

## 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.

26. — **Arthroleptis stenodactylus** PFEFFER.

(Pl. V, 2.)

*Arthroleptis stenodactylus* PFEFFER, 1893, Jahrb. Hamburg Wiss. Anst.,  
10, p. 93, pl. 1. fig. 11 — Kihengo, Tanganyika.

Taxonomic notes. — Existing definitions of subspecies appear rather weak. The principal difference between *s. whytii* and *s. stenodactylus*, according to LOVERIDGE (1953), involve size, shape of finger tips and metatarsal tubercle, and coloration of the breast in females. Snout-vent of adult *whytii* are given by LOVERIDGE as : males 23-35 mm, females 29-44 mm; and for *stenodactylus* as 23 mm and 30-34 mm. The Upemba sample is almost exactly intermediate, mature males ranging from 21 to 35 mm and females from 29 to 38 mm. LOVERIDGE himself refers to much variation in the digit tips and metatarsal tubercle without presenting data illustrating a statistical difference. The dusky marbling of the breast of *whytii* females is the only character given by LOVERIDGE that seems to hold good. Females from the Upemba are usually immaculate white or cream-colored below, thus resembling the typical form.

Diagnosis. — Habitus stocky; head as broad as long; obtusely pointed; tympanum visible, about two-fifths eye diameter; maxillary teeth present.

Tips of fingers obtuse, first two fingers subequal; third finger elongated in adult males; tips of toes obtuse; a very slight web at bases of toes; subarticular tubercles prominent; blade-like inner metatarsal tubercle equal to or longer than first toe; no outer metatarsal tubercle.

Skin usually smooth above; a few tubercles scattered on sides; belly coarsely granular.

Color (in alcohol) above brown with a dark irregular mid-dorsal pattern; a few individuals with a light vertebral stripe; below immaculate white or cream-colored except for throat of male (see below).

Secondary sex characters. — Females with mature ova have a snout-vent range of 29.5-38.1 mm (mean=33.63±0.98; N=41). Mature males, i.e., those with gular modifications, range from 20.8 to 35.4 mm, though only one is smaller than 25.6; the mean of 85 is 29.71±0.21 mm.

Males have a median subgular vocal sac with a round opening on each side of the mouth. The gular skin becomes densely pigmented with melanin in a broad band just mesad of the mandible, and a cluster of small, colorless tubercles appears just behind the symphysis.

Male *stenodactylus* also develop elongated third fingers and, as in *Arthroleptis globosus*, the elongation is an indicator of maturity. Twelve males in the size range 25.0-29.0 mm and lacking vocal sacs and pigmented gular skin have third fingers equivalent to 0.178 to 0.199 (mean 0.187±0.002) of the snout-vent length. In fourteen from the same size range but having vocal sacs and pigmented throats the proportion of finger

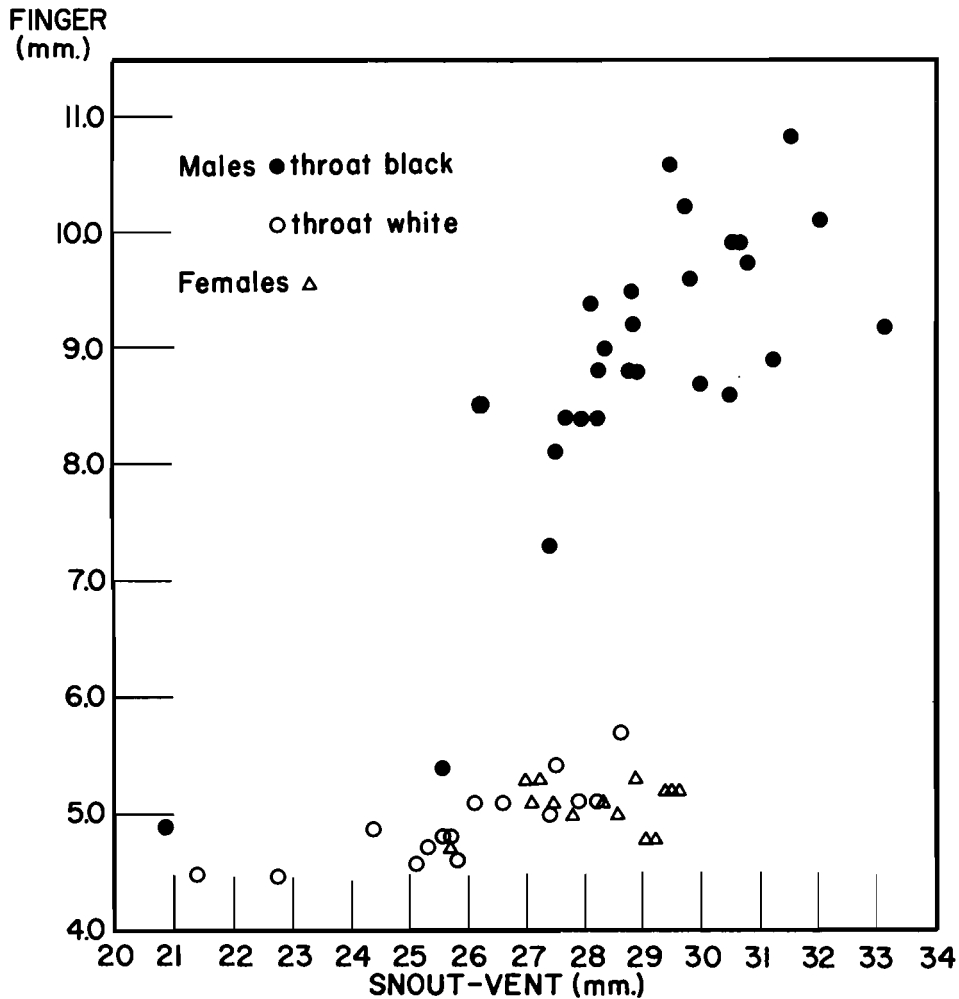


FIG. 54. — Relation between the length of the third finger and snout-vent length in *Arthroleptis stenodactylus* from Parc National de l'Upemba.

to snout-vent length varies from 0.211 to 0.335 (mean  $0.302 \pm 0.008$ ). As Fig. 54 shows, there seems to be a sudden spurt in the growth of the third finger shortly after the development of vocal sacs. In females, on the contrary, growth of the third finger apparently ceases after the animal reaches a length of 27 mm (Fig. 54).

The masculine secondary sex characters of *stenodactylus* show no evidence of seasonal regression. All males with pigmented gular skin have well-developed vocal sacs and vice versa. All males in that stage

of development and only those males have elongated third fingers. And, as shown in Table 25, about half of the males collected in the dry period have fully developed sex characters.

Only the fifteen adult-sized males listed in the second column of Table 25 can constitute evidence for seasonal regression. None of them has a vocal sac or an elongate third finger. Since we know of no documented case of seasonal disappearance of vocal sacs and since it is unlikely that the phalanges undergo seasonal shrinkage, the best interpretation of these males is that they are immature. This interpretation is supported by the fact that 59 of the 84 males listed in the first (i.e., mature) column are larger than the largest (28.6 mm) individual of the second (i.e., theoretically immature) column.

Ecological notes. — *Arthroleptis stenodactylus* has been collected in open country (LOVERIDGE, 1933, 1942, 1953) and in rather dry forest (LOVERIDGE, 1933, 1953), but never in rain forest. The altitudinal range as reported by LOVERIDGE is extensive, running from sea level to 1,800 m. In the Parc de l'Upemba *stenodactylus* is found at all elevations from 585 m to 1,830 m, with the following frequency :

Meters.	Individuals.
585- 750	2,634
751-1,000	197
1,001-1,250	314
1,251-1,500	80
1,501-1,830	3

The eggs of *stenodactylus* are deposited in small protected burrows away from bodies of water (LOVERIDGE, 1953). In the Upemba breeding appears to begin in November, when the proportion of adult females containing enlarged ova rises sharply (Table 25), and ends in January, when the proportion falls.

Range. — Probably confined to East Africa (Fig. 55) from north-eastern Belgian Congo (WITTE, 1934) southeastwards to Northern Rhodesia (FITZSIMONS, 1939) and central Portuguese East Africa (PARKER, 1930). ANGEL (1940) lists specimens from Sierra Leone and the Cameroons, but these localities are so far off from the main body of the range that the identification requires confirmation.

#### Upemba localities and specimens :

Bowa (23); Bunda Bunda (3); Ganza (3); Kabenga (4); Kabwe (17); Kalule Nord (3); Kalumengongo (2); Kande (14); Kankunda (59); Kanonga (216); Kaswabilenga (914); Kateke (89); Kaziba (281); Kiamakoto (1); Kilwezi (19); Kimiala (2); Kipondo (34); Lolie (1); Lukawe (11); Lupiala (11); Lusinga (1); Mabwe (1,467); Masombwe (5); Mokey (1); Munoi (46); Tumbwe (2).

TABLE 25. — Monthly frequency of adult *Arthroleptis stenodactylus* from the Upemba in different stages of sexual competence.

	Males (*)		Females (**)	
	Gular skin pigmented	Gular skin non-pigmented	Ova mature	Ova immature
January ... ..	7 (26.2-31.5 mm)	1 (25.6 mm)	3	2
February ... ..	6 (28.2-30.8 mm)	5 (25.4-28.2 mm)	0	8
March .. ...	1 (29.5 mm)	4 (26.0-27.8 mm)	0	4
April ... ..	0	1 (25.9 mm)	—	—
May ... ..	2 (27.2-29.4 mm)	0	—	—
June ... ..	1 (31.6 mm)	3 (25.7-27.6 mm)	0	1
August ... ..	—	—	0	2
October ... ..	6 (25.6-29.5 mm)	1 (28.6 mm)	6	7
November .. ...	23 (27.0-33.1 mm)	0	22	4
November-December ...	36 (27.6-33.2 mm)	0	7	1
December .. ...	2 (30.7-35.4 mm)	0	3	0

(\*) All individuals larger than 25.4 mm.

(\*\*) All individuals larger than 29.4 mm.

### 27. — *Arthroleptis globosa* WITTE.

(Pl. V, 3.)

*Schoutedenella globosa* WITTE, 1921, Rev. Zool. Afr., **9**, p. 18, pl. 5, fig. 1  
— Lofoi, Katanga, Belgian Congo.

*Arthroleptis lameerei* WITTE, 1921, Rev. Zool. Afr., **9**, p. 12, pl. 4, fig. 1  
— Lofoi, Katanga, Belgian Congo.

*Schoutedenella muta* WITTE, 1933, Rev. Zool. Bot. Afr., **24**, p. 101 — Kando, Katanga, Belgian Congo.

Taxonomic notes. — In the original description of *muta*, WITTE (1933) states that it differs from *globosa* in having longer hind limbs and in lacking both vocal sacs and sex dimorphism in the length of the third finger. Snout-vent length of the holotypes are 17 and 21.5 mm, respectively (WITTE, 1921, 1933). The Upemba collection contains upwards of 15,000 frogs of a single arthroleptine species, this immense sample demonstrating conclusively that *muta* is merely a juvenile of *globosa*.

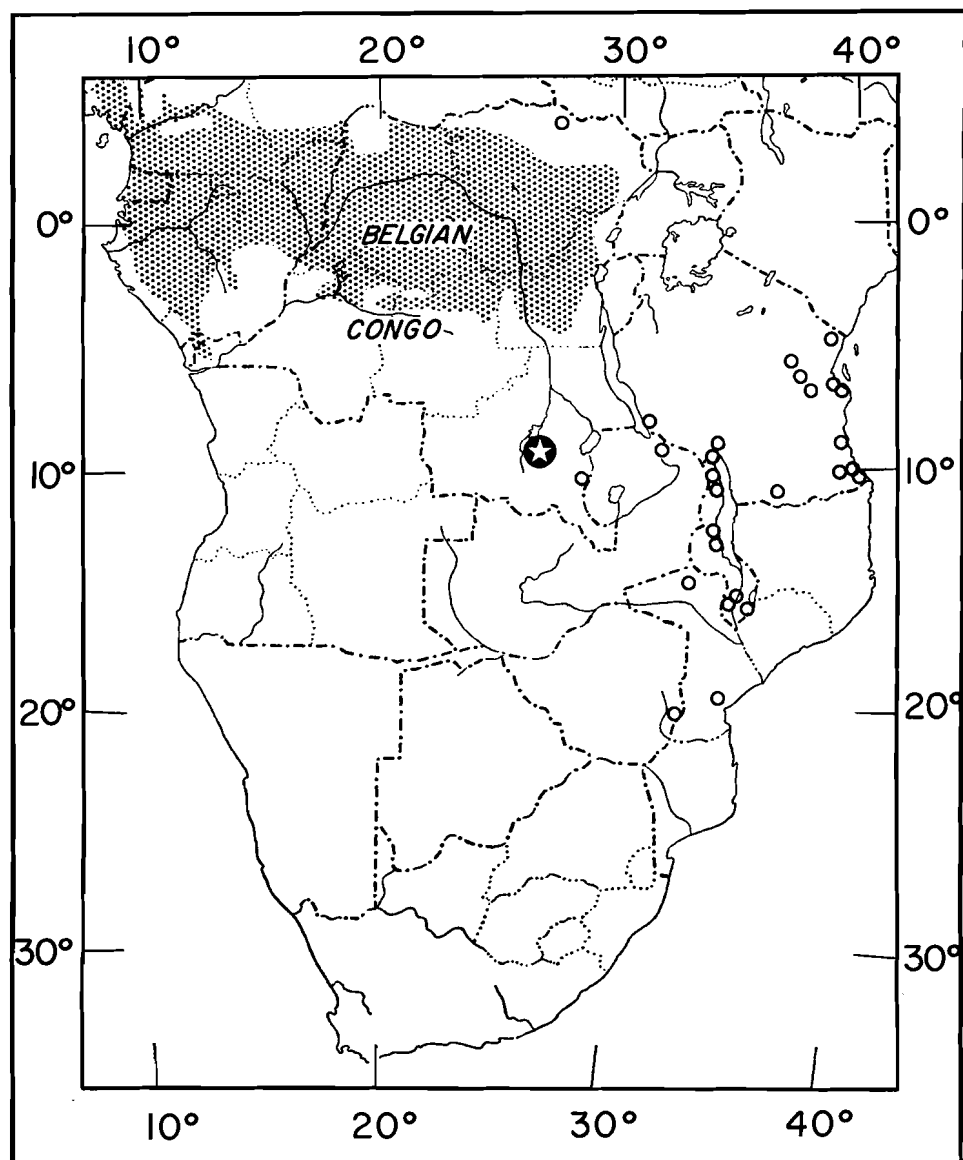


FIG. 55. — Distribution of *Arthroleptis stenodactylus*.  
Parc National de l'Upemba indicated by symbol with open star.

As Fig. 56 shows, a continuous size gradation spanning the lengths of the holotypes is present in our series. Elongation of the third finger in males is clearly a function of size and, hence, of age; the finger grows continuously and at a steadily increasing rate. The third finger of 13 males in the snout-vent interval 16.5-17.5 mm represents 0.201-0.320 (mean=0.262) of snout-vent length, whereas in 9 from the interval 20.5-21.5 the proportion is 0.361-0.447 (mean=0.399). Thus the difference between *muta* and *globosa* in this character is easily accounted for by the difference in size.

In Fig. 57 the lengths of tibia and foot are plotted against snout-vent length. Neither the tibia nor the foot grows appreciably after the frog has reached a certain size (ca. 17 mm). Therefore, the segments of the hind limb are relatively shorter in the larger specimens than in the smaller ones, i.e., precisely the difference between *muta* and *globosa*.

In much of the literature of the 1930's and earlier the term « vocal sac » was used loosely and customarily referred to some externally visible modification of the gular skin. The gular skin of adult, male *globosa* is heavily pigmented and distinctly wrinkled. This is true of all Upemba males over 17.1 mm and all of these have openings into true vocal sacs in the floor of the mouth. Twelve in the size range 14.0-17.1 mm have gular skin identical to that of the females; i.e., smooth and nonpigmented except, possibly, at the symphysis. Only one (14.9 mm) of the twelve actually lacks a vocal sac. If, as is highly probable, WITTE's examination was confined to the exterior of the animal, the absence of vocal sacs refers to modification of the gular skin and, as just skown, is characteristic of young males.

Paratypes of *muta* (MCZ 19420-23; 21801-09) have been compared directly with Upemba frogs and agree with the small individuals so closely as to leave no doubt of the indentification. But as these small frogs are merely juveniles of adults that, in turn, agree with description of *globosa*, *muta* must be considered a synonym of *globosa*.

According to WITTE, both *muta* and *globosa* have a large papilla in the center of the tongue. All the specimens we have seen-paratypes of *muta*, examples of *globosa* identified by WITTE, and the Upemba frogs-lack this structure.

One final point in the *globosa-muta* question should be mentioned. The two type localities are 100 miles apart but four of the five additional *globosa* localities listed by WITTE (1934, p. 181) are also places from which he records *muta* (1934, p. 182).

*Arthroleptis lameerei* WITTE, described in the same paper and from the same locality as *globosa*, is also based on juveniles (14 mm). The original description agrees with that of *muta* point for point and LAURENT (1954 A) recognized the similarity, if not identity, of these nominate forms. Following the arguments presented above, *lameerei* and *globosa* are juvenile and adult of the same species. We retain the name *globosa* because the type series includes adults.

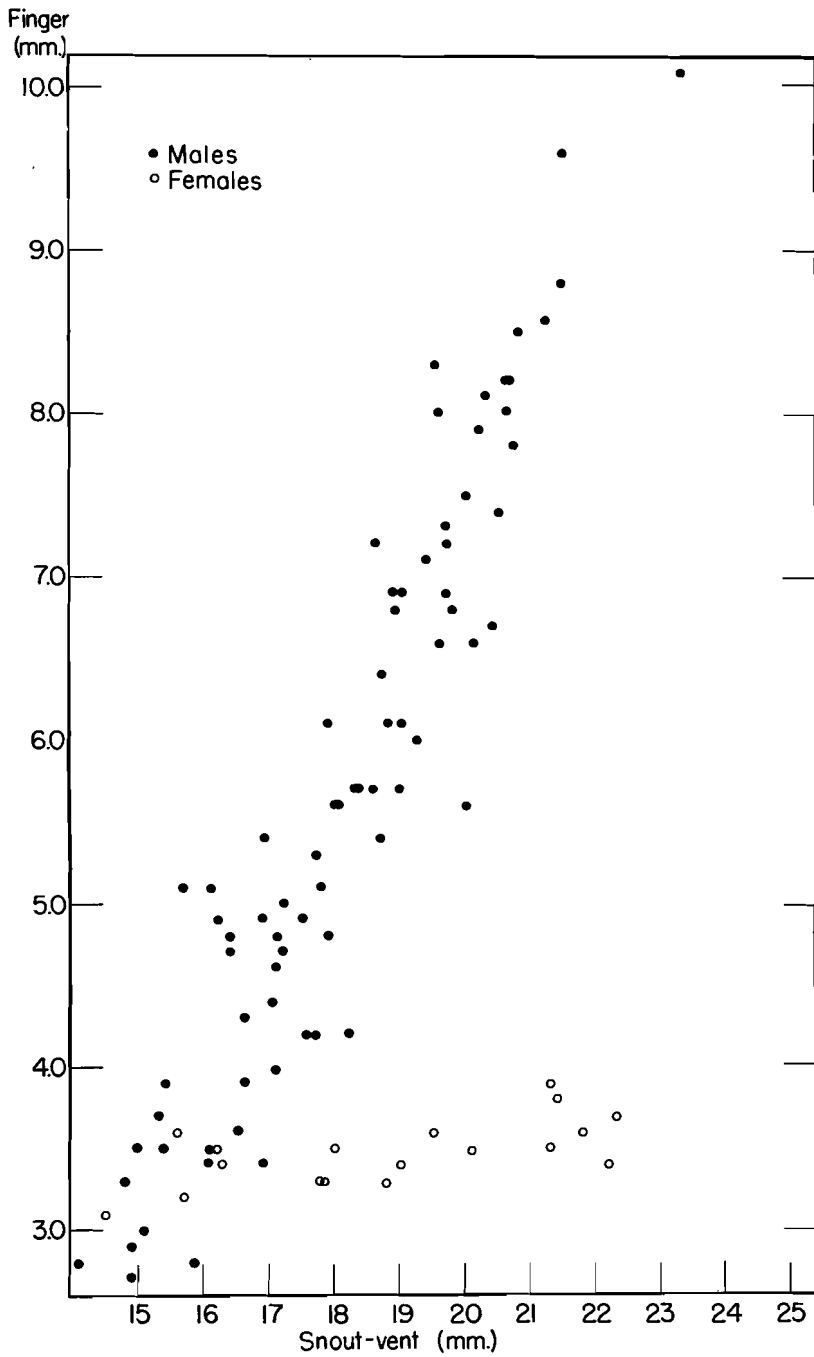


FIG. 56. — Relation between the length of the third finger and snout-vent length in *Arthroleptis globosa* from Parc National de l'Upemba.



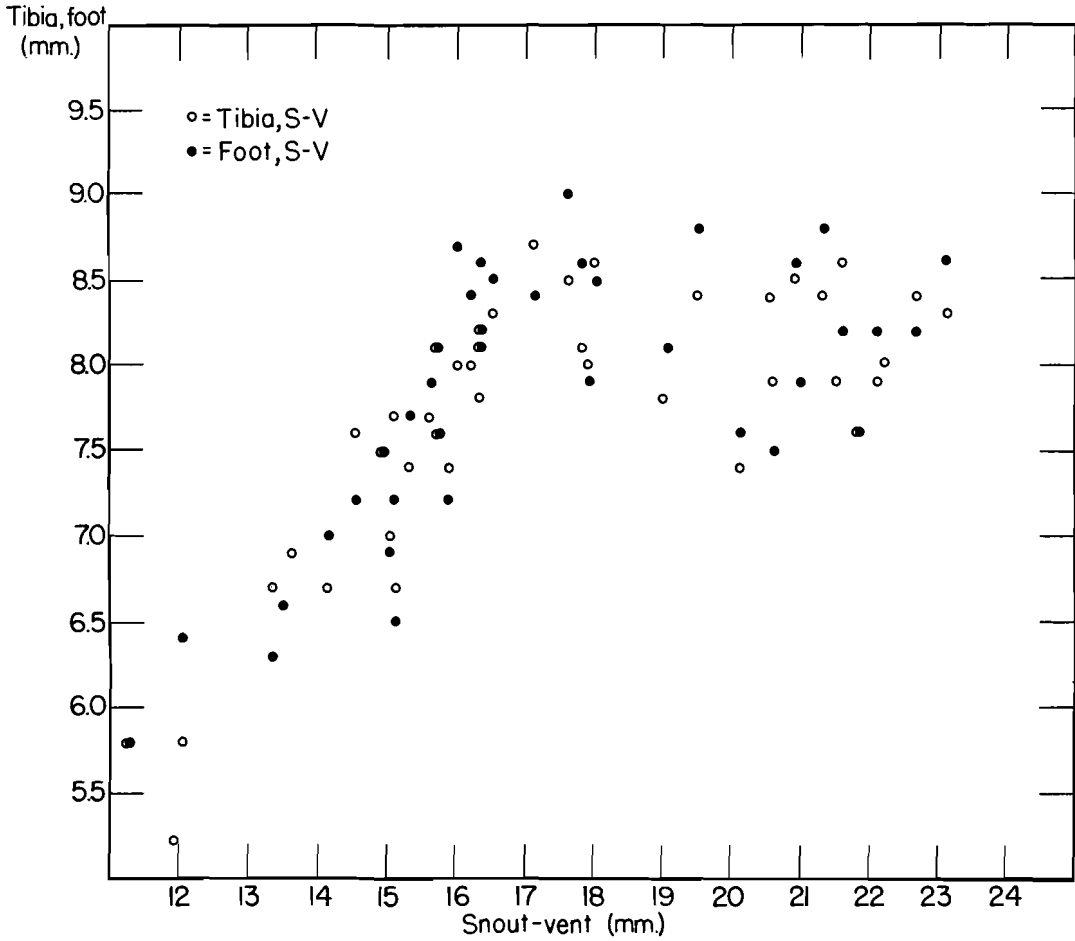


FIG. 57. — Relations of the lengths of foot and tibia to snout-vent length in *Arthroleptis globosa* from Parc National de l'Upemba.

**Diagnosis.** — Habitus moderate (juveniles) to stocky (large females); head as broad as long; snout obtusely pointed; tympanum visible, one-half to two-thirds diameter of eye; teeth absent.

Tips of fingers obtuse or slightly swollen; first finger shorter than second; third finger elongated in adult males (see below); tips of toes obtusely pointed or swollen; no web; subarticular tubercles prominent; oval inner metatarsal tubercle as long as first toe or somewhat shorter; no outer metatarsal tubercle.

Skin usually smooth above with a few irregularly distributed tubercles; sides coarsely granular; underside smooth except granular near groin.

Coor (in alcohol) brown above, uniform or with a double hourglass figure; below cream-colored, immaculate or with a few melanophores on throat (for adult males see below).

Secondary sex characters. — Females with mature ova vary in size from 18.4 to 24.3 mm; the mean of 32 is  $21.15 \pm 0.85$  mm. Considering as mature only individuals with modified gular skin (see below), males have a snout-vent range of 15.4-23.3 mm but have a smaller mean ( $18.66 \pm 0.21$ ;  $N=64$ ) than the females. The difference between the means is statistically significant ( $t=2.835$ ;  $P=0.006$ ).

Seventy-six males, 14 mm and up, were examined for the condition of the secondary sex characters; 11 were less than 16.0 mm long. All but one (14.9 mm) has a median subgular vocal sac with round or oval openings on each side of the floor of the mouth just behind the commissure of the jaws. The gular skin of most males is densely pigmented and wrinkled. As stated above (p. 129), gular skin modified in this fashion is absent in only 12 and these fall in the range 14.1-17.1 mm. Fourteen others in the size class 15.4-17.1 mm have the typical adult modification.

Elongation of the third finger in males is a feature of many *Arthroleptis* species. Males and females of *globosa* below 16.5 mm do not differ in the length of the third finger (Fig. 56). But above this size the finger of males becomes progressively larger whereas it scarcely grows at all in females. The relation of finger length to snout-vent for males is given by the formula :  $Y = +12.478 + 0.994 X$ , where Y equals the length of the third finger and X the snout-vent. By contrast the corresponding formula in females is :  $Y = +2.521 + 0.051 X$ .

Now, the coefficient of X (snout-vent length) is the rate of change in Y (finger length) with respect to change in X, expressed in absolute terms. Naturally, an increase of one millimeter in finger length is relatively a much greater change than the same increase in snout-vent length. Comparing the coefficients of X in the two formulae, we find that in the males' formula the coefficient is about 20 times that of the females'. This means that in the size range covered the third finger in males grows at roughly 20 times the rate in females.

Although the morphology of this sexual dimorphism has been described often, its ontogenesis has not been understood. Various authors write of the presence or absence of this character without regard to the developmental stages of the specimens at their disposal. As shown above (see *taxonomic notes*), this failure in part led to the erroneous description of *muta* as a distinct species. Even LAURENT (1954 A) in his brief review of *Schoutedenella* remarks that dimorphism in finger length varies from species to species and uses *muta* as an example of one totally lacking this modification. Clearly, reasonably large series (ca. 30 or more) of males of each species must be treated in a statistical manner before comparisons are made between species.

The distribution of points in Fig. 56 indicates that the third finger does not regress seasonally. However, the elongated finger in males bears small spines on its inner margin and these spines evidently are not permanent. Of the 45 males lacking these spinules 20 are less than 17.1 mm snout to vent, 16 are 17.1 to 19.0 mm, and 9 are larger than 19.0 mm. Similarly, somewhat less than one-half of the males lacking spinules have third fingers under 4.0 mm long and about one-eighth have fingers longer than 6.0 mm. Thus, while the spinules tend to be more common in larger and, therefore, older males, they may be absent in otherwise mature individuals. A sharp pattern of seasonal distribution of the spinules does not emerge from Table 26 although the relative abundance of males without spinules is greater during the dry season (May-September).

A pink linea masculina is present along the ventral margin of the obliquus muscle in mature males. The six lacking this secondary sex character (see Table 26) fall in the size range 14.1-17.1 mm. The single male (14.9 mm) lacking vocal sacs also lacks lineae masculinae.

TABLE 26. — Monthly frequency of males of *Upemba Arthroleptis globosa* in various stages of development. All have vocal sacs.

Character	Stage of development			
	Present	Present	Present	Absent
Lineae masculinae ... ..	Present	Present	Present	Absent
Gular skin ... ..	Modified	Modified	Unmodified	Unmodified
Spinules, third finger .. ..	Present	Absent	Absent	Absent
Months	Number of individuals			
January .. .. .	2	0	0	0
February ... .. .	10	5	0	0
March ... .. .	17	1	0	0
April ... .. .	1	4	0	0
May . ... .. .	0	2	0	0
June ... .. .	0	2	0	0
October .. .. .	9	13	5	6
November ... .. .	16	3	0	0
November-December ... .. .	4	3	0	0
December ... .. .	0	1	0	0

Table 26 suggests the order in which the secondary sex characters develop. Since all males with any of the sex characters has vocal sacs, these structures appear first in ontogeny. This is the same pattern observed in other Upemba frogs. The lineae masculinae develop next and are followed by modification of the gular skin and then by the appearance of spinules on the third finger. The elongation of the third finger does not readily fit into this sequence because the finger continues to grow after the other sex characters have appeared.

Ecological notes. — All the localities from which *globosa* has been reported by WITTE are in the upland savanna region of southeastern Belgian Congo. In the Upemba, *globosa* occurs at all elevations from 585 to 1,830 m, with the following frequency :

Meters.	Individuals.
585- 750	2,597
751-1,000	6,680
1,001-1,250	2,815
1,251-1,500	1,978
1,501-1,750	1,066
Above 1,751	441

The proportion of sexually competent individuals in this collection rises sharply in November and continues high until February or March (Tables 26, 27), suggesting that breeding begins in November.

TABLE 27. — Monthly frequency of adult female *Arthroleptis globosa* from the Upemba with respect to development of ova. All exceed 18.0 mm., snout-vent.

Months	Ova		
	mature	intermediate	immature
February . . . . .	6	0	2
March . . . . .	0	0	1
April . . . . .	3	0	3
May .. . . .	0	0	1
October ... . .	4	2	8
November ... . .	13	4	0
November-December ... . .	3	0	0
December ... . .	3	0	1

Range. — Known only from southeastern Belgian Congo.

Upemba localities and specimens :

Bowa (3); Buye-Bala (467); Bwalo (1); Difiringi (2); Dipidi (7); Ganza (1,400); Kabenga (57); Kabwe (1,425); Kabwekanono (117); Kagomwe (1); Kankunda (2); Kalubamba (1); Kalumengongo (6); Kalungwe (65); Kambi (35); Kamitungulu (14); Kamitunu (1); Kamusanga (87); Kande (611); Kankunda (172); Kanonga (805); Kanpungu (44); Kaswabilenga (491); Kateke (51); Katongo (60); Kavizi (40); Kayumbwe (16); Kaziba (373); Kenia (58); Kiamakoto (29); Kilolomatenibo (11); Kilwezi (1,671); Kimapongo (5); Kipondo (261); Loie (146); Lufira (17); Lukawe (103); Lukoka (13); Lukorami (138); Lupiala (476); Lusinga (138); Mabwe (2); Manda (13); Masombwe (120); Mitoto (1); Mubale (140); Mukana (21); Mukelengia (285); Mukukwe (3); Munoi (2,729); Munte (3); Munte-Mubale (377); Muye (30); Mware (114); Pelenge (2,188); Senze (67); Tumbwe (1).

Genus **CACOSTERNUM** BOULENGER.

28. — **Cacosternum leleupi** LAURENT.

*Cacosternum leleupi* LAURENT, 1950, Rev. Zool. Bot. Afr., **44**, p. 138 — Kundelungu, Katanga, Belgian Congo.

Taxonomic notes. — The present series of juveniles agrees well with the original description. A lateral black band is present in the eleven at hand and each has a transverse pectoral fold. Since neither character is mentioned by LAURENT (1950), the Upemba series may differ somewhat from the type, which is the only other specimen known.

Diagnosis. — Tongue narrow, not notched; no teeth; a distinct pectoral fold; two metatarsal tubercles; subarticular tubercles conspicuous; third, fourth, and fifth toes webbed to basal tubercles. A white line from shoulder forward below eye; a dark lateral band from eye to groin. Snout-vent 12.1-15.3 mm.

Ecological notes. — These young frogs were collected at altitudes between 1,750 and 1,830 m. The type locality is at 1,750 m.

Range. — As yet known only from the Katanga.

Upemba localities and specimens :

Bwalo (1); Kabwekanono (4); Kalumengongo (1); Katongo (1); Lusinga (1); Mukana (2); Mukelengia (1).

Genus **CARDIOGLOSSA** BOULENGER.29. — **Cardioglossa** sp.

A juvenile (9.6 mm) too small for reliable identification. Mubale (1).

Genus **PHRYNOBATRACHUS** GÜNTHER.

Probably no genus of African Salientia, with the exception of *Hyperolius*, gives taxonomists as much difficulty as *Phrynobatrachus*. Some species, such as *perpalmatus* and *natalensis* are easily distinguished, but they are exceptional. The principal sources of the trouble are relatively obvious: the species are numerous, the animals small in size, and the older descriptions inadequate. Although we have been able to examine the types of many nominate forms while on a brief tour of European museums, we are certain that before most of the species are satisfactorily defined the majority will have to be examined in one laboratory at one time. Another prerequisite is large series of both sexes.

But in addition to these requirements, more rigorous definition of frequently used characters, elimination of certain characters from consideration, and use of still others will be necessary. WITTE's synopsis (1919) of *Phrynobatrachus*, which is the most recent attempt to cover the whole genus though it included less than half the species, employed the old but ambiguous method of describing the extent of webbing in terms of proportion of the toes webbed, e.g., two-thirds or one-fourth webbed. LOVERIDGE recognizes the inadequacies of this method and in his most recent paper (1953), as well as in earlier ones, uses the number of digits free of web as a more accurate means of describing this character. Because the web may extend distally as a narrow fringe for varying distances, we prefer to note the extent of broad web, which varies less, relative to the subarticular tubercles.

Similarly, greater care should make the tympanum more helpful. Commonly keys and descriptions note that the tympanum is hidden. Such statements assume the presence of the structure but usually it is not explicitly indicated that a tympanum was found. In some species, as in three small ones reported on here, the tympanum is indeed hidden; it is present but covered by rather thick skin obliterating all external signs of its presence. On the other hand, in our fourth dwarf form, and this is probably true of some species from other areas, the tympanic annulus is not present, as determined by actual dissection.

The spacing of the tarsal and metatarsal tubercles, another character used by WITTE, has not facilitated our work though it may be of help in distinguishing species of other regions. Four small species have been

especially troublesome to us and we have tried to use every conceivable character including the spacing of the tubercles. The ratio of the distance between the metatarsal tubercles to the distance between the outer metatarsal tubercle and the tarsal tubercle varies within species from 0.46 to 0.78, for example, whereas the means only vary from 0.59 to 0.62. Considering that the measurements involved are less than 2.0 mm, the differences between means are hardly significant taxonomically. Similar results were obtained for all ratios among these distances. For the small species, therefore, this character is not promising.

Male secondary sex characters, as a rule, have not been exploited by students of Salientia. Though use of them has the practical disadvantage of requiring both sexes, in view of the muddle that now exists in this genus that requirement is probably a blessing in disguise. PARKER (1936 A) has pointed out that a femoral gland is present in males of some species; among the six covered by this report, four have femoral glands.

The lineae masculinae have been especially helpful in corroborating distinctions made on the basis of other characters. *Phrynobatrachus natalensis*, *gutturosus*, and *perpalmatus* males have lineae masculinae at both dorsal and ventral borders of the obliquus muscle. Those of *parvulus* have a single linea and that at the ventral border of the obliquus. One of the new forms described below has a dorsal linea only and the second new form none at all. As with all secondary sex characters, the lineae masculinae must be explicitly defined. We have applied the term only to a transparent narrow band of tissue, sometimes pinkish otherwise colorless, paralleling the longitudinal edges of the obliquus. In some instances the ventral line may be overlain by the pars abdominis of the pectoralis and this muscle must be carefully lifted when a ventral line is not immediately visible. The final condition to the use of these structures is that only mature males should be examined, a structure applying equally to other secondary sex characters. If the male being examined has nuptial pads, then its lineae masculinae should be in definitive condition since, as will be shown below, the last always develop before the nuptial pads.

In describing *Phrynobatrachus* species, authors often refer to black or dark throats in males. The black pigment may be on one or both of two layers, though the distinction has not been recognized previously. Males of *Phrynobatrachus parvulus* and *gutturosus* both have dark throats, usually darker in the former. In *parvulus* the melanophores are concentrated on the gular skin, in *gutturosus* on the vocal sac and its investing muscle. Admittedly the difference in appearance is trivial; nonetheless a genetic distinction exists and has been helpful in our study.

The common ambiguity of taxonomic literature with regard to the vocal sac should be mentioned. The vocal sac is never external in the sense of superficial. Invariably it is covered by the gular skin and with few exceptions by the subhyoideus muscle as well. In examining the

throat of male *Phrynobatrachus*, the gular skin should not be confused with the vocal sac. The former has its own specializations, such as folds and asperities (Fig. 58), and, though these have a definite developmental time relationship to the vocal sac, they are not physically part of the latter.

Despite the small number of species included in this collection, a diagnostic key is given because of the difficulties commonly encountered in identifying members of this genus.

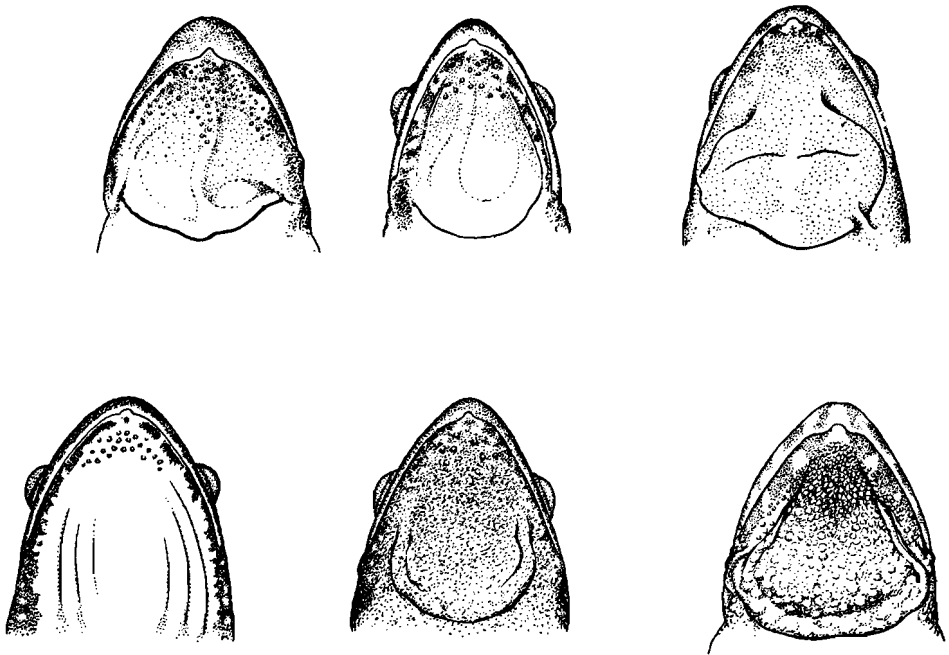


FIG. 58. — Gular regions of male *Phrynobatrachus* from Parc National de l'Upemba.

Upper left, *P. cryptotis* ( $\times 4$ ). Upper center, *P. guttuosus* ( $\times 4$ ).

Upper right, *P. perpalmatus* ( $\times 4$ ). Lower left, *P. anotis* ( $\times 5$ ).

Lower center, *P. parvulus* ( $\times 5$ ). Lower right, *P. natalensis* ( $\times 2\frac{1}{2}$ ).

#### KEY TO UPEMBA *PHRYNOBATRACHUS*.

- 1A. Toes broadly webbed to base of disks ..... *perpalmatus*.  
 B. Toes not webbed beyond subarticular tubercles ..... 2
- 2A. Toes broadly webbed to distal subarticular tubercles of third and fifth toes ..... *natalensis*.  
 B. Web at most reaching distal subarticular tubercles of third and fifth toes as a narrow fringe ..... 3



- 3A. Tips of toes expanded into disks having circummarginal grooves; broad web extending beyond basal subarticular tubercles of third and fifth toes; never with silvery streak below tympanum ..... 4
- B. Tips of toes not expanded, lacking circummarginal grooves; web usually not extending beyond basal subarticular tubercles of third and fifth toes, at most extending distally as a narrow fringe; silvery streak below tympanum present or absent ..... 5
- 4A. Tympanum absent; posterior third of abdomen usually mottled or spotted with brown pigment; adult males with white throats, no transverse fold behind modified gular skin (Fig. 58) ..... *anotis*.
- B. Tympanum present though usually not visible through skin; posterior third of abdomen usually without dark pigment; adult males with black pigment at least under chin and often over entire throat, a transverse fold behind modified gular skin (Fig. 58) ..... *gutturosus*.
- 5A. A silvery streak below tympanum from eye to arm insertion (Fig. 62); posterior fourth of abdomen with dark spots; tympanum present though hidden under skin; throat of adult male blackish (Fig. 58) ..... *parvulus*.
- B. No silvery infratympanic streak; posterior fourth of abdomen without dark spots; tympanum present though hidden under skin; throat of adult male blackish at least at chin (Fig. 58) ..... *eryptotis*.

30. — ***Phrynobatrachus anotis*** n. sp.

(Pl. V, 4.)

**Holotype.** — Institut des Parcs Nationaux du Congo Belge, No. 1958, adult male from Lusinga, 1,810 m, Parc National de l'Upemba, Katanga, Belgian Congo, collected May 22, 1945, by the Mission G. F. DE WITTE. Allotype, 1958, female, same data.

**Diagnosis.** — A small *Phrynobatrachus*, adults 15-23 mm; tympanic annulus absent; tips of toes with small disks having circummarginal grooves; broad web extending beyond basal subarticular tubercles of third and fifth toes but not reaching distal tubercles; no silvery infratympanic stripe (Fig. 59); throats of males whitish (Fig. 58), with at most a faint dusting of small spots.

**Description of holotype.** — Habitus of *Phrynobatrachus*, with a moderately pointed snout, projecting slightly beyond mouth; body stocky, limbs relatively long; lingual papilla present; vomerine teeth absent, maxillary teeth present; tympanum absent; tips of fingers and toes slightly expanded, with subterminal horizontal grooves; second finger a little longer than first, third finger once and a half as long as second; subarticular tubercles well-defined; webs between toes well developed, web between

third and fourth toes at level of a point midway between the basal and the second tubercle of the fourth toe; web extended along fourth toe as a flap of skin on both sides of penultimate phalanx of fourth toe; dorsal skin with low tubercles; ventral skin entirely smooth.

Dark brown above, with an obscure line across head at the middle of the eyelids, anterior to which the snout is lighter; a broad yellowish line along the posterior face of the thigh; upper surface of thighs and tibia with obscure dark bars; sides of head with obscure dark bars radiating from eye; a dark line, with an obscure light line below it, from eye to shoulder; ventral surfaces pale yellow, with brown spots on breast and abdomen.



FIG. 59. — Male *Phrynobatrachus anotis* new species.  
Left, side view of head ( $\times 6$ ). Right, nuptial pad ( $\times 8$ ).

Throat (Fig. 58) with two strong lateral folds, one parallel to the labial border, the other curved toward the mid-line posteriorly; no transverse posterior gular fold; gular skin very lightly pigmented; vocal sac and muscle not pigmented; tip of chin with a few white asperities; back (Fig. 59) with numerous white asperities from snout to above anus; nuptial pad (Fig. 59) on first finger; femoral gland present; no linea masculina.

#### Measurements of holotype and allotype.

	Holotype. (mm)	Allotype. (mm)
Length from snout to vent ... ..	17.0	24.0
Length of arm ... ..	8.0	13.0
Length of leg . ... ..	26.0	33.0
Length of tibia ... ..	9.0	11.0
Width of head at angles of mouth ...	6.2	8.5

Paratypes. — Approximately 1,970 specimens from various localities in the Parc National de l'Upemba form a remarkably uniform series. Significant variation is described in the section on secondary sex characters (below).

Comparisons. — The character of presence or absence of the tympanum proper (to be observed when a flap of skin over the tympanic region is reflected) has not been ascertained for most of the species of *Phrynobatrachus*. The tympanum is definitely absent in *ogowensis* BOULENGER and in *keniensis* BARBOUR and LOVERIDGE. In *ogowensis*, from the Gaboon, the toes are more extensively webbed, and the gular sac is bounded posteriorly by a transverse fold. *Phrynobatrachus keniensis*, from Mount Kenya, was described without a male; males subsequently associated with this species by LOVERIDGE lack longitudinal folds on the gular pouch. *Phrynobatrachus anotis* is not *scheffleri*, in which the tympanum is present beneath the skin (partly further concealed by a slip of muscle). This new form is thoroughly distinct from all other *Phrynobatrachus* in the Katanga region; its nearest relatives may be found among some of the still inadequately described species of the East African region and of the Congo Forest.

Secondary sex characters. — Adult females (with large pigmented ova) are distinctly longer than mature males (with complete secondary sex characters). The former have a snout-vent range of 17.6-22.8 mm (mean  $20.83 \pm 0.12$ ; N=84), and the latter one of 15.0-20.2 mm (mean  $17.62 \pm 0.11$ ; N=95). Maximum size for all females is 23.4 mm.

Surrounding the vent of adult females is a cluster of whitish spinules similar to those occurring in female *gutturosus* (see below). A small proportion of males have similar structures though they are smaller and fewer in number than those of females.

The male secondary sex characters are typical of the genus. Median subgular vocal sacs, opening through longitudinal slits, and horizontally oval femoral glands are present in males larger than 15.0 mm. The gular skin (Fig. 58), which in females bears rather large brown spots, loses its pigmentation in adult males and becomes almost immaculate cream-colored. Pigment never appears on the vocal sac or on the subhyoideus muscle. One or two longitudinal folds develop laterally in the gular skin, but not a single male of the hundreds examined has a transverse fold such as characterizes *gutturosus*, *parvulus*, and *cryptotis*.

The nuptial pad (Fig. 59) is a velvety structure covering the dorsal and median surfaces of the first finger from its base to the end of the proximal phalanx. At its maximum development, that is, when its detailed structure is most easily seen under the microscope, the pad is yellowish. At other times it is dark gray. Small whitish spinules or asperities, like those of *parvulus* and *gutturosus*, are present in a cluster on the chin, and similar ones are more widely scattered over the dorsal surfaces of head, trunk, and hind limbs. No lineae masculinae were seen.

The vocal sac and femoral gland appear in all males having any other secondary sex characters. On the other hand, ten of 123 males examined in detail have vocal sacs and femoral glands only, so that these two

structures must develop first just as they do in *gutturatus* and other species. The folds in the gular skin probably develop next and probably do not regress. Of the twelve males lacking these folds, nine are smaller than 15.7 and three others measure 16.2, 16.9, and 17.7 mm. All except the last may be judged young adults. Only two (15.7, 16.9) of the twelve have nuptial pads.

By contrast six of the sixteen lacking nuptial pads have gular folds. The sixteen include five in the size range 17.1-18.1 mm, certainly fully adult in size, which suggests that the pads may regress. Aside from ten males having vocal sacs and femoral glands only, thirteen lack mental asperities (nine in the size range 17.1-18.5) and fifteen lack dorsal asperities (twelve in the size range 17.1-18.5). These two classes do not coincide exactly as one without the spinules on the chin has them on the back and four without spinules on the back have them on the chin. Since the two classes include many individuals that are fully mature with respect to size, it is reasonable to assume that asperities on both regions of the body develop later than the other sex characters and that they undergo regression. The distribution of male secondary sex characters with respect to one another is shown in Table 28.

TABLE 28. — **Monthly frequency of adult male *Phrynobatrachus anotis* with respect to development of secondary sex characters. All have vocal sacs and femoral glands.**

	Present	Present	Present	Present	Present	Absent	Absent
Gular folds .. ...	Present	Present	Present	Present	Present	Absent	Absent
Nuptial pad . ...	Present	Present	Present	Absent	Absent	Present	Absent
Mental asperities . ...	Present	Present	Absent	Present	Absent	Absent	Absent
Dorsal asperities .. ...	Present	Absent	Absent	Absent	Absent	Present	Absent
January ... ..	18	0	0	0	0	0	0
February ... ..	2	0	0	0	0	0	0
March ... ..	8	0	0	0	0	0	5
April ... ..	18	0	2	0	0	1	0
May ... ..	15	2	3	0	0	0	0
June ... ..	17	1	0	1	0	0	1
July ... ..	11	0	1	0	5	0	2
October . ... ..	7	0	0	0	0	1	2
	96	3	6	1	5	2	10

Ecological notes. — Though five specimens in this collection were caught at 860 m, *Phrynobatrachus anotis* is much more abundant at the higher elevations within the Parc National de l'Upemba as shown by the following tabulation of this sample.

Meters.	Individuals.
751-1,000	10
1,001-1,250	58
1,251-1,500	109
1,501-1,750	803
1,751-1,830	994

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

Upemba localities and specimens :

Babagi (1); Buye-Bala (29); Dipidi (8); Ganza (5); Kabenga (4); Kabwe (37); Kabwekanono (20); Kagomwe (35); Kakolwe (1); Kamamulongo (15); Kamatshya (24); Kambi (31); Kamitungulu (15); Kamitunu (47); Kanpungu (24); Karibwe (9); Kasandendeko (157); Kavizi (232); Kayumbwe (24); Kaziba (2); Kenia (56); Kilolomatambo (63); Kimapongo (51); Kimiala (2); Kipangaribwe (74); Luanana (1); Lufwa (1); Lusinga (784); Manda (1); Masombwe (2); Mitoto (8); Mukana (88); Munoi (2); Munte-Mubale (71); Pelenge (50).

31. — *Phrynobatrachus cryptotis* n. sp.

(Pl. V, 5.)

*Arthroleptis schoutedeni* WITTE, 1934, Ann. Mus. Congo Belge, Zool., (1), 3, p. 178 (part).

*Arthroleptis 'scheffleri*, idem, p. 178 (part).

Holotype. — Institut des Parcs Nationaux du Congo Belge, No. 1926, adult male from the upper Bwalo River (an affluent from the left of the Muye, which is an affluent from the right of the Lufira), 1,750 m, Parc National de l'Upemba, Upper Katanga, Belgian Congo; collected April 9, 1948, by the Mission G. F. DE WITTE. Allotype, 1926, with the same data.

Diagnosis. — A small *Phrynobatrachus*, adults 13-22 mm; tympanum present, but normally not visible through skin; tips of digits without expansions and lacking circummarginal grooves; broad web not usually extending beyond basal subarticular tubercle of third and fifth toes; no silvery infratympanic stripe (Fig. 60); gular skin of males (Fig. 58) pigmented near chin, usually free of pigment posteriorly; vocal sac densely powdered with melanophores.

Description of holotype. — Habitus of *Phrynobatrachus*; with moderately pointed and projecting snout, stocky body, and relatively short

limbs; lingual papilla present; tongue emarginate behind; vomerine teeth absent, maxillary teeth present; tympanum not distinguishable externally, present beneath the skin; tips of fingers and toes entirely without expansion; second finger about as long as first, third finger half again the length of the first and second; subarticular tubercles well developed; a basal web between toes, its margin between the third and fourth and fourth and fifth toes at the level of the basal tubercle of the fourth toe, extending along toes as a narrow membrane to the second tubercle of the third and fifth toes, a little beyond the basal tubercle of the fourth; dorsal skin with low tubercles, ventral skin entirely smooth.

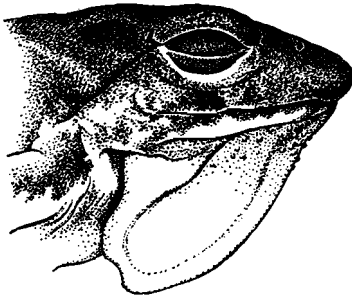


FIG. 60. — Side view of head of male *Phrynobatrachus cryptotis* ( $\times 6$ ).

Lighter and darker gray above, with a narrow light line from snout to vent, and from vent along upper faces of the thighs, reappearing on the lower half of the tibiae and over the heel to the foot; a broader less sharply defined line parallel to the upper narrow one on the otherwise dark posterior faces of the thighs; an obscure light line from below the eye to the insertion of the arm; ventral surfaces light (very pale yellow), the chin with dark fine spotting, and lateral brown spotting on breast and abdomen; under surfaces of arms, thighs, and tibiae immaculate, yellowish; border of lower lip strongly barred with subequal dark and light vertical maculation.

Vocal sac conspicuous, black, showing through the thin skin of the posterior part of the throat, which is pigmented only anteriorly; a curved transverse fold bounds the throat posteriorly, behind which is a parallel curved band, a millimeter wide on which (as on the edge of the fold) there is fine black punctulation; chin (Fig. 58) with fine white asperities; a dark gray nuptial pad of extremely fine and close-set asperities on the inner basal portion of the first finger; an oval femoral gland.

**Measurements of holotype and allotype.**

	Holotype. (mm)	Allotype. (mm)
Length from snout to vent ... ..	17.9	19.5
Length of arm ... ..	9.0	10.0
Length of leg . ... ..	24.0	26.5
Length of tibia ... ..	8.4	9.0
Width of head at angles of mouth ...	5.6	6.0

**Paratypes.** — An enormous sample of 11,659 specimens from the Parc National de l'Upemba comprise the type series. Variation is limited to minor differences in pigmentation of the throat and abdomen and to the characters discussed under *secondary sex characters*.

**Comparisons.** — Examination of the lectotype and twenty additional specimens of *Phrynobatrachus scheffleri* NIEDEN, from Kibwezi, Kenya Colony, shows *cryptotis* to be very similar to this species, at least as concerns female specimens. Though faded, the ventral pattern of *scheffleri* is distinctive and very unlike that of *cryptotis*. It is pale brown with numerous small white spots over the whole underside. Definitive description of *scheffleri* must await collection of adult males from the type locality, for the original collection contains only females and juveniles.

Specimens of *cryptotis* from the Katanga region, in the collections of the Musée du Congo Belge, have been identified as *minutus*. We find this Abyssinian species to be distinguished from the new form by its more extensive webbing, its distinct tympanum, and by the unmodified gular skin of the male. The ventral surface of *minutus* is immaculate. The type, in the British Museum (Natural History), has been examined. In addition to the characters named, it has a distinctive dorsal pattern of paired dark markings.

**Secondary sex characters.** — Adult females (with enlarged pigmented ova) have a snout-vent range of 15.2-22.2 mm and a mean of  $19.26 \pm 0.15$  mm (N=99). This mean is significantly larger, statistically, than that of adult males (those with completely developed sex characters). The snout-vent range in adult males is 13.4-20.3 mm and the mean  $17.05 \pm 0.11$  mm (N=107).

Females of *cryptotis* have pre-anal spinules similar to those described for *gutturosus* (see below).

Male secondary sex characters closely resemble those of *gutturosus*. A median subgular vocal sac opens into the mouth through longitudinal slits. The outer layer of the vocal sac and the investing subhyoideus muscle are heavily dusted with melanophores as is the gular skin, though the pigment of the last may be restricted to the chin. In this stage of development the gular skin (Fig. 58) has a conspicuous transverse fold marking its

TABLE 29. — Monthly distribution of male *Phrynobatrachus cryptotis*  
In each cell, in vertical order, are given: the number of specimens, the

Vocal sacs ... ..	Present	Present	Present
Femoral glands ... ..	Present	Present	Present
Linea masculina ... ..	Present	Present	Present
Gular skin ... ..	Modified	Modified	Modified
Nuptial pads .. ...	Present	Present	Present
Mental asperities .. ...	Present	Present	Absent
Dorsal asperities ... ..	Present	Absent	Absent
January .. ...	26 16.2-19.7 17.68	3 17.6-18.6 17.9	0
February ... ..	6 17.3-18.7 17.80	4 18.0-18.7 18.2	1 18.2
March ... ..	16 15.7-18.6 17.08	0	0
April ... ..	15 15.7-18.8 17.61	1 16.4	0
May . ... ..	1 18.3	0	1 18.2
July . ... ..	0	0	1 17.7
August ... ..	1 20.3	0	1 19.4
September ... ..	14 14.5-17.2 16.05	2 14.5-15.2 14.85	0
October .. ...	20 13.4-17.2 15.86	0	0
November ... ..	3 17.3-18.8 18.23	3 17.2-17.6 17.47	1 17.6
December ... ..	5 16.4-17.8 17.14	10 16.3-17.7 17.33	0
Totals ... ..	107 13.4-20.3 17.05±0.11	23 14.5-18.7 17.33±0.20	5 17.6-19.4 18.22±0.32

with respect to development of secondary sex characters.  
range of snout-vent (mm.), and the average snout-vent length.

Present	Present	Present	Present	Present
Present	Present	Present	Present	Absent
Present	Absent	Present	Absent	Absent
Modified	Modified	Unmodified	Unmodified	Unmodified
Absent	Absent	Absent	Absent	Absent
Absent	Absent	Absent	Absent	Absent
Absent	Absent	Absent	Absent	Absent
0	0	0	0	0
0	0	0	0	0
0	0	0	0	0
1 16.7	0	0	0	0
16 15.3-18.9 17.34	0	0	1 13.8	1 14.5
12 15.9-18.7 17.02	0	0	2 15.4-15.7 15.55	0
17 14.4-17.3 16.16	1 16.6	1 16.3	1 13.8	0
1 13.8	0	2 12.0-13.0 12.5	2 10.6-11.5 11.05	0
0	0	0	0	0
0	0	0	1 16.0	0
0	0	0	0	0
47 13.8-18.9 16.74±0.15	1 16.6	3 12.0-16.3 13.77	7 10.6-16.0 13.83±0.80	1 14.5



TABLE 30. — Seasonal distribution  
of certain sex characters in male *Phrynobatrachus cryptotis* having vocal sacs and femoral glands.  
Numbers in table refer to number of specimens.

	Nuptial pads		Mental asperities		Dorsal asperities		Gular folds		Linea masculina	
	Present	Absent	Present	Absent	Present	Absent	Present	Absent	Present	Absent
	January ... ..	29	0	29	0	26	3	29	0	29
February .. ...	11	0	10	1	6	5	11	0	11	0
March ... ..	16	0	16	0	16	0	16	0	16	0
April .. ...	16	1	16	1	15	2	17	0	17	0
May .. ...	2	18	1	19	1	19	18	2	18	2
July .. ...	1	14	0	15	0	15	13	2	13	2
August ... ..	2	20	1	21	1	21	20	2	20	2
September ... ..	16	5	16	5	14	7	17	4	19	2
October ... ..	20	0	20	0	20	0	20	0	20	0
November. ... ..	7	1	6	2	3	5	7	1	7	1
December . ... ..	15	0	15	0	5	10	15	0	15	0

posterior border and, usually, a short lateral fold. Immediately behind the transverse fold of some males is a narrow band of transparent skin.

Horizontally oval femoral glands and a linea masculina at the dorsal border of the obliquus muscle are present. There is no ventral linea maculina.

A grayish, velvety nuptial pad covers the dorsal and median surfaces of the first finger from its base to the end of the basal phalanx. A dense cluster of small whitish spinules or asperities occurs on the chin (Fig. 58) and similar, though much more widely spread, ones are distributed over the entire dorsal surface.

As in other species, the vocal sacs of *cryptotis* develop early, probably before the femoral glands become discernible and certainly before all other secondary sex characters. All males with any secondary sex characters have vocal sacs and, almost invariably, femoral glands (Table 29). One male (14.5 mm) has vocal sacs only, seven others (10.6-16.0, mean 13.8 mm) vocal sacs and femoral glands. The linea masculina probably is the next sex character to develop. Two small males (12.0, 13.0 mm) have this structure in addition to vocal sacs and femoral glands. Another individual (16.3 mm) having the same secondary sex characters also has feeble lateral folds on the throat representing initiation of modification of the gular skin; the vocal sac lacks chromatophores completely.

Many specimens have lineae masculinae, gular skin folds, and pigmented vocal sacs but lack nuptial pads and mental and dorsal asperities. A male in this condition could be either a young adult in which the last three structures had not yet developed, or a fully mature individual in which these structures had regressed between breeding periods. Both interpretations probably apply to the present sample, for some males in this condition are quite small (nine in the range 13.8-15.9 mm) and others larger (six in the range 18.0-18.9 mm) than the average adult male. Furthermore the seasonal incidence of males having fully developed sex characters (Table 30) strongly suggests regression of the nuptial pads.

Most of the males in the most abundant stage collected in May (Table 29) are fully mature, judging by size, as ten of sixteen are larger than 17.5 mm (mean of all fully developed males 17.05 mm). Presumably in these ten the nuptial pads and mental and dorsal asperities have regressed. July males of the same category include only three larger than 17.5 mm, two in the range 17.0-17.5 mm, six between 16.0 and 16.9 mm, and one 15.9 mm. In August this category is divided as follows: three in the range 17.0-17.5, ten 16.0-16.9, four 15.0-15.9, and one 14.4 mm. Thus the proportion of young adults increases from May through August as juveniles of the preceding year class become mature.

The movement of the new adults into the class of all adults is also reflected in the monthly changes in average size of males having completely developed sex characters (Table 29, column 1).

Ecological notes. — The range in altitude of specimens collected is from 585 m to 1,850 m, distributed as follows :

Meters.	Individuals.
585- 750 ... ..	2,584
751-1,000 ... ..	683
1,001-1,250 ... ..	291
1,251-1,500 ... ..	863
1,501-1,750 ... ..	2,460
1,751-1,850 ... ..	4,778

Probably the low numbers collected between 751 and 1,500 m reflect lack of a suitable habitat rather than an effect of altitude.

The largest single lots are from Mabwe, on Lake Upemba at 585 m (1,545), and from Mukana, at 1,810 m (2,803). Both the Mabwe and Mukana series are from marshes.

Apparently *cryptotis* has a more sharply delimited breeding season than *gutturosus* or *parvulus*. The proportion of adults in breeding condition (females containing mature ova; males with fully developed sex characters) drops sharply after April and rises in September (see Table 31).

TABLE 31. — Monthly frequency of adult *Phrynobatrachus cryptotis* from Parc National de l'Upemba with respect to breeding condition.

	Males (*)		Females (**)	
	Secondary sex characters		Ova	
	complete	incomplete	mature	immature
January .. .. .	26	3	23	0
February ... ..	6	5	12	0
March ... .. .	16	0	8	8
April ... .. .	15	2	6	8
May . ... .. .	1	18	4	10
July . ... .. .	0	15	3	12
August ... .. .	1	21	0	8
September ... ..	14	5	15	3
October .. ... .	20	0	7	1
November ... ..	3	5	6	8
December ... ..	5	10	15	0

(\*) All with vocal sacs and femoral glands.

(\*\*) All over 15.0 mm; smallest with pigmented ova = 15.2 mm.

Range. — The vast numbers of *Phrynobatrachus cryptotis* from the Upemba region, and its past confusion with *schoutedeni* (= *parvulus*) and *scheffleri*, as well as with *minutus*, indicate that this species ranges far beyond the Upemba region. Specimens in the Musée du Congo Belge, identified as *Arthroleptis moorei* BOULENGER by LOVERIDGE, though juveniles, can be positively identified as *cryptotis*. They came from Nyamruado, Northern Rhodesia. Specimens in the Musée du Congo Belge from Dilolo (Lulua District, Belgian Congo), in the Kasai drainage, far to the west of the Katanga include positively identifiable males of *cryptotis*, associated with *parvulus*.

Upemba localities and specimens :

Bunda-Bunda (1); Buye-Bala (897); Bwalo (184); Dipidi (48); Ganza (200); Kabenga (10); Kabwe (22); Kabwekanono (1,345); Kafwe (17); Kalubamba (2); Kalumengongo (136); Kalungwe (7); Kamitungulu (2); Kamitunu (2); Kampadika (117); Kamusanga (11); Kande (146); Kanonga (473); Karibwe (1); Kaswabilenga (147); Kateke (2); Katongo (8); Kaziba (14); Kenia (6); Kiamakoto (188); Kilwezi (123); Kipondo (42); Loie (6); Luangalele (6); Lufira (44); Lufwa (37); Lukawe (77); Lupiala (86); Lusinga (602); Mabwe (1,545); Manda (10); Masombwe (60); Mokey (7); Mubale (132); Mukana (2,803); Mukelengia (612); Mukukwe (1); Munoi (78); Munte (277); Munte-Mubale (837); Mwema-Mabole (1); Pelenge (19); Sanga (96); Senze (173).

32. — *Phrynobatrachus gutturosus* CHABANAUD.

(Pl. V, 6.)

*Arthroleptis gutturosus* CHABANAUD, 1921, Bull. Com. Études Hist. Sci. Afr. Occ. Française, 1921, p. 452, pl. 2, fig. 2-4 — SANIKOLÉ, Liberia; NOBLE, 1924, Bull. Amer. Mus. Nat. Hist., 49, p. 315; WITTE, 1934, Ann. Mus. Congo Belge, (1), 3, p. 180.

*Phrynobatrachus gutturosus* LAURENT, 1941, Rev. Zool. Bot. Afr., 34, p. 207, fig. 3g.

Taxonomic notes. — The redescription of this species by WITTE, with his careful comparison of Katanga specimens with the West African types, convinces us that this is the proper allocation of the Upemba series. It is to be presumed that the range is not actually so discontinuous, and that the species will yet be found in the region between Liberia and the Katanga. There are differences between the Liberian types and our large Upemba series, but these cannot be evaluated without additional specimens from the intermediate region.

Diagnosis. — A small *Phrynobatrachus*, adults 16-25 mm; tympanum present, but not visible through skin; tips of fingers slightly dilated; tips of toes with small, yet distinct disks having circummarginal grooves; broad web extending well beyond basal subarticular tubercles of third and fifth toes but not reaching distal tubercles except as a narrow fringe; no silvery infratympanic stripe; gular skin of male black near chin; vocal sac with dark chromatophores.

Descriptive notes. — Snout triangular in outline from above, rounded in profile, longer than eye; nostril a little closer to tip of snout than to eye; interorbital space equal to upper eyelid; tongue with a strong median papilla; dorsal skin strongly glandular, with raised rounded tubercles; a pair of elongate tubercles on shoulders; first finger shorter than second; three strong metacarpal tubercles.

General color dark above and light beneath; a pale streak often present from eye to shoulder, but never silvery as in *Phrynobatrachus parvulus*; upper lip distinctly barred, the dark bars about equal to the light interspaces; dark bars of lower lip usually wider than interspaces; venter spotted anteriorly, posterior part of abdomen usually without dark spots.

Secondary sex characters. — Adult females (with pigmented ova) are distinctly larger than males having nuptial pads. Adult males (93) range in snout-vent length from 16.2 to 22.7 mm (mean  $19.78 \pm 0.12$  mm); adult females (72) range from 19.5 to 25.3 mm (mean  $22.60 \pm 0.17$  mm).

Adult females have a cluster of conical, whitish spinules on a dark triangle surrounding the anus. A few spinules may occur outside the triangle laterally on the rear of the thighs. The dark triangle is present in males but is devoid of spinules, though a few low glandules sometimes occur.

Median subgular vocal sacs and oval femoral glands are invariably present in males larger than 16.0 mm. The gular skin (Fig. 58) forms a loose pouch that is sharply defined posteriorly by a transverse fold in front of the chest. Frequently the pouch is bordered laterally by a longitudinal fold on each side. Anteriorly the gular pouch is heavily pigmented, the chromatophores becoming less dense posteriorly so that the rear portion of the throat is only faintly dusted or immaculate whitish. The vocal sac and its investing muscle usually bear numerous melanophores and, when especially dark, give the gular skin a dark gray appearance.

A pinkish linea masculina forms the ventral border of the obliquus muscle and is ordinarily visible superficially although in some males the pars abdominis of the pectoralis overlaps it as in *parvulus* (see below). Usually a linea masculina appears at the dorsal border of the obliquus.

A grayish or yellowish velvety nuptial pad appears on the dorsal and medial surfaces of the first finger from its base to the middle or end of the proximal phalanx. Small whitish spinules or asperities occur in a dense group near the chin (Fig. 58) on the gular skin and much more diffusely on the back.

As in other *Phrynobatrachus* the vocal sac and femoral gland are developed in all males having any other secondary sex characters and apparently develop before the other structures. Only three of the males examined lacked lineae masculinae; nuptial pads were present in these three. In three others lineae masculinae were present but nuptial pads absent. Seven males possessing both lineae masculinae and nuptial pads

lacked mental spinules, whereas only one having mental asperities lacked a linea masculina and none was without nuptial pads. Therefore, mental spinules probably develop after the nuptial pads and lineae masculinae. Dorsal asperities evidently appear last for, with one exception, all males having them also have all the other secondary sex characters while the converse is not true. The exceptional individual has dorsal asperities but not mental spinules. The distribution of secondary sex characters with respect to one another is given in Table 32.

TABLE 32. — Monthly frequency of adult male *Phrynobatrachus guttuerosus* from the Upemba with respect to development of secondary sex characters. All have vocal sacs and femoral glands.

Nuptial pad . . . . .	Present	Present	Present	Present	Present	Present	Absent
Linea masculina .. . . .	Present	Present	Present	Present	Absent	Absent	Present
Mental asperities . . . . .	Present	Present	Absent	Absent	Absent	Present	Absent
Dorsal asperities .. . . .	Present	Absent	Absent	Present	Absent	Absent	Absent
February ... .. . . .	22	2	0	0	0	1	0
March ... .. . . .	13	0	0	0	0	0	0
April ... .. . . .	16	1	0	1	0	0	0
May ... .. . . .	4	0	1	0	0	0	0
June ... .. . . .	1	1	0	0	1	0	0
July ... .. . . .	1	1	4	0	0	0	0
October . . . . .	0	1	1	0	0	0	3
November-December ..	12	1	0	0	1	0	0
<b>Total ... .. . . .</b>	<b>69</b>	<b>7</b>	<b>6</b>	<b>1</b>	<b>2</b>	<b>1</b>	<b>3</b>

Ecological notes. — The range in altitude of specimens collected is from 585 m to 1,780, distributed as follows :

Meters.	Individuals.
585- 750 ... .. . . .	470
751-1,000 ... .. . . .	359
1,001-1,250 ... .. . . .	685
1,251-1,500 ... .. . . .	19
1,501-1,750 ... .. . . .	19
1,751-1,780 ... .. . . .	2

The proportion of females with enlarged, pigmented ova remains high throughout the year (see Table 33), suggesting that breeding may take place during any month. The proportion of males with fully developed secondary sex characters is relatively high except in June, July, and October.

TABLE 33. — **Monthly frequency of adult *Phrynobatrachus guttuosus* from the Upemba with respect to breeding condition.**

	Males (*)		Females (**)	
	Secondary sex characters		Ova	
	complete (***)	incomplete	mature	immature
February ... ..	22	3	19	0
March ... ..	13	0	12	0
April ... ..	16	2	14	0
May . ... ..	4	1	7	0
June ... ..	1	2	1	0
July . ... ..	1	5	5	0
September ... ..	—	—	1	1
October .. ...	0	5	2	1
November-December ... ..	12	2	16	0

(\*) All having vocal sacs and femoral glands.

(\*\*) All larger than 19.5 mm, the minimum for females with pigmented ova.

(\*\*\*) The first column of Table 32.

Range. — The discontinuity in the known range of *guttuosus* — from Liberia to the Katanga — is almost certainly apparent rather than real. Part of the difficulty may be a result of the taxonomic muddle involving some of the smaller species of *Phrynobatrachus*.

#### Upemba localities and specimens :

Difirinji (2); Ganza (19); Kabenga (288); Kabwe (13); Kafwe (1); Kambi (16); Kamusanga (1); Kande (4); Kankunda (2); Kanonga (307); Kaswabilenga (137); Kateke (158); Kaziba (358); Kiamakoto (10); Kilwezi (19); Kipondo (78); Lukoka (1); Lupiala (19); Lusinga (3); Mabwe (2); Masombwe (29); Mokey (5); Mukukwe (1); Munoi (80); Mware (1).

33. — *Phrynobatrachus natalensis* SMITH.

(Pl. VI, 1.)

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

*Phrynobatrachus natalensis* GÜNTHER, 1862, Proc. Zool. Soc. London, **1862**, p. 190; LOVERIDGE, 1953, Bull. Mus. Comp. Zool., **110**, p. 378.

*Phrynobatrachus ranoides* BOULENGER, 1894, Proc. Zool. Soc. London, **1894**, p. 644, pl. 39, fig. 2 — Pietermaritzburg, Natal.

*Phrynobatrachus natalensis* forma *gracilis* ANDERSSON, 1904, in Jägerskiöld, A.L.K.E., Res. Swedisch Zool. Exped. Egypt White Nile, Part 1, No. 9, p. 10, figure — Ghrab el Aish, south of Kaka, White Nile.

*Phrynobatrachus boulengeri* WITTE, 1919, Rev. Zool. Africaine, **6**, p. 6 — Beira and Cogono, Portuguese East Africa.

*Phrynobatrachus maculatus* FITZSIMONS, 1932, Ann. Trans. Mus., **15**, p. 40 — Rain Forest, Victoria Falls; idem, **16**, p. 391, fig. 27.

Taxonomic notes. — The species *Phrynobatrachus natalensis* has an enormous range from Senegal to the Egyptian Sudan, southward to Natal and Cape Colony, and westward south of the Congo forest to Angola (Fig. 61). The supposed species *ranoides*, regarded by LAURENT so lately as 1941 as distinguishable from *natalensis*, has been referred to *natalensis* by various authors, and most lately by LOVERIDGE (1953). DE WITTE's *P. boulengeri* has been referred to *natalensis* by NOBLE (1924) and LOVERIDGE (1925). We find no distinctions, except those of juveniles, between *Phrynobatrachus maculatus* and *natalensis*; we have examined a paratype of *maculatus* in Chicago Natural History Museum. The original description of this form compares it only with *ranoides*, which is clearly a synonym of *natalensis*.

Diagnosis. — A medium-sized *Phrynobatrachus*, adults 25 to 40 mm; tympanum present, usually hidden under skin; tips of digits not dilated, without circummarginal grooves; toes broadly webbed to distal subarticular tubercle of third and fifth toes; no silvery infratympanic stripe; lower lip barred with brown or brown with light spots; throat spotted with brown in females, black in adult males.

Secondary sex characters. — Females are slightly but distinctly larger than males. One hundred ninety-nine females with pigmented ova vary from 26.6 to 38.6 mm (mean  $33.00 \pm 0.16$  mm) snout to vent, although only one measures less than 28.2 and one female lacking mature ova measures 39.3 mm. The size range of males having fully developed secondary sex characters (see below) is 26.2-36.3 mm (mean  $30.86 \pm 0.13$  mm; N=211).

Adult males have median subgular vocal sacs (LIU, 1935) joining the oral cavity by means of bilateral round or slit-like openings. The smallest



male with vocal sacs measures 26.2 mm and the largest lacking them 32.8 mm. The mean of the snout-vent length of males larger than 26.0 lacking vocal sacs is  $28.45 \pm 0.18$  mm (N=59); the difference between this mean and that of males having vocal sacs (see above) is statistically significant.

The nuptial pad consists of a velvety cluster of minute white or cream-colored spinules. When fully developed the pad covers the entire dorsal and median surfaces of the first finger from its base to the end of the basal phalanx.

The gular skin (Fig. 58) in breeding males is thrown into longitudinal folds, the deepest of which are lateral. Numerous round white asperities, each tipped by a minute spicule, cover the throat in such males. Finally, these males have a layer of black pigment on the dorsal (i.e., inner) surface of the gular skin. This black pigment is quite distinct from the brown pigment of the gular region of females and juveniles males, for the latter is concentrated on the ventral (i.e., outer) surface of the gular skin. Femoral glands are not found in this species.

In *Phrynobatrachus natalensis* the vocal sac develops prior to the other secondary sex characters. Fifty-four males have vocal sacs but lack nuptial pads, black gular pigment, gular asperities, or some combination of one or more of the three. On the other hand, all males having one or more of the last three characters also have vocal sacs. The temporal distribution (Table 34) of the five combinations in which the secondary sex characters (excluding the vocal sac) appear is best explained in the following manner.

The nuptial pads seem to go through a seasonal cycle of development and regression, the crest of the cycle occurring from September through January and the trough from May through July. The black gular pigment and the gular asperities, once they develop, apparently do not normally regress, for the proportion of adult males (i.e., those with vocal sacs) having these structures remains high except in August and September (Table 34).

Nineteen males collected in August and September have vocal sacs but lack one or more of the other secondary sex characters. They range in size from 26.6 to 30.5 mm (mean  $28.06 \pm 0.27$ ), all therefore falling below the mean (30.86 mm) of the fully developed males. Consequently it is reasonable to view the 19 as newly adult. The sharp drop in August in the proportion of adult males having black gular pigment and gular asperities probably results from a lag between the time males acquire vocal sacs (and thus move into the « adult » category) and the time they develop the other sex characters.

Three males collected in April lack secondary sex characters other than vocal sacs, and their small size (30.0, 30.4, 30.8 mm) suggests that they,

TABLE 34. — Monthly frequency of adult-sized (over 26.0 mm.) male *Phrynobatrachus natalensis* from the Upemba in various stages of development of the secondary sex characters.

	Present	Present	Present	Present	Present	Present	Absent	
Vocal sac .. ...	Present	Present	Present	Present	Present	Present	Absent	Total
Nuptial pad ... ..	Present	Absent	Absent	Present	Present	Absent	Absent	
Black gular pigment ...	Present	Present	Absent	Absent	Absent	Absent	Absent	
Gular asperities ... ..	Present	Present	Present	Present	Absent	Absent	Absent	
January ... ..	26	0	0	0	0	0	0	26
February .. ...	19	4	0	0	0	0	0	23
March ... ..	15	4	0	0	0	0	2	21
April . ... ..	10	8	0	0	0	3	6	27
May .. ...	3	6	0	0	0	0	4	13
June .. ...	3	5	0	0	0	1	22	31
July .. ...	1	3	0	0	0	0	20	24
August ... ..	7	1	1	5	2	3	4	23
September ... ..	44	0	1	4	0	2	1	52
October ... ..	29	0	0	1	0	0	0	30
November ... ..	28	0	0	0	0	0	0	28
November-December ...	19	0	0	0	0	0	0	19
December . ... ..	7	0	0	0	0	0	0	7
Total . ... ..	211	31	2	10	2	9	59	324

too, are in this intermediate stage of development. The only other male preserved in this stage is too large (33.6 mm, June) to be considered a new adult.

Of the 12 new adults from August, 5 lack gular asperities, 5 lack nuptial pads, and 11 black gular pigment (Table 34). Only 2 of the 7 new adults collected in September lack gular asperities, 3 lack nuptial pads, and all lack black gular pigment. Evidently gular asperities and nuptial pads develop at approximately the same time, to be followed by the appearance of black pigment.

Ecological notes. — *Phrynobatrachus natalensis* is an inhabitant of savannah swamps, ponds, and flood plain lakes outside of the rain

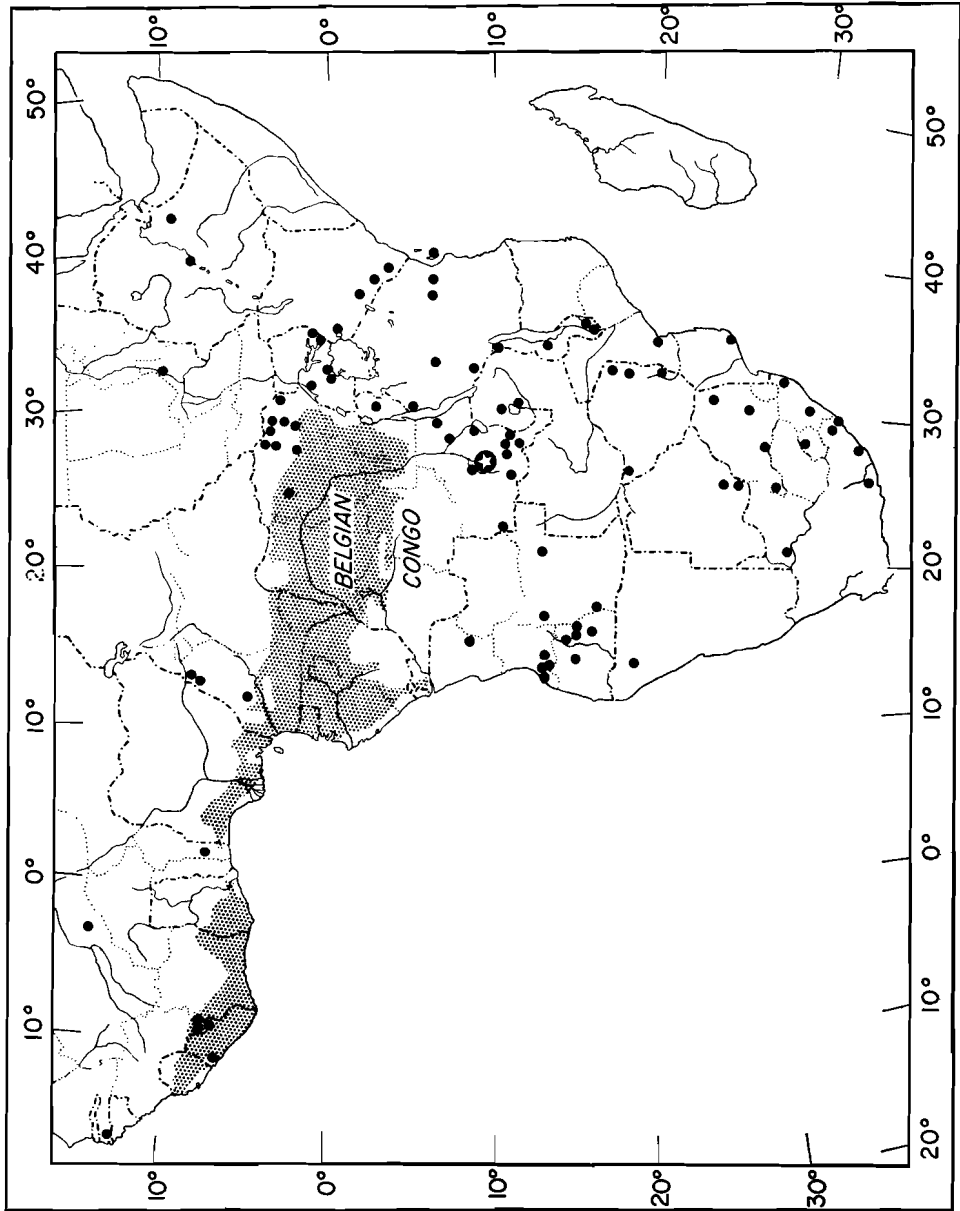


Fig. 61. — Distribution of *Phrynobatrachus natalensis*.  
Parc National de l'Upemba indicated by symbol with open star.

forest region (LOVERIDGE, 1942; NOBLE, 1924). CHABANAUD (1921 A) and LOVERIDGE (1941) have recorded it from the West African forest and NOBLE (1924) and WITTE (1934) note localities at the edge of the Ituri forest. It has been reported from sea level (MONARD, 1937; POWER, 1935) to 2,100 m (LOVERIDGE, 1936). In the Parc de l'Upemba it occurs at all elevations; specimens in the present collection show the following distribution :

Meters.	Individuals.
585- 750	2,989
751-1,000	2,065
1,001-1,250	1,275
1,251-1,500	767
1,501-1,750	661
1,751-1,830	356

Table 35 presents the monthly frequencies of *natalensis* adults according the stage of development of the ova, in the case of females, and of the secondary sex characters (which are indicators of breeding condition), in the case of males. The pattern is the same for both sexes although the proportion of males in breeding condition never falls as low as that of females (see also Fig. 74). The high proportion of females in breeding condition in October and November, followed by a gradual decrease in that proportion in the period December-March, suggests that breeding takes place from November to March. From March to July, the low proportion of sexually competent adults indicates the ebb period of the cycle. In August, September, and probably October both sexes move into breeding condition as shown by the rise in the curves of Fig. 74.

The reproductive cycle is synchronized with the rainfall cycle (Fig. 74) although the upsurge in the former precedes the beginning of the rains by several months.

Range. — South of the Sahara, which forms the northern boundary of the range, *natalensis* is found throughout Africa save only the rain forest regions (with the exceptions noted above) and, probably, the Kalahari area (Fig. 61).

#### Upemba localities and specimens :

Bowa (49); Bunda-Bunda (3); Buye-Bala (216); Bwalo (6); Difirinji (6); Dipidi (20); Ganza (358); Kabenga (99); Kabulumba (2); Kabwe (54); Kabwekanono (42); Kafwe (57); Kalubamba (5); Kalumengongo (38); Kalungwe (330); Kamatshya (2); Kambi (22); Kamitunu (19); Kampadika (17); Kamusanga (36); Kande (583); Kankunda (27); Kanonga (1,022); Karibwe (5); Kasandendeko (2); Kaswabilenga (275); Kateke (157); Katongo (6); Kaziba (351); Kenia (9); Kiamakoto (455); Kilwezi (591); Kimiala (9); Kipondo (186); Loie (46); Lufira (75); Lufwa (28); Lukawe (70); Lukoka (13); Lukorami (6); Lupiala (231); Lusinga (260); Mabwe (662); Manda (1); Masombwe (303); Mokey (45); Mubale (36); Mukana (46); Mukelengia (154); Mukukwe (21); Munoi (101); Munte (9); Munte-Mubale (677); Muye (12); Mware (20); Mwemba-Mabole (1); Pelenge (18); Sanga (64); Senze (156).

TABLE 35. — Monthly frequencies of adults of Upemba *Phrynobatrachus natalensis* in various stages of sexual competence.

	Males		Females	
	Secondary sex characters		Ova	
	complete	incomplete	pigmented	not pigmented
January .. ...	26	0	24	3
February ... ..	19	4	16	5
March ... ..	15	4	14	10
April ... ..	10	11	6	20
May . ... ..	3	6	0	24
June ... ..	3	6	1	28
July . ... ..	1	3	0	39
August ... ..	7	12	8	13
September ... ..	44	7	49	16
October .. ...	29	1	36	0
November ... ..	28	0	31	0
November-December ...	19	0	6	0
December ... ..	7	0	8	1

34. — *Phrynobatrachus parvulus* BOULENGER.

(Pl. VI, 2.)

*Arthroleptis parvulus* BOULENGER, 1905, Ann. Mag. Nat. Hist., (7), **16**, p. 109, pl. 4, fig. 3 — Bange Ngola, northeastern Loanda, Angola; NOBLE, 1924, Bull. Amer. Mus. Nat. Hist., **49**, p. 202, 316; LOVERIDGE, 1933, Bull. Mus. Comp. Zool., **74**, p. 386; WITTE, 1934, Ann. Mus. Congo Belge, Zool., (1), **3**, fasc. 4, p. 180 (part); PARKER, 1936, Nov. Zool., **40**, p. 142; MERTENS, 1937, Abh. Senck. Naturf. Ges., **435**, p. 20; 1940, Zool. Anz., **131**, p. 247; 1955, Abh. Senck. Naturf. Ges., **490**, p. 27.

*Phrynobatrachus parvulus* LAURENT, 1941, Rev. Zool. Bot. Africaine, **34**, p. 206.

*Arthroleptis schoutedeni* WITTE, 1921, Rev. Zool. Bot. Africaine, **9**, p. 13, pl. 4, fig. 3 — Lofoi, Katanga, Belgian Congo; NOBLE, 1924, Bull. Amer. Mus. Nat. Hist., **49**, p. 317; WITTE, 1934, Ann. Mus. Congo Belge, Zool., (1), **3**, fasc. 4, p. 178; MERTENS, 1937, Abh. Senck. Naturf. Ges., **435**, p. 20.

*Phrynobatrachus schoutedeni* LAURENT, 1941, Rev. Zool. Bot. Africaine, **34**, p. 205 (?).

*Arthroleptis minutus* WITTE, 1934, loc. cit., p. 178 (part).

*Arthroleptis scheffleri* WITTE, 1934, loc. cit., p. 178 (part).

**Taxonomic notes.** — The distinction of the smaller species of *Phrynobatrachus* of the Katanga requires attention especially to the characters of the male, to the size of the digital discs, to the amount of webbing between the toes, and to the coloration, particularly of the ventral surfaces and the side of the head. The very large series of these smaller species in the collections reported upon by DE WITTE in 1934 have been critically examined after making our discrimination of four species (in addition to *natalensis* and *perpalmatus*) as set forth in our key. The collections, preserved in the Musée du Congo Belge under the names *schoutedeni*, *minutus*, and *scheffleri*, all prove to be mixtures in varying proportions, of *Phrynobatrachus parvulus* and our new species *cryptotis*. The confusion of the two species under different designations is the result of the very large proportion of juvenile specimens and females and the inadequate representation of males. When the males are sorted out and carefully defined, it becomes possible to distinguish most, though not quite all, of the juveniles and females as well.

The recognition of *Phrynobatrachus parvulus* as a species ranging from Angola to Lake Tanganyika (LOVERIDGE, 1933) calls attention to the probability, indeed the certainty, that this species is present in the Katanga. Examination of the types of *parvulus* in the British Museum and the fortunately uniform series of five co-types of *Phrynobatrachus schoutedeni* in the Musée du Congo convinces us that these forms are conspecific. Both bear, in every specimen, the silvery facial stripe characteristic of the species; and the distinctive femoral gland of the adult male, described by PARKER (1936 A) is present in our Katanga males. The dorsal coloration of *parvulus*, figured by BOULENGER in the original description, can be matched as a frequent variant in our series; it is found in only two of the four co-types.

**Diagnosis.** — A small *Phrynobatrachus*, adults 12-25 mm; tympanum present, but usually not visible through skin; tips of digits not dilated, no circummarginal grooves; web not extending beyond basal subarticular tubercles of third and fifth toes, sometimes extending farther distally as a narrow fringe; a distinct silvery infratympanic stripe (Fig. 62); throat of female mottled with dark brown, of mature male finely and densely punctate with black (Fig. 58); vocal sac usually without pigment.

**Descriptive notes.** — Limbs relatively short; snout somewhat flattened and pointed; dorsal skin often with symmetrically arranged, low, oval glands.

General color dark brown above; pale beneath with dark brown spots, most dense anteriorly, often with a light median area and with more scattered spotting extending to the posterior part of the abdomen; a light vertebral stripe often present; some specimens with the back uniform gray, sharply set off from the darker sides; upper and lower lips dark with

light, often silvery, spots, rarely with dark and light bars of equal width; the silvery infratympanic stripe sometimes reduced to a row of spots.

Secondary sex characters. — Females with pigmented ova range in size from 12.6 to 24.8 mm snout to vent (mean  $18.37 \pm 0.13$ ;  $N=255$ ). Although these figures are similar to the corresponding ones of the males (range 12.3-20.4 mm; mean  $16.18 \pm 0.12$ ;  $N=219$ ), the difference between the means is statistically significant.

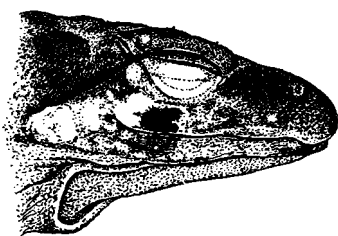


FIG. 62. — Side view of head of male *Phrynobatrachus parvulus* from Parc National de l'Upemba ( $\times 6$ ).

PARKER (1936 A) has described an oval femoral gland in males; all adult males in the present collection have these glands. Males also have median subgular vocal sacs with bilateral slit-like openings into the mouth. Usually the vocal sac and the investing subhyoideus muscle are devoid of pigment, but in a small proportion of individuals a few melanophores may be present.

Though the gular skin is usually spotted in females, it is much darker and the pigment more or less uniformly distributed in males (Fig. 58). Some males, preserved with an inflated throat, have lighter appearing skin because the stretching separates the chromatophores. The gular skin in mature males normally has several shallow, longitudinal folds laterally and a transverse fold posteriorly. Towards the chin several whitish conical tubercles develop. Similar asperities appear on the rear of the dorsum in many, though not all, mature males.

The nuptial pad consists of a grayish velvety pile on the dorsal and median surfaces of the first finger from the wrist to the base of the first finger. Finally, a pinkish linea masculina appears sporadically along the ventral border of the obliquus muscle but, because it is covered by the pars abdominis of the pectoralis, it is not visible superficially.

With the exception of the last one, the male secondary sex characters have a relatively simple developmental relationship. The vocal sac and

TABLE 36. — Monthly frequency of adult male *Phrynobatrachus parvulus* from the Upemba with respect to development of secondary sex characters.

Femoral glands ... ..	Present	Present	Present	Present	Present	Present	Present	Total
Vocal sacs ... ..	Present	Present	Present	Present	Present	Present	Present	
Nuptial pads ... ..	Present	Present	Present	Absent	Absent	Absent	Absent	
Mental asperities ... ..	Present	Present	Absent	Present	Present	Absent	Absent	
Dorsal asperities ... ..	Present	Absent	Absent	Present	Absent	Present	Absent	
January ... ..	12	9	2	0	0	0	0	23
February .. ...	13	0	0	0	0	0	0	13
March ... ..	9	2	1	0	0	0	2	14
April . ... ..	0	5	4	0	0	0	0	9
May .. ...	7	4	0	1	0	0	5	17
June .. ...	14	0	1	0	0	0	0	15
July .. ...	1	2	1	0	1	1	15	21
August ... ..	4	0	0	0	1	0	3	8
September ... ..	13	0	0	0	0	0	0	13
October ... ..	2	4	3	0	0	0	7	16
Total . ... ..	75	26	12	1	2	1	32	149

femoral gland develop earliest. On the basis of the present material, a decision as to which of these two appears first is impossible; all males having one of these structures has the other. However, thirty-two males with vocal sacs and femoral glands lack other secondary sex characters (Table 36). The femoral gland in these particular males is rather thin though its area is not reduced.

As shown by Table 36, only four males lacking nuptial pads have mental or dorsal asperities or both, whereas thirty-eight with nuptial pads lack one or both of those characters. Three explanations of these observations are possible : (1) normally the nuptial pads develop prior to both types of asperities; (2) the asperities undergo regression whereas the pads do not; (3) a combination of (1) and (2). As Tables 36 and 37 contain little evidence of regression, we reject the last two explanations. By analogous reasoning the mental asperities appear to develop before those of the dorsum.



Ecological notes. — *Phrynobatrachus parvulus* inhabits open country south of the rain forest, for the most part in regions more than 500 m above sea level. LOVERIDGE (1933) reports it at an elevation of 2,400 m. Within the Parc National de l'Upemba, *parvulus* is present at all but the lowest elevations, the observed range being 695-1,830 m and the frequency within zones as follows :

Meters.	Individuals.
585- 750	1,270
751-1,000	1,692
1,001-1,250	11,300
1,251-1,500	245
1,501-1,750	1,945
1,751-1,830	1,788

TABLE 37. — Monthly frequency of adult *Phrynobatrachus parvulus* from the Upemba in various stages of reproductive condition.

	Males			Females (**)	
	Secondary sex characters (*)			Ova	
	complete	incomplete	absent	mature	immature
January ... ..	12	11	0	40	1
February ... ..	13	0	0	33	0
March ... ..	9	3	2	47	1
April ... ..	0	9	0	32	5
May ... ..	7	5	5	41	8
June ... ..	14	1	0	24	4
July ... ..	1	5	15	13	10
August .. ...	4	1	3	10	3
September ... ..	13	0	0	11	3
October . ... ..	2	7	7	15	4
November ... ..	0	0	0	0	10
	75	42	32	256	49

(\*) Excluding vocal sacs and femoral glands, which are present in all males listed in this table.

(\*\*) All females 12.0 mm or larger; smallest female with mature ova 12.6 mm.

The monthly frequency of adults in various stages of reproductive condition is given in Table 37. A large proportion of males are apparently in an inactive reproductive state in July and October, but the incidence of these proportions in these particular months is probably a matter of chance since, besides the separation in time, the two months are in totally different seasons with respect to rainfall. The picture is made even more irrational by the lack of correspondence between the two sexes. September and October are months of equal sexual development for the females, whereas for the males these two months are at opposite extremes. The irregular pattern that emerges from Table 37 leads to the conclusion that *parvulus* does not have a sharply defined breeding period in the Upemba.

Range. — From the mouth of the Congo (NOBLE, 1924) eastward through Angola and southeastern Belgian Congo to central Tanganyika (LOVERIDGE, 1933) and southward to the Zambezi (WITTE, 1934, as *schoutedeni*) and northeastern South West Africa (MERTENS, 1955). WITTE (1934) also gives Buta, Lower Uelle, as a locality (see Fig. 63), but that is so far north of all other records, besides lying within the rain forest, that the identification needs confirmation.

#### Upemba localities and specimens :

Bunda-Bunda (2); Buye-Bala (379); Dipidi (140); Ganza (957); Kabenga (913); Kabwe (209); Kabwekanono (22); Kafwe (13); Kagomwe (84); Kakolwe (1); Kalala (9); Kalungwe (64); Kamamulongo (22); Kamatshya (90); Kambi (146); Kamitungulu (217); Kamitunu (184); Kampadika (94); Kande (30); Kankunda (1); Kanonga (949); Kanpungu (184); Karibwe (12); Kasandendeko (71); Kaswabilenga (219); Katongo (2); Kavizi (80); Kayango (2); Kaziba (5,048); Kenia (368); Kiamakoto (18); Kilolomatamba (232); Kilwezi (165); Kimapongo (64); Kimiala (28); Kipangaribwe (15); Kipondo (40); Lufira (1); Lufwa (1); Lupiala (36); Lusinga (1,106); Masombwe (1,389); Mitoto (135); Mokey (45); Mubale (21); Mukana (24); Mukelengia (18); Mukukwe (1); Munoi (167); Munte (2); Munte-Mubale (33); Pelenge (3,925); Sanga (36); Senze (214); Tumbwe (8).

#### 35. — *Phrynobatrachus perpalmatum* BOULENGER.

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

*Phrynobatrachus perpalmatum weneri* AHL, 1924, Zool. Anz., **60**, p. 273 — El Grassi and the White Nile (Tonga, Renk, and Kaskawal).

Taxonomic notes. — No species of the genus *Phrynobatrachus* has suffered less from taxonomic confusion than *perpalmatum*. The subspecies *weneri* proposed by AHL in 1924 for the northernmost populations has been referred to the synonymy by LOVERIDGE (1933). The name *weneri* was preoccupied in *Phrynobatrachus* by *P. weneri* NIEDEN (described as an *Arthroleptis*).

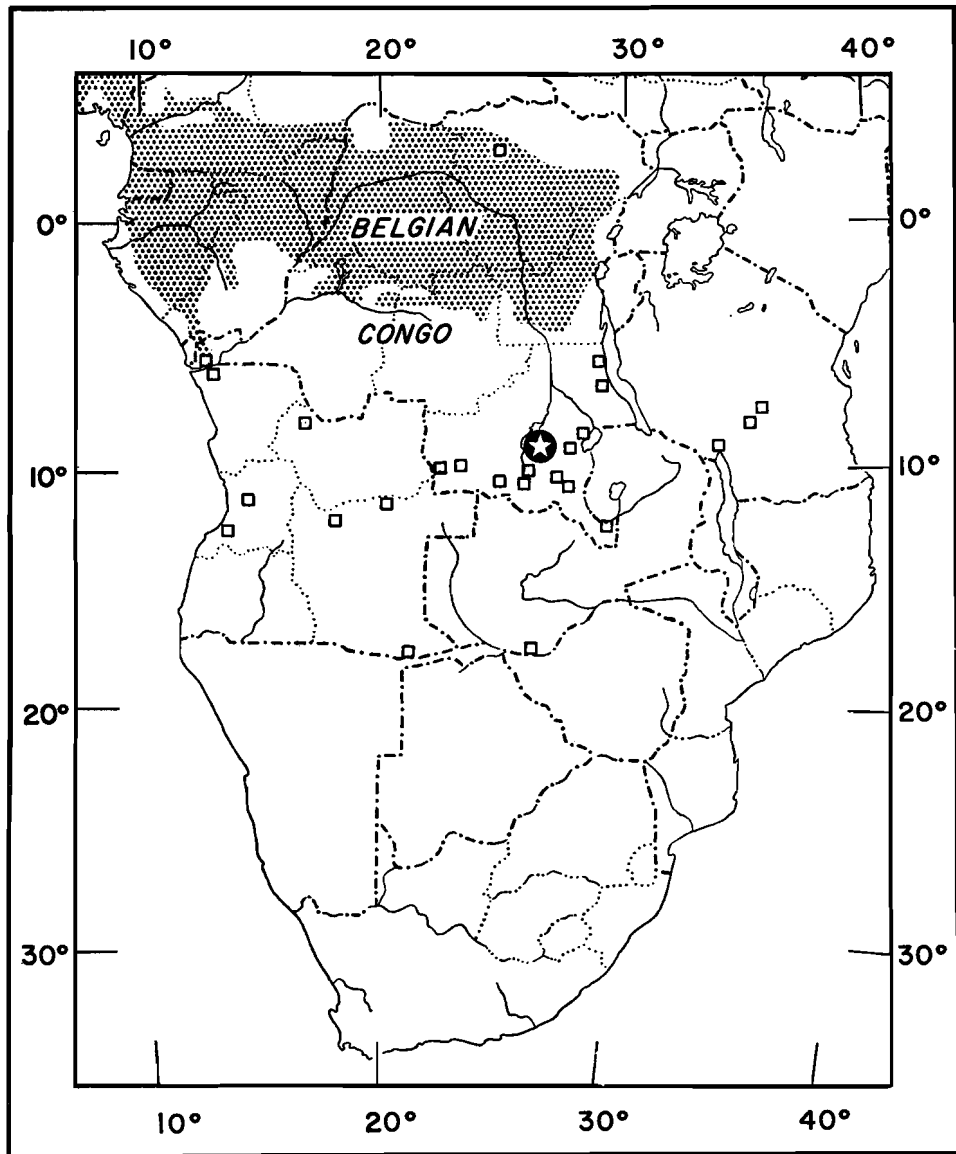


FIG. 63. — Distribution of *Phrynobatrachus parvulus*.  
Parc National de l'Upemba indicated by symbol with open star.

**Diagnosis.** — A medium-size *Phrynobatrachus*, adults 20-30 mm; tympanum present, usually visible through skin; tips of fingers not dilated; toes with small disks having weakly indicated circummarginal grooves; toes, except fourth, broadly webbed to disks, fourth commonly with one phalanx free; no infratympanic silvery stripe; throats of females densely mottled with grayish color, of males sparsely dotted with dark pigment or immaculate whitish (Fig. 58).

**Secondary sex characters.** — Adult females average larger in size than males though there is much overlap. Fifty-two females containing mature ova have a snout-vent range of 20.8 to 29.2 mm and a mean of  $24.29 \pm 0.24$  mm. Forty-nine males having nuptial pads measure from 18.8 to 25.0 mm and have a mean of  $22.44 \pm 0.19$  mm.

The median subgular vocal sac of males is connected with the oral cavity through a pair of round openings at the corners of the mouth. The gular skin has no distinct folds, but usually lacks pigmentation in contrast to the dark-spotted throat of females. Feebly developed mental asperities appear in a few males; in the others they are totally lacking. A mature male has a pair of pinkish lineae masculinae, one each at the dorsal and ventral edges of the obliquus muscle. The ventral band is overlain by the pars abdominalis of the pectoralis muscle. A velvety, yellowish nuptial pad covers the dorsal and median surfaces of the first finger from its base to the beginning of the basal phalanx. No femoral gland is present.

As in other species of *Phrynobatrachus*, the vocal sac and lineae masculinae may be present when nuptial pads are absent; this occurs in 12 out of 62 males. However, the converse is never true.

**Ecological notes.** — *Phrynobatrachus perpalmatus* usually inhabits swampy grasslands (LOVERIDGE, 1933, 1942) and river flood plain pools (LOVERIDGE, 1953) of the savanna country though it has also been found along streams deep in rain forest territory (NOBLE, 1924). LOVERIDGE's observations indicate that swampy shores of lakes seem to be especially favorable to this frog, whose fully webbed toes are functionally related to its thoroughly aquatic habits. About three-fourths of the Upemba series was collected at Mabwe, which is on the shore of Lake Upemba.

This species evidently is confined to low and moderate elevations, the highest literature record for it being 860 m (LOVERIDGE, 1942; 2,800 feet). Altitudinal range in the Parc National de l'Upemba is limited; 2,020 specimens were taken at 585 m and 597 at 695 m. The absence of *perpalmatus* from the marshes at Mukana (1,810 m) is evidence that the meteorological conditions of high altitudes are decidedly unfavorable.

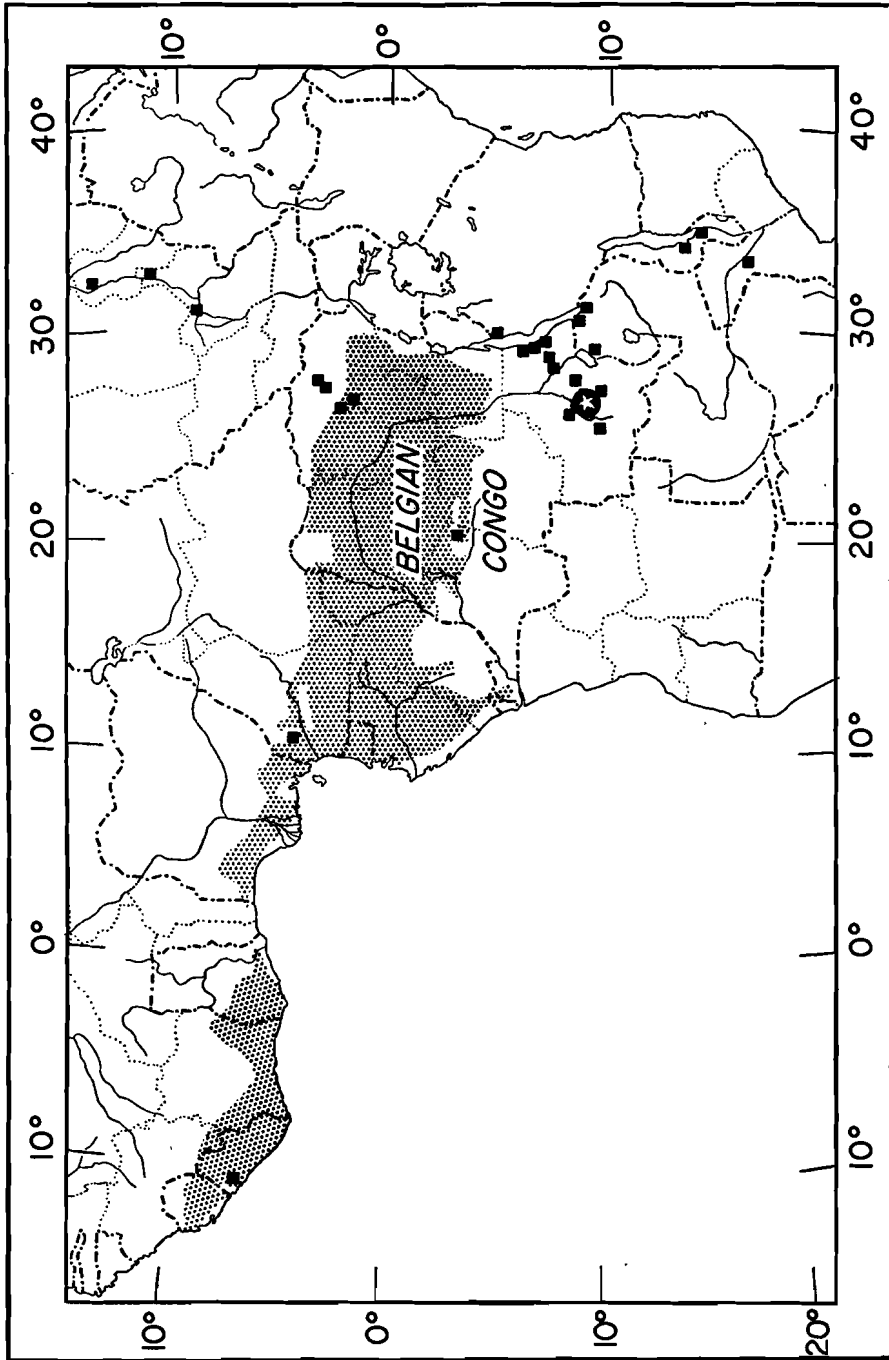


FIG. 64. — Distribution of *Phrynobatrachus perpalmatatus*.  
Parc National de l'Upemba indicated by symbol with open star.

Specimens were available from only a limited portion of the calendar year. However, the frequency of females with mature ova and that of males having nuptial pads (Table 38) indicate that breeding begins after September.

TABLE 38. — **Monthly frequency of adult *Phrynobatrachus perpalmatu* from the Upemba in various stages of sexual competency.**

	Males (*)		Females (**)	
	Nuptial pads		Ova	
	present	absent	mature	immature
January .. ...	17	0	15	2
February ... ..	15	0	11	0
March ... ..	—	—	1	0
July . ... ..	4	2	—	—
August ... ..	—	—	1	0
September ... ..	0	7	0	16
November ... ..	11	1	11	1
December ... ..	3	2	13	6
	50	12	52	25

(\*) All males having vocal sacs.

(\*\*) All females larger than 20.8 mm (the smallest containing mature ova).

Range. — From Sudan (Fig. 64) just south of Khartoum (ANDERSSON, 1904) to central Mozambique (LOVERIDGE, 1953), and from the Rift Valley to central Belgian Congo (BARBOUR and LOVERIDGE, 1930 A). The last two authors (1930) also record *perpalmatu* from Liberia.

Upemba localities and specimens :

Kanonga (597); Mabwe (2,020).