

NOTES ON THE BIOLOGY OF *BREVICEPS* (ANURA: MICROHYLIDAE)

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ABSTRACT

Breviceps verrucosus and *B. adpersus* are taken to represent the two ends of the morphological and ecological spectrum of this genus of burrowing frogs. Both occur in the Durban area, but *verrucosus* is typically limited to forest and *adpersus* to savanna. *B. adpersus* appears to have adapted itself to savanna-living by digging deeper burrows than *verrucosus* and by gearing its time of seasonal emergence to the swarming of termites which form its main type of food.

INTRODUCTION

Breviceps Merrem is a genus of burrowing frogs confined to the southern half of Africa. Large yolky eggs are laid underground, and in the species so far investigated, the male during mating becomes glued by a very sticky secretion to the sacral region of the female before an egg chamber is dug. The tadpole stage is passed in the underground chamber.

Some thirteen species of *Breviceps* can be recognized, and they may conveniently be arranged in a sequence according to the degree of digital reduction and a shift of habitat from forest to savanna (Poynton 1964). *B. verrucosus* Rapp can be placed at one end of this sequence, *B. adpersus* Peters at the other. This paper deals with field studies conducted on these two species.

B. verrucosus appears to exhibit the more primitive features of the genus. It seems that *Breviceps* can be derived from *Probreviceps* Parker, currently known from forests in Tanzania and eastern Rhodesia. The southernmost member of this genus, *P. rhodesianus* Poynton & Broadley, has shorter limbs than the Tanzanian species, suggesting a southward tendency towards limb shortening that is evidently associated with a burrowing habit – a tendency developed still further in *Breviceps*. *P. rhodesianus* does burrow: a female was found on a clutch of eggs in a chamber hollowed out in humus beneath a 7-cm layer of leaves (Poynton & Broadley 1967). But the tendency to burrow becomes much more marked in *Breviceps*, and is shown morphologically in the more strongly developed digging metatarsal tubercles and the shortening of the inner and outer toes. *B. verrucosus*, however, is the longest-toed member of the genus, and, like *P. rhodesianus*, is sylvicolous. It has been collected in forested areas of the eastern

plateau slopes from the southern Transvaal to the eastern Cape, which (assuming that *Breviceps* evolved from a *Probreviceps* stock) is where one might expect a primitive member of the genus to occur.

B. adspersus is one of the shortest-toed members of the genus, and the digging metatarsal tubercle is much more sharply ridged than in *verrucosus* (Figure 1). It has a wide distribution from the Kalahari across to Moçambique and down into Natal, and tends to avoid true forest, although occasionally it can be heard calling in scrub, for example in *Brachylaena* coastal dune forest. It shows no avoidance of completely open situations, and has accommodated itself very successfully to suburban gardening: on wet nights early in the breeding season (notably October), both sexes may be found on lawns and streets of Durban suburbs. *B. verrucosus* has not been recorded in such open situations. Its distribution is very patchy in the Durban–Pietermaritzburg area, being largely confined to remaining clumps of natural forest, although it is sometimes relatively common in established shrubberies, plantations and even fields of densely matted grass where forest previously stood.

Despite the habitats of these two species being accessible even to the town-bound naturalist, their ecology is still very poorly known. This is particularly true of *verrucosus*, which calls only for short periods during summer and is very rarely seen above ground. There is no difficulty in plotting the distribution of either species, because on wet summer nights their presence is loudly advertised by a distinctive call for each species. But in other respects the frogs are extremely secretive, making ecological work heavily dependent on chance observation.

This paper is based on observations made in the Durban–Pinetown area. There are indications that times of emergence and habitat selection are not uniform throughout the range of either species, and therefore we would advise against making broad generalizations on the material offered here. We hope, however, that this paper will encourage more penetrating and wide-ranging studies on this most interesting but poorly known element of the southern African

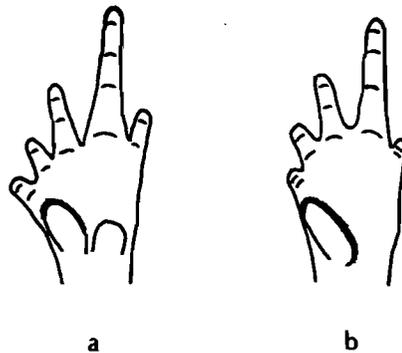


FIGURE 1
Plantar surface of left foot of *Breviceps verrucosus* (a) and *B. adspersus* (b), showing shape of metatarsal tubercles and relative lengths of digits and phalanges.

fauna. These two species represent the morphological and ecological ends of the spectrum of the genus, and therefore invite a very broad biological approach. The apparent invasion of savanna by *Breviceps* can indeed be viewed as part of the general shift of southern and eastern African faunal elements into the savanna as savanna replaced forest during the Tertiary.

BURROWS

Burrows of *verrucosus* have been examined both in true forest and in dense grassland during the breeding season. No uniform layout of burrows has yet been detected, but a typical feature of them is that they are shallow, running only 2–4 cm below the surface of the soil. Their length varies from about twice the length of the individual (about 5 cm) to 11 cm in the case of the longest tunnel so far examined. One or two side branches may be present, with or without openings at the surface. So far, only one male has been found to occupy a burrow in the breeding season. A calling male has been found in the mouth of a surface burrow of the golden mole *Amblysomus hottentotus* (Smith) in forest, and as these burrows are very common in Durban forests, their use by *verrucosus* may be frequent.

B. adspersus burrows can be considerably longer than those of *verrucosus*, and they tend to go deeply into the soil. Two burrows we examined during the breeding season had a double entrance at the surface, placed 23 cm and 28 cm apart respectively, the average length of each fork being 21 cm, and the total length of the burrow being 51 and 56 cm respectively. A female was found in one, and a male in the other, both about 30 cm below ground level. Two other long burrows (51 and 60 cm) had a side branch not reaching the surface. All these burrows differed notably from *verrucosus* burrows in that they did not run horizontally below the surface of the ground, but at an angle of about 45° from the horizontal. Shorter burrows also showed this tendency. The shortest burrows, about twice the length of the individual, appeared to be 'stop-over' shelters and were not necessarily returned to after a night's excursion.

In the breeding season, males have not been found sharing burrows, and in fact a struggle develops if a second male enters an occupied burrow, resulting in one or the other being evicted. The situation is evidently different during the time of hibernation, since there have been occasional reports of several hibernating individuals being found together in a burrow (personal communications; Burton & Burton 1968).

We are not able to add anything to the little that is known about egg chambers. These have not yet been discovered in *verrucosus* burrows, but, judging from the very similar *B. sylvestris* FitzSimons, they are probably shallow. Wager (1965) quotes a correspondent who found *sylvestris* egg clusters in the Woodbush forest of the eastern Transvaal: they were found 'usually at the base of a rock, or the roots of some sturdy plant' (page 120). As with *Probreviceps rhodesianus*, the female was reported to perch on the egg mass, at least if the chamber was disturbed. *sianus*, the female was reported to perch on the egg mass, at least if the chamber was disturbed. Egg chambers of *adspersus* in the Durban area have been reported by Wager (1965) at a depth of 30–45 cm below ground level.

MATING BEHAVIOUR

As breeding does not take place in water, *Breviceps* males do not form breeding aggregations. Calling nevertheless tends to be of a chorus type, the calling of one individual (or a simulated call) causing a burst of calling all round. No work has yet been done to determine whether the calling is more important in attracting females or spacing males, but it is noticeable that burrows tend to be regularly spaced in uniform surroundings, their closeness being dependent on population density (the minimum so far encountered being about 15 cm between burrows of *adspersus* in a cultivated garden).

In the Durban area, *verrucosus* males begin calling earlier in the season than *adspersus*, namely towards the end of August as soon as the first few millimetres of soil have been wetted. *B. adspersus* usually starts calling late in September, or even October in a dry season, its activity appearing to coincide (as Wager 1965 has noted) with the swarming of termites, which seem to be the most important prey of this savanna species. This will be discussed further in the next section. Calling in both species ceases during January.

In *verrucosus*, males have been heard to call only when rain or drizzle is falling, except at the beginning of the breeding season, when bursts of calling can also be heard between showers on rainy nights. Greater readiness to call at the beginning of the season is a common feature of anurans (Poynton 1964; Balinsky 1969). In *adspersus*, however, calling may continue for several nights after a heavy downpour even though no further rain falls. Daytime calling occurs in both species in wet weather.

Males of both species call from burrows or while out in the open. Somewhat surprisingly, in dense grassland during drizzle in the early part of the breeding season, male *verrucosus* have been found clambering to a height of some 30 cm in dense tussocks from where they call.* In forests, males have been seen moving about actively on the forest floor during rainy weather, pausing at intervals to call. A tendency to call from elevated positions in forest has so far not been observed, but this might be due to the lack of opportunity to clamber (such as is provided by grass tussocks), for in true forest in the sandy Durban area the forest floor is largely an expanse of leaf and twig litter. It may be noted that the ecologically similar *Arthroleptis wahlbergi* Smith shows a tendency to call from elevated positions; and being a much smaller and more agile frog, it has many more opportunities for doing this in forest.

In *adspersus*, whose behaviour has been better studied, calling and emergence from burrows in the evening follows a sequence: the frogs call while invisible in the burrows, then call while visible at the burrow mouth, and then call out of the burrows in the open, usually while moving about actively. Clambering behaviour has not been observed in *adspersus*. Conditions associated with full emergence from burrows, chorus calling and mating are low barometric pressure (about 1 010 mbar), relatively high temperature (at least 20°C), and high relative humidity (at least 85 per cent). Such conditions are normally accompanied by drizzle or rain. Our preliminary impression is that barometric pressure is the most important factor determining whether or not frogs emerged from their burrows, and the general role of this factor in the behaviour of both species seems to deserve further study.

* J. Visser reported at this symposium the same behaviour in *B. montanus* of the south-western Cape.

As *adpersus* is not normally found out of burrows during daylight, and as calling tends to become more sporadic after about 10h00 even on wet days, it might be thought that light is an important factor governing emergence and calling. Yet in well-lit gardens and streets, emergence, calling and mating seem to follow the same pattern as anywhere else, and shining a torch on males of either species does not markedly inhibit calling. At least at a relatively weak intensity, then, light does not appear to have a very definite influence on behaviour.

Once male and female *adpersus* have emerged from their burrows, they move about freely. Males encountering other males show apparent aggressive behaviour in that one male will push against the other with its vocal sac while calling. But males will also attempt to mount each other. A moving female will be followed by males, and mounting is initiated by a pelvic grip.

So far, it has not been shown that a recently-coupled pair return to a previously dug burrow. Two couplings have been observed in this study. The first was disturbed by handling, and the pair buried itself as soon as it was released. Wager (1965) also reports an immediate attempt to burrow, noting that such disturbed pairs tend to uncouple themselves without laying eggs. The second pair was observed from the beginning of amplexus. This pair covered a distance of about 78 cm in no constant direction, and then became stationary for about half an hour, after which it was lost from sight while other individuals were being studied. It is possible that burrowing is delayed after coupling, allowing time for the male to become 'glued' to the female before digging commences.

FEEDING

Stomachs of 12 *verrucosus* in the Natal Museum collection contained a wide variety of arthropods, mostly amphipods, isopods, juvenile myriapods, various endopterygote caterpillars, beetles and worker ants. Ninety-six specimens of *adpersus* in the Durban and Natal Museums were examined, and a count of recognizable individual animals in the stomach contents showed the following food composition: alate termites 48 per cent; worker ants 27 per cent; worker and soldier termites 19 per cent. Frogs killed in October contained a higher proportion of alate termites than those killed in November and December: in other words, at the beginning of the season, alate termites tend to be the most common prey, but later in the season the frogs rely more on worker ants and worker termites.

No termites were found in the *verrucosus* stomachs, which is possibly not surprising, as termites are not a marked feature of southern African forests: they are not discussed at all in Lawrence's (1953) work on forest cryptozoa. But they are very much a feature of savannas, and it appears that *adpersus* has taken advantage of this source of food to the extent of tending to gear its time of seasonal emergence to the swarming of termites, which in Durban commences about the end of September.

DISCUSSION

It is not yet clear exactly what mechanisms are at work maintaining the habitat differences between *verrucosus* and *adpersus*. Granted that *verrucosus* may occur in dense grassland and

adpersus in scrub, no site has yet been found where the two species occur together. Grass-living *verrucosus* have been studied in Pinetown. The patches of grass where they occur adjoin the remains of riverine forest, and show no sign of recent burning. These patches also support populations of the typically sylvicolous *Arthroleptis wahlbergi*. Adjoining grassland that is regularly burnt has no *verrucosus* or *Arthroleptis*, although *adpersus* is usually present. Presumably both *B. verrucosus* and *A. wahlbergi* are showing a preference for dense cover, perhaps particularly in the early part of the breeding season (August–September) when there is a very marked difference between burnt and unburnt grassland.

Given the tendency to make shallow burrows in *verrucosus*, the survival value of its habitat preference is fairly evident. Shallow burrows and egg chambers would provide little protection against the hazards of a savanna environment, notably desiccation, predation, and trampling by large ungulates. *B. verrucosus* could hardly be expected to maintain populations in anything but densely overgrown forest margins or true forests, where these dangers are minimized. The same is no doubt true of the essentially sylvicolous *Arthroleptis* and *Anhydrophryne* Hewitt, which also have shallow burrows and egg chambers.

By making deeper burrows, *adpersus* is better protected from these dangers. This behavioural tendency, which is reflected in the morphology of the digging hind limb, allows it to live successfully in open country, and so join a savanna association of animals that takes advantage, amongst other things, of the massive swarming of termites.

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