

19. — *Rana oxyrhyncha* SMITH.

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

*Rana (Ptychadena) gribinguiensis* ANGEL, 1922, Bull. Mus. Hist. Nat. Paris, 28, p. 399, fig. — Fort Crampel, French Equatorial Africa.

*Rana oxyrhynchus gribinguiensis* LOVERIDGE, 1936, Bull. Mus. Comp. Zool., 79, p. 416.

Taxonomic notes. — In view of SMITH's excellent description (1849), it is surprising that this widespread species should still have been confused in the literature of the last 20 years. ANGEL's description and figure of *gribinguiensis* (1922) fit SMITH's description remarkably well. Angel states that *gribinguiensis* is distinguished by the length and proportions of the hind limb. According to his measurements the leg of *gribinguiensis* is 2.12 times the snout-vent length; SMITH's measurements give a ratio of 2.04, hardly a significant difference. SMITH states that *oxyrhyncha* has « long rather robust » hind limbs, which is the phrase (« long, robustes ») used by ANGEL to describe *gribinguiensis*. The distinct interorbital bar, the light triangle of the forehead, and the vermiculation of the posterior face of the thighs, all diagnostic of *gribinguiensis*, are either figured or mentioned by SMITH. There is no reason to consider *gribinguiensis* ANGEL other than a strict synonym of *oxyrhyncha* SMITH, an opinion supported by comparison of a Natal specimen collected by SMITH and now in the British Museum (1858.11.25.96), with the type of *gribinguiensis*.

LOVERIDGE (1936) recognizes two forms in British East Africa, *oxyrhyncha oxyrhyncha* and *o. gribinguiensis*, distinguished by size (females rarely over 50 mm with a maximum near 55 in *o. oxyrhyncha*; females 59 to 67 mm in *o. gribinguiensis*) and extent of webbing (fourth toe with 1 ½ to 2 phalanges free in *o. oxyrhyncha*; 1 to 1 ½ free in *o. gribinguiensis*). In subsequent papers LOVERIDGE reports the two subspecies from Liberia (1938, 1941), Belgian Ruanda (1942), and Nyasaland (1953). These papers call attention to another character distinguishing the two forms : the posterior surface of the thigh is striped in *o. oxyrhyncha* and vermiculated in *o. gribinguiensis*. The important point here is that the characteristics LOVERIDGE attributes to *o. gribinguiensis* are those of *oxyrhyncha* SMITH. SMITH's type is 57 mm long; its thighs are, to use SMITH's phrase, « reticulated or freckled » posteriorly; and its web leaves little more than one phalanx of the fourth toe free.

But the characters noted by LOVERIDGE certainly define two forms and, considering that they are sympatric from Liberia to Kenya and Mozambique, we treat them as full species. LOVERIDGE's *o. gribinguiensis* is clearly *oxyrhyncha* SMITH and his *o. oxyrhyncha* is almost certainly *superciliaris*

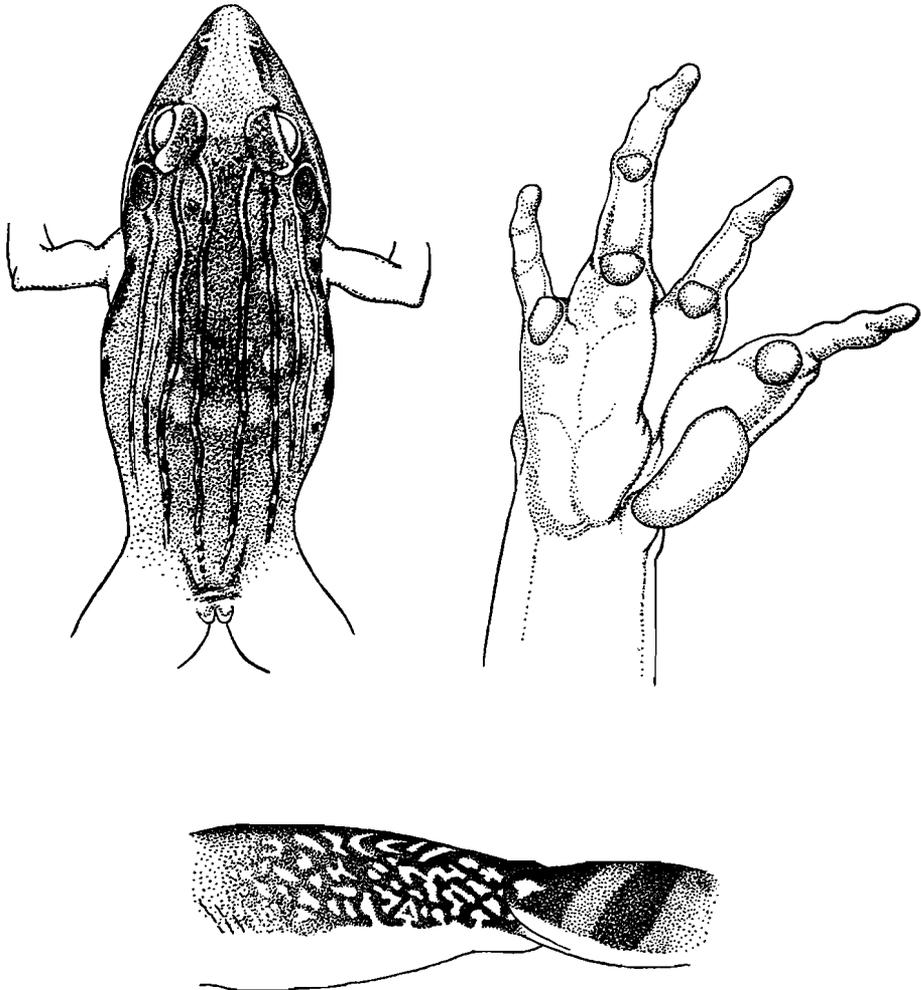


FIG. 43. — *Rana oxyrhyncha* from Parc National de l'Upemba.  
 Upper left, dorsal view ( $\times 1\frac{1}{2}$ ). Upper right, ventral surface of hand ( $\times 5$ ).  
 Lower right, posterior surface of thigh ( $\times 2$ ).

GÜNTHER. We have examined the type of the last and it agrees in every detail with the diagnoses of *o. oxyrhyncha* LOVERIDGE of the previously listed papers and with Congo and East African specimens LOVERIDGE had identified as *oxyrhyncha* elsewhere (1936 A).

Diagnosis. — Body moderately stocky, limbs heavy; head obtusely pointed; snout projecting; nostril nearer to eye than to tip of snout; vomerine teeth in transverse series, in contact with antero-median borders of choanae; tympanum distinct, about  $\frac{3}{4}$  diameter of eye, slightly less than distance

between eye and nostril; back with 6 or 8 longitudinal folds, folds ending behind orbits, mid-dorsal pair continuous (Fig. 43); tips of fingers (Fig. 43) and toes bluntly rounded; first finger slightly shorter than second; usually no supernumerary metacarpal tubercles; toes almost completely webbed; fourth toe with one to one and one-half phalanges free of web on lateral border; fifth toe usually webbed to tip; no external metatarsal tubercle; no row of small tubercles on fourth metatarsal.

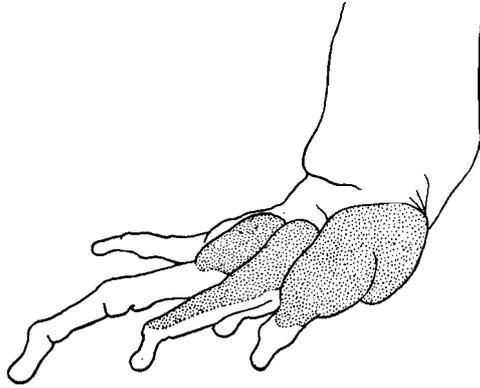


FIG. 44. — *Rana oxyrhyncha*.  
Hand of male showing nuptial pads ( $\times 5$ ).

Back with alternating rows of small squarish black spots, each of which is smaller than the tympanum; no mid-dorsal band or line; no light line on thigh or tibia; posterior surface of thigh dark brown or black with a vermiculation of white (Fig. 43); 4 to 6 interrupted black bars across tibia; 3 tarsal bars; underside of foot dark brown, occasionally small light areas at base of web; lower jaw barred with black.

Secondary sex characters. — The nuptial pads (Fig. 44) have the same gross appearance as in all members of the subgenus *Ptychadena*; that is, they consist of velvety cream-colored clusters of spinules. At the height of development the nuptial pad covers the entire dorsal and lateral surfaces of the first finger from its base to the end of the basal phalanx, the dorsal surface of the second finger from its base to the first phalanx, and a circular area on the dorsal surface of the third finger not extending beyond the level of the proximal subarticular tubercle.

The slits of the gular pouches begin slightly anterior to the tympanum and end at the ventral border of the insertion of the arm. The length of the slits varies from 0.15 to 0.19 of snout-vent (mean = 0.164) in seven mature males. The gular pouches are usually black or black anteriorly and gray

or white posteriorly in mature males; in one male the pouches are light gray. Fine ventral asperities are feebly developed in only four males.

The slit of the gular pouch develops before the nuptial pad. The latter appears only in males having fully developed vocal sacs and gular pouches; on the other hand, fifteen males with fully developed gular pouches (snout-vent 43.6-53.5 mm) have no trace of nuptial pads (Table 17). Initially the slits for the pouches appear as a short and shallow fold on each side of the throat. Thirty-one males (32.3-52.1 mm) are in this stage; only one male (28.4 mm) has no indication of these folds. None of these last 32 males has a trace of nuptial pad.

The females are significantly larger than the males. Thirty-one adult females (all individuals with pigmented ova) measure 49.2-62.0 mm (mean=58.22±0.48 mm) and 27 mature males (all individuals with vocal sacs and nuptial pads) measure 43.6-53.2 mm (mean=49.71±0.47 mm).

**Ecological notes.** — Because significant portions of the literature have misidentified this species, one gains a false impression of the relative abundance of *oxyrhyncha*. It is far less common than the literature indicates. For example, LOVERIDGE lists 101 *o. oxyrhyncha* from Kenya and Uganda (1936), 18 from Uganda and Tanganyika (1942), and 148 from Nyasaland (1953). But, as we have shown above, all of these specimens were misidentified. The true *oxyrhyncha* (*o. gribinguiensis* of LOVERIDGE) listed in those three papers number 4, 1, and 11 respectively. The Upemba collection contains 142 *oxyrhyncha*, a modest number in terms of this enormous collection; by contrast the Upemba material includes over 1,000 *Rana porosissima*, a high altitude form, and over 500 *R. mascareniensis* from low altitudes.

As its wide geographic range suggests, *oxyrhyncha* is able to live in several vegetation formations. PARKER (1936 A) and SANDERSON (1936) report it from rain forest and more open forest in Angola and the Cameroons, and LOVERIDGE (1942, 1953) from forested areas of East Africa. All of the localities given by ANGEL (1922), CHABANAUD (1921), and MERTENS (1938) lie outside the rain forest belt, but their specimens may have come from gallery forest. Reports from southern and southeastern Africa (SMITH, 1849; POWER, 1927) locate *oxyrhyncha* in savannah country.

*Rana oxyrhyncha* has been found from sea level (SMITH, 1849; LOVERIDGE, 1941) to 2,150 m (LOVERIDGE, 1936). Specimens in the Upemba collection show the following altitudinal distribution :

Meters.	Specimens.
500- 750	30
751-1,000	77
1,001-1,250	16
1,251-1,500	13
Above 1,500	9

The development of the secondary sex characters and the monthly distribution of females with pigmented ova indicate that in the Upemba the breeding season of *oxyrhyncha* begins with the rains in October and continues at least into November. Only 2 of the 35 adult females collected from May through August, in the dry season, has pigmented ova; however, by September most of them have pigmented ova and by October (the start of the rainy season) and November all of them are reproductively competent (see Table 17). Similarly, the males of the dry season do not usually have the secondary sex characters fully developed. In September most of them show maximum development of these structures, and in October and November all do.

TABLE 17. — Frequency by months of *Rana oxyrhyncha* from the Parc National de l'Upemba in various developmental stages of reproductive competence.

	Males (*)			Females (**)	
	Vocal sacs and nuptial pads	Vocal sacs only	No vocal sacs or pads	Pigmented ova present	No pigmented ova
February ... ..	1	0	0	—	—
April ... ..	0	1	1	—	—
June ... ..	0	5	6	0	17
July ... ..	1	2	5	0	4
August .. ...	1	6	9	2	12
September ... ..	12	1	1	12	2
October . ... ..	2	0	0	12	0
November ... ..	10	0	0	6	0

(\*) All larger than 43 mm; smallest with nuptial pads 43.6 mm.

(\*\*) All larger tahn 49 mm; smallest with pigmented ova 49.2 mm.

Range. — *Rana oxyrhyncha* is known with reasonable certainty from Cape Province (POWER, 1935) in the south to Ethiopia (PARKER, 1930) in the north and from Kenya (LOVERIDGE, 1936) and Mozambique (PARKER, 1930) in the east to Angola and Liberia in the west.

#### Upemba localities and specimens :

Ganza (22); Kabenga (3); Kalala (1); Kalungwe (1); Kaluwamba (2); Kande (6); Kankunda (13); Kanonga (7); Karibwe (2); Kaswabilenga (6); Kiamakoto (5); Kilwezi (36); Kipondo (5); Loie (1); Lufira (4); Lukawe (4); Lupiala (2); Lusinga (5); Mabwe (6); Masombwe (8); Mukukwe (2); Munoi (4); Muye (1); Mware (3); Senze (2).

20. — **Rana porosissima** STEINDACHNER.

*Rana porosissima* STEINDACHNER, 1867, Reise Novara, Amph., p. 19, pl. 1, figs. 9-13 — Angola.

*Rana loveridgei* LAURENT, 1954, Ann. Mus. Congo Belge, **34**, p. 14, pl. 1, fig. 4, pl. 2, fig. 1, pl. 3, figs. 3-4, pl. 4, figs. 2, 7 — Tare, Busanza, Ruanda.

Taxonomic notes. — LAURENT (1954) notes that males of *loveridgei* have the strong spinosity of *porosissima* but distinguishes the two forms on the basis of differences in the positions of the external slits of the gular pouches. Actually, a close comparison of STEINDACHNER's description and figures with those of *loveridgei* presented by LAURENT reveals agreement in even minute details. Dr. J. EISELT has very kindly compared two males from the Upemba with the holotype of *porosissima* and informs us that in coloration, webbing, body proportions, and in the position of the gular pouches our specimens agree with *porosissima*. Dr. EISELT specifically notes (in litt.) that, contrary to LAURENT's opinion, the openings of the gular pouches of *porosissima* end near the ventral border of the insertion of the arm and, hence, are arranged exactly like those of *loveridgei*.

We have compared the frogs sent to Dr. EISELT with a male paratype of *loveridgei* (CNHM 74922) and can find no significant differences. However, the longitudinal light line on the dorsal surface of the thigh, said by LAURENT to be characteristic of *loveridgei*, is sporadic in appearance within the entire Upemba series. Approximately one-sixth of our frogs have a complete line on the thigh, an additional one-sixth have an incomplete line, and the rest have no line at all. The absence of this line from the thigh of the holotype of *porosissima* is one of the trivial differences between it and the description of *loveridgei*.

LOVERIDGE (1953) states that *porosissima* is a synonym of *subpunctata* BOCAGE. The two forms differ in so many respects that we must disagree with that opinion. The webbing is much more extensive in *subpunctata*, leaving at most one-half of the last phalanx of the fifth toe free whereas in *porosissima* one to two complete phalanges are free. Males of *porosissima* rarely reach a length of 45 mm and females rarely exceed 55 mm. On the other hand males of *subpunctata* often exceed 50 mm and females commonly exceed 60 mm. BOCAGE (1866) states clearly (and is supported by our *subpunctata*) that the posterior face of the thigh is striped; in *porosissima* this area has round light spots that occasionally coalesce into a light network. The two forms also differ in the pattern on the lower jaw.

Diagnosis. — Body moderate to slender, limbs moderate; head pointed; snout greatly projecting; nostril nearer to eye than to tip of snout; vomerine teeth in transverse series, in contact with antero-median borders of choanae; tympanum distinct,  $\frac{3}{4}$  to  $\frac{4}{5}$  diameter of eye, about equal to

distance between eye and nostril; back with 8 folds ending behind orbits, mid-dorsal folds continuous (Fig. 45); tips of fingers and toes bluntly rounded; first finger equal to second; supernumerary metacarpal tubercles usually present, distinct; toes about two-thirds webbed; fourth toe with 3 to  $3\frac{1}{4}$  phalanges free of web on lateral border; fifth toe with  $1\frac{1}{3}$  to  $1\frac{1}{2}$  phalanges free; external metatarsal tubercle usually absent; a row of small tubercles on fourth metatarsus present in about half of individuals.

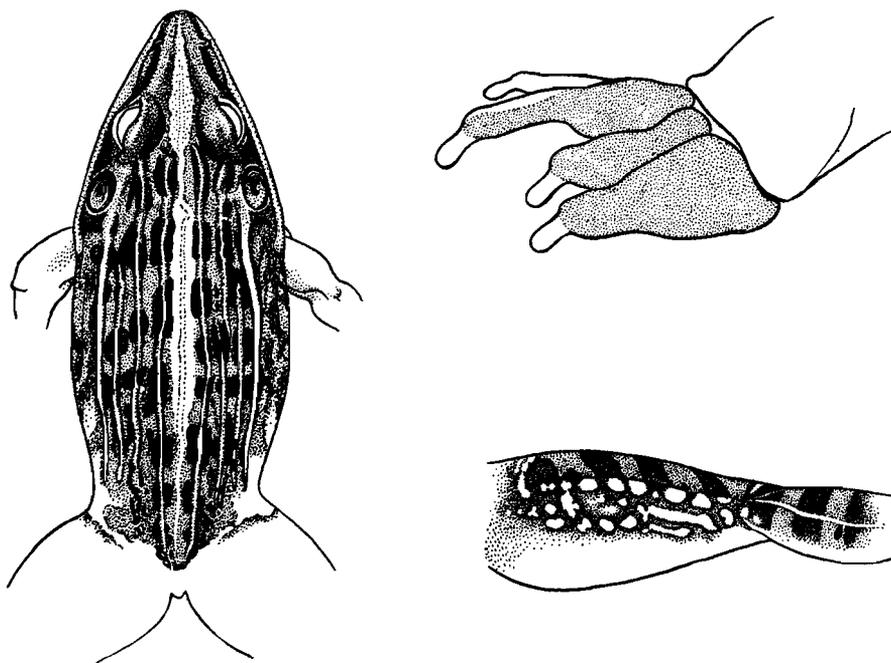


FIG. 45. — *Rana porosissima* from Parc National de l'Upemba.  
Left, dorsal view ( $\times 2$ ). Right upper, hand of male showing nuptial pads ( $\times 6$ ).  
Right lower, posterior surface of thigh ( $\times 2$ ).

Back with alternating rows of squarish black spots, each of which is subequal to tympanum; a broad mid-dorsal band of light color through which a still lighter vertebral line is visible; a light line always present on dorsal surface of tibia; thigh with or without light line (see Taxonomic notes); posterior face of thigh dark brown with roundish or oval light spots (Fig. 45); 4 to 6 black bars across tibia, usually complete; 2 or 3 black tarsal bars; underside of foot uniform brownish; lower jaw with continuous blackish streak that widens abruptly just before axilla.

Secondary sex characters. — The nuptial pads (Fig. 45) are cream-colored velvety clusters of spinules. At the height of development the pads cover the entire dorsal surfaces of the first and second fingers from the wrist to the base of the terminal phalanx and the medio-dorsal surface of the third finger from its base to the proximal end of the terminal phalanx. Most males with nuptial pads also have well-developed spines uniformly distributed over the venter from the chin to the groin. At the climax of development the ventral spines are tipped with black pigment.

As in other *Ptychadena* the vocal sac apparatus consists of paired vocal sacs and gular pouches. The openings for the pouches run from a point opposite the middle of the eye to the antero-ventral corner of the arm insertion. In 15 males with fully developed pouches and nuptial pads, the slits of the gular pouches vary from 0.15 to 0.21 of the snout-vent length (mean =  $0.177 \pm 0.004$ ).

The development of the masculine secondary sex characters follows a clear sequence. First, in males about 29 mm snout-vent, a fold appears in the skin on each side of the gular region; these folds develop into shallow invaginations that gradually deepen into the gular pouches that protrude during vocalization. The blind apex of each gular pouch then partially evaginates, becomes wrinkled, and acquires the dark pigment typical of

TABLE 18. — Frequency by size classes of male *Rana porosissima* in different stages of development of the gular pouch.

Snout-vent (mm)	Gular skin		
	No modification	Fold to complete invagination	Mature gular pouch
22.4-24.9 ... ..	6	1	0
25.0-26.9 ... ..	3	0	0
27.0-28.9 ... ..	10	1	0
29.0-30.9 ... ..	2	15	0
31.0-32.9 ... ..	0	16	1
33.0-34.9 ... ..	0	29	1
35.0-36.9 ... ..	0	29	12
37.0-38.9 ... ..	0	20	31
39.0-40.9 ... ..	0	4	28
41.0-42.9 ... ..	0	0	6
Totals .. ..	21	115	79

adults. Only in males having the gular pouches in the last stage are there opening to the vocal sacs in the floor of the mouth. The relation between snout-vent length and the development of the gular pouches is shown in Table 18.

A sharp distinction must be made between the gular pouches, which are invaginations of gular skin, and the vocal sacs, which presumably are evaginations from oral epithelium (LJU, 1935). One hundred thirty-six males (snout-vent 22.4-42.9 mm) in various stages of gular pouch development prior to the appearance of wrinkled, pigmented skin were examined; none has vocal sac openings in the floor of the mouth and none has recognizable vocal sacs under the floor of the mouth. On the other hand all 79 males with fully developed gular pouches have vocal sacs and openings to them in the floor of the mouth. Since no intermediate stages of vocal sac development were found, the development of the sacs is probably rapid. A more detailed account of the anatomy and development of the vocal sac apparatus is given elsewhere (INGER, 1956 A).

The nuptial pads develop after the vocal sacs. All 59 males (snout-vent 34.0-42.1 mm) with nuptial pads in some stage of development have mature vocal sacs (that is, the openings are present in the mouth) whereas 20 males (32.7-42.3 mm) have the vocal sac apparatus fully formed but no trace of nuptial pads. The ventral spinules are the last of the secondary sex characters to appear and are found only on males having fully developed nuptial pads. The sequence of development of the secondary sex characters is shown in Table 19.

As the first two columns of Table 19 show, nuptial pads and ventral spines have a cyclic development and are absent in males collected during most of the dry season (late April through August), during which *porosissima* does not breed (see *Ecological notes*). The cyclic appearance of these two structures corresponds with the periodicity in the nuptial pads of *Rana graeca* (CEI, 1944), *R. esculenta* (ARON, 1926), and *R. pipiens* (GLASS and RUGH, 1944), which have been shown to be controlled by periodic changes in hormone production. The nuptial pads of the Holarctic species are well-developed only immediately before, during, and immediately after the breeding period. Well-developed gular pouches and vocal sacs are found in male *porosissima* even during the dry season (third column of Table 19). Conceivably, the development of these gular structures might be initiated by androgens and their appearance in the dry season could be explained merely by a failure to regress. But this hypothesis would leave unexplained the initiation of development of the gular pouches in males from the dry season (see fourth column) when production of androgens is at an ebb. The data of Table 19 suggest that the development of vocal sacs and gular pouches is under direct genetic control.

The mature females are larger than adult males. Nineteen with pigmented ova measure 39.3-48.9 mm snout-vent (mean=44.3±0.64 mm) and 59 males with nuptial pads 34.0-42.1 mm (mean=39.2±0.22 mm).

TABLE 19. — Monthly frequency and size range (mm.) of male *Rana porosissima* in various stages of development of secondary sex characters.

	Fully developed	Fully developed	Fully developed	Early stages	Absent
Gular pouches . . . . .	Fully developed	Fully developed	Fully developed	Early stages	Absent
Vocal sacs . . . . .	Present	Present	Present	Absent	Absent
Nuptial pads . . . . .	Present	Present	Absent	Absent	Absent
Ventral spines . . . . .	Present	Absent	Absent	Absent	Absent
Number and size (mm) of males					
January . . . . .	21 (35.6-40.7)	0	0	0	0
February .. . . .	0	0	1 (38.3)	11 (30.1-37.3)	3 (27.0-28.0)
March . . . . .	8 (38.1-42.1)	4 (37.5-40.1)	3 (38.8-42.3)	25 (24.5-40.5)	12 (22.8-29.5)
April . . . . .	0	0	7 (37.5-41.9)	16 (34.0-38.9)	3 (23.4-30.1)
May .. . . .	0	0	2 (35.7-37.3)	30 (30.8-39.8)	1 (24.0)
June .. . . .	0	0	0	18 (29.0-37.4)	0
July .. . . .	0	0	6 (36.6-39.6)	15 (32.3-38.2)	0
September . . . . .	19 (35.9-41.7)	0	0	0	2 (22.4-23.3)
October . . . . .	6 (34.0-38.2)	0	0	0	0
November-December . . . . .	0	1 (39.2)	1 (32.7)	0	0
Totals . . . . .	54 (34.0-42.1)	5 (37.5-40.1)	30 (32.7-42.3)	115 (24.5-40.5)	21 (22.4-30.1)

Ecological notes. — *Rana porosissima* lives at moderate to high elevations. The lowest elevation reported by LAURENT (1954) is 1,285 m and the highest 2,200 m. In the Upemba collection the lowest elevation for *porosissima* is 1,250 m and the highest 1,830 m. BOGAGE (1895) reported *porosissima*, which he considered to be a variety of *mascareniensis*, from the high plateaus of Angola. The altitudinal distribution of the Upemba specimens and those listed by LAURENT as *loveridgei* is as follows :

Meters.	LAURENT (1954).	Upemba collection.
— 1,250 . . . . .	—	2
1,251-1,500 . . . . .	6	61
1,501-1,750 . . . . .	27	313
1,751-2,000 . . . . .	64	746
Above 2,001 . . . . .	3	—

The breeding season of *porosissima* probably begins in the Upemba in October, coinciding with the beginning of the rains, and continues through March. The monthly frequency of adult females in two stages of the reproductive cycle is given in Table 20. Only females larger than 39 mm are considered mature; the smallest female with ripe ova is 39.3 mm. The distribution of females with pigmented ova thus agrees with that of males having nuptial pads (first two columns of Table 19) and supports the view that *porosissima* is ready to breed in September immediately before the onset of the rains. The collection of 21 transforming young in March gives added confirmation. Only one other transforming juvenile was caught, and that in January. No larvae were obtained.

TABLE 20. — Monthly frequency of adult female *Rana porosissima* from the Parc National de l'Upemba in two phases of the reproductive cycle.

	With pigmented ova	Without pigmented ova
January . . . . .	4	0
February . . . . .	3	4
March . . . . .	4	18
April . . . . .	0	28
May . . . . .	0	12
June . . . . .	0	12
July . . . . .	0	8
September . . . . .	7	0
October .. . . .	1	0
November-December .. . . .	0	2

Range. — *Rana porosissima* occurs with certainty from northeastern Angola to Tanganyika and Uganda.

Upemba localities and specimens :

Between Buye-Bala and Katonga (43); Buye-Bala (86); Bwalo (18); Dipidi (20); N'Gozie (7); Kabwe (10); Kabwekanono (302); Kafwe (20); Kagomwe (1); Kalumengongo (34); Kamitunu (1); Kampadika (1); Kanpungu (1); Karibwe (23); Kasandendeko (1); Katombwe (14); Katonga (15); Kayango (1); Kenia (6); Kipangaribwe (2); Luangalele (7); Lufira (11); Lufwa (11); Lusinga (340); Mitoto (2); Mubale (1); Mukana (142); Mukelengia (1); Munte-Mubale (40); Pelenge (2).

21. — *Rana subpunctata* BOCAGE.

(Pl. V, 1.)

*Rana subpunctata* BOCAGE, 1866, Jour. Acad. Sci. Lisbonne, **1**, p. 73 — Duque de Bragança, Angola.

*Rana katangae* WITTE, 1921, Rev. Zool. Afric., **9**, p. 3, pl. 2, figs. 1-4 — Lofoi, Katanga, Belgian Congo.

*Rana chobiensis* FITZSIMONS, 1932, Ann. Transvaal Mus., **15**, p. 39 — Kasane, Chobe River, Bechuanaland.

Taxonomic notes. — LOVERIDGE has suggested that *katangae* (1936) and *chobiensis* (1953) are synonyms of *subpunctata*. We concur in these opinions. The Upemba specimens agree with the original description of *subpunctata* in all details. Nothing in WITTE's description (1921) of *katangae* will distinguish it from *subpunctata*. The same applies to FITZSIMONS' description (1932) of *chobiensis* and the 7 paratypes of the latter available (CNHM 18028-29). WITTE's description and figure (of *katangae*) and the paratypes of *chobiensis* show the characteristic pigmentation of venter, thighs, and plantar surfaces, the relatively large size, the extensive webbing, the absence of supernumerary metacarpal tubercles (see *Diagnosis*, p. 104), and the fringe of web along the second and third fingers (see below, p. 104).

WITTE (1921) does not describe clearly the position of the opening of the gular pouch. Although at one point (p. 4) he notes that it ends near the upper border of the arm (« ... près du bord supérieur du bras ») and at another (p. 6) that it ends above the lower border of the arm (« ... au-dessus du bord inférieur du bras »), the figure of the type (pl. 2, fig. 3) distinctly shows the opening running at an angle to the lower lip or gape of the mouth, which is the critical fact. A young male paratype of *chobiensis* (CNHM 18029; 42 mm) has the gular pouch in an early stage of development, yet clearly oblique to the lower lip. The opening in fully mature males from the Upemba (IPN-1262 B; 54.6 mm) is also oblique to the lower lip. BOCAGE (1866, 1895) did not describe the position of the gular pouch in *subpunctata*, but overall agreement of the present specimens with his descriptions oblige us to identify them as *subpunctata*.

In many ways this species is very similar to *Rana m. mascareniensis*. BOTH have bicolored plantar surfaces and striped thighs; neither has supernumerary metacarpal tubercles normally; both have the tibia bars broadly interrupted; both have continuous mid-dorsal skin folds that end behind the eyes; neither has an outer metatarsal tubercle; etc. However, minor but consistent differences do separate the two. *Rana subpunctata* has slightly more extensive webbing than the most fully webbed *mascareniensis* (i.e., those from the Upemba). The difference is more readily seen and more easily described on the hands than on the feet. The hand of *subpunctata* (Fig. 27) has a distinct rudiment of web between the first and

second fingers and a distinct though narrow fringe along the median edges of the second and third fingers, giving these fingers a somewhat flattened appearance. A few *mascareniensis* have a rudiment of web between the first two fingers but none of the many examined had a fringe on the sides of the second and third fingers (Fig. 28). The ventral spotting, confined to the throat in *mascareniensis*, usually occupies the chest and often the abdomen of *subpunctata*.

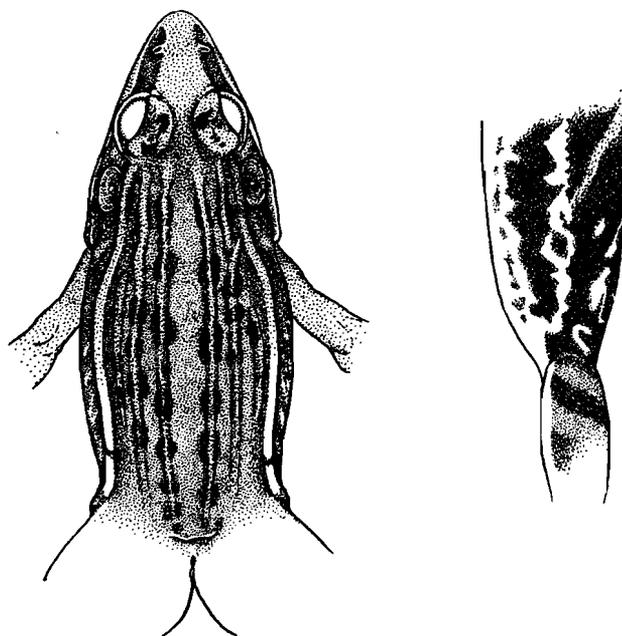


FIG. 46. — *Rana subpunctata* from Parc National de l'Upemba ( $\times 1$ ).  
Left, dorsal view. Right, posterior face of thigh.

Males of the two species are readily differentiated. In *mascareniensis* the openings of the gular pouches are parallel to the lower lip and end at the upper border of the insertion of the arm; in *subpunctata* the opening makes a distinct angle with the lower lip and ends more ventrally. The males of *subpunctata* lack the light spinules that in *mascareniensis* cover the plantar surfaces, sides, and often the throat.

Diagnosis. — Body and limbs moderately stocky; head obtusely pointed; snout projecting; nostril nearer to tip of snout than to eye; vomerine teeth in transverse series, in contact with anterior borders of choanae;

tympanum distinct, three-fourths to four-fifths diameter of eye, slightly shorter than eye-nostril distance; back (Fig. 46) with 8 continuous skin folds, the mid-dorsal pair beginning behind eyes; fingers and toes bluntly rounded; first finger slightly shorter than second which is slightly shorter than fourth; a rudiment of web between first and second fingers; second and third fingers with a narrow fringe of skin along median edges; no supernumerary metacarpal tubercles; toes almost completely webbed; fourth toe with two phalanges free of web on lateral border; fifth toe webbed to tip or with one-half phalanx free; no external metatarsal tubercle; no row of small tubercles on fourth metatarsal.

Back with alternating rows of squarish black spots; half of specimens with a light vertebral line or band; dorsal surface of tibia usually with a light, longitudinal line; thigh with light line dorsally in half of individuals; posterior face of thigh (Fig. 46) dark brown with two light longitudinal stripes; 4 to 6 broadly interrupted dark crossbars on tibia; usually 2 dark tarsal bars; underside of foot bicolored, the toes dark and the web mostly cream-colored; lower jaw with a black network.

Secondary sex characters. — Only two fully mature males are included in this sample. The nuptial pads are cream-colored and cover the entire dorsal and median surfaces of the first finger from its base to the beginning of the terminal phalanx, the dorsal surface of the second finger from its base to the base of the terminal phalanx, and a dorso-median area of the third finger from its base to a point mid-way between the two subarticular tubercles. Light spinules are not present on any part of the body.

The opening of the gular pouch runs from below the center of the eye to a point near the ventral border of the insertion of the arm. The opening is 0.16 of the snout-vent length in both males. The wrinkled skin of the pouch is black.

These males measure 50.8-54.6 mm and the two females with ripe ova 64.1-67.6 mm.

Ecological notes. — All recorded localities of *subpunctata* and its synonyms are in the open country south of the rain forest belt. All Upemba specimens were collected at 585 m.

Range. — Known only from northern Angola (BOCAGE, 1866), southeastern Belgian Congo, and Bechuanaland (FITZSIMONS, 1932).

Upemba locality and specimens :

Mabwe (14).

22. — *Rana superciliaris* GÜNTHER.

*Rana superciliaris* GÜNTHER, 1848, Cat. Batr. Brit. Mus., pp. 17 and 132, pl. 1, fig. B — Sierra Leone.

*Rana (Ptychadena) superciliaris* GUIBÉ and LAMOTTE, 1955, Bull. Mus. Nat. Hist. Nat., (2), 27, p. 363.

*Rana mascareniensis* (part), BOULENGER, 1882, Cat. Batr. Brit. Mus., p. 52.

*Rana oxyrhynchus oxyrhynchus* (non SMITH) LOVERIDGE, 1936, Bull. Mus. Comp. Zool., 79, p. 415.

Taxonomic notes. — Until the recent publication of GUIBÉ and LAMOTTE (1955 A), the status of *superciliaris* has been obscure. GÜNTHER himself (1858, p. 132) contributed to the difficulty by stating that it was probably a synonym of *bibroni* HALLOWELL. The name was subsequently buried in the catch-all synonymy of *mascareniensis* by BOULENGER (1882). More recently the species has been misidentified by LOVERIDGE as *oxyrhynchus* (see p. 91). But GUIBÉ and LAMOTTE have firmly and clearly reestablished *superciliaris* as a distinct species.

Without knowing that GUIBÉ and LAMOTTE had been working on this problem, we examined the type of *superciliaris*, thanks to the courtesy of Miss GRANDISON of the British Museum, and arrived at precisely the same conclusions. As noted by GUIBÉ and LAMOTTE, *superciliaris* has much more extensive webbing than *bibroni* and differs from *mascareniensis* in the position of the opening of the gular pouch. The striped rear face of the thigh, the absence of an outer metatarsal tubercle, the interruption of the mid-dorsal skin folds, the transverse arrangement of the vomerine teeth, and the fully webbed fifth toe, taken in combination, distinguish *superciliaris* from all members of the subgenus *Ptychadena*.

Liberian specimens (CNHM 57940-63) agree with the type of *superciliaris* remarkably well and leave no doubt as to their identity. About one-half of this series has a broad vertebral stripe. As in the type, the web of the Liberian frogs reaches the tip of the fifth toe but leaves two phalanges of the fourth, one and one-third phalanges of the third, and one phalanx on each of the second and first toes free (on lateral borders of first to fourth toes).

East African specimens apparently lack any light vertebral marking; we have examined 9 from Tanganyika, 3 from Kenya, 2 from Ethiopia, and 13 from French Somaliland, as well as 72 from the Upemba. The eastern populations also differ in having slightly more extensive webbing. The fourth toe has 1 ½ to 2 phalanges free and the third, second, and first toes are either webbed to the tips or have one phalanx free. Considering only males with the secondary sex characters fully developed (see Secondary sex characters below), the openings of the gular pouches are relatively longer in the West African population. In five males from Liberia and

Sierra Leone (the type), these slits are 0.17 to 0.19 of the snout-vent length (mean= $0.180\pm 0.004$ ), whereas in 11 from East Africa the corresponding figures are 0.14-0.17 (mean= $0.150\pm 0.003$ ). This small difference is statistically significant. Otherwise the eastern frogs are like the type and Liberian specimens; the two groups are certainly conspecific.

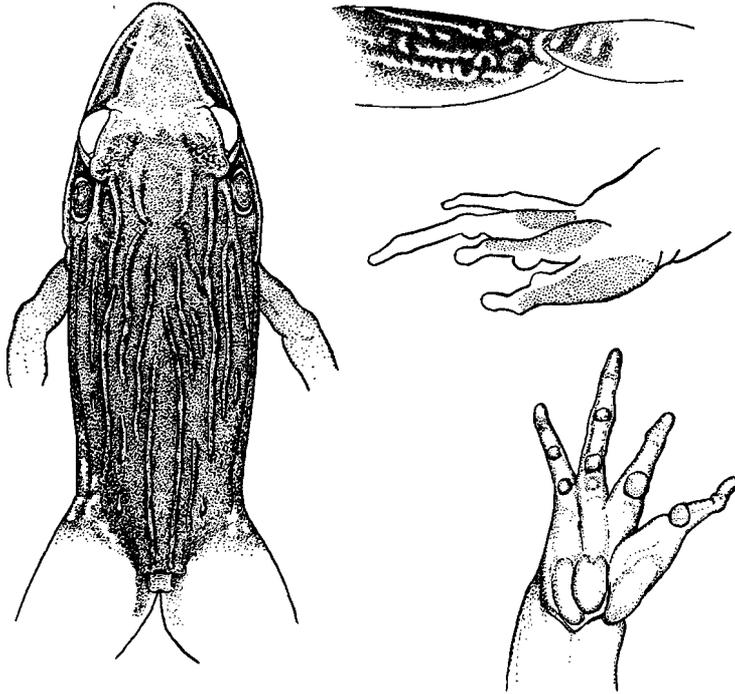


FIG. 47. — *Rana superciliaris* from Parc National de l'Upemba. Left, dorsal view ( $\times 2$ ). Right upper, posterior face of thigh ( $\times 2$ ). Right center, nuptial pads of male ( $\times 4$ ). Right lower, ventral surface of hand ( $\times 4$ ).

**Diagnosis.** — Body raniform; limbs moderately long; head obtusely pointed; snout projecting slightly; nostril nearer to tip of snout than to eye; vomerine teeth in transverse series, in contact with antero-median borders of choanae; tympanum distinct, about  $\frac{4}{5}$  diameter of eye, slightly less than eye-nostril distance; back (Fig. 47) with 6 or 8 longitudinal folds, folds ending behind orbits, mid-dorsal pair interrupted or present only in posterior half of body; tips of fingers and toes bluntly rounded; first finger equal to or shorter than second; usually no supernumerary metacarpal tubercles; toes almost completely webbed; fourth toe with one and one-half

to two phalanges free of web on lateral border; fifth toe usually webbed to tip; no external metatarsal tubercle; no row of small tubercles under fourth metatarsal.

Back with alternating rows of oblong black spots equal to tympanum diameter (West African frogs) or smaller than tympanum (East African individuals), or with spots absent (East African frogs); mid-dorsal band common in West African population only; no light line on thigh or tibia; posterior surface of thigh (Fig. 47) dark brown or black with yellowish or whitish, irregular stripes or with light spots arranged in longitudinal series; 3 to 6 usually interrupted black bars on tibia; 2 or 3 tarsal bars; underside of foot dark brown, small light areas at base of web; lower jaw barred with black.

Secondary sex characters. — At maximum development the nuptial pad of *superciliaris* is cream-colored and covers the dorsal and median surfaces of the first finger from its base to the end of the proximal phalanx, the dorsal surface of the second finger from its base to the end of the proximal phalanx, and an oval area on the dorsal surface of the third finger not extending beyond the level of the basal subarticular tubercle (Fig. 47). The smallest male with fully developed pads measures 33.6 mm snout to vent.

The slit-like openings of the gular pouches begin below the posterior half of the eye and end near the ventral border of the insertion of the arm. In six adult males from the Upemba collection these slits are 0.14 to 0.17 of the snout-vent length. The range for 16 males from scattered localities (see Taxonomic notes above) is 0.14-0.19. The skin of the gular pouches varies from black to black and white. Ventral asperities were not seen in any male.

The sequence of development of the male secondary sex characters is as in other species of this group. The gular pouches develop before the nuptial pads. Six males (35.1-39.3 mm) from the Upemba have fully developed gular pouches and vocal sacs but not a trace of nuptial pads. On the other hand, no male lacking the gular pouches has nuptial pads.

Males are distinctly smaller than females. Six Upemba males with nuptial pads measure 33.6-37.8 mm snout to vent (mean=35.13±0.61); 13 additional mature males from other localities extend the range to 31.4-42.8 mm (mean=36.70 mm). Only one Upemba female contains ripe ova, and it measures 49.0 mm; 9 other Upemba females vary from 40.2 to 48.4 mm. Two Liberian females with pigmented ova measure 51.9 and 52.5 mm.

Ecological notes. — Published habitat information associate *superciliaris* with streams and their immediate vicinity (LOVERIDGE, 1936, 1942, 1953 as *o. oxyrhyncha*).

In the Upemba 13 *superciliaris* were obtained at altitudes between 680 and 750 m and 60 at altitudes between 800 and 860 m.

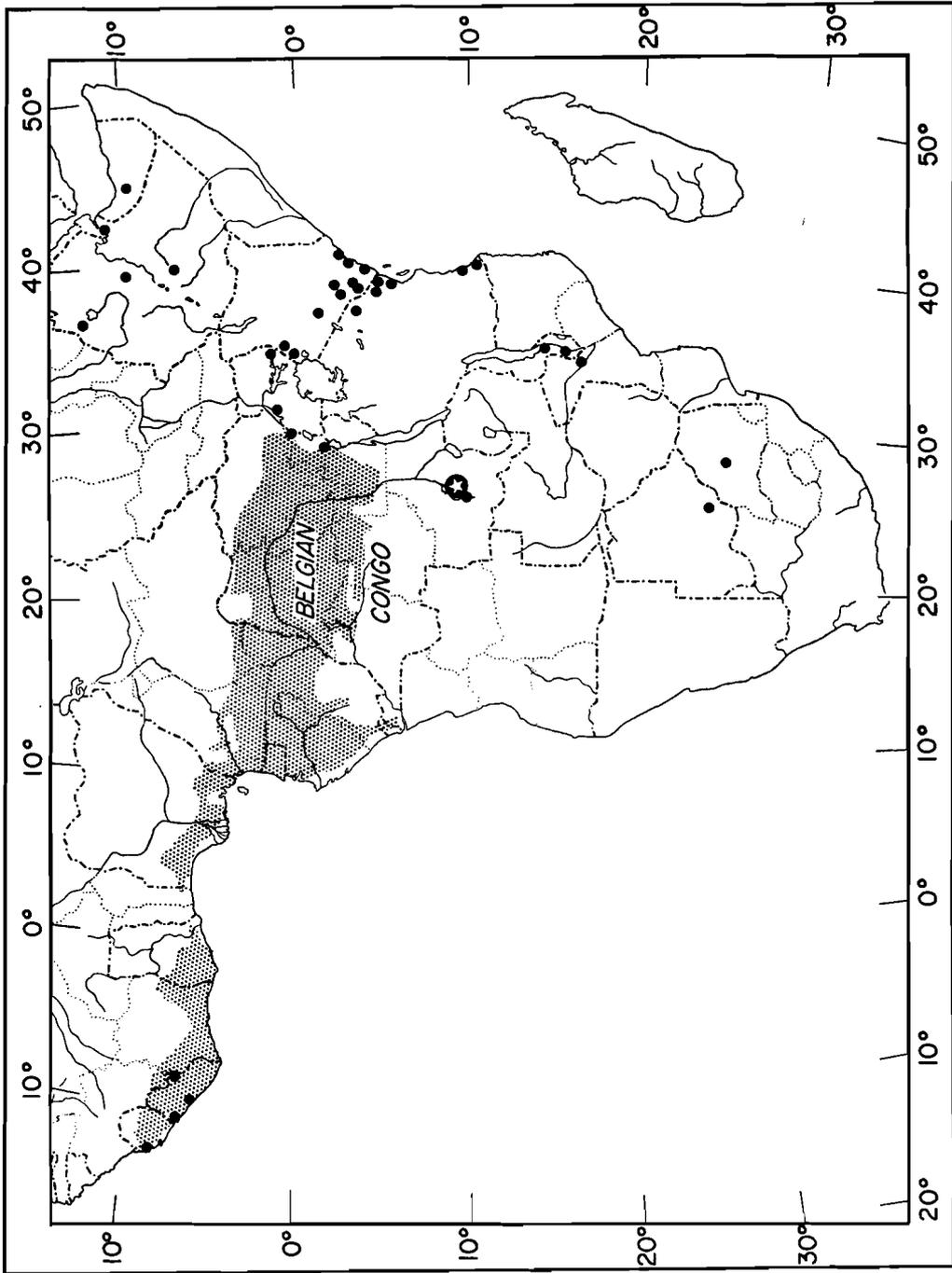


FIG. 48. — Known distribution of *Rana superciliaris*, based on collections of Chicago Natural History Museum and papers of Loveridge (as *R. o. oxyrhynchus*).

Too few specimens were available to determine the breeding period adequately, but the data fit the cycle worked out for other species of the genus (e.g., *oxyrhyncha*, *porosissima*). Nuptial pads, which are indicators of sexual activity, are absent in all 13 adult males of June and all 7 of July, but are present in 1 of 4 adult August males, in all 4 September males, and in the single October male. The only female with ripe ova was collected in September; the collection includes only 10 females.

Range. — In the west *Rana superciliaris* is known with certainty only from Sierra Leone and Liberia. In East Africa it occurs from Bechuanaland (CNHM 18026) in the south to Ethiopia in the north (Fig. 48).

Upemba localities and specimens :

Ganza (47); Kande (1); Kaswabilenga (1); Kilwezi (3); Kipondo (4); Loie (2); Lufira (2); Lukoka (3); Mware (8); Senze (2).

23. — *Rana taenioscelis* LAURENT.

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

Taxonomic notes. — The specimens at hand agree remarkably well with the type series, which we have examined. Though resembling the sympatric *uzungwensis*, as LAURENT points out, the two species differ in coloration of the feet and thighs, in the position of the openings for the gular pouches, and in the supernumerary metacarpal tubercles (present only in *uzungwensis*). In those characters, *taenioscelis* recalls *m. mascareniensis*. However, *taenioscelis* is readily distinguished by its smaller size (maximum of males near 35 mm, of females 40 mm), the extension of the mid-dorsal skin folds on to the snout (Fig. 49), the presence of prefrontal spots, and the restriction of the nuptial pad of the third finger to the metacarpus (Fig. 49). In fact, the forward extension of the skin folds in combination with the light longitudinal stripes behind the thighs distinguishes *taenioscelis* from all other forms of *Rana* (*Ptychadena*).

Diagnosis. — Body and limbs moderately slender; head pointed; snout projecting; nostril equidistant between eye and tip of snout or closer to latter; vomerine tooth groups transverse or slightly oblique, in contact with antero-median corners of choanae; tympanum distinct, three-fourths to four-fifths diameter or eye, equal to or shorter than eye-nostril distance; back (Fig. 49) with 8 continuous skin folds, the mid-dorsal pair beginning on snout and ending in anal region; tips of fingers and toes bluntly rounded; first finger shorter than second, second shorter than fourth; no supernumerary metacarpal tubercles; toes about two-thirds webbed; fourth toe with 3 phalanges free of web on lateral border; fifth toe with one to

1  $\frac{1}{3}$  phalanges free; no external metatarsal tubercle present; no row of small tubercles on fourth metatarsal.

Back with alternating rows of obscure, squarish or oblong, black spots whose longest axes are subequal to tympanum; a vertebral light line or band usually present, never with both band and line; a pair of dark, prefrontal spots usually present; dorsal surface of tibia with obscure, light,

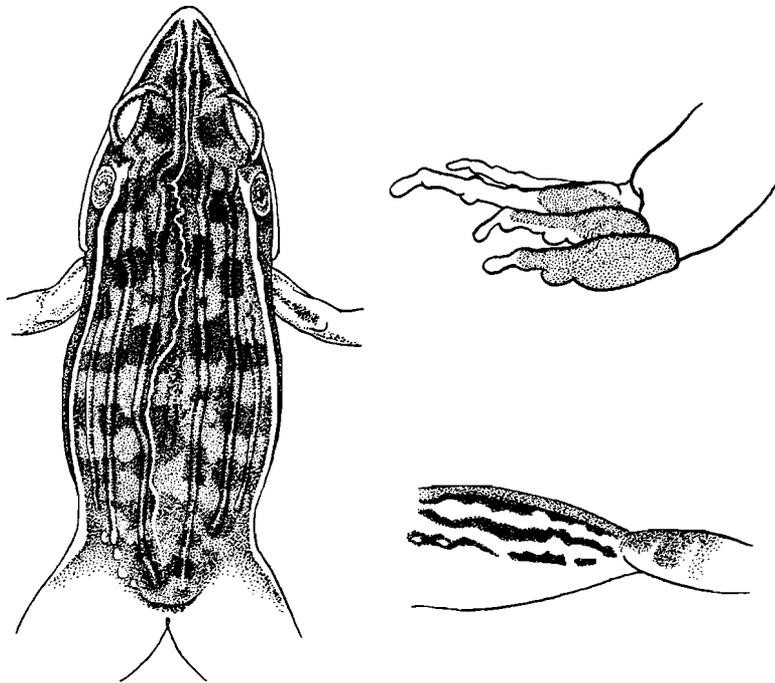


FIG. 49. — *Rana taenioscelis* from Parc National de l'Upemba.

Left, dorsal view ( $\times 2\frac{1}{2}$ ). Right upper, hand of male showing nuptial pad ( $\times 6$ ). Right lower, posterior face of thigh ( $\times 2\frac{1}{2}$ ).

longitudinal line; dorsal surface of thigh occasionally with light line in distal half; posterior face of thigh (Fig. 49) dark brown with two longitudinal light stripes; 4 to 7 usually uninterrupted black bars on dorsal surface of tibia; 3 or, less often, 2 black tarsal bars; underside of foot distinctly bicolored, the toes dark brown or black, the web cream-colored except distally between the outer toes; lower jaw barred with black; throat sometimes with small dark spots; chest and abdomen immaculate cream-colored.

Secondary sex characters. — Males have cream-colored or dusky nuptial pads. At the peak of their development, the pads (Fig. 49) cover the entire dorsal and median surfaces of the first finger from its base to the beginning of the terminal phalanx, the dorsal surface of the second finger from its base to the beginning of the terminal phalanx, and an oval, dorso-median area on the third metacarpal but not extending beyond the level of the basal subarticular tubercle. Males at this stage usually have feeble, translucent spinules scattered over the throat. They never develop such spinules on the back, sides, or on the feet (see *mascareniensis*, p. 81).

The vocal sac apparatus consist of paired vocal sacs and gular pouches. The openings of the latter are parallel to the lower lip and run from below the center or posterior half of the eye to the upper border of the insertion of the arm. The skin of the gular pouches is black or black and gray. In 5 males with mature nuptial pads, the openings of the pouches vary from 0.13 to 0.18 of the snout-vent length (mean=0.155).

The females are slightly but consistently larger than the males, as suggested by LAURENT (1954), who cites 40 mm as the maximum snout-vent length of females and 35 mm as the maximum for males. Nine females at hand have a range of 30.7-36.7 mm (mean=34.71±0.75 mm), the smallest with pigmented ova measuring 31.1 mm. The seven males at hand have a range of 30.2-32.6 mm (mean=31.49±0.30 mm) and even the smallest has fully developed gular pouches but no nuptial pads. The difference between the two means is statistically significant ( $t=3.594$ ,  $n=14$ ,  $P<.01$ ).

Ecological notes. — The 22 frogs available were collected between 1,700 and 1,810 m above sea level. The localities LAURENT cites are in moderately high country south of the rain forest province.

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

Upemba localities and specimens :

Kafwe (1); Kalumengongo (1); Kampadika (1); Lufwa (11); Lusinga (7); Mubale (1).

#### 24. — *Rana upembae* n. sp.

Holotype. — Institut des Parcs Nationaux du Congo Belge number 1304. An adult male collected at Kaswabilenga, Parc National de l'Upemba, Province Katanga, Belgian Congo on January 5-9, 1949, by the Mission G. F. DE WITTE.

Diagnosis. — A *Rana* (*Ptychadena*) (Fig. 50) with one to two phalanges of fifth toe free of web, mid-dorsal pair of skin folds continuous from occiput to the anal region, strongly projecting snout, uniformly dark lower lip, posterior face of thigh striped, and no longitudinal light line on dorsal face of tibia.

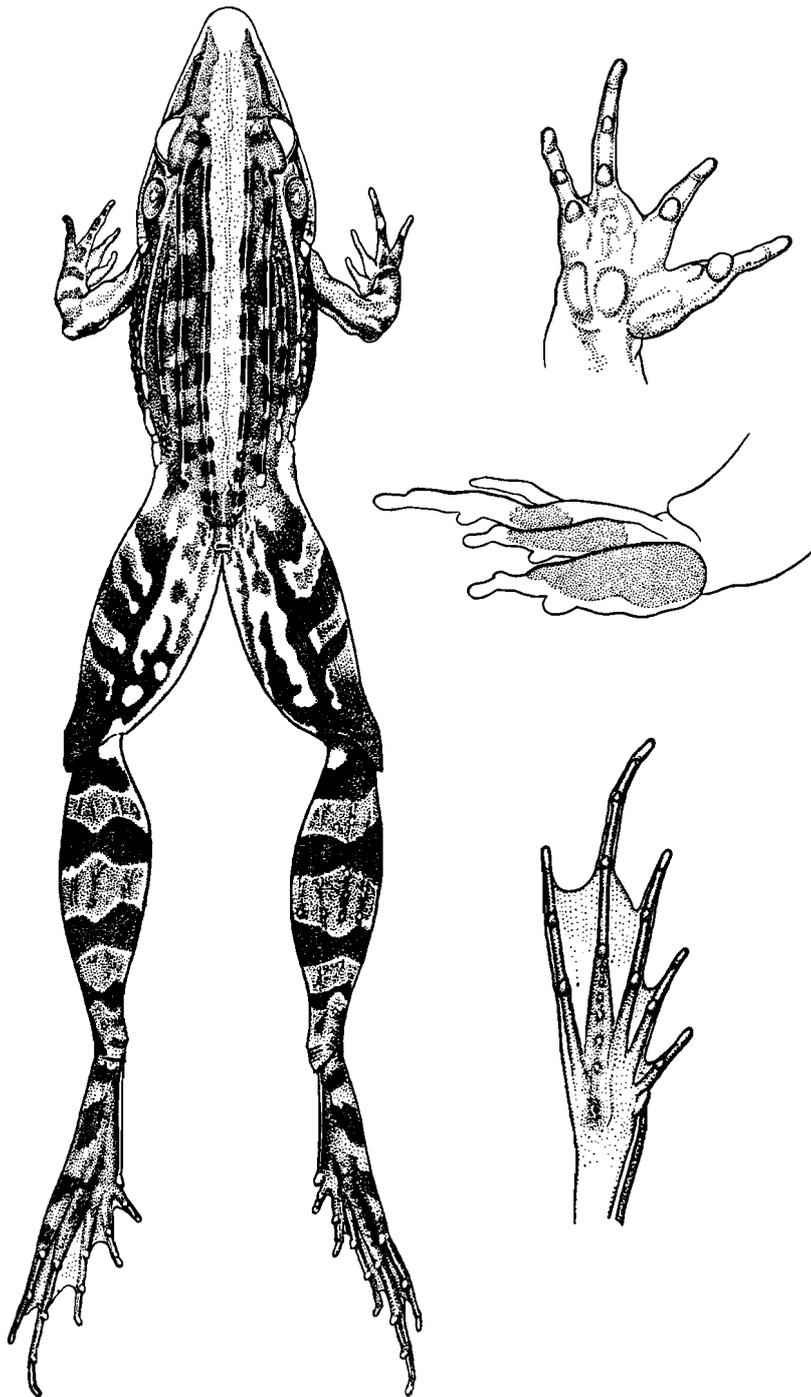


FIG. 50. — *Rana upembae* new species.

Left, dorsal view ( $\times 2$ ). Right upper, ventral surface of hand ( $\times 5$ ).  
Right center, hand of male showing nuptial pad ( $\times 6$ ). Right lower,  
ventral surface of foot ( $\times 3$ ).

Description of holotype. — Body and limbs slender; head long and narrow, roundly pointed in profile; snout long, projecting beyond tip of mandible more than diameter of tympanum; nostril slightly closer to eye than to tip of snout; internarial distance subequal to eye-nostril distance but much greater than interorbital; width of upper eyelid equal to interorbital; canthus rostralis rounded; lores oblique, distinctly concave; long diameter of eye equal to eye-nostril distance; tympanum distinct, equal to  $\frac{4}{5}$  eye diameter, separated from orbit by half its diameter; vomerine teeth in transverse groups, in contact with antero-median borders of choanae.

Fingers and toes bluntly rounded; first and second fingers equal, fourth slightly shorter than second, third much longer than fourth; subarticular tubercles distinct; metacarpals with supernumerary tubercles. Toes about two-thirds webbed; first toe with 2, second with  $1\frac{1}{2}$ , third with  $1\frac{2}{3}$ , and fourth with 3 phalanges free of web on lateral borders; fifth toe with  $1\frac{1}{2}$  phalanges free; subarticular tubercles distinct; inner metatarsal tubercle oval, less than half the length of first toe; a small but distinct, round external metatarsal tubercle; fourth metatarsal with a row of small tubercles, third with a shorter row of feebler ones.

Back with prominent folds; median pair beginning at postero-lateral corner of interorbital and continuing without interruption to anal region; a second fold beginning at posterior edge of upper eyelid and running without break almost to inguinal region; a somewhat heavier dorso-lateral fold beginning in a glandular swelling above tympanum and running to inguinal region with several interruptions; a short fold between dorso-lateral fold and next long fold above; round and oval swellings between all folds; sides coarsely granular with relatively large round warts anteriorly; a thick glandular swelling from beneath tympanum to upper border of axilla; skin below smooth except for secondary sexual spinules (see below); postero-ventral surface of thigh coarsely granular.

Color (in alcohol) of dorsal surfaces of head, body, and limbs light brown; a broad, light mid-dorsal band from tip of snout to vent; a thin lighter vertebral line from internasal to vent; back with two staggered rows of dark oblong spots; dorso-lateral fold becoming whitish posteriorly; sides of body dark brown anteriorly, becoming pale brownish posteriorly; a narrow dark brown streak from tip of snout, through upper half of lores, covering entire temporal region except for slightly lighter tympanum; upper lip grayish brown; lower jaw black almost from symphysis to insertion of arm, the black streak gradually widening posteriorly; all other ventral surfaces immaculately cream-colored; dorsal surfaces of lower arm and outer fingers barred with dark brown; no light longitudinal line on dorsal surfaces of hind limbs; dorsal surface of thigh with narrow dark crossbars; posterior face of thigh (Fig. 50) dark brown with two irregular, light, longitudinal stripes; dorsal surface of tibia with 4 uninterrupted dark bars; two dark tarsal bars; underside of foot dark brown except for lighter subarticular and metatarsal tubercles.

Dimensions (mm) of holotype : snout-vent 40.8; head length (to angle of jaw) 16.8; head width (at center of tympanum) 12.0; length of gular pouch opening 7.6; tibia 25.2; foot (less tarsus) 22.0.

Secondary sex characters of holotype. — The nuptial pads (Fig. 50) are cream-colored, velvety clusters of spinules occupying 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 from its base to the end of the penultimate phalanx, and an oval area on the medio-dorsal surface of the third finger from its base to a point just beyond the level of the basal subarticular tubercle. Very feeble, colorless, translucent spinules are scattered over the gular and pectoral regions and on the plantar surface of the foot. Dorsal or lateral nuptial spinules are absent.

The gular pouch openings begin below the posterior third of the eye and run somewhat oblique to the lower jaw ending near the ventral border of the axilla. The wrinkled skin within the gular pouch is black. Oval vocal sac openings are situated in the floor of the mouth, near the corners.

Paratypes. — All of the following specimens are from the Parc National de l'Upemba or immediately adjacent localities. IPN 1244 B (3), 1273 (6), 1296, 1297 (2), 1299 (4), 1302, 1304 (3), 1313 (11), 1315, 1320-21 (3), 1322 A, 1323-30 (17), 1334 (2), 1385, 1391, 1398, 1402-03 (3), 1419-23 (8), 1424 A, 1425 A, 1428 (11), 1430-35 (22), 1437, 1557 A.

This series is remarkably uniform despite the fact that two-thirds are juveniles. The vomerine teeth may be in transverse or slightly oblique groups. The dorso-lateral fold is usually interrupted, but the positions of the breaks vary from the anterior third of the fold to its posterior third. Approximately one-sixth of the sample lacks the external metatarsal tubercle and the row of smaller tubercles on the fourth metatarsal.

The outer edge of the thigh usually has a dark streak connecting the ends of the dark dorsal crossbars. The whitish stripes on the rear of the thigh are sometimes broken up. A few specimens have a pair of dark prefrontal spots. Nevertheless, the basic pattern varies but little. Characteristically, these frogs have a light mid-dorsal band and line, a dark loreal stripe, a dark lower jaw, uninterrupted bars on the tibia, light stripes behind the thigh, but no light line on the dorsal surface of the leg.

Adult males with fully developed nuptial pads are 38.0-43.9 mm long (mean of 10 =  $40.58 \pm 0.61$  mm). Another male with pads incompletely developed measures 36.3 mm. Two females containing pigmented ova are 42.8 and 45.9 mm. Four additional females without ripe ova have snout-vent lengths of 46.0-50.8. Body proportions (given as decimals of snout-vent) vary as shown in Table 21.

TABLE 21. — Variation in body proportions (as decimals of snout-vent) among paratypes of *Rana (Ptychadena) upembae*.

	No	Range	Mean $\pm$ SE
Tibia ... ..	9	0.58-0.63	0.608 $\pm$ 0.006
Foot ... ..	9	0.52-0.58	0.549 $\pm$ 0.006
Head width ..	10	0.30-0.35	0.315 $\pm$ 0.005
Snout ... ..	10	0.19-0.21	0.202 $\pm$ 0.002
Gular pouch opening ..	10	0.15-0.20	0.178 $\pm$ 0.006

For the above calculations the foot was measured from the proximal edge of the inner metatarsal tubercle to the tip of the fourth toe, the head width taken at the center of the tympanum, and the snout measured from the eye forwards.

Comparisons. — This discussion is limited to those forms of the subgenus *Ptychadena* having between 1 and 2 phalanges of the fifth toe free of web and the median pair of skin folds continuous from occiput to anal region. The species thus eliminated from consideration (e.g., *oxyrhyncha*, *superciliaris*, *bibroni*, *chrysogaster*, *mossambica*, etc.) differ in one or more additional characters from *upembae*. There still remain 8 species to be disposed of. Two, *mascareniensis* and *taenioscelis*, differ from *upembae* in the position of the gular pouch openings and in the coloration of the lower jaw (barred in the first two) and plantar surface of the foot (bicolored in the first two). *Rana grandisonae*, *venusta*, and *vernayi* differ from *upembae* in coloration of the lower jaw (barred in the first three) and tibia (crossbars interrupted in the first three) and in the shape of the snout. *Rana uzungwensis* is distinguished from *upembae* by the extension of the median skin folds on to the snout, by the presence of prefrontal spots, and by the barred lower jaw. *Rana submascareniensis* is a much smaller frog, with adult males averaging 26.4 mm, according to GUIBÉ and LAMOTTE (1953), as compared to a range of 36-43 mm in *upembae*, and lacks vomerine teeth. A shorter snout, smaller dorsal spots, and the dorsal spinules of sexually competent males separate *obscura* from *upembae*.

Probably *upembae* is more likely to be confused with *porosissima* than with any other species. They are approximately the same size and similar in coloration, especially in such details as the dark brown or black lower jaw, the conspicuous dark loreal stripe, and the uninterrupted crossbars

on the tibia. But *upembae* lacks the light longitudinal streak so characteristic of the dorsal surface of the tibia in *porosissima*; the light markings on the posterior face of the thigh are usually in the form of isolated round spots in *porosissima* (Fig. 45) and in the shape of irregular longitudinal stripes in *upembae* (Fig. 50). The tibia and snout are relatively longer in *upembae* as shown in Table 22; though not large, the differences are statistically significant at the one percent level. The two species also differ in the male secondary sex characters. The ventral spinules in sexually active *upembae* are much weaker and are not black as in male *porosissima*. The nuptial pad on the third finger covers one more phalanx in *porosissima*, reaching the terminal phalanx, whereas in *upembae* it ends at the base of the penultimate one.

TABLE 22. — **Body proportion differences between *Rana porosissima* STEINDACHNER and *R. upembae* n. sp. All specimens from Parc National de l'Upemba.**

	Tibia/snout-vent			Snout/snout-vent		
	No.	Range	Mean	No.	Range	Mean
<i>upembae</i> ... ..	9	0.58-0.63	0.608 ± 0.006	10	0.19-0.21	0.202 ± 0.002
<i>porosissima</i> ... ..	20	0.52-0.63	0.581 ± 0.005	9	0.15-0.20	0.172 ± 0.005

A comparison with *bibroni*, fortunately facilitated by the recent redescription by GUBÉ and LAMOTTE (1955), is necessary in view of the confusion centering around that species. The fifth toe of *bibroni* has 2 phalanges free of web whereas only 1 to 1  $\frac{3}{4}$  are free in *upembae*. According to GUBÉ and LAMOTTE *bibroni* has a short mid-dorsal pair of skin folds that do not extend anterior to the sacral region. The mid-dorsal folds of *upembae* are continuous from the occiput to the anal region. The dorsum of *upembae* bears alternating rows of distinctly quadrangular dark spots while the back of *bibroni* has a distinctly striped appearance given it by small elongated dark streaks.

Secondary sex characters. — The holotype represents the most advanced condition of these characters. Counting the holotype, only ten males (38.0-43.9 mm) have fully developed nuptial pads and all were collected during the months January-March. All but three of these have gular and plantar spinules. Another male (39.4 mm) collected in February has a nuptial pad on the first finger only and has no sign of gular or plantar spinules. Five presumably adult males (38.2-40.8 mm), collected

in August and September, have fully developed vocal sac apparatus but no other secondary sex characters. A slightly smaller male (36.3 mm) caught in April has nuptial pads on the first two fingers, but no gular spinules. Males without nuptial pads and in the size range 35-37 mm were taken in April, September, and October.

**Ecological notes.**— Though the small sample size limits confidence in the speculation, the seasonal distribution of males with well developed secondary sex characters suggests that breeding in the Upermba starts after October and continues through March. The sole female with a full complement of ripe ova was collected in January. Another female, apparently caught very shortly after oviposition, has a few ovulated ova; this frog was collected on April 7.

*Rana upembae* is most abundant at middle and low elevations as the following tabulation shows.

Meters.	Individuals.
500- 750	30
751-1,000	56
1,001-1,250	12
1,251-1,500	0
1,501-1,750	11

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

**Upemba localities and specimens :**

Ganza (9); Kabenga (7); Kalungwe (2); Kambi (11); Kande (17); Kanonga (5); Kaswabilenga (6); Kaziba (4); Kilwezi (19); Lupiala (2); Munoi (26); Tumbwe (1).

#### 25. — *Rana uzungwensis* LOVERIDGE.

*Rana mascareniensis uzungwensis* LOVERIDGE, 1932, Bull. Mus. Comp. Zool., **72**, p. 384 — Dabaga, Uzungwe Mountains, Tanganyika; 1933, idem, **74**, p. 370; 1936, idem, **79**, p. 418; 1953, idem, **110**, p. 372.

*Ptychadena uzungwensis* LAURENT, 1954, Ann. Mus. Roy. Congo Belge, **34**, p. 9, pl. 1, fig. 1, pl. 4, fig. 4.

*Rana mascareniensis subpunctata* (non BOCAGE) SCHMIDT, 1936, Ann. Carnegie Mus., **25**, p. 129.

**Taxonomic notes.** — The availability of a large series convinces us that LOVERIDGE (1936) is right in disagreeing with the senior author's placing of *uzungwensis* in the synonymy of *subpunctata* BOCAGE. The latter differs from *uzungwensis* not only in the extent of webbing (LOVERIDGE, 1953), but also in size, coloration, and relative length of dorsal skin folds (c.f., Figs. 29 and 46).

However, we also agree with LAURENT (1954) that *uzungwensis* is a distinct species and not, as LOVERIDGE has it, a form of *mascareniensis*. LAURENT correctly points out that *mascareniensis* and *uzungwensis* differ sharply in the position of the opening of the gular pouch. Furthermore they differ in coloration, the anterior extent of the mid-dorsal folds, the development of supernumerary metacarpal tubercles (usually absent in *mascareniensis*), and the extent of webbing. On the basis of morphology alone, *uzungwensis* is no more closely related to *mascareniensis* than many others of their congeners and less so than some.

Although LAURENT (1954) states that *uzungwensis* and *mascareniensis* are sympatric, we are able to glean only one instance of their occurring together from the literature. SCHMIDT (1936, p. 129) reported a *mascareniensis* (CNHM 21163; reexamined by us) and LAURENT (1954, p. 9) an *uzungwensis* from Chitau, Angola. The large series NOBLE (1924, p. 221) lists under *mascareniensis* actually includes *uzungwensis* (AMNH 11213, 11217-18) and *mascareniensis* from Faradje, Belgian Congo. Despite the fact that both species occur in the Upemba, we do not have both from a single locality. At least in the Upemba differences in altitudinal distributions isolate the two frogs (see pp. 83 and 121).

The extension of the mid-dorsal folds onto the snout distinguishes *uzungwensis* (Fig. 29) from all forms of *Rana* (*Ptychadena*) except *taenioscelis* (Fig. 49) and *ansorgei* (Fig. 32). The last differs from *uzungwensis* in having less extensive webbing and the black pigment of the lower jaw continuous. *Rana taenioscelis* differs in the position of the gular pouch opening, in coloration, and in the absence of supernumerary metacarpal tubercles.

Contrary to LAURENT's statement (1954, p. 31) that *uzungwensis* has neither an external metatarsal tubercle nor a row of small tubercles under the fourth metatarsus, about half of the specimens at hand have both structures, though not as well developed as in *grandisonae*.

Our material agrees well with a male paratype (CNHM 18345) from the type locality. The specimen (CNHM 12515) from Kitete, Tanganyika listed by LOVERIDGE (1936 A) is a *Rana porosissima*.

**Diagnosis.** — Body and limbs moderately slender; head pointed; snout rather strongly projecting; nostril usually mid-way between eye and tip of snout; vomerine teeth slightly oblique, in contact with anteromedian corners of choanae; tympanum distinct, one-half to two-thirds eye diameter, much shorter than distance between eye and nostril; back (Fig. 29) with 8 folds, the mid-dorsal pair beginning between nostrils and continuous to anal region; tips of fingers and toes bluntly rounded; first, second, and fourth fingers subequal; supernumerary metacarpal tubercles present, distinct; toes about two-thirds webbed; fourth toe with 3 phalanges free of web on lateral border; fifth toe with 1 to 1 ½ phalanges free; about half

of the individuals with a small, round, external metatarsal tubercle; a row of feebly distinct, small, light-colored tubercles on the fourth metatarsus.

Back with alternating rows of squarish black spots, each of which having the transverse axis subequal to tympanum; occasionally spots of adjacent rows fuse forming irregular transverse bands; a narrow, vertebral line in almost all individuals; thigh and tibia without light lines on dorsal surfaces; posterior face of thigh (Fig. 51) dark brown with round light spots that occasionally coalesce into a network; 4 to 6 uninterrupted black bars on dorsal surface of tibia; 2 or 3 black tarsal bars; underside of foot uniformly brownish except for lighter tubercles; lower jaw barred with black; a pair of black prefrontal spots usually present.

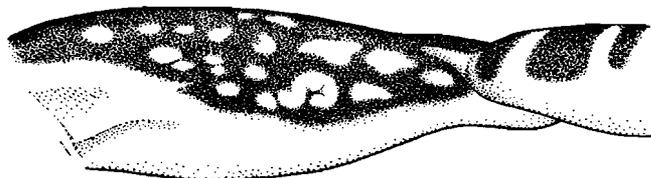


FIG. 51. — *Rana uzungwensis* from Parc National de l'Upemba.  
Posterior face of thigh ( $\times 4$ ).

Secondary sex characters. — The vocal sacs of *uzungwensis* are paired as in other *Rana* (*Ptychadena*). The wrinkled skin of the gular pouches is customarily uniformly black, although in some males the posterior half of the pouch may be distinctly lighter than the anterior. The openings of the gular pouches begin below the posterior half of the eye and end near the antero-ventral border of the insertion of the arm. In 15 males with fully developed nuptial pads, the slits of the gular pouches vary from 0.15 to 0.19 of the snout-vent length (mean =  $0.165 \pm 0.003$ ).

The nuptial pads (Fig. 52) consist of cream-colored or dusky velvety clusters of spinules. The pads at the peak of development cover the dorsal and median surfaces of the first finger from its base to the end of the first phalanx, the dorsal surface of the second finger from its base to the end of the first phalanx, and an oval area on the dorso-median edge of the distal half of the third metacarpus. Males with pads in this condition usually have translucent, colorless, widely spaced spinules under the head and body and small, whitish spinules uniformly distributed over the dorsal surfaces of the head, trunk, and hind legs.

These secondary sex characters have the usual sequence of development. Only after the gular pouches and vocal sacs develop do the nuptial pads and the dorsal and ventral spinules appear. Eighteen males have com-

TABLE 23. — Correlation of the development of two secondary sex characters of male *Rana uzungwensis* (\*).

	Nuptial pad			
	Absent	On first finger only	On first two fingers	On three fingers
Dorsal and ventral spinules :	Number of individuals			
Absent ... ..	18	2	0	2
Present ... ..	0	0	2	24

(\*) All males with mature gular pouches and vocal sacs.

pletely formed gular pouches but have no trace of nuptial pads or spinules. On the other hand, all males having pads or spinules in any stage of development have mature gular pouches. The ventral and dorsal spinules develop simultaneously. The correlation between their development and the nuptial pad is shown in Table 23. Apparently the spinules and the nuptial pads begin development at approximately the same level of hormone production.

The females are distinctly larger than the males. Only 4 females with pigmented ova were available and these range in size from 41.9 to 45.7 mm. Nineteen additional females had snout-vent lengths in excess of 40 mm,

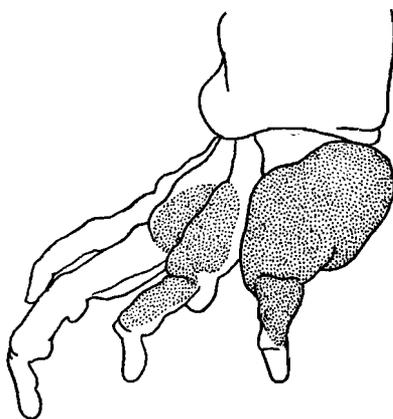


FIG. 52. — Hand of male *Rana uzungwensis* showing nuptial pad ( $\times 8$ ).

the largest measuring 47.6 mm. By contrast, 26 males with fully developed secondary sex characters have a snout-vent range of 31.6 to 35.7 mm (mean=33.54±0.22 mm). LAURENT (1954) gives similar size ranges : 39-49 mm for females, and 31.5-36.5 mm for males.

Ecological notes. — *Rana uzungwensis* is apparently most abundant at elevations between 1,000 and 2,000 m. Records from the literature place the lowest known elevation at 1,600 m and the highest at 2,000 m (both from LAURENT, 1954). The Upemba series shows the following distribution :

Meters.	Individuals.
890-1,000	6
1,001-1,250	22
1,251-1,500	75
1,501-1,750	13
1,751-1,815	31

All known localities lie outside the rain forest province.

Too few specimens are available for working out the reproductive cycle in the Upemba but the indications are that, like other species of *Rana*, the breeding season ends in March or April. As shown by Table 24, the proportion of adult males with nuptial pads drops sharply after March, suggesting a decrease in sexual activity.

Range. — This species is known with certainty from central Angola (SCHMIDT, 1936) to Tanganyika (LOVERIDGE, 1932) and from Southern Rhodesia to Ruanda (LAURENT, 1954) (Fig. 53).

TABLE 24. — Monthly frequency of adult male *Rana uzungwensis* with respect to nuptial pad development.

	Nuptial pads		
	complete	incomplete	absent
January .. .. .	12	1	0
March ... .. .	7	1	0
April . ... .. .	4	2	4
May .. ... .. .	2	0	13
June . ... .. .	0	0	1

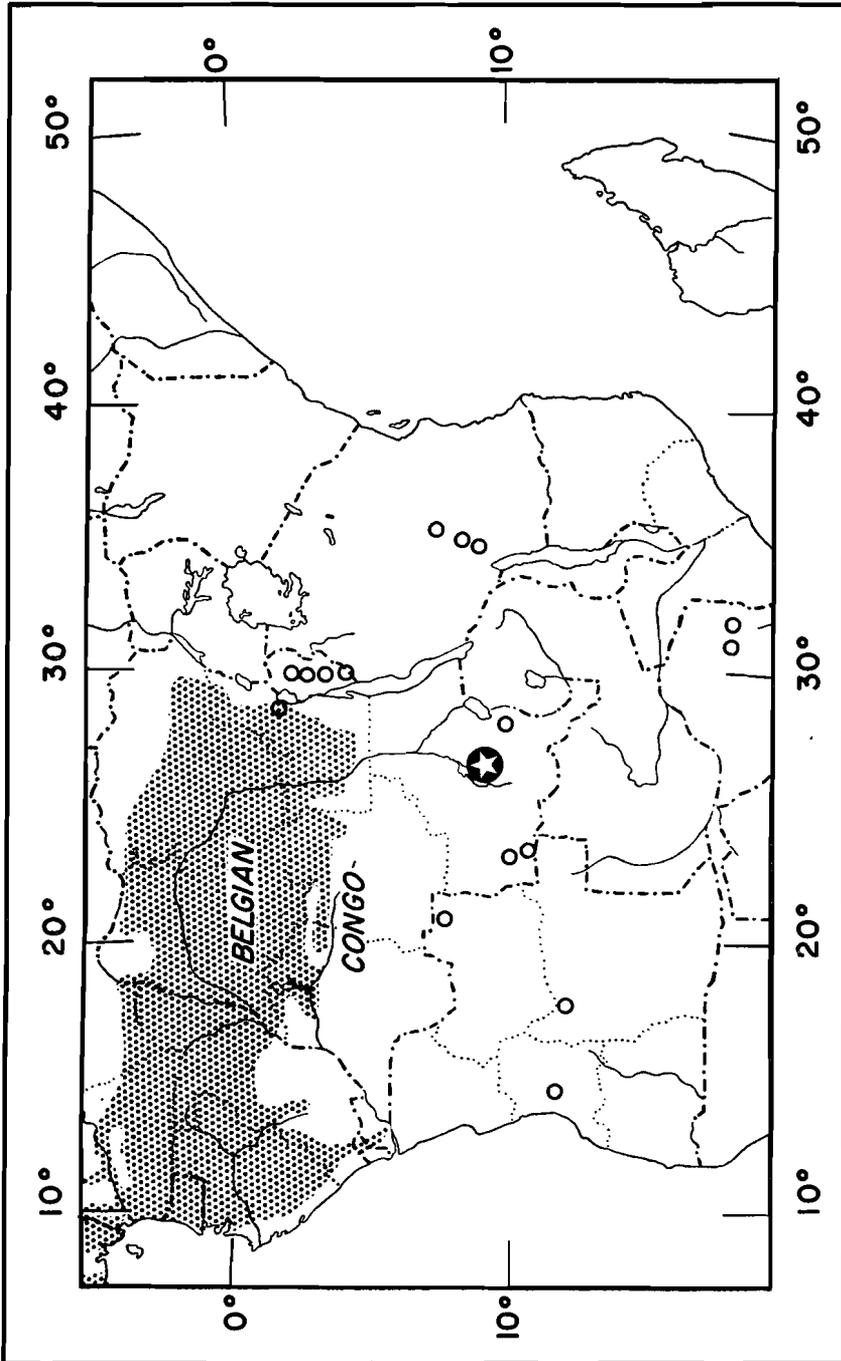


FIG. 53. — Distribution of *Rana uzunguensis*.  
Parc National de l'Upemba indicated by symbol with open star.

## Upemba localities and specimens :

Buye-Bala (4); Bwalo (1); Kabenga (7); Kabwe (56); Kabwekanono (6); Kafwe (4); Kagomwe (1); Kamitungulu (1); Kampadika (15); Kankunda (1); Katongo (1); Kaziba (1); Kimiala (2); Lufwa (6); Lusinga (4); Mubale (1); Munoi (4); Munte-Mubale (18); Pelenge (14).

Genus **ARTHROLEPTIS** SMITH.

The species most authors have grouped in the genus *Arthroleptis* (after removing those belonging to *Phrynobatrachus*) were divided into the genera *Cardioglossa* BOULENGER, *Schoutedenella* WITTE, and *Arthroleptis* SMITH by LAURENT (1940, 1954 A). The last he considered to include the subgenera *Abroscaphus*, *Coracodichus*, and *Arthroleptulus* (LAURENT, 1940), the last being absorbed later by *Schoutedenella* (LAURENT, 1954 A). In his most recent paper on this group, LAURENT (1957 A) merges *Schoutedenella* with *Arthroleptis* and elevates *Abroscaphus* and *Coracodichus* to full generic status.

These taxonomic opinions have been based wholly on osteological data, the principal characters being the degree of ossification of the ethmoid, the degree of bifurcation of the coracoid, and the relative size and compression of the inner metatarsal tubercle. But the species of this group can be arranged to form a gradual transition from one extreme condition to another in each character. With the exception of the last one, the characters used are of doubtful or at least uncertain phylogenetic, morphological, and ecological significance.

An enlarged, compressed inner metatarsal tubercle is characteristic of fossorial frogs and, within the present group, is best developed in the forms LAURENT places in *Coracodichus*. These forms, such as *stenodactylus* PFEFFER (see below), are fossorial, but according to LAURENT (1957 A, p. 275) so are species assigned to *Arthroleptis* (*sensu* LAURENT) and *Abroscaphus*. In fact, one of the last, *variabilis* MATSCHIE, has a tubercle essentially the same relative size and form as that of *stenodactylus*.

In summary, the differences noted by LAURENT do not suggest the more or less fundamental evolutionary divergence that should be required for generic recognition. Until an analysis indicating the evolutionary significance of the differences is presented, we refer LAURENT's new genera to the synonymy of *Arthroleptis* SMITH.