ANURAN ECOLOGY IN RELATION PARTICULARLY TO OVIPOSITION AND DEVELOPMENT OUT OF WATER

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From the foregoing paper (The Zoocartographic Approach to Anuran Ecology) and an earlier paper in this symposium by Mr. B. R. Stuckenberg (Effective Temperature as an Ecological Factor in southern Africa) it will be seen that there are arguments in favour of a fresh approach to anuran ecology in southern Africa. An approach based on the major activities of the animals is suggested.

Animals are involved in a number of activities which must be performed with some degree of efficiency if they are to survive and leave progeny. Each species has a particular set of behaviour patterns which enable it to survive. In attempting to assess the limiting effect of environmental factors we need to know what is likely to affect the efficiency of such activities as feeding, predator avoidance and breeding. It is therefore reasonable to approach the ecology of each species of a group of animals by studying these activities comparatively.

LOCOMOTORY MODES, AND MICROHABITATS

It is to be expected that considerable differences in behaviour, and hence ecology, between anuran genera should be demonstrable, since differences in both anatomy and behaviour are implied by separation at generic level. It appears to be possible to separate the genera of southern African *Anura* into small groups according to the types of locomotion employed by the adults. This is shown diagrammatically in Figure 1. In Figure 2 the habitats and microhabitats of the anuran genera are illustrated. It will be seen that there is considerable diversity in microhabitats and that genera with similar modes of locomotion tend to be found in similar microhabitats.

FEEDING

The food of anurans varies with their mode of locomotion and, of course, also with their habitat. Thus the jumpers and swimmers of grassy verges often take flying insects by leaping out of water. Anurans of reeds, bushes and trees take cursorial animals on the vegetation or insects flying about in the vegetation, Cott (1932), for instance, observing that *Hyperolius* takes ants frequently (cursorial prey), while *Afrixalus fornasinii* takes more *Diptera* and *Lepidoptera* (flying prey). Burrowers such as *Breviceps* take cursorial ground prey, such as alate termites emerging for the nuptial flight, while hoppers such as *Bufo* take, in addition to cursorial ground prey, insects flying near the ground. *Xenopus*, an aquatic genus, eats a variety of prey, such as drowning insects, while humus-dwellers such as *Arthroleptis* may subsist largely on one food – amphipods. Feeding has been considered indiscriminate:

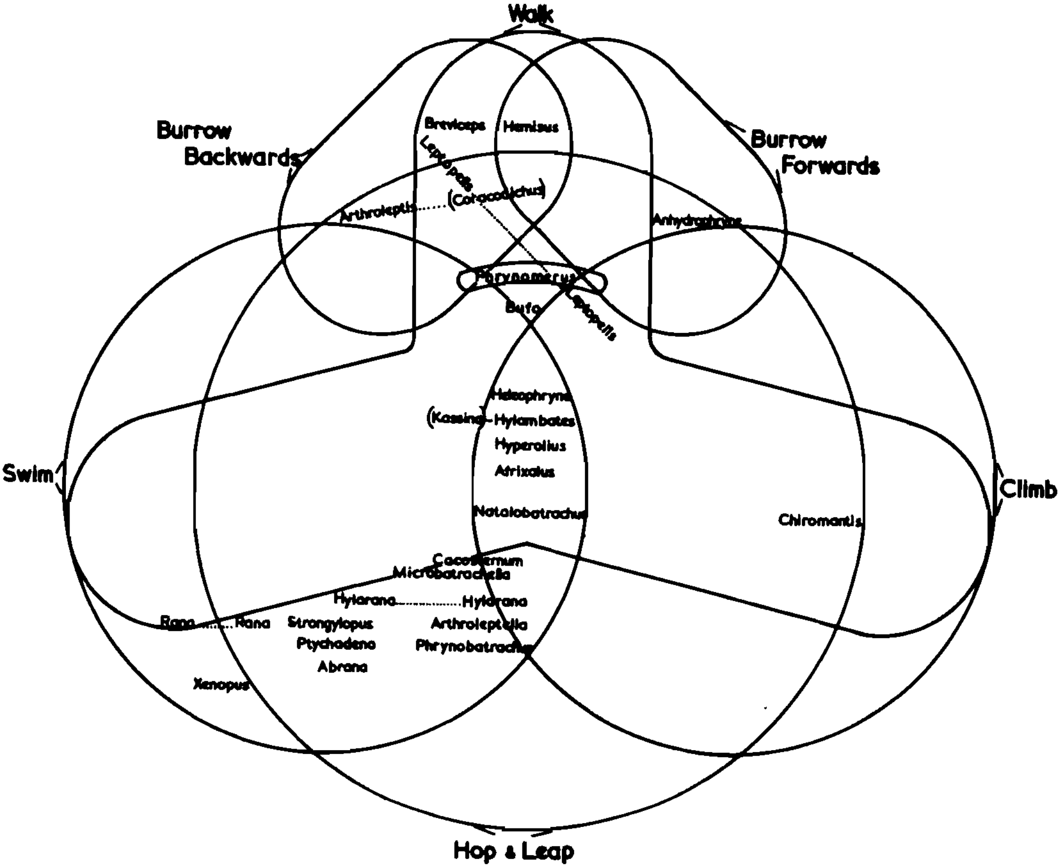

FIGURE 1

Locomotory combinations in the genera of southern African *Anura*. Note that *Phrynomerus* does not hop. This genus also walks backwards very efficiently. Tendencies to use a particular mode of locomotion are represented by overlapping the name of the genus into the appropriate area. Thus *Cacosternum* and *Microbatrachella* tend to walk and climb, but are basically hoppers and swimmers.

"The amphibian food supply, which consists of whatever insects of the right size happen to be available (see Inger and Marx 1961), has also not suffered at the hands of man." (Poynton 1964a, p. 208.) Inger and Marx should be referred to in the original in this regard as the above is not the only interpretation of their findings possible, since they record a considerable variety of animals, other than insects, as anuran food.

PREDATOR AVOIDANCE

Predator avoidance also varies with the habitat of the anuran concerned and with its mode of locomotion. Thus the grassy-verge and rocky-stream anurans typically escape predators by

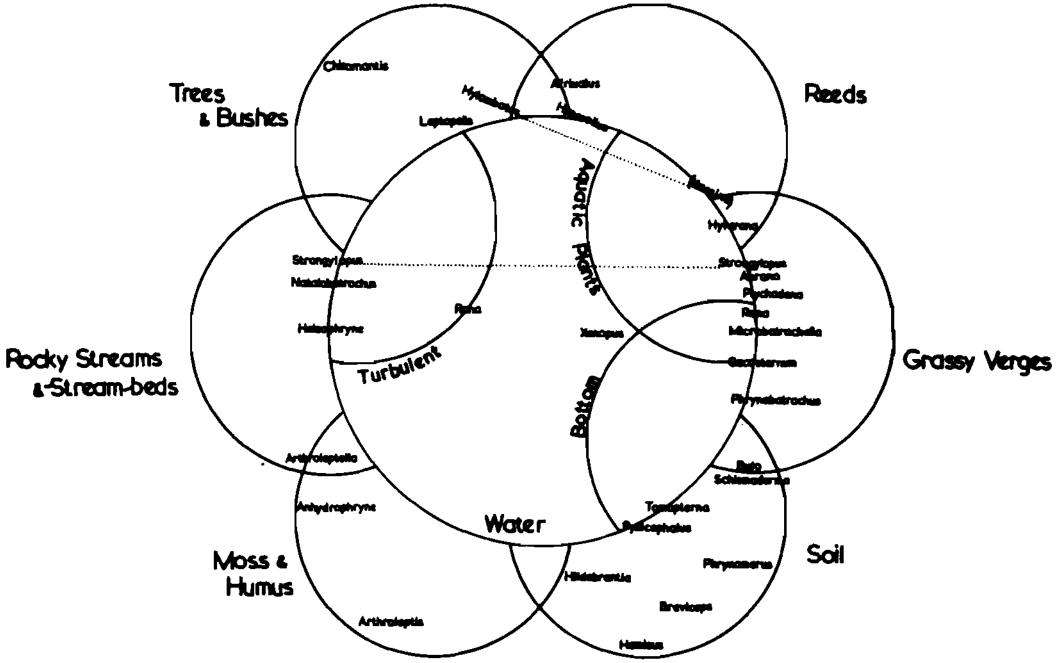

FIGURE 2
The habitats and microhabitats of southern African anurans.

leaping into water and their sliminess makes them difficult to hold if caught. Leaf-frogs rely on camouflage, concealment in leaf axils, being relatively inaccessible on high branches, smooth broad leaves or slender reeds, and on their ability to leap about accurately in the vegetation. The secretion of poison is well-developed among ground-dwellers such as *Phrynomerus*, *Breviceps*, *Bufo* and *Schismaderma* (and *Hemisus?*), *Phrynomerus* showing marked aposematic colouration. These anurans, including *Hemisus*, are crepuscular or nocturnal in habit and have in common the tendency to inflate themselves when captured or threatened, this being particularly marked in the burrowers *Breviceps* and *Hemisus* which are in any case plump. (Laurent 1964, p. 458, comments on the plumpness and inflation of burrowers.)

OVIPOSITIONAL SITES

Figure 3, when compared with Figure 2, shows that ovipositional sites tend to separate the genera with similar modes of locomotion and similar microhabitats. This may be seen, for instance, in the ovipositional sites of the group *Strongylopus*, *Ptychadena*, *Abrana*, *Rana*, *Microbatrachella*, *Cacosternum* and *Phrynobatrachus* (the swimming, leaping group) – *Ptychadena* (and *Abrana?*) and *Phrynobatrachus* oviposit at the surface of water, *Rana* at

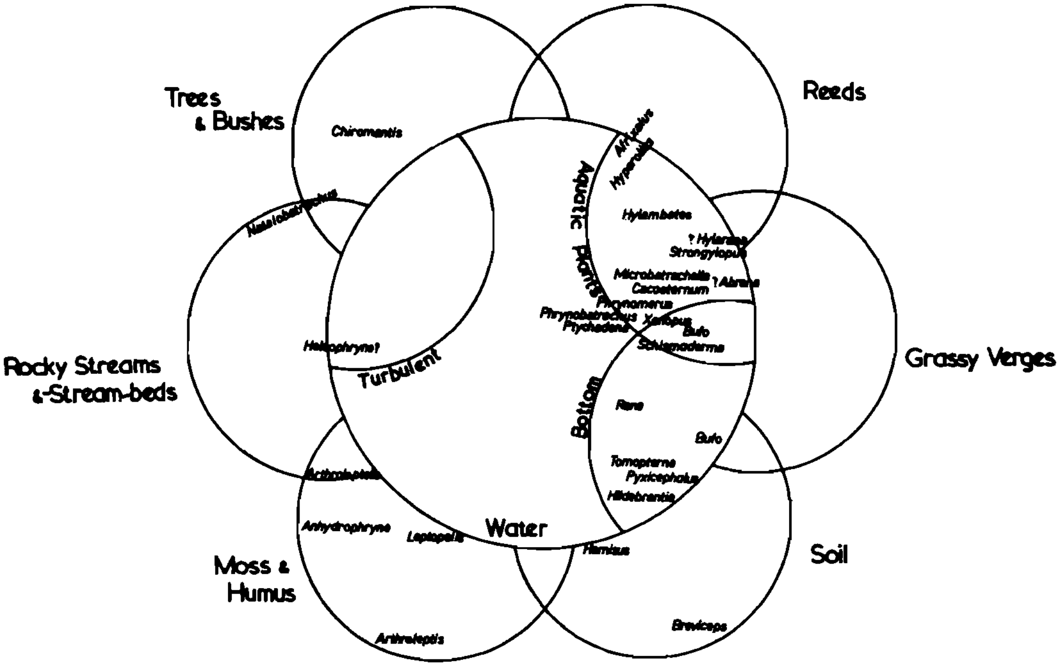

FIGURE 3A
The ovipositional sites of southern African anurans.

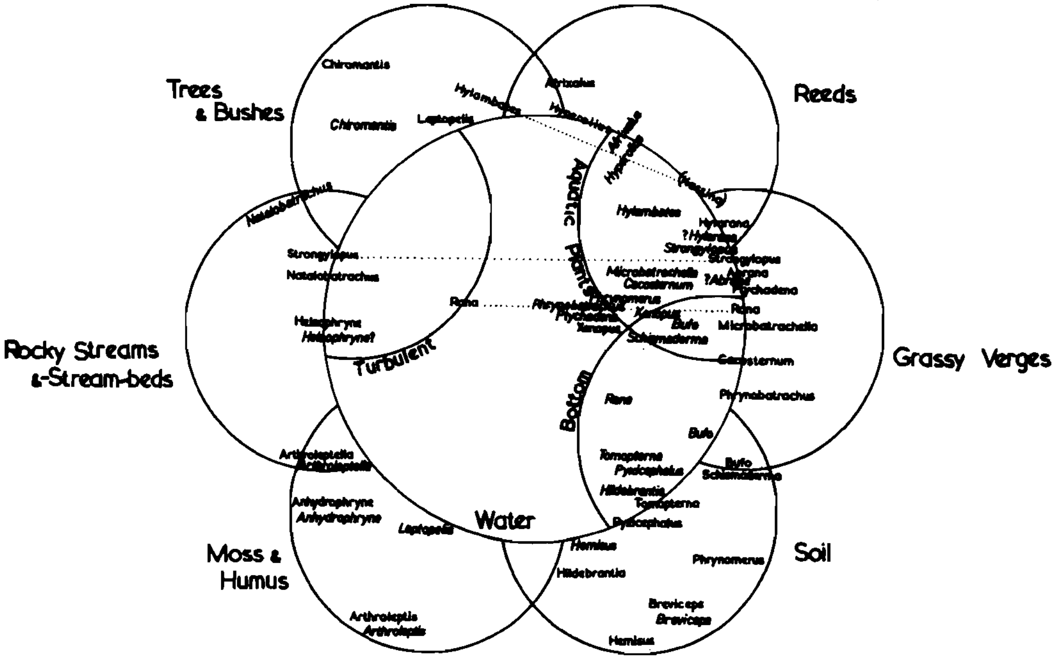

FIGURE 3B
Figure 3a superimposed on Figure 2 to allow comparison.

the bottom, *Microbatrachella* and *Cacosternum* attached to submerged vegetation and *Strongylopus* at the water's edge (or attached to vegetation in swift streams).

MICROHABITATS AND ECOLOGICAL ISOLATION

Together the microhabitats occupied by the adult anurans and their ovipositional sites determine, for each genus, a rather definite habitat which appears to be closely linked to physiography, season- and type of rainfall (e.g. summer storms), soil type and vegetation. Thus *Phrynobatrachus* does not appear to occur on the grassless verges of the Cape Macchia, but only on the grassy verges in the summer rainfall areas. *Ptychadena* is apparently similar in its requirements. *Heleophryne* appears to be confined to clear, fast-flowing, shallow, fairly cool streams typically with stones about 10–20 cms in diameter on the stream floor; vegetation type is not important in this case. It may be noted that Schiøtz (1967) finds West African tree-frogs (Rhacophoridae) to show preferences for particular types of vegetation, and Laurent (1964) has analysed the anuran habitats of an African highland area. A full analysis of all the genera – and the species, for vegetation preferences particularly appear to vary with the species – would not be appropriate in the present paper. One example at subspecific level will illustrate the sort of distributional phenomenon observed for which an ecological explanation should be sought. The distributions of four subspecies of *Bufo vertebralis* in South-West Africa are illustrated on p. 272 of Poynton (1964a), from which it may be seen that there is one subspecies to the South-East of the Waterberg range (which is the western limit for other anurans as well), one to the North-West of this range, one on the highlands South-West of this range, and one South-East of these highlands. Unfortunately collecting is mainly concentrated near the road northwards from Reheboth (a phenomenon observed in relation to other anurans and other national roads, e.g. the Umtali-Beira road) and the habitats cannot at present be clearly defined.

ASSOCIATION BETWEEN HABITATS AND EXTRA-AQUATIC OVIPOSITION AND DEVELOPMENT

Extra-aquatic oviposition and development, and the origin of the cleidoic "egg", has been linked with avoidance of various hazards, oxygen lack in swamps in conditions such as those studied by Carter and Beadle (1930), desiccation (Roner 1957), predation (Tihen 1960; Lutz 1948), difficulty in swift streams of ensuring fertilisation and danger of embryos being washed away (Goin and Goin 1962). Regarding southern African *Anura*, Poynton writes as follows: "The various specializations in oviposition shown by the savanna species give no indication of being adaptations to escape desiccation, since in almost every case the eggs become more exposed to aerial conditions. Clearly these specializations are a response to predation, the trend being to remove the eggs and as much of the larval stage as possible from the dangers of pond life. This trend is probably reinforced by the low oxygen tension in tropical swamps (Carter 1960), a factor which will be particularly important in the immobile egg stage. But as the amphibian egg is poorly protected, an exposure to the elements evidently cannot be tolerated for a long enough time to allow the entire pre-metamorphic stage to be passed out of water in open savanna conditions. Additional protective devices shown by *Afrixalus*, *Hyperolius nasutus* and *Hemisus* could conceivably in time overcome this difficulty, but in general the attainment of a completely protected pre-metamorphic stage is a near-impossibility in the open savannas. Forest conditions, however, automatically offer all the protection that is needed. The eggs can be laid out of water in humid and sheltered situations, and development can proceed to the adult stage away from water. There is therefore a close correlation between the completely terrestrial life cycle and the sylvicolous habit " (Poynton 1964a, p. 210.) Goin and Goin (1962) refer to southern African examples emphasising the correlation, as elsewhere, between montane conditions and terrestrial development. Their conclusions have been criticised by Poynton 1964b, p. 131: "But this correlation appears to be an incidental one. The amphibians referred to, all thrive in gently sloping areas provided that there is a heavy covering of vegetation, and there is no reason to suppose that their terrestrial habits could not have been evolved in such protected areas chiefly as a response to larval predation. The purely incidental correlation between terrestrial breeding habits and the montane environment shown in southern Africa is probably typical of the situation in all fundamentally savanna areas." On the basis of distributional data in the above quotation the suggestion that "this correlation appears to be an incidental one" becomes a firm conclusion: "The purely incidental correlation . . .". There are thus two firm conclusions which have been expressed on specialisations in the breeding of southern African *Anura*, viz. that the correlation between terrestrial breeding and montane conditions is "purely incidental" and "Clearly these specializations are a response to predation".

The arguments on predation are expressed as follows: "The attempt to make the best of two worlds by having an aquatic larval stage and a terrestrial adult stage has the disadvantage of exposing the individual to two successive sets of predators. Furthermore, the individual is particularly exposed to vagaries in the rainfall and other upsets in the physical environment. The tadpole stage appears to be normally passed amid an abundance of food, but a rather clumsy method of locomotion renders a tadpole particularly vulnerable to predation, and the eggs possess little inherent protection. Also, both egg and tadpole are unable to defend themselves against desiccation. The trend has therefore developed in a number of different amphibians groups to remove the eggs away from at least normal predation, and to reduce the length of the free larval stage to a minimum, or even to zero. Possibly the most primitive method of keeping the eggs out of harm's way is that adopted by *Ptychadena* and *Phrynobatrachus*. In these two genera the eggs float on the surface of the water, thereby avoiding much of the scavenging, which is concentrated at the water's bottom. The practice amongst many amphibians of attaching their eggs to submerged vegetation has probably been selected for the same advantage." (Poynton 1964a, pp. 208–209.)

In contrast to the above comments on floating eggs and those attached to submerged vegetation, it can be pointed out that the albumen (gelatinous covering) of anuran eggs apparently offers good protection against predation (and a certain amount of protection against desiccation). As far as predation is concerned observations on *Bufo bufo* ovipositing in permanent forest pools at Lenglerne, near Göttingen, Germany, during 1965, showed that potential predators, such as dragon-fly and may-fly nymphs, become entangled in the albumen. Oviposition at the water's surface or on submerged objects away from the bottom removes the embryos from the lower oxygen concentrations which may occur at the bottom of ponds (where decay is at a maximum) and places the embryos at a level where development may proceed more rapidly due to higher temperatures. In this connection the findings of Savage (1950; 1961, p. 16) on the function of the albumen and Guyétant (1966) on oviposition of *Rana temporaria* under various conditions are relevant: "Dans certaines conditions (groupement de pontes, bonne exposition aux rayons solaires) la gelée permet un échauffement supérieur à celui de l'eau ambiante; il s'en suit que la durée du développement embryonnaire est légèrement écourtée pour les oeufs de la surface." (Guyétant 1966, p. 18.) Concerning the Alaskan wood frog Herreid and Kinney (1967) write as follows: "The egg mass absorbs and retains radiant energy and has a higher temperature than the surrounding water. The temperature increase speeds the rate of development. The mass is laid on stalks of vegetation a few centimetres under water. In this position they are less subject to the freezing and heat of surface waters. It is likely that grouped egg masses characteristic of the wood frog also modify temperature extremes." (1967, p. 589.)

OVIPOSITION IN RIVERS

Oviposition in rivers in southern Africa is uncommon because of the frequent changes in level and hence the danger for the eggs, embryos or tadpoles of being washed away. Where breeding does occur in rivers it is often in small streams, at the verges, in back-waters, and also not infrequently during the season when the river is low. Thus *Rana fuscigula* breeds in summer in the Western Cape and *Strongylopus fasciatus* tadpoles metamorphose before the spring in the summer-rainfall areas.

OVIPOSITION IN TEMPORARY POOLS AND PREDATION

Temporary pools are very frequently used by anurans as breeding sites although such pools frequently dry up partially or completely before development of tadpoles is complete. Besides being much more common than permanent pools, temporary pools may offer the advantage for anurans that established populations of animals which might prey on tadpoles, such as fish, adult *Xenopus*, turtles, resident water-birds, leeches and large water-bugs, are absent. Predation of advanced tadpoles is much more frequently seen than predation of young tadpoles and this might not be an observational artefact. Certainly a large proportion of embryos become tadpoles, while predation can be seen to reduce the number of these which reach metamorphosis in a mature pool. The preference of anurans for temporary pools might thus be dictated not only by their greater availability, but also by the advantage conferred on anurans by their fast development which enables them to grow faster, at least in the early stages, than such predators as dragon-fly nymphs and various water-bugs and so escape more or less completely predation by these predators in pools where development of anurans and predators commences simultaneously. The habit of some water-bugs (e.g. of the families

Nepidae and Belostomatidae) and water-beetles of flying from pools apparently perfectly suitable to them to newly-formed pools may have evolved in response to this situation.

OVIPOSITION IN TEMPORARY POOLS AND COMPETITION

The frequency with which temporary pools dry up and broods of tadpoles are desiccated may account, at least in part, for an interesting phenomenon, the secretion of growth-inhibiting substances by advanced tadpoles (Hodler 1958; Rose 1959; Rose and Rose 1961; West 1960) which may totally inhibit development of younger tadpoles. If an earlier brood is still surviving in a temporary pool when rains again induce oviposition, the new brood will be prevented from competing with the older one, but the new brood could develop if the earlier brood had failed. The use of temporary pools naturally also limits competition to animals, of various groups, which invade newly-formed pools or develop in them.

OVIPOSITION OUT OF WATER WITH DEVELOPMENT CONTINUING IN WATER

Where oviposition occurs outside water and the embryos survive until further rain falls, if this is not too long delayed, and the embryos are released into the water (e.g. *Chiromantis* which makes a foam nest overhanging water, *Strongylopus grayi* and *S. fasciatus* which oviposit next to water), oviposition may take place following rain which forms temporary pools, thus indicating to the anurans where to oviposit, and release of the embryos into the pools will usually occur when the pools have been replenished by further rains or re-established if they had dried up. (Wetting and enzyme action both play parts in releasing the embryos; in some cases one factor may predominate. The albumen of the foam nest of *Leptodactylus* from S. America limits growth according to Pisanó, 1965 and 1966, and Pisanó and Barbieri 1965). Besides shortening the time required in the pools (because part of the development has already taken place) synchronisation of release of tadpoles with the formation or replenishment of pools has the advantage that the tadpoles are immediately able to seek out the most favourable sites in the event of the pools beginning to dry again. Release of tadpoles, i.e. embryos capable of feeding, into pools, even if predators were present, would offer the advantage that non-feeding stages are not exposed to predation. Where oviposition occurs out of water in association with swiftly-running water, e.g. *Natalobatrachus*, the tadpoles released into the water would be better able to cope with the swiftly flowing water than embryos developing in the water would be. It is significant that, in the case of *Natalobatrachus*, and, apparently, *Heleophryne* (judging from the gravid females), the eggs and young tadpoles are large and thus less at the mercy of swiftly flowing water than smaller eggs and tadpoles would be.

DEVELOPMENT OUT OF WATER

Under conditions of good oxygenation water contains less oxygen than an equal volume of air, and in swamps the degree of oxygenation of water may be very low, as Carter and Beadle (1930) have emphasized. Rotting vegetation deprives water of oxygen both by producing reducing substances and by darkening the water and hence reducing photosynthesis which produces oxygen. In water on forest floors rotting vegetation may be expected and photosynthesis would be reduced by the low light intensity. Oxygen-poor water with few green plants, macroscopic or microscopic, will be the only water available in forests except in streams and in pools in glades. In southern Africa, forests strike a student of tadpoles as having few bodies of standing water suitable as breeding sites for anurans. This is partly due to the paucity of level ground. "In South Africa it is exceptional to find smooth and level stretches within the forest; the forest 'glades' and 'aisles' of palaeartic regions are terms almost unknown in South Africa, where the forests are usually situated on the rugged slopes of mountains and in ravines and kloofs;" (Lawrence 1953, p. 25). Dr. R. F. Lawrence and Dr. O. M. Hilliard both confirm the rarity of pools in the forests they have studied. Correlated with the paucity of standing water is the infrequency with which dragon-flies, some nymphs of which are tadpole predators, are seen in forests, except near streams. The forest-floor has an abundant cryptic fauna, but cursorial or low-flying animals suitable as food for such an anuran as *Bufo* are rarely seen. The specialised anuran fauna of southern African forests is thus not attributable primarily to unique opportunities offered by a humid environment, but rather to the necessity of breeding in streams or out of water because of the scarcity of standing water and the lack of oxygen and plant food in that which is available.

LEVELS OF ADAPTATION TO EXTRA-AQUATIC DEVELOPMENT

Genera with distinctly extra-aquatic development

Anhydrophryne is the only genus apparently confined to forest-floors, and its development is entirely extra-aquatic. Burrowing forwards has apparently been developed by this genus to aid in the production of a shallow burrow for extra-aquatic development. *Arthroleptis* is the genus in which the extra-aquatic development is furthest evolved, the tail being much reduced and the fore-limbs developing externally. This genus is not confined to forest-floors according to Loveridge (1957, p. 352, footnote 273) and Laurent (1964, p. 459), who separates the less forest-bound species, *A. stenodactylus*, as the genus *Coracodichus*, but Poynton (1964a, p. 159) states: "There indeed appear to be no noticeable differences between the ecology of *wahlbergi* and *stenodactylus*". The forest-dwelling *Bufo anotis* may be a terrestrial breeder to judge from the small number of fairly large eggs in gravid females (Poynton 1964a, p. 68, notes 85 eggs 2·4 mm in diameter).

GENERA WITH ILL-DEVELOPED EXTRA-AQUATIC DEVELOPMENT

Arthroleptella is a recent recruit to the ranks of extra-aquatic breeders to judge by the persistence of lateral line organs and rostral cartilages although the cornified mouthparts (rostrodonts) which these cartilages normally support are absent (De Villiers 1929, pp. 488 and 496). *Arthroleptella* develops on damp moss in association with swiftly-flowing streams. *Natalobatrachus* shows a stage in the evolution of such a mode of development, the tadpoles dropping into water and developing further. *Heleophryne* probably has similar early development to *Natalobatrachus*, but is not confined to forests, but rather to torrents.

BURROWING AND EXTRA-AQUATIC DEVELOPMENT

The burrowing genera *Breviceps* and *Hemisus* show extra-aquatic oviposition, development in *Breviceps* continuing to metamorphosis in the burrow, while *Hemisus* continues its development in water, apparently when the burrow is flooded. (Wager describes the tadpoles as wriggling down to water along a tunnel made by the female, but the animals are found at least sometimes on level ground where this is scarcely possible and Wager does not state the circumstances under which he made his observations.) (See Wager 1929, pp. 127–135; Loveridge 1933, p. 388; Loveridge 1936, p. 427.) It would seem that the burrowing habit tends to produce extra-aquatic oviposition, since the burrows are humid and hence provide a suitable microenvironment for development. Wager (1965, p. 120) quotes observations of burrows of *Breviceps* containing a frothy mass in which the tadpoles wriggled. This has been confirmed by Dr. J. H. Swanepoel (personal communication, D.Sc. thesis in the press). Morphologically *Breviceps* tadpoles are not nearly as far along the terrestrial path as *Arthroleptis*, and it is not surprising to find confirmation of the essentially tadpole nature of the developing embryos.

BURROWING TREE-FROGS AND EXTRA-AQUATIC DEVELOPMENT

Early development of *Chiromantis xerampelina* and some other species takes place in foam nests on branches overhanging pools; *Chiromantis petersi kelleri* of North Africa oviposits on stones or grassy banks close to water (Cherchi 1958), the tadpoles falling into water as in *Chiromantis xerampelina* in southern Africa. *Chiromantis kachowskii* in Somaliland is described as having a large fossorial metatarsal tubercle (Parker 1932, p. 366), and it is possible that development will be found to occur in burrows, or at least to begin in them. *Leptopelis natalensis* and *L. karissimbensis* ovipost on humus near water and development continues in water. It would be interesting to learn whether *Leptopelis bocagei*, which burrows, has developed the habit of ovipositing in burrows and whether the tadpoles are further developed before entering water than in the non-burrowing species.

INCIPIENT EXTRA-AQUATIC DEVELOPMENT

Oviposition at the margins of pools occurs in *Strongylopus grayi* and *S. fasciatus*, in the latter also in vegetation at the margins of streams, while *S. grayi* also deposits strings of eggs (C. Gow, South African Museum, personal communication) and is very variable in its choice of site and the degree of cohesion of the eggs. Since *S. grayi*, in particular, may oviposit in shady sites and on humus, it is possible that oxygen-lack will act as a factor to prolong extra-aquatic development beyond the early stages. It is interesting that *S. hymenopus* attaches the eggs to vegetation in swiftly-flowing streams. Oviposition on vegetation above, as well as below, water is seen in species of *Hyperolius* and *Afrixalus*. It should be noted that transpiration may maintain a humid microenvironment for the early stages of development of these species, just as transpiration probably accounts for the ability of the adults of these genera to spend hours in direct sunlight. (The animals have been observed to desiccate when removed from vegetation.)

Oviposition at the surface of pools, such as occurs in *Ptychadena* and *Phrynobatrachus*, appears to be associated with summer rainfall and grassy pools and apparently serves to bring the embryos to the feeding stage very rapidly by virtue of the higher temperatures and oxygen concentrations at the surface. There is no immediately apparent advantage to be derived from prolongation of the part of the development occurring at the surface.

ANURANS AS SUCCESSFUL TERRESTRIAL ANIMALS

The conclusion to be drawn from the occurrence of various degrees of extra-aquatic adaptation in the development of anurans is not that these modes of development are incomplete advances towards fully terrestrial life (as suggested by Lutz 1948), but rather that they are necessary compromises to meet conditions where the typically amphibian mode of development is not as highly efficient as it is in the conditions experienced by the majority of amphibians. The assumption that the cleidoic egg is better adapted than the amphibian egg to terrestrial conditions is not entirely justified. Reptilian eggs, particularly those with horny shells, are notoriously difficult to culture, tending either to desiccate or to develop fungus when the humidity is too low or too high respectively. Comparative studies of the limits of tolerance of developing snake or lizard eggs and those of such anurans as *Arthroleptis* and *Breviceps* would be interesting. As far as the adult animals are concerned, Mosaurer (1936) and subsequent authors have pointed out that heat-tolerance of Reptilia appears to have been overestimated, while Brattstrom (1963, p. 251) remarks: "In terrestrial amphibians water loss is an almost unavoidable concomitant of their dermal respiration, yet only one group of workers (Kirk and Hogben 1946) has suggested the possibility of water loss in amphibians as being an aid to thermo-regulation." (See also Cloudsley-Thompson 1967.) Estimates for any area of the numbers or biomasses of terrestrial reptiles and anurans seldom entering or not entering water would be interesting. In southern Africa it would be surprising in any area other than the Namib desert to find reptiles markedly more successful on these criteria than anurans.

The following conclusions and suggestions regarding southern African *Anura* are offered as a basis for further study.

1. Factors affecting anuran ecology do so by their action on the efficiency of locomotion, predator avoidance, feeding and breeding.
2. The genera of southern African anurans are characterised primarily by particular combinations of locomotory modes.
3. The genera with similar locomotory modes often show differences in their modes and sites of oviposition.

4. Modes of predator avoidance differ primarily according to the locomotory mode.
5. Feeding is not indiscriminate; feeding techniques are related to the modes of locomotion and to the microhabitat.
6. Oviposition in temporary pools reduces predation and competition since resident populations of predators and competitors are generally absent.
7. Rapid development in temporary pools reduces predation and competition.
8. Rapid development in temporary pools is aided by oviposition at the surface or on submerged vegetation, and by oviposition in clusters.
9. The egg albumen functions in speeding development by its effect on the temperature regime of the eggs and by providing access for oxygen to massed eggs.
10. Predation of early stages is virtually eliminated by the egg albumen.
11. Removal of early stages in development from water makes it possible for the tadpoles entering water actively to select the most favourable sites in the event of partial drying up of a pool commencing, and also makes feeding immediately on entry to a pool possible.
12. Production of growth-inhibitory substances by advanced tadpoles could be advantageous as a device for limiting competition from a later brood, in addition to its function in placing a premium on fast development. If younger tadpoles can perceive the substance/s involved they may respond by moving away from the most favourable sites because these are occupied by older tadpoles and thus exploration of other microhabitats may result.
13. Oviposition and partial or complete development out of water tend to evolve in burrowing anurans, the burrows being used as brood-chambers.
14. Development out of water in turn tends to induce burrowing habits involved in the production of brood-chambers.
15. Swiftly-flowing water induces oviposition out of water and the production of fewer, larger embryos.
16. Swiftly-flowing water may induce full development out of water.
17. Of the explanations hitherto offered for terrestrial breeding in *Anura* those of Goin and Goin (response to sloping ground), and of Romer (response to desiccation) are the most acceptable.
18. Development out of standing water is induced by the absence of suitable standing water (in forests in southern Africa).
19. Terrestrial breeding of forest-dwelling anurans enables them to utilise a habitat that is not available to aquatic-breeding anurans, because the latter require standing water.
20. Anurans living outside of forests are sometimes terrestrial breeders, but they have to meet competition from aquatic-breeders. Their extra-aquatic adaptation does not, therefore, have as much survival value in savanna areas as in forests.
21. Terrestrial development adaptations are greatest in *Arthroleptis*, followed by *Anhydrophryne*, *Breviceps* and *Arthroleptella* in that order.
22. The "typical" aquatic anuran mode of development is highly successful, making possible rapid increase in size of a large number of offspring and utilising sources of food not available to other terrestrial vertebrates (nor to fish in the case of temporary

pools) by reason of the initially herbivorous, and often subsequently saprozoic, feeding habit.

23. A comparison of the humidity tolerances of terrestrial embryos of anurans such as *Breviceps* and of reptiles such as lizards and snakes would be of great interest in attempting to account for the apparent success of anurans as compared with living reptiles.

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