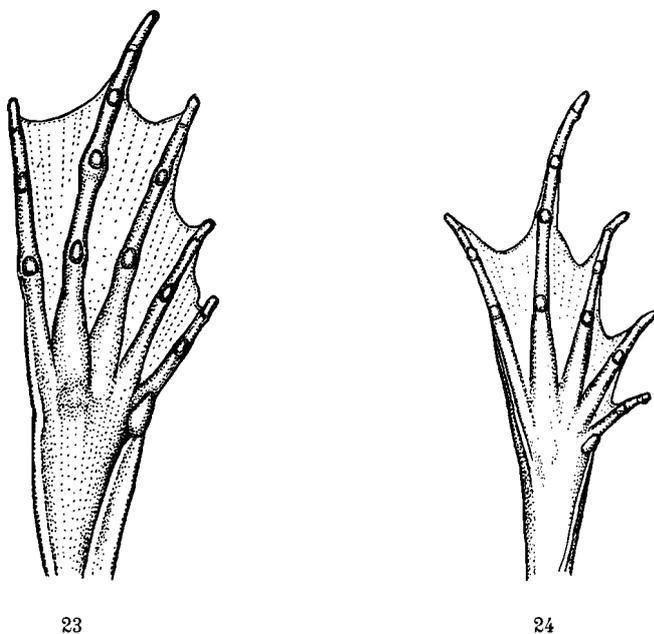
Range. — *Rana fuscigula* is distributed throughout Africa south of a line connecting Kenya with northern Angola (Fig. 22).

Upemba localities and specimens :

Babagi (6); Bowa (15); Bwalo (15); Difiriji (11); Dipidi (10); Ganza (8); Kabenga (134); Kabwe (21); Kafwe (7); Kagomwe (4); Kakolwe (1); Katamshya (2); Kamitungulu (12); Kamitunu (10); Kande (10); Kankunda (38); Kanonga (2); Karibwe (94); Kasandendeke (1); Kaswabilenga (2); Kateke (8); Kavizi (2); Kayumbwe (2); Kaziba (4); Kiamakoto (46); Kimapongo (1); Kimiala (19); Kipangaribwe (63); Loie (1); Lukawe (15); Lukorami (2); Lupiala (5); Lusinga (476); Mabwe (1); Masombwe (42); Mukelengia (1); Mukukwe (3); Munte (3); Mware (6); Pelenge (249); Tumbwe (1).

Subgenus **PTYCHADENA.**

The work of LAURENT (1954) demonstrates that many forms of this remarkable group remain to be discovered. In addition to four of the new species found by LAURENT, the Upemba collection includes two others described for the first time below. Unfortunately the literature prior to 1950 cannot be relied upon. As the papers of GUIBÉ and LAMOTTE (1953, 1954, 1955, 1955 A) have shown, many good species have been erroneously

FIG. 23. — Webbing of *Rana subpunctata* ($\times 1\frac{1}{2}$).FIG. 24. — Webbing of *Rana taenioscelis* ($\times 3$).

buried in the synonymies of other forms, while still others, e.g., *longirostris*, have been described under several names (GUIBÉ and LAMOTTE, 1954). In the course of this study, we examined the series identified by NOBLE (1924) as *mascareniensis* and found not only that species, but also *maccarthyensis*, *taenioscelis*, *uzungwensis*, and *mossambica*.

Some measure of the remarkable ecological success of *Ptychadena* is given by the fact that thirteen full species occur in the Parc National de l'Upemba. Because of the unreliability of the literature, a key to the Upemba species follows.

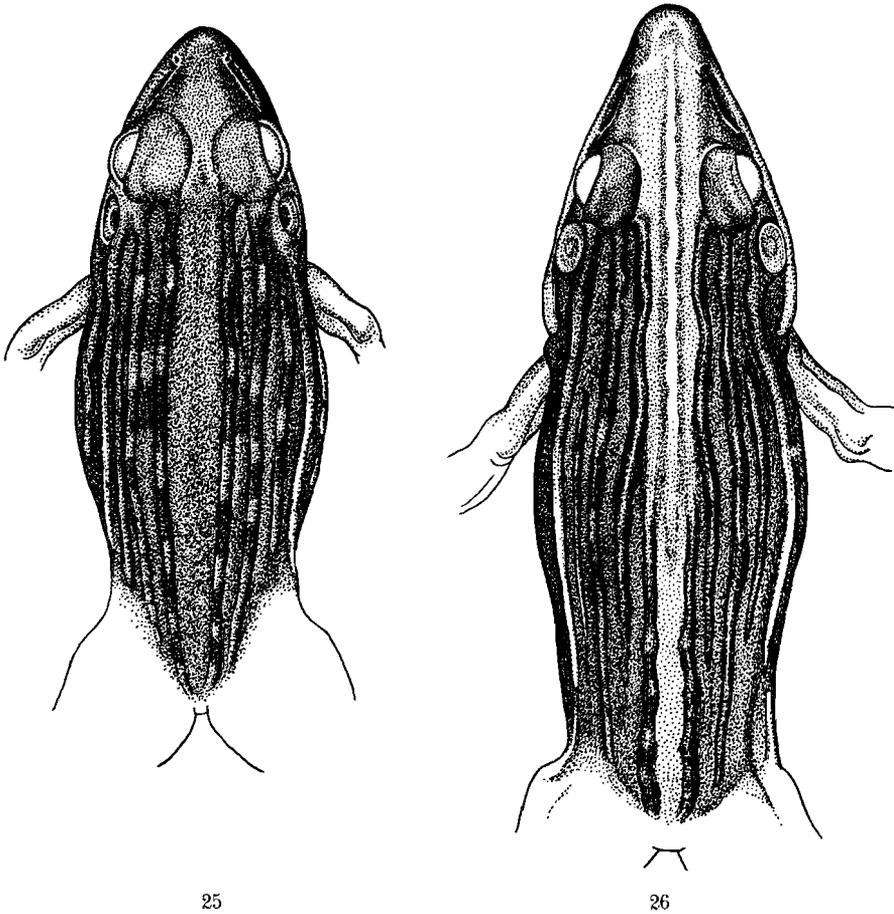


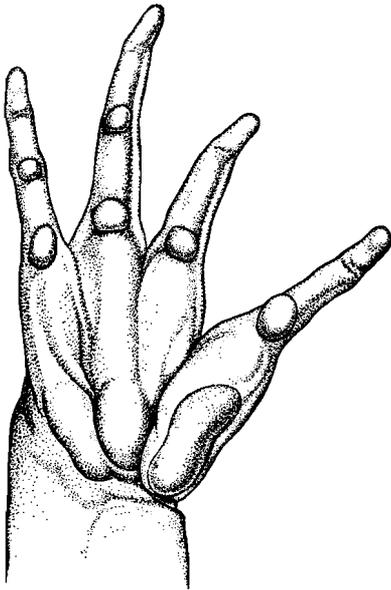
FIG. 25. — Dorsal skin folds of *Rana mascareniensis* ($\times 2$).

FIG. 26. — Dorsal skin folds of *Rana chrysogaster guibei* ($\times 3$).

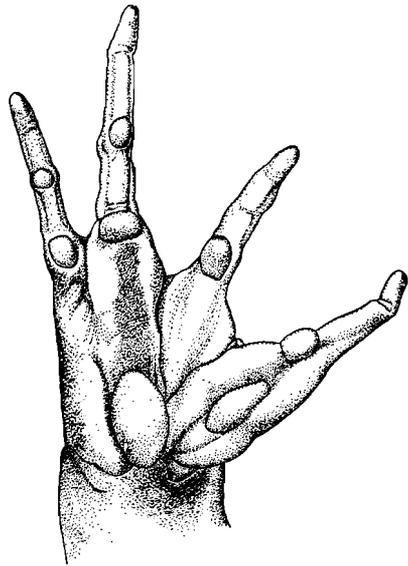
KEY TO UPEMBA SPECIES OF *RANA* (*PTYCHADENA*).

- 1A. Less than one phalanx of fifth toe free of web (Fig. 23) 2
 B. One or more phalanges of fifth toe free of web (Fig. 24) 7
- 2A. Mid-dorsal pair of skin folds continuous from occiput to supra-anal region (Fig. 25) 3
 B. Mid-dorsal pair of skin folds interrupted or present on posterior half of body only (Fig. 26) 6
- 3A. At most one transverse row of spots on back *obscura*.
 B. At least two transverse rows of dorsal spots 4

- 4A. Posterior face of thigh with light vermiculation or network
oxyrhyncha.
- B. Posterior face of thigh with distinct longitudinal light stripes 5
- 5A. Median edges of second and third fingers with a distinct, narrow fringe of skin (Fig. 27); gular pouch openings oblique to mandible
subpunctata.



27



28

FIG. 27. — Ventral view of hand of *Rana subpunctata* (×4).

FIG. 28. — Ventral view of hand of *Rana mascareniensis* (×4).

- B. Median edges of second and third fingers without a fringe of skin (Fig. 28); gular pouch openings parallel to mandible
mascareniensis.
- 6A. An outer metatarsal tubercle and, usually, a row of small tubercles on fourth metatarsal
frontalis.
- B. No outer metatarsal tubercle and no row of tubercles on fourth metatarsal
superciliaris.
- 7A. Mid-dorsal pair of skin folds interrupted or present only posteriorly (Fig. 26)
chrysogaster guibei.

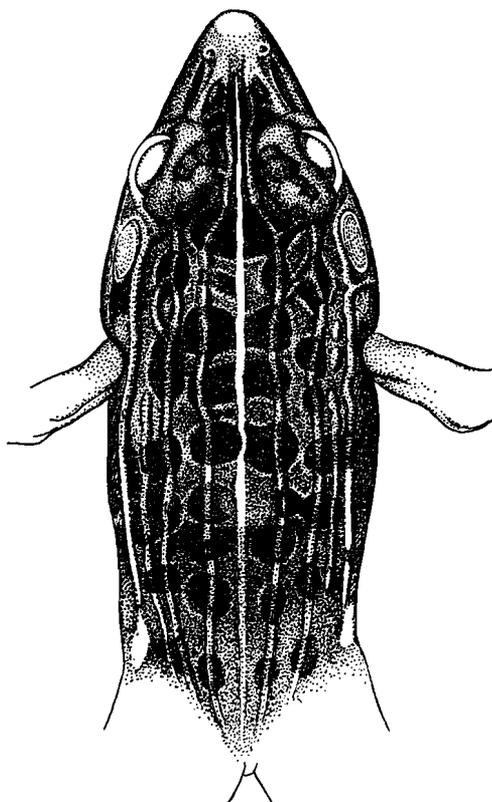


FIG. 29. — Dorsal skin folds of *Rana unguensis* ($\times 3$).

- B. Mid-dorsal pair of skin folds continuous from occiput to anal region 8
- 8A. Mid-dorsal pair of skin folds extending forward on to snout (Fig. 29) 9
- B. Mid-dorsal pair of skin folds ending between or behind eyes 10
- 9A. Posterior face of thigh with longitudinal light stripes ... *taenioscelis*.
- B. Posterior face of thigh with light network or spots *zungwensis*.
- 10A. At least two phalanges of fifth toe free of web 11
- B. Less than two phalanges of fifth toe free of web 12
- 11A. Posterior face of thigh with longitudinal light stripes *upembae*.
- B. Posterior face of thigh with rows of light spots *ansorgei*.

- 12A. No outer metatarsal tubercle 13
 B. Outer metatarsal tubercle present 14
- 13A. Posterior face of thigh with round light spots *porosissima*.
 B. Posterior face of thigh with longitudinal light stripes
mascareniensis.
- 14A. Dorsal face of tibia with longitudinal light line *porosissima*.
 B. Tibia without longitudinal light line 15
- 15A. Back without dark spots or with one or two transverse rows of
 spots *obscura*.
 B. Back with more than four transverse rows of dark spots
grandisonae.

13. — *Rana ansorgei* BOULENGER.

Rana ansorgii BOULENGER, 1905, Ann. Mag. Nat. Hist., (7), 16, p. 107, pl. 4,
 fig. 1 — between Benguella and Bihé, Angola.

Taxonomic notes. — In appearance this well defined species resembles both *uzungwensis* LOVERIDGE and *porosissima* STEINDACHNER, but has less extensive webbing than either and differs in certain aspects of coloration. The three species occur at the same localities in the Upemba.

The Upemba series differs slightly from the type in the color pattern on the rear face of the thigh. In the type, which we have examined, this surface is marbled whereas in the Upemba frogs it bears small light spots.

In the greatly reduced webbing, elongate snout, and size *ansorgei* resembles *stenocephala* BOULENGER, of which we have examined two cotypes. But the coloration of *stenocephala* is very different. The lower jaw of *ansorgei* bears a broad continuous dark band that reaches the lower lip.



FIG. 30. — Pattern on mandibles
 of (left) *Rana stenocephala* and (right) *Rana ansorgei* (×2).

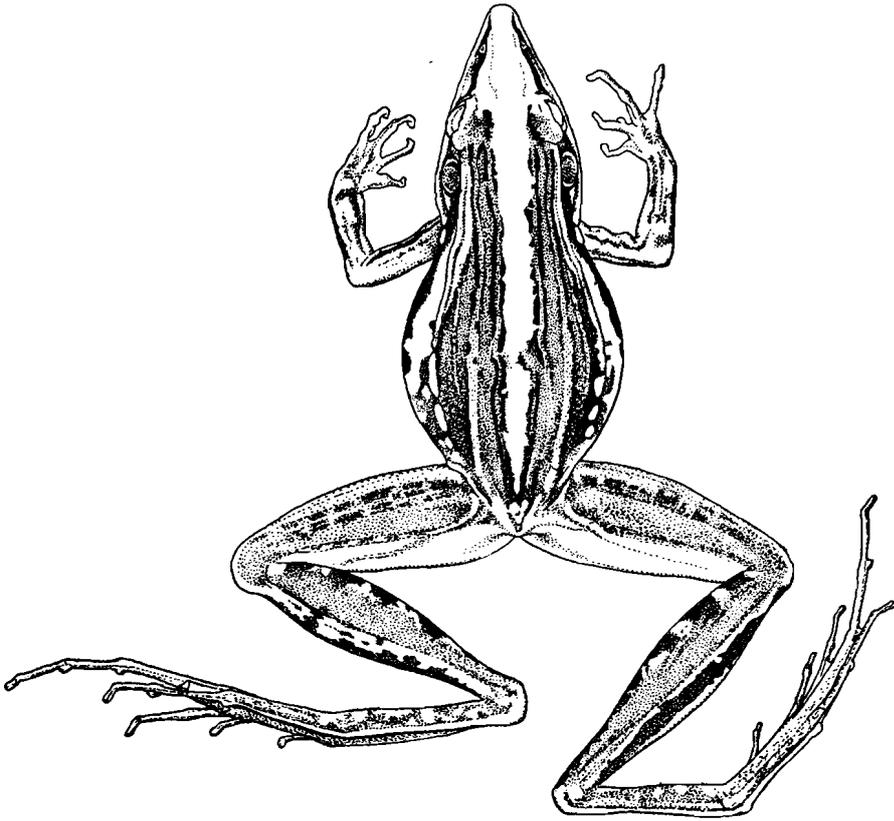


FIG. 31. — Dorsal view of *Rana stenocephala* ($\times 1\frac{1}{2}$).

Although *stenocephala* (Fig. 30) too has a black stripe on the mandible, it is much narrower than that of *ansorgei* (Fig. 30) and widely separated from the mouth by a broad light area. The dark markings on the hind limbs of *stenocephala* (Fig. 31) are arranged longitudinally with a long dark streak along the anterior face of the thigh, a similar one along the outer edge of the calf, and a row of spots on the inner edge of the calf. The mid-dorsal surface of the calf has no dark markings. On the other hand, *ansorgei* (Fig. 32) has transverse bars on the legs, those of the calf usually continuous across the dorsal surface, and no longitudinal dark streak on the thigh.

Similar differences are shown by the pattern of the body (Figs. 31, 32). *Rana stenocephala* has a broad oblique dark band on the sides and, though *ansorgei* also has dark lateral markings, these are in the form of square spots. On the back, too, *stenocephala* has longitudinal dark streaks whereas *ansorgei* has square spots.

Diagnosis. — Body moderately slender; legs slender; head pointed; snout strongly projecting; nostril mid-way between eye and tip of snout or closer to eye; vomerine teeth in short transverse groups, in contact with antero-median corners of choanae; tympanum distinct, one-half to two-thirds eye diameter, shorter than eye-nostril distance; back with 8 longitudinal folds, the mid-dorsal pair usually beginning between the anterior borders of the orbit and continuous to anal region (Fig. 32); tips of fingers and toes bluntly rounded; first finger equal to or slightly shorter than second, which is equal to fourth; supernumerary metacarpal tubercles present, distinct; toes about half webbed; fourth toe with $3\frac{1}{3}$ to $3\frac{1}{2}$ phalanges free of web on lateral border; fifth toe with 2 phalanges free; a small proportion of individuals with a small, round, external metatarsal tubercle; a round light spot present in the corresponding position in other individuals; a row of feeble, distinct, small tubercles present or absent on fourth metatarsal.

Back with alternating rows of squarish black spots, each of which is larger than tympanum; almost all specimens with a thin, light vertebral line or (more rarely) a vertebral band; thigh and tibia without light lines on dorsal surfaces; posterior face of thigh chocolate brown with longitudinal rows of small, round, light spots; 4 to 6 usually uninterrupted black bars on tibia (Fig. 32); usually 3 black tarsal bars; underside of foot uniformly brown except for row of light tubercles; lower jaw (Fig. 30) with a continuous black band, narrow near chin and broadening posteriorly; a pair of prefrontal spots occasionally present.

Secondary sex characters. — The vocal sac apparatus is typical of *Rana* (*Ptychadena*). The openings of the gular pouches begin below the center of the eye and run obliquely to near the ventral border of the insertion of the arm. In four males the openings are 0.18 to 0.21 of the snout-vent length. The skin in the gular pouches is intense black.

No males were collected during the breeding season and, consequently, our specimens do not have nuptial pads or other nuptial asperities.

Females are evidently larger than males but the extent of the difference cannot be determined from the present sample because no female contains ripe ova, preventing determination of maturity. The four males with gular pouches measure 30.6-33.3 mm, and 10 females 32.4-37.3 mm snout to vent. LOVERIDGE (1953) records a male 36 mm and females 35-43 mm.

Ecological notes. — All records of *ansorgei* are from south of the rain forest areas. However, one locality (PARKER, 1931) is in dense gallery forest and three others (LOVERIDGE, 1933, 1953; PARKER, 1936 A) in montane forest. The region between Benguella and Bihé, Angola (the type locality) includes montane and deciduous broadleaved forests and tree savanna. Several of LOVERIDGE's localities (1953) are in tree savanna.

The species has a moderately high altitudinal distribution. Literature records range from 610 to 1,830 m. The Upemba series was collected



FIG. 32. — Dorsal view of *Rana ansorgei* from Parc National de l'Upemba ($\times 2$).

between the elevations of 1,250 and 1,750 m, with three-fourths of the material from the lowest elevation and only one-twentieth from the highest.

LOVERIDGE (1953) collected *ansorgei* along small streams and in grassy swamps.

Range. — From western Angola (BOULENGER, 1905) to Zululand (PARKER, 1931) and Uganda (LOVERIDGE, 1936).

Upemba localities and specimens :

Buye-Bale (2); Kabwe (11); Pelenge (28).

14. — *Rana chrysogaster guibei* LAURENT.

Ptychadena chrysogaster guibei LAURENT, 1954, Ann. Mus. Roy. Congo Belge, **34**, p. 23 — Muita, Luemba, Angola.

Taxonomic notes. — This series of frogs resembles *chrysogaster guibei* LAURENT very closely. They differ from the Congo paratypes (Musée Royal du Congo Belge 175, 627, 36222, 36289-90), which we have examined, in two details of coloration. Whereas all the paratypes have a distinct longitudinal light line on the dorsal surface of the tibia, only 2 (4 %) of the present series have this line. Also, the black crossbars of the tibia are narrowly interrupted in the Upemba frogs but broadly so in the Congo paratypes.

The great similarity in other characters enumerated in the diagnosis (see below) argues against considering the Upemba frogs distinct from the subspecies *guibei*.

The range of the latter is the open country of northeastern Angola and southern Belgian Congo, and one locality given by LAURENT (1954), Lofoi, is approximately 100 kilometers from the Parc National de l'Upemba.

This form bears a slight resemblance to *porosissima* STEINDACHNER but differs in the coloration of the thighs (posteriorly with round spots in *porosissima*) and tibia (bars not interrupted in *porosissima*), and in the short median pair of sacral folds (absent in *porosissima*).

Diagnosis. — Body and limbs moderately slender; head pointed, snout strongly projecting; nostril mid-way between eye and tip of snout or nearer to eye; vomerine teeth in transverse or slightly oblique groups, in contact with antero-median borders of choanae; tympanum distinct, $\frac{3}{4}$ to $\frac{4}{5}$ diameter of eye, much shorter than eye-nostril distance; back anteriorly with 6 longitudinal skin folds, posteriorly with 8-10; median pair of skin folds interrupted or with a short mid-dorsal pair of folds in sacral region (Fig. 26); anteriorly median pair of folds ending behind interorbital; tips of fingers and toes bluntly rounded; first, second, and fourth fingers subequal, or first slightly shorter; supernumerary metacarpal tubercles

usually present; toes about two-thirds webbed; fourth toe with 3 or, less often, $3\frac{1}{3}$ phalanges free of web on lateral border; fifth toe with $1\frac{1}{2}$ to 2 phalanges free; external metatarsal tubercle present; a row of small tubercles under fourth metatarsal in $\frac{4}{5}$ of specimens.

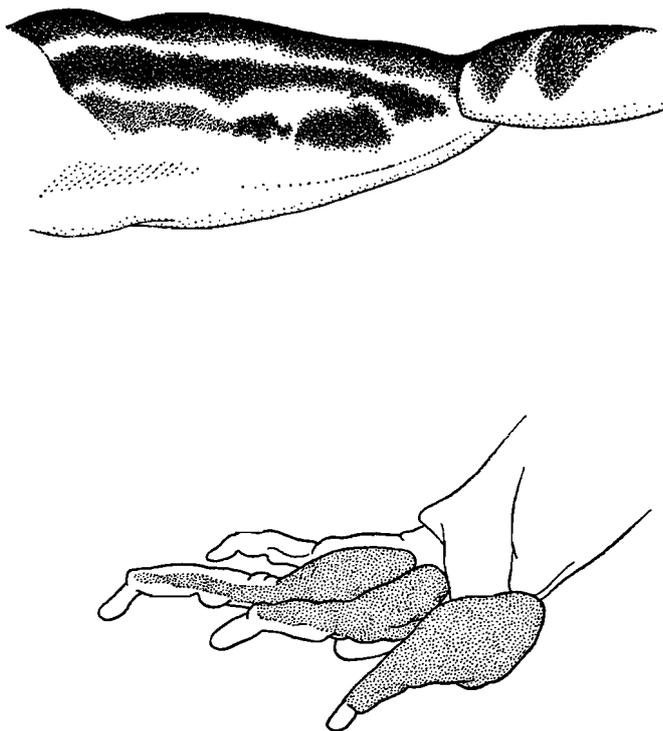


FIG. 33. — *Rana chrysogaster guibei* from Parc National de l'Upemba.
Above, posterior face of thigh ($\times 4$). Below, nuptial pads ($\times 8$).

Back with alternating rows of black oblong spots, each usually longer than diameter of tympanum; a broad mid-dorsal light band with a more or less distinct light vertebral line (Fig. 26); dorsal surfaces of tibia and thigh with or without (in Upemba series) longitudinal light lines; posterior face of thigh dark brown with two regular light longitudinal stripes (Fig. 33); tibiae with 4 to 6 interrupted crossbars; 2 or, occasionally, 3 tarsal bars; underside of foot uniformly dark brown except for light metatarsal and subarticular tubercles; lower jaw usually with a continuous dark streak; throat and anterior portion of abdomen suffused with dark brown to varying degrees.

Secondary sex characters. — The nuptial pads (Fig. 33) are cream-colored or dusky velvety clusters of spinules. At their maximum development the pads cover the dorsal and median surfaces of the first finger from its base to the beginning of the last phalanx, the dorsal surface of the second finger from its base to the beginning of the last phalanx, and a tapering area of the dorso-median surface of the third finger over the metacarpal and proximal phalanx. Males with nuptial pads developed to this degree have small, translucent, colorless spinules distributed over the throat and chest and whitish spinules on sides and back. Males in which the pad does not extend beyond the third metacarpal usually lack the ventral spinules. Neither type of spinule is present in males without pads. Characteristic of the subgenus, only males with fully developed gular pouches have nuptial pads.

The vocal sac apparatus consists of paired vocal sacs and corresponding gular pouches lined with black or black and gray wrinkled skin. The slit-like openings of the pouches are oblique to the lower jaw, beginning below the center of the eye and ending near the ventral border of the insertion of the arm. In six males with nuptial pads, the length of the opening varies from 0.13 to 0.18 of the snout-vent length (mean 0.159 ± 0.007).

Mature females are larger than mature males. LAURENT (1954) gives 49 mm as the maximum snout-vent length of females and 35.5 mm as the maximum in males. Only the three largest females of the Upemba series contain pigmented ova and they measure 45.1-47.7 mm. The six adult Upemba males range from 35.5 to 37.5 mm (mean = 36.55 ± 0.33 mm).

Ecological notes. — The twenty-four Upemba specimens were collected between 585 and 700 m above sea level. The nominate form of this species is apparently restricted to higher elevations, the localities given for *c. chrysogaster* by LAURENT (1954) ranging in altitude from 1,650 to 2,600 m. The recorded localities of *guibei* all lie south of the rain forest belt in savanna country (Fig. 34).

The three females with pigmented ova were collected in December and the six males with nuptial pads in the months of November, December, and February. The males in the adult size range (35.1, 36.8 mm) collected in October had fully developed gular pouches but no nuptial pads. Evidently the breeding season does not begin until November.

Range. — Known only from northeastern Angola and southern Belgian Congo (LAURENT, 1954).

Upemba localities and specimens :

Kande (1); Kanonga (1); Lupiala (2); Mabwe (20).

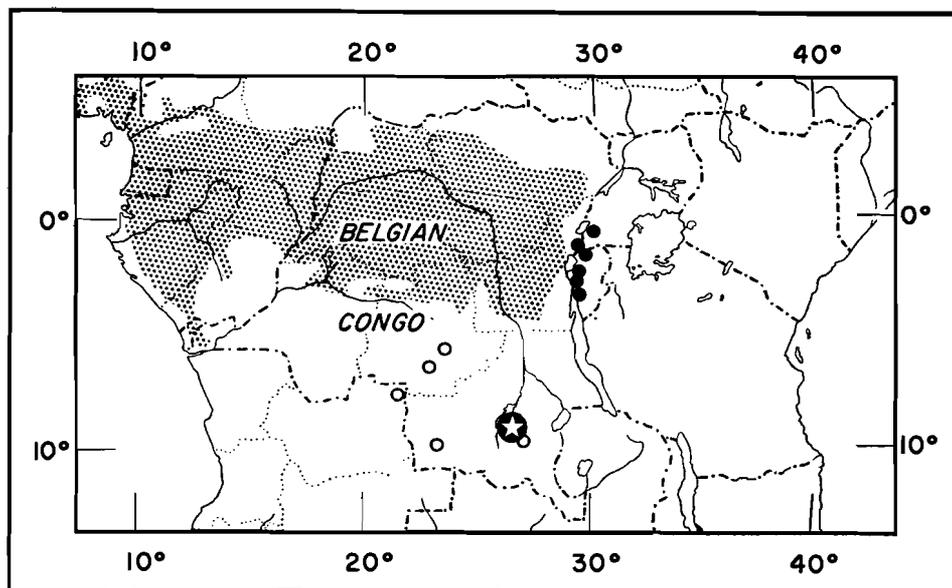


FIG. 34. — Distribution of *Rana chrysogaster*.

R. chrysogaster chrysogaster shown by solid circles; *R. c. guibei* by hollow circles.
Parc National de l'Upemba indicated by symbol with open star.

15. — *Rana frontalis* LAURENT.

Ptychadena frontalis LAURENT, 1954, Ann. Mus. Roy. Congo Belge, **34**, p. 26, pl. 4, fig. 8, pl. 5, fig. 2 — Kiambi, Tanganika, Belgian Congo.

Taxonomic notes. — The large series of Upemba *frontalis* agree with LAURENT's description (1954) and with the type series, which we have seen, in all significant details. We have confirmed the difference in the pectoral girdles of *floweri* BOULENGER and *frontalis* mentioned by LAURENT. Both *floweri* and *frontalis* are characterized by short legs and feet and are similar in habitus, coloration, and arrangement of skin folds. But, in addition to the difference in ossification of the clavicle, the two forms differ in the position of the opening of the gular pouch. That of *frontalis* is oblique to the mandible and ends near the ventral border of the insertion of the arm, whereas that of *floweri* is parallel to the mandible, ending near the upper border of the axilla.

Diagnosis. — Body moderately stocky; legs short, stocky; head obtusely pointed; snout projecting; nostril nearer to tip of snout than to eye; vomerine teeth in transverse or slightly oblique series, in contact with antero-median borders of choanae; tympanum distinct, about two-

thirds diameter of eye, shorter than eye-nostril; back with 8 longitudinal folds, the median pair beginning behind interorbital and interrupted in sacral region (Fig. 35); tips of fingers and toes bluntly rounded; first finger slightly longer than second, second equal to or longer than fourth; supernumerary metacarpal tubercles usually present and distinct; toes almost completely webbed; fourth toe with $2\frac{1}{2}$ to $2\frac{2}{3}$ phalanges free of web on lateral border; fifth toe with one-third to one-half phalanx free; a small, round external metatarsal tubercle; usually a row of small tubercles on fourth metatarsal.

Back with rows of alternating, squarish black spots each usually larger than tympanum; only very rarely (less than one percent of individuals) with a light mid-dorsal stripe or line; no light line on dorsal surface of tibia or thigh; posterior face of thigh dark brown with two or three irregular, light, longitudinal stripes (Fig. 35); 4 or 5 dark crossbars on tibia, usually uninterrupted; underside of foot dark brown, often with small light areas at base of web; lower jaw barred with black.

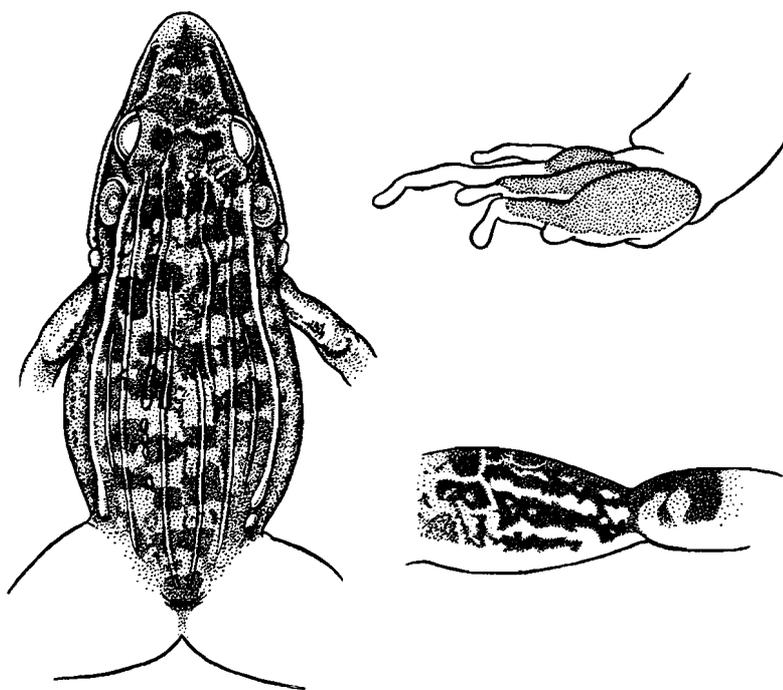


FIG. 35. — *Rana frontalis* from Parc National de l'Upemba.

Left, dorsal view ($\times 2$). Right upper, hand of male showing nuptial pads ($\times 6$).
Right lower, rear face of thigh ($\times 2$).

Secondary sex characters. — Fully developed males have dusky or cream-colored nuptial pads on the entire dorsal and median surfaces of the first finger from its base to the beginning of the last phalanx, on the dorsal surface of the second finger from its base to the beginning of the terminal phalanx, and on an oval area on the dorso-median surface of the third finger not extending beyond the level of the basal subarticular tubercle (Fig. 35). Males in this stage have small, translucent, colorless spinules uniformly scattered over the throat and chest.

The vocal sac apparatus consists of paired vocal sacs and corresponding gular pouches. The openings of the latter are oblique to the mandible and run from below the posterior half of the eye to near the ventral border of the insertion of the arm. The length of the openings varies from 0.15 to 0.21 of the snout-vent in 10 males (mean=0.186±0.005). The wrinkled skin inside the gular pouches is black or, more often, black anteriorly and gray or white posteriorly.

Females are distinctly larger than males. Fifty-five mature females vary from 39.5 to 46.7 mm, snout to vent (mean=42.98±0.20 mm). Forty-two adult males vary from 35.0 to 40.3 mm (mean=36.96±0.18 mm).

Ecological notes. — Reported localities are in the savanna provinces of the southern Congo. One of the Upemba specimens was collected at 620 m and the remaining 432 at 585 m.

Two females, collected in July-August, lack pigmented ova though the frogs are mature in size (see above). The rest of this large sample was taken during the months of November to January. All males had fully developed secondary sex characters and approximately ninety percent of females examined (51/55) had ripe ova.

Range. — The type locality, in southeastern Belgian Congo, is the only other recorded locality.

Upemba localities and specimens :

Mabwe (432); Mwema-Mabole (1).

16. — *Rana grandisonae* LAURENT.

Ptychadena grandisonae LAURENT, 1954, Ann. Mus. Roy. Congo Belge, **34**, p. 11, pl. 1, figs. 2, 5, pl. 3, figs. 1-2, pl. 4, figs. 1, 9 — Muita, Luemba, Angola.

Taxonomic notes. — In the original description, LAURENT (1954) compared *grandisonae* to *macCarthyensis* and called attention to the difference in the extent of webbing, relative length of the tibia, and pattern of the posterior face of the thigh. Although we can confirm the first distinction, the other two differences are not borne out by our examination of several hundred *grandisonae* and seven *macCarthyensis*.

However, we observe the following additional differences between the two species. The two median dorsal skin folds are continuous from the interorbital to the anal region in *grandisonae* but are interrupted in the sacral region of *macCarthyensis* (Fig. 36). Our six *macCarthyensis* males have a large nuptial pad on the distal portion of the lower arm near the

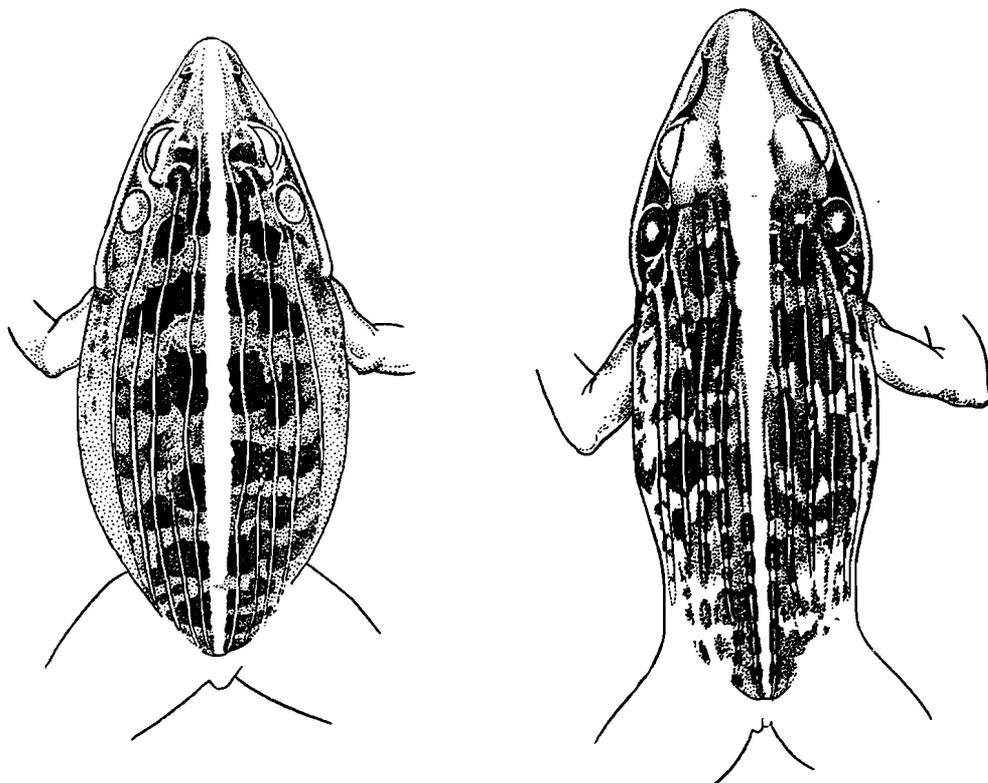


FIG. 36. — Dorsal views of *Rana grandisonae* (left) and *Rana macCarthyensis* (right) (both 2 \times).

base of the first finger; fully developed *grandisonae* males have nuptial pads on the fingers only (Fig. 37). The gular pouch of mature *grandisonae* males is distinctly bicolored, the anterior half of the wrinkled skin being black and the posterior half white. The gular pouch of *macCarthyensis* is either uniformly black or black and dark gray.

The present species also resembles *vernayi* FITZ SIMONS, which has similar webbing and an outer metatarsal tubercle. But *vernayi*, of which we have seen seven half-grown paratypes, has the mid-dorsal skin folds interrupted over the sacrum (as in Fig. 36, right) and lacks the row of small tubercles under the fourth metatarsus.

Rana mossambica PETERS (Fig. 38), though similar to *grandisonae* in habitus, webbing, and position of the gular pouch opening, differs from the latter in the position of the nostril (which is nearer the tip of the snout in *mossambica*), in the shape of the black spots on the back (longitudinally elongate in *mossambica*, squarish or transversely elongate in *grandisonae*), in the color of the gular pouch (not bicolor in *mossambica*), and in the absence of an outer metatarsal tubercle and the row of small tubercles on the fourth metatarsus. Comments on *mossambica* are based on examination of the type and three paratypes from the type locality.

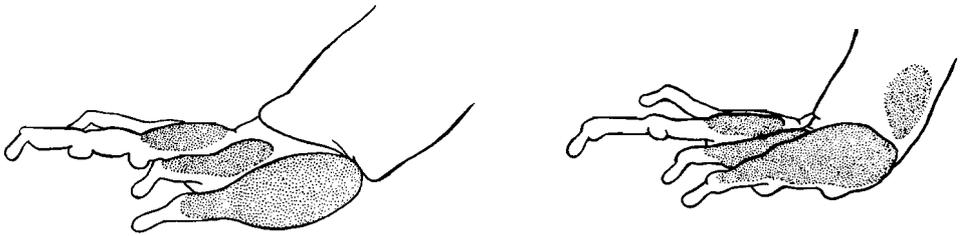


FIG. 37. — Male *Rana grandisonae* (left) and *Rana macCarthyensis* (right) showing nuptial pads on fingers and lower arm ($\times 5$).

Diagnosis. — Body and limbs moderate; head pointed; snout moderately projecting; nostril slightly closer to tip of snout than to eye; vomerine teeth just off a transverse line, in contact with antero-median corners of choanae; tympanum distinct, three-fourths to four-fifths eye diameter, shorter than distance between eye and nostril; back with 8 folds, the mid-dorsal pair ending between the orbits and continuous from interorbital to anal region (Fig. 36, left); tips of fingers and toes bluntly rounded; first finger slightly shorter than second; supernumerary metacarpal tubercles present, distinct; toes about two-thirds webbed; fourth toe usually with 3 phalanges free of web on lateral border; fifth with 1 phalanx free, rarely $1\frac{1}{4}$ free, a small but distinct, round external metatarsal tubercle present; a row of small, light-colored tubercles on fourth metatarsus.

Back with alternating rows of squarish black spots, each of which having the transverse axis subequal to the tympanum; a broad mid-dorsal light band, usually without a lighter vertebral line; thigh and tibia without light line on dorsal surfaces; posterior face of thigh dark brown with longitudinal series of light spots; 4 to 6 black bars on dorsal surface of tibia, bars always interrupted in mid-line; 2 or 3 black tarsal bars; underside of foot uniformly brownish except for light tubercles; lower jaw barred with black.

Secondary sex characters. — The vocal sacs, as in all *Ptychadena*, are paired. The wrinkled skin of the gular pouches is bicolored, black anteriorly and white posteriorly. The extent of the black pigment varies although most commonly the entire posterior half of the pouch is

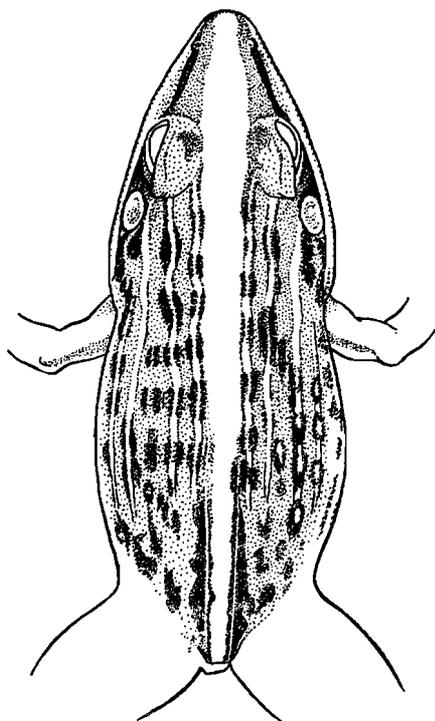


FIG. 38. — *Rana mossambica* PETERS, paratype ($\times 2$).

white. The openings of the gular pouches are oblique to the mouth gape and run from below the center of the eye to the medio-ventral border of the insertion of the arm. In 20 males with fully developed nuptial pads, the slits of the gular pouches vary between 0.16 and 0.21 of the snout-vent length (mean = 0.190 ± 0.001).

The nuptial pads resemble those of other *Rana* (*Ptychadena*) in appearance, consisting of light colored, velvety clusters of minute spines. At their maximum development the pads cover the dorsal and median surfaces of the first finger from its base to the end of the basal phalanx, the dorsal and median surfaces of the second finger from its base to the end of the basal phalanx, and a small oval area near the end of the third metacarpus

on its dorso-median edge (Fig. 37, left). Males with nuptial pads in this condition usually have translucent, colorless, widely spaced spinules on the entire underside of the head and on the chest. These spinules are inconspicuous and very feeble compared to those of male *Rana porosissima*.

The developmental sequence of the male secondary sex characters is as outlined in detail for *porosissima* (p. 99). The vocal sac apparatus (sacs plus gular pouches) appears in ontogeny before the nuptial pads. As shown in Table 12, males may have partially or fully developed gular pouches and completely lack nuptial pads; on the other hand, all males having nuptial pads in any stage of development always have fully developed gular pouches.

TABLE 12. — **Monthly frequency of adult male (*) *Rana (Ptychadena) grandisonae* from the Upemba in various developmental stages.**

Gular pouch	Mature	Mature	Mature	Immature
Nuptial pads	Complete	Incomplete	Absent	Absent
January	51	0	0	0
February	2	0	0	0
March	34	1	0	0
April	22	2	0	1
May	8	3	2	2
June	0	4	3	0
July,	2	0	1	0
November-December	3	0	0	0

(*) All males larger than 33.6 mm, the smallest with fully developed nuptial pads.

Mature females are larger than adult males. Fifty-eight females with pigmented ova measure from 37.5 to 49.4 mm, snout to vent (mean = 42.10 ± 0.32 mm); 122 males with fully developed nuptial pads vary from 33.6 to 43.5 mm (mean = 38.63 ± 0.18 mm). The difference between the means is statistically significant.

Ecological notes. — This little known species has been reported (LAURENT, 1954) only from localities along the southern and eastern borders

of the rain forest. In the Upemba it is primarily an inhabitant of the higher elevations, only 48 of the 603 specimens coming from below 1,500 m. The lowest Upemba record is 900 m. One of LAURENT's localities has an elevation of 1,650 m; the others are on plateaus presumably at altitudes in excess of 1,000 m.

Although our material gives no definite information as to the inception of the breeding period of Upemba *grandisonae*, Table 13 suggests that breeding ends in April. The proportions of females with pigmented ova and of sexually active males drop sharply in May.

TABLE 13. — Monthly frequency of adult *Rana grandisonae* from the Parc National de l'Upemba in various stages of reproductive competency.

	Mature males (*)		Mature females (**)	
	Nuptial pads fully developed	Nuptial pads incomplete or absent	Pigmented ova present	Pigmented ova absent
January	51	0	16	1
February	2	0	3	0
March	34	1	18	3
April	22	2	18	4
May	8	5	3	10
June	0	7	0	5
July	2	1	0	3

(*) Includes all males with fully developed gular pouches.

(**) Includes all females as large as or larger than the smallest having pigmented ova (37.5 mm). Five females (January through May) with only a few pigmented ova are listed in the left hand column.

Range. — *Rana grandisonae* is known so far only from northeastern Angola, Ruanda, and southeastern Belgian Congo (LAURENT, 1954).

Upemba localities and specimens :

Buye-Bala (186); Bwalo (12); N'Gongozi (2); Kabwekanono (49); Kalumengongo (3); Katongo (3); Kimiala (2); Luangalele (5); Lufwa (131); Lusinga (139); Mubale (91); Mukana (146); Munte-Mubale (46).

17. — **Rana mascareniensis mascareniensis** DUMÉRIL and BIBRON.

Rana mascareniensis DUMÉRIL and BIBRON, 1841, Erp. Gén., **8**, p. 350 — Mascarene Islands.

Rana mascareniensis mascareniensis LOVERIDGE, 1933, Bull. Mus. Comp. Zool., **74**, p. 369.

Taxonomic notes. — LOVERIDGE (1933) recognized three subspecies of *mascareniensis* : the nominate form from the non-forested regions of eastern Africa, a large western subspecies whose range he found to be roughly coincident with the rain forest, and *mascareniensis uzungwensis*. After separation of *uzungwensis* as a distinct species (see p. 118), we find support for the first two subspecies in the frogs available to us.

LOVERIDGE (1933, 1936 A) distinguished the western, « forest » subspecies on the basis of size and applied the name *venusta* WERNER to it. Though LOVERIDGE suggested that the western form had less webbing than *m. mascareniensis*, he subsequently (1942) changed his opinion. There is also an oblique reference (LOVERIDGE, 1941, p. 136) to a difference in leg length.

Our material is divisible into western and eastern ⁽²⁾ groups. In the former we place 126 from northeastern Belgian Congo (AMNH ex series 11122-259, CNHM 12232, 12759-60, 12793), 7 from the Cameroons (CNHM 59156-60, 59163, 59166), and 9 from Liberia (CNHM 57816, 57939, 57943, 57948, 57951, 57955, 57958, 57960, 57965). In the eastern group are 20 from eastern Tanganyika (CNHM 12263-68, 27792-93), 3 from Uganda (CNHM 12001-03), 26 from Egypt (CNHM 68861-86), and over 500 from the Upemba. Four were at hand from Madagascar (CNHM 18229).

The differences between the two groups in snout-vent length shown in Table 14 are statistically significant if the combined « western » sample is compared with the Upemba series (males $\text{diff./SE}=6.46$, $P<.001$; females $\text{diff./SE}=8.88$, $P<.001$). LOVERIDGE also found the western form to be larger. For example, he gave the following size ranges (1942) : Uganda-Ruanda males 40-53 mm, females 52-65 mm; Kenya-Tanganyika males 41-42 mm, females 34-48 mm. The difference between the Upemba and western sample in relative length of tibia is also statistically significant ($\text{diff./SE}=13.70$, $P<.001$).

The plantar surface of the foot in this species may be either uniformly brownish or distinctly bicolored. In the latter instance the toes are dark brown or black and the web, particularly those portions between the first and second and second and third toes, is cream-colored. The light areas usually cross the bases of the first three metatarsi so that the median half

(2) Actually « eastern » should be « eastern and southern ». We use « eastern » for the sake of simplicity.

TABLE 14. — Comparison of forest (or western) and non-forest (or eastern) samples of adult *Rana mascareniensis*.

Sample	Snout-vent length (mm)						Tibia/snout-vent		
	Males			Females			Sexes combined		
	No.	Range	Mean ± SE	No.	Range	Mean ± SE	No.	Range	Mean ± SE
Eastern :									
Upemba	85	36.9-46.3	41.73 ± 0.22	59	41.4-57.9	47.80 ± 0.52	20	0.49-0.57	0.532 ± 0.004
Tanganyika	2	35.7-40.1	37.9	5	44.1-49.0	46.2	6	0.51-0.54	0.519
Madagascar	1	38.5	38.5	3	41.6-49.7	45.5	4	0.51-0.62	0.569
Western :									
Northern Congo	21	40.1-50.6	46.1	26	47.7-62.9	56.0	46	0.56-0.66	0.607
Cameroons	3	42.1-44.6	43.7	1	53.3	53.3	3	0.55-0.66	0.605
Liberia	3	45.5-50.3	47.6	1	55.7	55.7	5	0.58-0.62	0.604
Combined western	27	40.1-50.6	45.64 ± 0.56	28	47.7-62.9	55.86 ± 0.74	54	0.55-0.66	0.606 ± 0.003

of the foot bears two or three dark, longitudinal streaks that are isolated by lighter areas from the lateral half. The striped, bicolored pattern is characteristic of the Upemba, Tanganyika, Uganda, and Egyptian frogs. The uniform pigmentation characterizes the western frogs although a few individuals have striped feet. The Madagascan specimens are too faded for analysis.

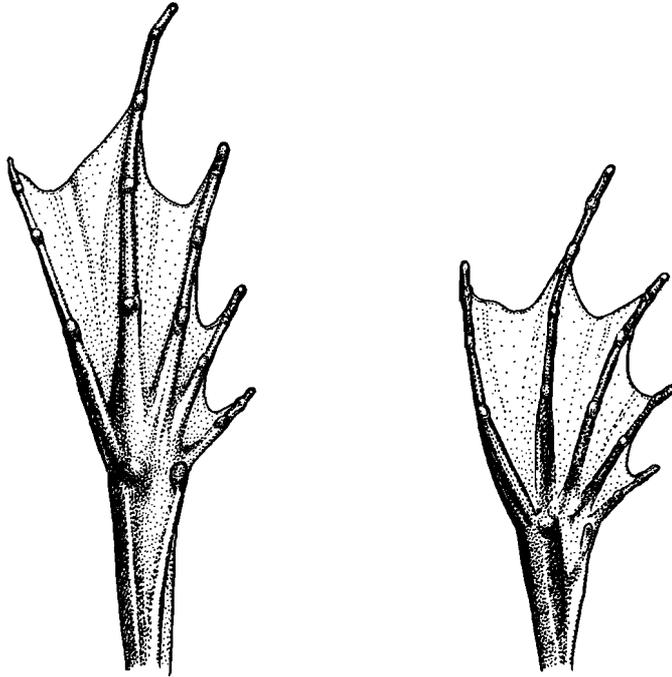


FIG. 39. — Ventral view of feet of *Rana mascareniensis hylaea* (left) and *R. m. mascareniensis* (right) ($\times 2$).

Adult males of *mascareniensis* have a number of distinctive secondary sex characters (see below, p. 81), of which one does not occur in all populations. Only males having fully developed nuptial pads have been used in the following comparison. Males of the western samples have colorless, translucent spinules scattered uniformly over the venter. These structures are absent in males of the eastern samples, but present in the single male from Madagascar.

As noted above (p. 76) LOVERIDGE originally thought the western and eastern populations differed in the extent of webbing. This character varies geographically in our material, but the pattern of variation does not fit a west versus east dichotomy and, consequently, does not coincide with

the variation in the preceding characters. The Upemba population (Fig. 39, right) seems to have the most extensive webbing; usually less than one phalanx of the fifth toe and only 2 phalanges on the lateral border of the fourth toe are free of web. The frogs from Liberia (Fig. 39, left) Cameroons, and the four from Madagascar have one phalanx of the fifth toe and 2 to 2 ½ phalanges of the fourth toe free. Those from northeastern Belgian Congo and Tanganyika have one to 1 ½ phalanges of the fifth toe and 2 ½ to 3 phalanges of the fourth toe free.

Two subspecies of *mascareniensis* are clearly recognizable on the basis of size, relative leg length, pigmentation of the foot, and development of ventral spinules in the males. So far we have called these two groups « western » and « eastern ». But as noted earlier (p. 76) LOVERIDGE referred to them as « forest » and « non-forest » as well as « western » and « eastern ». Their relationships to these phytogeographic divisions appear complex even on the basis of the little information now available.

Besides drawing attention to the rough correspondence of the range of the « western » form to the main rain forest region of central and western Africa, LOVERIDGE (1942) reported this subspecies from one of the isolated montane forests (Magrotto Mountains) in extreme eastern Tanganyika. LOVERIDGE (1937) previously had related the insular distribution of forest forms in East Africa to the contraction of the once much more extensive rain forest belt.

LOVERIDGE also pointed out that some of the forest animals persisted for a few decades after deforestation especially if scattered clumps of trees were left. One of the places LOVERIDGE specifically mentioned as a locality at which this phenomenon was evident is Entebbe, Uganda, now outside the forest belt and one of the non-forest localities for the western subspecies of *mascareniensis*. The same phenomenon probably explains the presence of the western subspecies at Faradje, Niangara, and Garamba in the Belgian Congo, about 120 kilometers from the northern boundary of the rain forest.

On the whole, the western subspecies may with justice be referred to as a forest form that is now contracting its range. But if we are dealing with true subspecies and, therefore, with interfertile populations, the contraction of the range should be viewed not as a movement of populations but as a change in local frequencies of genotypes resulting from changing selective values.

It is not possible to find existing names for both subspecies. The eastern, non-forest race is obviously *m. mascareniensis*. But the western, forest form presents a problem. LOVERIDGE (1933) referred to the latter as *m. venusta* WERNER. But the type locality of *venusta* is Mongalla, Sudan, and not Entebbe, Uganda, as LOVERIDGE (1933) stated. Mongalla is in savanna country about 420 kilometers northeast of the rain forest boundary. Although the forest form has persisted in eastern Tanganyika at much greater distances from the main forest region, it has done so only where

forest now or very recently existed. We have no evidence that Mongalla has had the same recent history. But the principal reason for rejecting the name *venusta* for the forest subspecies is the fact that WERNER's description (1908, pp. 1,899, 1,892) does not permit *venusta* to be related to any *Ptychadena* with confidence, and certainly allows no choice between a relationship with *mascareniensis* and one with *chrysogaster* LAURENT, for example.

Only five named forms of the subgenus *Ptychadena* are known to have the openings of the gular pouches parallel to the mandible and ending near the upper border of the insertion of the arm : *mascareniensis*, *newtoni* BOCAGE, *floweri* BOULENGER, *cooperi* PARKER, and *taeniofelis* LAURENT. Only *floweri* and *taeniofelis* resemble *mascareniensis* in the striped pattern behind the thigh. Additional characters distinguish *cooperi* (no vomerine teeth, reduced web) and *newtoni* (interruption of skin folds) from *mascareniensis*. Both *floweri* and *taeniofelis* are sympatric with the eastern, non-forest race of *mascareniensis* and specifically distinct from it.

Accordingly, in the absence of an available name, the western, forest subspecies is described below (p. 83) as *Rana mascareniensis hylaea*.

Diagnosis of *m. mascareniensis*. — (Based on Upemba specimens only.) Body moderately slender (males) to somewhat stocky (gravid females); limbs moderately slender; head obtusely pointed; snout projecting; nostril nearer to tip of snout than to eye; vomerine teeth in transverse or slightly oblique series, in contact with antero-median borders of choanae; tympanum distinct, two-thirds to three-fourths diameter of eye, about equal to distance between eye and nostril; back with 8 continuous, longitudinal folds, folds ending behind orbits (Fig. 25); tips of fingers and toes bluntly rounded; first finger sometimes equal to but usually shorter than second, fourth longer than second; no supernumerary metacarpal tubercles (Fig. 28); toes extensively webbed (Fig. 39, right); fourth toe with 2 or (rarely) 2 ½ phalanges free of web on lateral margin; fifth toe with ½ to (rarely) 1 phalanx free; no external metatarsal tubercle; no row of small tubercles on fourth metatarsal.

Back with alternating rows of black squarish or oblong spots that may fuse across rows; usually with a mid-dorsal light line or band or both; a dorsal light line present on tibia, though sometimes very faint; occasionally a short dorsal light line on distal portion of thigh; posterior surface of thigh dark brown or black with two or three longitudinal light stripes; 4 to 6 continuous or broadly interrupted dark crossbars on tibia; underside of foot bicolored, dark pigment usually confined to the toes, the web usually cream-colored except distally between the outer toes; lower jaw barred or vermiculated with black.

Secondary sex characters. — The nuptial pads (Fig. 40) consist of velvety, cream-colored or dusky clusters of fine spinules. At the peak of their development, the pads cover the entire dorsal and median surfaces of the first finger from its base to the beginning or middle of the last phalanx, the same portions of the second finger, and the dorso-median edge of the third finger from its base to the end of the penultimate phalanx. The width of the pad on the third finger is greater over the metacarpal than distally.

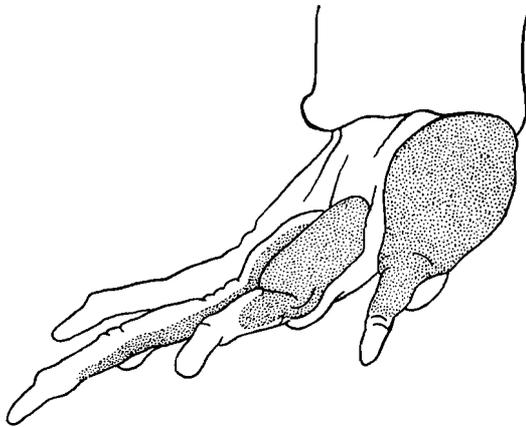


FIG. 40. — Hand of male *Rana m. mascareniensis* showing nuptial pads ($\times 8$).

The vocal sac apparatus consists of paired vocal sacs and corresponding gular pouches. The slit-like openings of the last are parallel to the lower lip, beginning below the posterior half of the eye or opposite the hind corner of the eye and ending near the upper border of the insertion of the arm. The lengths of the slits vary from 0.12 to 0.19 of the snout-vent (mean = 0.145 ± 0.005) in 14 mature males from the Upemba. In 4 males from Madagascar, Tanganyika, and Kenya the proportion ranges from 0.12 to 0.16. The wrinkled skin within the gular pouches is black.

Males with fully developed nuptial pads also have pale, translucent spinules scattered on the undersides of the toes. (These are much smaller than the tubercles confined to the ventral surface of the fourth metatarsal of *grandisonae*; the tubercles of the latter occur in both sexes.) Similar spinules are found on the dorsal and lateral surfaces of the body. Females usually have a few spinules on the sides.

As noted above (p. 78) Upemba males lack the spinules present on the ventral surfaces of head and body in males of the western, forest subspecies.

TABLE 15. — Monthly frequency of adult *Rana mascareniensis mascareniensis* from the Parc National de l'Upemba in various stages of sexual competency.

Males (*)			
Gular pouch	Fully developed	Fully developed	Early stages
Nuptial pad	Fully developed	Absent	Absent
August	0	9	8
September	2	3	5
November	26	0	0
December	25	0	0
January	29	0	0
February	4	0	0
Females (**)			
Ova	Pigmented	Intermediate	Immature
August	1	0	23
September	0	1	6
November	19	0	1
December	16	2	1
January	20	0	1
February	3	0	0

(*) All as large as or larger than 36.9 mm, the smallest with fully developed nuptial pads.

(**) All as large as or larger than 41.4 mm, the smallest with mature ova.

The temporal relationships among the male secondary sex characters follow the pattern of other species of *Rana* (*Ptychadena*) (see p. 99). The vocal sacs and gular pouches develop first and only later do nuptial pads appear. Twelve males had mature vocal sac apparatus but no trace of nuptial pads; all males with nuptial pads have fully developed gular pouches and vocal sacs (Table 15). The spinules under the foot and on the back develop synchronously with the nuptial pads.

The males are distinctly smaller than the females. The former average 41.73 ± 0.22 mm and the latter 47.80 ± 0.52 mm (Table 14). The difference between these means is statistically significant.

Ecological notes. — As stated above, this form of *mascareniensis* is distributed through the non-forested portions of eastern Africa. LOVERIDGE (1933) found them in abundance in swampy, grassy areas. All Upemba material was collected in the vicinity of Lakes Upemba and Kabwe.

LOVERIDGE's localities (1933, 1936, 1942) range in altitude from sea level to 2,000 m. Within the Parc de l'Upemba, however, *mascareniensis* seems to be sharply limited to the lowest elevations. Nine specimens were collected at 695 m and 514 at 585 m.

The breeding season apparently begins in October or November in the Upemba. Practically no adults are sexually competent (i.e., females with pigmented ova; males with fully developed nuptial pads) in August or September. No data are available for October, but from November through February a high proportion of adults are sexually active (Table 15). The evidence from August and September suggests that there is no breeding during the dry period (April or May through September).

Range. — This subspecies is distributed through the drier portions of East Africa, from Egypt to the Cape of Good Hope Province (HEWITT, 1912) and Madagascar. We have seen no frogs from the dry areas of West Africa and are unable to allocate those populations to a subspecies.

Upemba localities and specimens :

Kanonga (9); Mabwe (514).

Reasons have been given in the preceding pages for recognizing two forms of *Rana mascareniensis*. The western subspecies is described here as.

***Rana mascareniensis hylaea* n. subsp.**

Holotype. — Chicago Natural History Museum number 57965 from Mount Nimba, Liberia. Adult male collected by Harry A. BEATTY, March, 1948, between 450 and 600 m.

Description of holotype. — Body slender, limbs slender; head obtusely pointed; snout projecting (slightly damaged); nostril distinctly closer to tip of snout than to eye; internarial distance equal to eye-nostril; vomerine teeth in slightly oblique series, in contact with anteromedian corners of choanae; tympanum four-fifths diameter of eye, equal to eye-nostril distance; back with 8 continuous folds (counting dorso-lateral ones), median pair beginning behind interorbital and ending above vent; first finger shorter than second, which is shorter than fourth; no supernumerary metacarpal tubercles; first toe with $1\frac{1}{2}$ phalanges free of web, second with one, third with $1\frac{1}{2}$, and fourth with $2\frac{1}{2}$ free on lateral margin, fifth toe with one free (Fig. 39, left); no external metatarsal tubercle.

Back with alternating rows of oblong black spots; anteriorly spots fuse across rows; a broad, light, mid-dorsal band and thin vertebral line present; dorsal surfaces of thigh and tibia without dark crossbars; tibia with a faint light line dorsally; posterior face of thigh blackish brown with two wavy; longitudinal light stripes; ventral surface of foot uniformly brownish.

The nuptial pad covers the entire dorsal and median surfaces of the first finger from the wrist to the base of the distal phalanx, the dorsal surface of the second finger to the base of the distal phalanx, and the dorso-median surface of the third finger as far as the base of the penultimate phalanx. Translucent spinules cover the ventral surfaces of the head, body, and foot, the sides of the body, and the posterior third of the back.

Paratypes. — Liberia : Mount Nimba CNHM 57816, 57951, 57955, 57958, 57960; a stream near Mount Nimba CNHM 57939, 57943, 57948.

French Camerouns : Sangmelina CNHM 19984; Ebolowa CNHM 59156-57; Mete CNHM 59158-60, 59163, 59166.

Belgian Congo : Beni CNHM 12759-60; 40 miles west of Beni CNHM 12793; 1,200 m on Mount Ruwenzori CNHM 12232 (13); Stanleyville AMNH 11122-54, 11156-64, 11167-68, 11170-73; Faradje AMNH 11174-85, 11187-99, 11201-09, 11211, 11214-16, 11219-20, 11223, 11225, 11234-35, 11238, 11240-42; Garamba AMNH 11243; Ngayu AMNH 11245; Avakubi AMNH 11246-47; Bafwasende AMNH 11248-49; Niangara AMNH 11250; Medje AMNH 11251, 11253-57, 11259.

Variation in size and relative tibia length among these is given in Table 14. All have uniformly brownish plantar surfaces. Variation in the size and disposition of dorsal spots in minor. Only one lacks both vertebral band and line. The fifth toe has from 1 to $1\frac{2}{3}$ phalanges free and the fourth toe 2 to 3 free.

Comparisons. — Differences between *hyla* and the typical form are discussed above (p. 79).

Remarks. — A male (CNHM 74214) from Huila in the highlands of southern Angola agrees with *hyla* in size, coloration, and secondary sex characters. On the other hand, a female (CNHM 21163) from Chitau

in central Angola resembles *m. mascareniensis*. Allocation of these Angolan populations to these subspecies cannot be made on the basis of single specimens.

We have seen no frogs from the savanna area of West Africa and, therefore, cannot comment on their relations.

Range. — Apparently limited to the rain forest province of Africa and the isolated forest islands of East Africa.

18. — ***Rana obscura*** n. sp.

Holotype. — Institut des Parcs Nationaux du Congo Belge number 1425. An adult male collected at Kaziba, Parc National de l'Upemba, Province Katanga, Belgian Congo, February 15-21, 1948, by the Mission G. F. DE WITTE.

Diagnosis. — A *Rana* (*Ptychadena*) with an external metatarsal tubercle and a cluster of small tubercles along the underside of the fourth and, usually, the third metatarsals (Fig. 42); a row of small tubercles on external face of tarsus; the fifth toe with one-half to one phalanx free of web; the mid-dorsal pair of skin folds continuous from occiput to anal region; and the dorsal pattern reduced to a few indistinct, small dark spots or no spots present (Fig. 41).

Description of holotype. — Body and limbs moderately stocky; head obtusely pointed; snout moderate, projecting less than a tympanic diameter beyond mandible; nostril closer to tip of snout than to eye; internarial distance less than eye-nostril, but much greater than interorbital width; width of upper eyelid equal to interorbital; canthus rostralis rounded, sloping; lores feebly concave; long diameter of eye equal to eye-nostril distance; tympanum distinct, equal to $\frac{2}{3}$ eye diameter, separated from orbit by slightly less than half of its diameter; vomerine teeth in transverse groups, in contact with antero-median corners of choanae.

Fingers and toes bluntly rounded; first finger slightly longer than second; second and fourth subequal; subarticular tubercles distinct; metacarpals with distinct supernumerary tubercles (Fig. 42). Toes about $\frac{3}{4}$ webbed; first toe with 2, second with $1\frac{1}{2}$, third with $1\frac{2}{3}$, and fourth with $2\frac{2}{3}$ phalanges free of web on lateral borders; fifth toe with one phalanx free; subarticular tubercles distinct; inner metatarsal tubercle oval, about equal to its distance from subarticular tubercle of first toe; a small, but distinct, round external metatarsal tubercle; a row of small tubercles under third and fourth metatarsals.

Back with prominent folds; median pair beginning on occiput and continuing without break to anal region; a second continuous fold beginning at posterior corner of upper eyelid and ending at groin; a dorso-lateral fold beginning above tympanum and reaching groin with a break

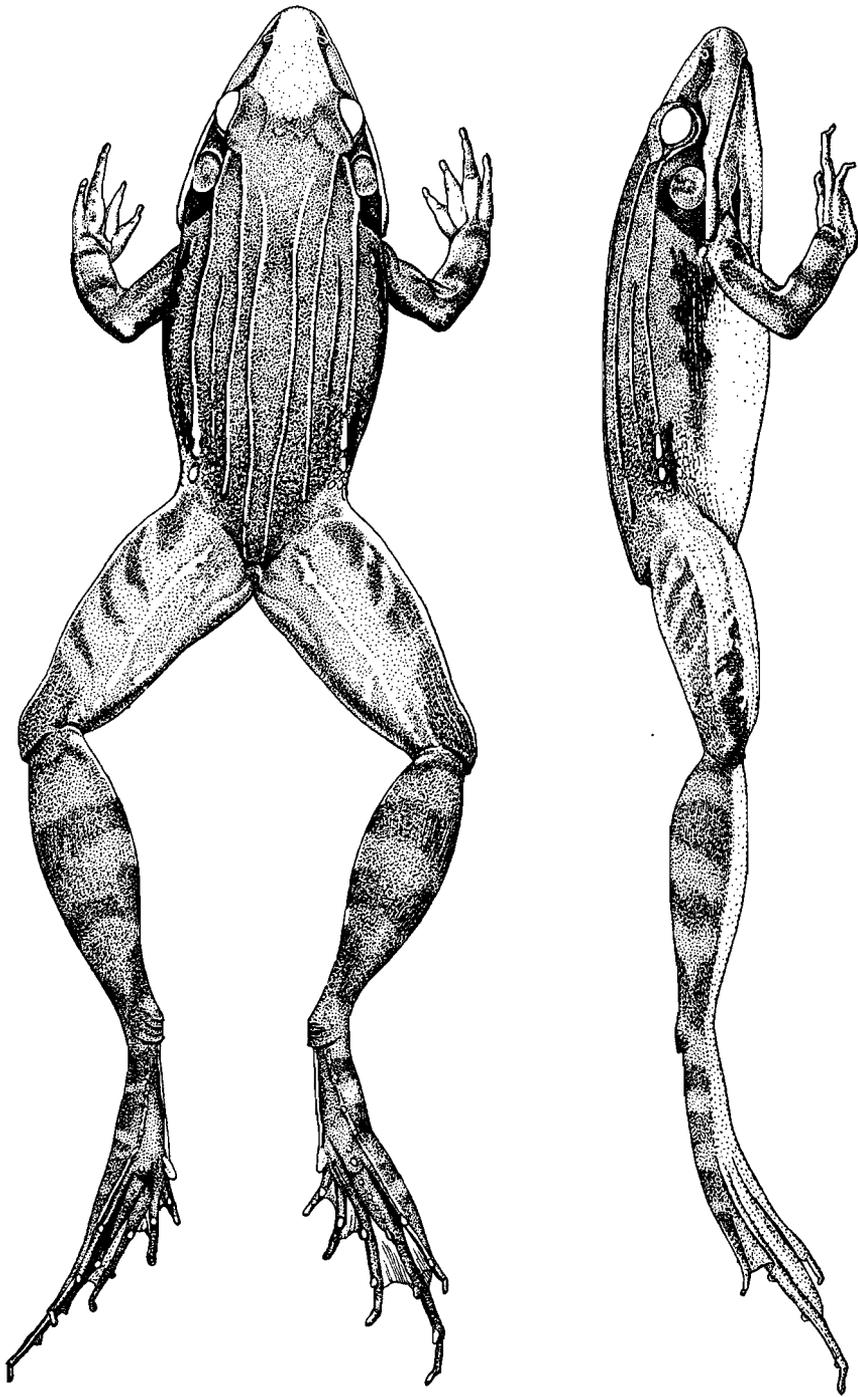


FIG. 41. — *Rana obscura* new species ($\times 2$).

near its end; a short fold in center of body between the last two folds; sides of body coarsely granular with several large rounded warts anteriorly; a glandular ridge from beneath tympanum to upper border of axilla; back and sides with fine spinules (see Secondary sex characters below); below smooth except for nuptial spinules.

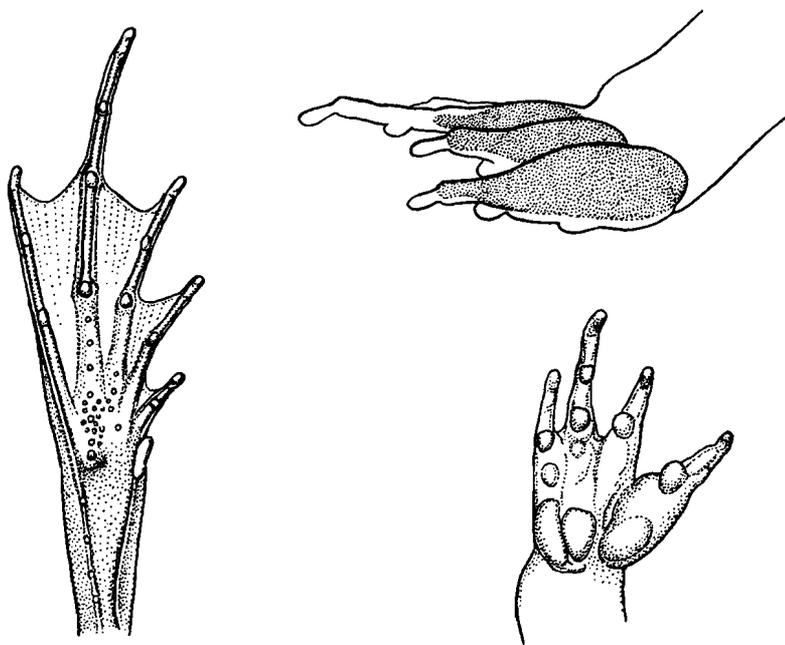


FIG. 42. — *Rana obscura*.

Left, underside of foot ($\times 3$). Right upper, hand of male showing nuptial pads ($\times 6$).
Right lower, underside of hand ($\times 4$).

Color (in alcohol) of dorsal and lateral surfaces dark brown, indistinctly mottled and with a pair of narrow black spots, one on each of the middle longitudinal folds above shoulders; dorso-lateral fold cream-colored; sides of body with several black spots anteriorly; a dark streak beginning at tip of snout, running in upper half of lores, narrowing below the eye, and expanding to cover entire temporal region except for slightly lighter tympanum; upper lip sooty grayish brown; infratympanic glandular swelling cream-colored, the streak continued forward as a narrow line between darkened lip and loreal stripe; lower jaw from symphysis to axilla black, enclosing a few light, round spots; all other ventral surfaces immaculate cream-colored; dorsal surface of lower arm barred with dark brown; no light longitudinal lines on dorsal surface of leg; dorsal surface of thigh with 6-7 short black bars; anterior face of thigh with a short dark stripe

distally, not in contact with dorsal bars; posterior face of thigh cinnamon brown with indistinct lighter spots; dorsal surface of tibia with 5 dark cross bars, 2 of which reach only to center of leg; two dark tarsal bars; underside of foot dark brown except for lighter tubercles.

Dimensions (mm) of holotype : Snout-vent 36.2; head length (to angle of jaw) 14.0; head width (at center of tympanum) 12.0; length of gular pouch opening 5.7.

Secondary sex characters of holotype. — Cream-colored, velvety nuptial pads (Fig. 42) cover the entire dorsal and median surfaces of the first finger from its base to the end of the penultimate phalanx, the dorsal surface of the second finger to the end of the penultimate phalanx, and the dorso-median edge of the third finger usually to the base of the penultimate phalanx (or opposite distal subarticular tubercle). Small, translucent, colorless spinules are uniformly distributed over practically every part of the animal except the inner surfaces of the arms, the ventral surface of the thigh and tibia, and the dorsal surface of the foot.

The round openings of the vocal sacs are situated in the floor of the mouth near the angle of the jaws. The gular pouch openings begin opposite the posterior half of the eye and run oblique to lower jaw, ending near the ventral insertion of the lower arm. The wrinkled skin within the pouches is dark gray.

Paratypes. — All of the following specimens were collected in the Parc National de l'Upemba or at immediately adjacent localities. IPN 793-797 (9), 1272, 1299 B (5), 1317 B (5), 1333, 1342, 1349, 1354 B, 1355 B, 1386 (12), 1408, 1424-25 (7), 1429 (11), 1436, 1439 (2), 1452 A (2), 1453, 1470, 1472 (6), 1474, 1495 A, 1496 A, 1497 C, 1536 (14), 1542 A, 1543 B, 1550 (46), 1563 (4), 1565 (2), 1568, 1571 (5), 1574, 1576-77 (3), 1587, 1590-91, 1596, 1598, 1600-02 (14), 1605 (2), 1622-23, 1625-29 (25), 1631 (4), 1709 A (2), 1712 A, 1716 A (32), 1731 A, 2693 (6).

The entire sample is relatively uniform. The dorsum is without any black spots in about $\frac{1}{5}$ of the series; one or two specimens each have two or three transverse pairs of spots. The great majority, however, are like the holotype and have a single pair of spots. Some ontogenetic variation shows up in the coloration of the lower jaw. Young specimens tend to have the black streak interrupted by two or three light crossbars.

The median pair of dorsal skin folds are uninterrupted in about $\frac{4}{5}$ of the paratypes. In a few these folds begin behind the usual origin, the occiput. One-fourth of the series lacks the small tubercles under the third metatarsal. Most specimens have one phalanx of the fifth free of web although only one-half phalanx is free in one-sixth. The number of free phalanges on the fourth toe varies from 2 $\frac{1}{2}$ to 3.

Variation in size and several body proportions are given in Table 16.

TABLE 16. — Variation in paratypes of *Rana obscura*.

Character	No.	Range	Mean \pm SE
Snout-vent (mm) :			
Males with nuptial pads	14	33.8-37.6	35.76 \pm 0.29
Females with mature ova	7	38.7-45.2	43.67 \pm 0.88
Gular pouch opening (males) (*)	10	0.15-.019	0.169 \pm 0.004
Tibia (males and females) (*)	22	0.59-0.67	0.628 \pm 0.005

(*) These dimensions given as proportions of snout-vent.

Comparison with other species. — The combination of the row of small tubercles under the fourth metatarsal with the reduction of the dorsal pattern to no more than 6 very small dark spots distinguishes *obscura* from all members of the *Rana* (*Ptychadena*) group. The fourth metatarsal has a row of tubercles in *grandisonae*, *frontalis*, *upembae*, *maccarthiensis*, *porosissima*, and *chrysogaster guibei* (as defined above, p. 65). But each of these has a conspicuous longitudinal dorsal pattern of quadrangular spots, and each differs from *obscura* in at least one other character. For example, in *grandisonae* the mid-dorsal folds end between the eyes (behind eyes in *obscura*), the lower jaw is distinctly barred (continuous black streak in *obscura*), and sexually active males do not have light spinules on the back. *Rana frontalis* has the lower jaw barred with black, the mid-dorsal folds interrupted (continuous in *obscura*), and no dorsal spinules in males. The same distinctions hold true for *maccarthiensis*, which also has more extensive webbing (at most 2 $\frac{1}{2}$ phalanges of fourth toe free; at least 2 $\frac{1}{2}$ phalanges free in *obscura*). Males of *porosissima* never have dorsal spinules, and both sexes have a light vertebral marking and a light longitudinal line on the tibia (both lacking in *obscura*). *Rana chrysogaster guibei* has less webbing (1 $\frac{1}{2}$ -2 phalanges of fifth toe free; at most 1 in *obscura*), discontinuous mid-dorsal folds or a short posterior median pair, and a vertebral light stripe. *Rana upembae* has less web, a vertebral stripe, but no dorsal spinules in males.

Other species with a greatly reduced or absent dorsal pattern are *christyi*, *longirostris*, and eastern populations of *superciliaris*. Besides lacking the row of tubercles under the fourth metatarsal, all three of these differ from *obscura* in having at most two phalanges of the fourth toe free of web (between 2 $\frac{1}{2}$ and 3 free in *obscura*) and in having the rear face of the thigh more conspicuously marked.

Secondary sex characters. — The holotype represents the maximum development of these characters. The sequence of development of the several male secondary sex characters is the roughly the same in *obscura* as in other species of the subgenus (see p. 89). The vocal sacs and gular pouches complete their development before the appearance of the other structures. The ventral and dorsal spinules develop concomittantly with the nuptial pads.

As indicated in Table 16, the females reach a larger size than the males.

Ecological notes. — In the Upemba, *obscura* is confined to elevations above 750 m and occurs only rarely below 1,000 m. The altitudinal distribution of the present sample is as follows :

Meters.	Specimens.
751-1,000	16
1,001-1,250	107
1,251-1,500	14
1,501-1,750	92
1,751-1,830	13

All males (14) with secondary sex characters fully developed and all females (7) containing pigmented ova were collected during the interval November-April. On the other hand, 6 adult-sized males (33-37 mm, c.f. Table 16) with mature gular pouches but totally lacking other secondary sex characters were obtained in the interval May-September. Thirteen females of mature size (38 mm or larger) were collected between March and July. No males were caught in July, August, or October and no females in August, September, or October. Apparently the breeding period coincides roughly with the rainy season and lasts from November to April.

Range. — Known only from the Parc National de l'Upemba.

Upemba localities and specimens :

Babagi (4); Buye-Bala (3); Ganza (1); Kabenga (2); Kabwe (10); Kabwekanono (8); Kafwe (1); Kagumwe (13); Kalumengongo (2); Kambi (11); Kamitunu (1); Kankunda (3); Karibwe (1); Kaziba (10); Kipangaribwe (1); Lufwa (2); Lusinga (62); Mokey (3); Munoi (8); Muye (1); Pelenge (95).