

## CONCLUSION

### ZOOGEOGRAPHIC RELATIONS.

The geographic distribution of the species contained in the Upemba collection <sup>(3)</sup> is given in Table 42. The division of Africa into faunal regions has been attempted many times, including once by the senior author (1923). The scheme presented now (Fig. 73) differs from that earlier one in containing more divisions corresponding to a finer division of the vegetation (modified from GOODE's School Atlas, New York, Rand McNALLY and Co., 1930, and BOUGHEY, 1957). For example, we now distinguish between the large area (V) dominated by savanna forest stretching from central Angola through Northern Rhodesia and central Tanganyika and the less wooded areas to the north (IV) and east (VII).

We also distinguish the semi-arid and arid region of southwestern Africa (XIII) and the temperate savanna and woodland at the extreme south (XIV, XV) from the tropical savannas. Contrary to the earlier paper, the grasslands of eastern Tanganyika are not separated from the similar formation in Mozambique, a decision justified by the similarities in vegetation and climate. For purposes of exposition, we have made arbitrary divisions between the western and eastern portions of the Sudan savanna and between the latter and the East African grasslands.

NOBLE's (1924) zoogeographic division of Africa is not suitable for present purposes because his separation of Angola and the Katanga runs counter to the distribution of many Upemba forms. On the other hand, the lack in NOBLE's system of a distinction between savanna and savanna forest regions obscures one aspect of the ecological distribution of the species with which we are concerned.

CHAPIN (1932) also divided Africa into faunal zones. Since his scheme was based upon roughly the same vegetational zones as ours, the two sets of faunal divisions correspond closely.

Zones XI and XII in the north, and XIII and the western half of XIV in the south are semi-arid, scrubby grasslands having less than twenty inches of rainfall annually. Zone X is primarily an area of temperate deciduous brush and woodland with some grassland. Zone VI is a region

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<sup>(3)</sup> Unless otherwise stated the genera *Afrizalus* and *Hyperolius* are omitted from the discussion. These two difficult genera have been reported on by LAURENT (1957).







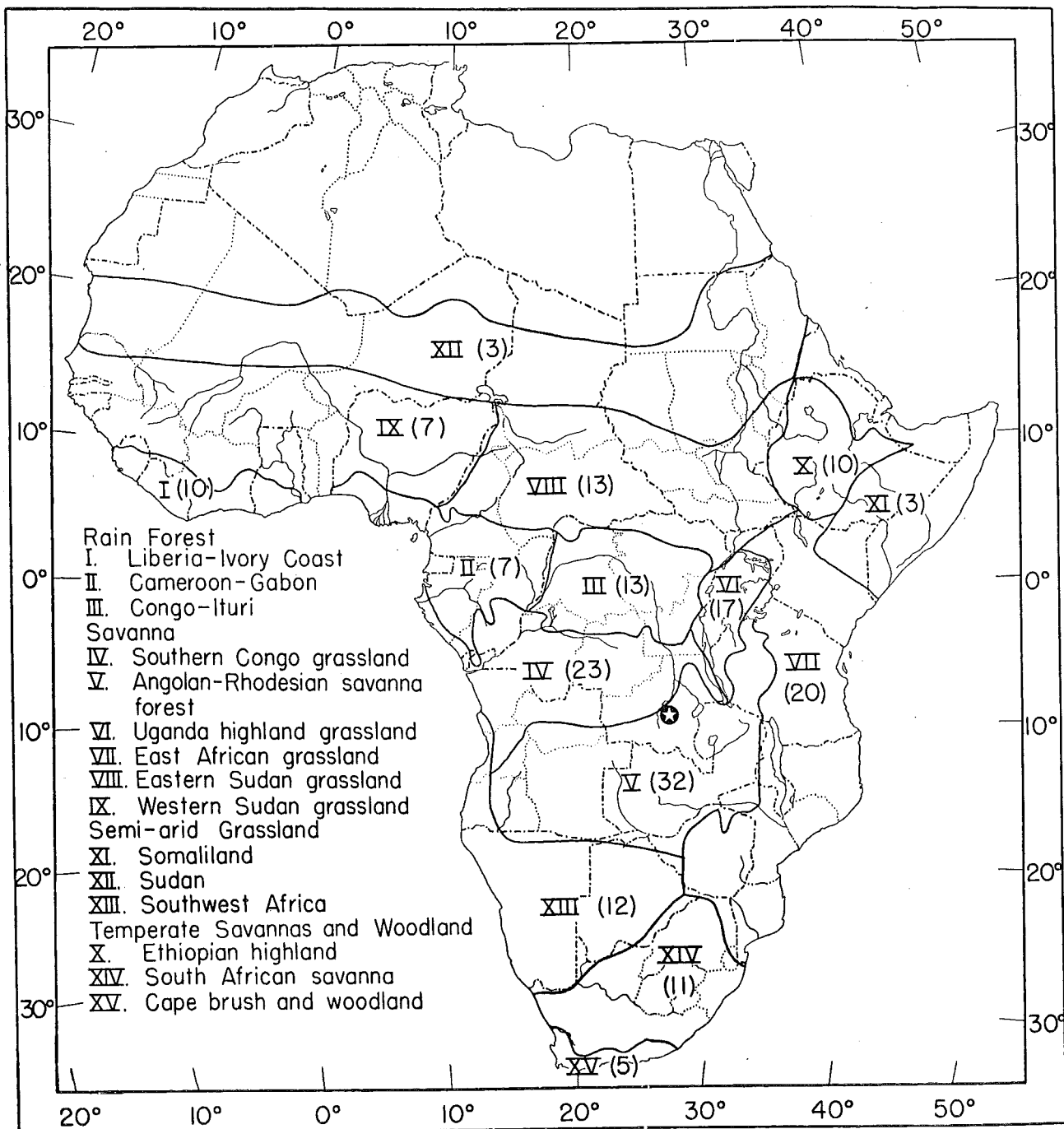


FIG. 73. — Suggested faunal division of Africa.  
 Roman numerals correspond to those of key. Arabic numerals in parentheses indicate number of Upemba amphibians occurring in each faunal zone.  
 Parc National de l'Upemba indicated by symbol with open star.

of high altitude grassland and scattered montane forests; the boundary between it and zone VII is somewhat arbitrary. Zones I, II, and III are lowland rain forest. Though the second two are separated by the Congo-Ubangi River, a number of the Cameroons-Gabon genera are not recorded east of the Ubangi. The other zones are defined above.

Finally, we make no claim of universality for the faunal zones of Figure 73. However, the distribution of the Upemba species in this scheme forms a rational and expected pattern.

The great preponderance of records on which Table 42 is based have been taken from many sources. Literature identifications unaccompanied by descriptive notes should always be regarded with scepticism. But in the cases of common wide-spread species untainted by taxonomic confusion (for example, *Bufo regularis*), little danger is risked in accepting literature records. We have avoided using literature reports of other names, such as *Rana mascareniensis*, that are known to have been collecting grounds for many valid species. Where valid reasons for doubt existed, we rejected a literature record.

Because of this limitation, some of the distributions in Table 42 are incomplete. A good example is the range of *Rana superciliaris*, only lately resurrected from the synonymy of *mascareniensis* by GUIBÉ and LAMOTTE (1955 A). The range in the table (and in Fig. 48) is based entirely on specimens we have examined. Since the type locality is in Sierra Leone (zone I) and since we have many specimens from zones V-VII, the species is certain to occur in the Sudanese savannas (zones VIII and IX). For similar reasons we expect the known range of *Rana porosissima* to be extended considerable.

As the Parc National de l'Upemba lies on the boundary between zones IV and V, one expects species occurring in the Upemba to be found in both zones. Excluding the six species described above as new and to date known only from the park, all but one Upemba species have been recorded from zone V previously. The exception is *Bufo ushoranus* known from zone VII in Tanganyika (LOVERIDGE, 1932). On the other hand, only 23 Upemba species have been reported from zone IV.

In general the number of Upemba species known from other zones diminishes with increasing distance so that, for example, 20 occur in zone VII (East African grasslands), 13 in zone VIII (eastern Sudan grasslands) and 7 in zone IX (western Sudan grasslands). The climatic and vegetational characteristics of the zones are factors modifying the influence of distance in the distributions shown in Figure 73. The semi-arid Somaliland grassland (zone XI) is only slightly more distant from the Parc National de l'Upemba than the eastern Sudan savanna (zone VIII) and is considerably closer than the western Sudan (zone IX). Yet zone XI has only one-fourth as many Upemba species as zone VIII and about one-half as many as zone IX. The reduction in numbers of Upemba species

in the Ituri lowland rain forest (zone III), which is relatively close to the Parc National de l'Upemba on this continental scale, is another example of the ecological effect. Although 14 of the Upemba species have been reported from lowland rain forest areas, only two, *Bufo funereus* (Fig. 6) and *Rana alboabris* (Fig. 20), are as generally distributed in the forest as out of it.

### ALTITUDINAL DISTRIBUTION.

The altitudinal distributions of the species samples in this collection are summarized in Table 43. Data on the genera *Afrixalus* and *Hyperolius* are from LAURENT (1957).

Many factors, such as relative proportions of land area and the duration of collecting time at various elevations, may so affect observed frequencies that the latter tell us little about the biology of the amphibians. This may be true, for example, of the observed distribution of *Rana obscura* (Table 43). It is probable that the small number collected in the 1,251-1,500 m interval indicates a small amount of collecting time and/or the small proportion of the park's area at that elevation. This suggestion is reinforced by the small total number (last column of Table 43) collected at that altitude.

A few of the observed gaps must be ignored. For instance, the absence of *Bufo ushoranus* from 1,001-1,250 m does not indicate an effect of altitude as it is found above and below that level. The same is to be said of the absence of *Bufo melanopleura* and *Rana grandisonae* from the same zone. In the following discussion it is assumed that the altitudinal range of every species is continuous.

For the most part, the broad outlines of the observed frequencies seem to reflect true altitudinal distributions, though some of course may be truncated at either the low or high end by the limitations of the park. Despite the fact that little ecological information on various localities in the park is now available, it may be determined in some instances whether the absence of a particular species at one elevation is to be explained by lack of a suitable biotope or by climatic differentiation. As an example, consider the distribution of *Phrynobatrachus perpalmatus*, which was obtained at only two Upemba localities, Kanonga (597 frogs) and Mabwe (2,020), both below 750 m. At these localities 473 and 1,545 specimens, respectively, of *Phrynobatrachus cryptotis* were also caught. Three hundred eight-four of the latter were collected at Lusinga in a marsh at 1,640 m. Since *cryptotis* is abundant at both altitudinal extremes and since *perpalmatus* apparently occupies the same biotope as *cryptotis*, it is reasonable to conclude that the absence of *perpalmatus* at high altitudes is explained by its inability to tolerate climatic conditions of high altitude and not by the absence of the habitat.

On the other hand, the relatively few numbers of *Phrynobatrachus cryptotis* collected at 1,001-1,250 m probably is explained by scarcity of the proper biotope. Obviously, since it is abundant above and below that level, climatic conditions do not restrict its abundance. The enormous numbers of *Phrynobatrachus parvulus* caught at 1,001-1,250 m demonstrate that considerable collecting effort was expended in that altitude.

Twenty-three of the 51 forms are distributed in five or more of the altitudinal zones and fifteen in only one or two zones. Ignoring discontinuities in observed distributions (see above), eight of the ten species spanning five zones are absent in the lowest one (585-750 m). On the other hand, most of the 22 species that range through three or fewer zones, that is, the specialized or stenokous forms, are concentrated in the lower altitudes. Fourteen occur only in the three lowest zones, six in the three highest zones, and only two in the middle zones.

*Bufo*, *Rana*, *Phrynobatrachus*, and *Hyperolius*, the only genera represented by more than two species, differ in the extent to which their species are restricted altitudinally (Table 44). The altitudinal ranges in Table 44 are given in terms of zones spanned. For example, *Hyperolius granulatus*, *Rana ansorgei*, and *Bufo carens* all occur in three altitudinal zones and are listed in the same column although they do not occur in the same zones. *Rana* clearly shows more altitudinal differentiation than the other genera. Conceivably, this extreme interspecific differentiation may explain the ability of such a small area to support so many species of *Rana*. Conversely, the lack of altitudinal specialization in *Phrynobatrachus* suggests that interspecific isolation in this genus has a different basis.

TABLE 44. — Number of species with indicated extent of altitudinal range in Parc National de l'Upemba.

Genus	Total number of species	Number of altitudinal zones spanned					
		1	2	3	4	5	6
		Number of species					
<i>Bufo</i> ... ..	6	—	—	2	1	2	1
<i>Rana</i> ... ..	17	4	4	1	2	4	2
<i>Phrynobatrachus</i> ..	6	1	—	—	—	1	4
<i>Hyperolius</i> ... ..	10	1	1	4	—	3	1



## REPRODUCTIVE CYCLES.

The reproductive cycle in amphibians generally is assumed to be geared to the seasonal incidence of rainfall in those areas, such as the Parc National de l'Upemba, having sharply defined wet and dry seasons. Most of the Upemba species fit this pattern, as has been indicated above (e.g., pp. 101, 159). The data presented separately for each species are best analyzed for each sex independently.

Nuptial pads and similar dermal secondary sex characters of males are known to fluctuate in development according to the production of

TABLE 45. — The nature of reproductive activity of male amphibians from the Parc National de l'Upemba as determined by the development of nuptial pads.

	Cyclic	Acyclic
<i>Xenopus laevis poweri</i> ... ..	+ (Oct.-Mar.)	—
<i>Bufo regularis</i> ... ..	+ (Aug.-Feb.)	—
<i>Bufo funereus upembae</i> ... ..	—	+
<i>Rana fuscigula</i> ... ..	—	+
<i>Rana albolabris lemairei</i> ... ..	—	+
<i>Rana grandisonae</i> . ... ..	+ (Nov.-May)	—
<i>Rana m. mascareniensis</i> ... ..	+ (Oct.-Feb.)	—
<i>Rana oxyrhyncha</i> .. ... ..	+ (Sept.-Feb.)	—
<i>Rana obscura</i> ... ..	+ (Nov.-Apr.)	—
<i>Rana porosissima</i> . ... ..	+ (Sept.-Mar.)	—
<i>Rana upembae</i> ... ..	+ (?-Mar.)	—
<i>Rana uzungwensis</i> ... ..	+ (?-Apr.)	—
<i>Arthroleptis globosus</i> ... ..	+ (Oct.-Mar.)	—
<i>Phrynobatrachus anotis</i> ... ..	—	+
<i>Phrynobatrachus parvulus</i> .. ... ..	—	+
<i>Phrynobatrachus gutturosus</i> ... ..	—	+
<i>Phrynobatrachus cryptotis</i> .. ... ..	+ (Sept.-Apr.)	—
<i>Phrynobatrachus natalensis</i> . ... ..	+ (Aug.-Mar.)	—

testicular hormones (ARON, 1926; GLASS and RUGH, 1944; GREENBERG, 1942; PONSE, 1924). These studies have shown that immediately before and during the breeding season, when secretion of testicular hormone is at a maximum, the nuptial pads and similar asperities reach their maximum development. With the end of the breeding season, production of testicular hormone wanes and the epidermal portions of the nuptial pads are sloughed off, to be redeveloped when hormone production rises before the next breeding season. If the species has acyclic reproductive activity, the nuptial pads do not regress (CEI, 1949). Thus nuptial pads are good indicators of reproductive competence in males.

Table 45 indicates the nature of the reproductive activity, as nearly as it can be determined from the development of nuptial pads and, in the case of *Arthroleptis globosus*, spines. Some of the Upemba species are

TABLE 46. — The nature of reproductive activity of female amphibians from the Parc National de l'Upemba as determined by the presence of enlarged ova.

	Cyclic	Acyclic
<i>Xenopus laevis poweri</i> ... ..	+ (June-Mar.)	—
<i>Bufo regularis</i> ... ..	+ (Aug.-May)	—
<i>Bufo funereus upembae</i> ... ..	+ (Oct.-Apr.)	—
<i>Rana fuscigula</i> ... ..	—	+
<i>Rana albolabris lemairei</i> ... ..	+ (Apr.-June)	—
<i>Rana grandisonae</i> . ... ..	+ (?-Apr.)	—
<i>Rana m. mascareniensis</i> ... ..	+ (Nov.-Feb.)	—
<i>Rana oxyrhyncha</i> . ... ..	+ (Sept.-?)	—
<i>Rana obscura</i> ... ..	+ (Nov.-Apr.)	—
<i>Rana porosissima</i> . ... ..	+ (Sept.-Jan.)	—
<i>Arthroleptis globosus</i> ... ..	+ (Nov.-Apr.)	—
<i>Arthroleptis stenodactylus</i> ... ..	+ (Nov.-Jan.)	—
<i>Phrynobatrachus anotis</i> ... ..	—	+
<i>Phrynobatrachus parvulus</i> .. ... ..	—	+
<i>Phrynobatrachus gutturosus</i> ... ..	—	+
<i>Phrynobatrachus cryptotis</i> .. ... ..	+ (Sept.-Mar)	—
<i>Phrynobatrachus natalensis</i> . ... ..	+ (Sept.-Mar.)	—
<i>Hemisus marmoratus</i> .. ... ..	+ (Nov.-Jan.)	—

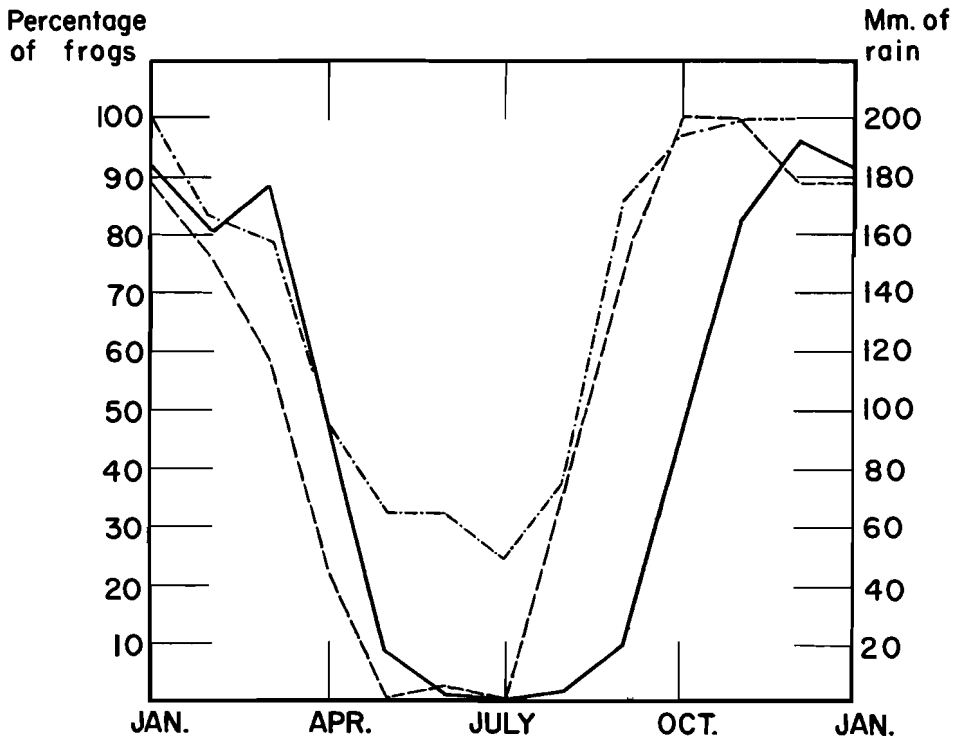


FIG. 74. — Relation between rainfall (—) in the Parc National de l'Upemba and percentage of *Phrynobatrachus natalensis* in breeding condition. Males with nuptial pads (---); females with enlarged ova (-.-.-).

excluded from the table because adults were not collected in a sufficient number of months; others, e.g., *Hemisus marmoratus*, are omitted because males never develop nuptial pads. If fifty per cent or more of the adult males obtained in a particular month had nuptial pads well-developed, that month was considered part of the breeding period.

Females were considered to be in reproductive condition if the eggs were fully pigmented and large. The ova of some species, for example, *Arthroleptis stenodactylus*, are pigmentless and in such cases size of ova was the criterion. The gonads of females are less reliable as indicators of the species reproductive behavior than the males' nuptial pads because enlarged and pigmented ova may not be fully mature. Furthermore, a week or two after a given female has spawned her gonads are at a low point in the cycle although other females may still be ready to breed. Nevertheless the females are tabulated (Table 46) in the same fashion as the males, using the fifty per cent criterion.

As stated above, most of the Upemba species have sharply defined, though extended, breeding periods. In general the patterns derived from both sexes agree. Only in *Bufo funereus* and *Rana albolabris* do the females show one pattern (cyclic in both cases) and the males another.

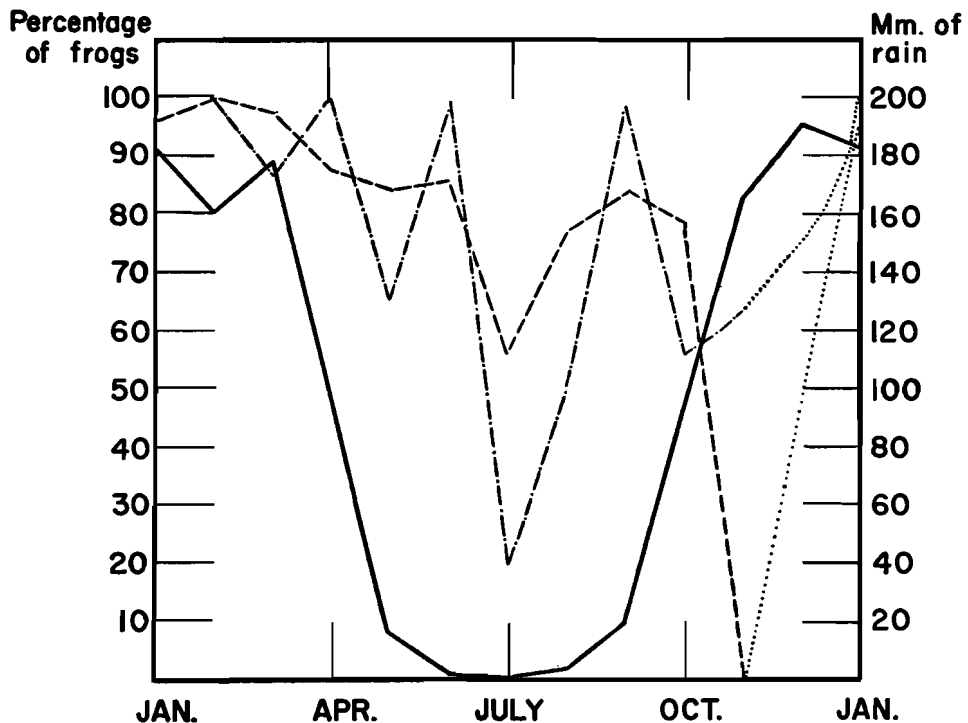


FIG. 75. — Relation between rainfall (—) in the Parc National de l'Upemba and percentage of *Phrynobatrachus parvulus* in breeding condition. Males with nuptial pads (—.—); females with enlarged ova (——). Dotted lines indicate periods for which data are not available.

With a few exceptions, the breeding seasons occupy most of the rainy season (October through April, Fig. 74). The presence of many suitable larval habitats during this interval is probably the ultimate factor controlling these reproductive cycles (INGER and GREENBERG, 1956). So little rain falls during the five dry months that many aquatic habitats must disappear with destruction of any amphibian larvae lacking the ability to aestivate. But rainfall is probably not the proximate factor stimulating secretion of reproductive hormones, for from one-third to one-half of the

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species appear to be in breeding condition in August or September, well in advance of the rains (Fig. 74). It is doubtful that these forms (e.g., *Bufo regularis*, *Rana porosissima*, *Phrynobatrachus natalensis*) actually begin to breed then. Conceivably, by being ready to spawn as soon as the rains begin, a given female could produce several clutches of ova in the interval from October to March.

With the possible exception of female *Rana albolabris*, the breeding periods of the cyclic species show no significant differentiation (Tables 45 and 46). Species isolation in this area is not promoted by this factor as it may be in other parts of the world (see MOORE, 1949, for an example).

The absence of a cycle in the development of sex characters in *Rana fuscigula*, *Phrynobatrachus anotis*, *P. parvulus* (Fig. 75), and *P. guttuosus* (Table 45) is well established by the data given on pages 54, 142, 164 and 154. All four range from the lowest to the highest altitudinal zones (Table 43). In the absence of field observation of the habits and habitats of these species, speculation on these data are not warranted.

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