

HABITATS AND DISPERSAL OF SOUTHERN AFRICAN ANURA*

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ABSTRACT

The data required to make it possible to relate dispersal of southern African Anura to the habitats occupied are considered. Habitat must be defined in terms of breeding populations; data on the breeding seasons of the taxon under consideration are needed, with comparative data on possible competitors in the breeding sites. Possible routes of dispersal under present conditions are considered; the distribution of the habitats of some taxa are considered in relation to presumed past conditions. Possible centres of origin and dispersal of genera and species endemic to southern Africa are discussed.

INTRODUCTION

There have been two publications in which distributions of individual southern African anuran taxa were related to parameters, viz. effective temperature (Stuckenberg 1969) and annual rainfall at the 800–801 mm boundary (Van Dijk 1971a). Common to these papers is emphasis on the need to consider the habitats of the individual taxa. The present paper examines this aspect in relation to dispersal.

HABITAT AND LOCALITY RECORDS

Locality records do not necessarily provide a good indication of habitat. The most important limitation is that a locality record, even if repeated, may not reflect the presence of a breeding population, although it may suggest that the locality might serve as a dispersal route, particularly if a suitable habitat for breeding is possible in especially favourable seasons. An example is afforded by *Xenopus*, the adults and even the large tadpoles of which may be found in pools created by the Kuiseb River near the Namib Research Station and further downstream, although the genus is not known to breed so far west in the Namib (Channing 1974), and the source of the specimens is flood-pools of the river further upstream, where breeding does occur. Distinction should be made between habitats, which include breeding sites, and locality records where the taxon is not viable, but from which it may invade new habitats, e.g. farm dams near rivers in arid regions in the case of *Xenopus*.

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ANADROMIC DISPERSAL

The tendency for transport of a species downstream to occur, as has been observed for the tadpoles of *Bufo angusticeps* on the Stellenbosch Flats, suggests that there might be an advantage for the species in having a behavioural mechanism which provides for movement up drainage systems when this is possible. That such a movement towards headwaters occurs is suggested by *Xenopus laevis* and *X. muelleri* populations meeting on a divide in the eastern Transvaal (Miss H. Francis, personal communication).

Such anadromic movements must not be thought of as occurring only via rivers although it might be expected to occur more readily in species in which the non-breeding adults may inhabit rivers, as applies to *Xenopus* spp., or in species breeding in rivers, such as *Rana fuscigula*. Consideration of Figures 3 and 4 (*Bufo* spp. of the *B. regularis* group and *Rana sensu stricto*) indicates invasion of South West Africa from the north-east (*B. garmani* and *B. pusillus*) via the rivers draining into the Okavango swamps and from the south (*Rana fuscigula*) via tributaries of the Orange River, respectively (cf. Figure 8).

BREEDING SEASON AND BREEDING SITES

The nature of the habitats of the various taxa, and the potentials for dispersal at any locality, are best understood when consideration is given to the breeding seasons of the taxa. Thus *Rana fuscigula* has been found breeding in late December and early January in the western Cape and this would suggest that movement upstream at these times of low flow-rate would be relatively easy, except in the upper reaches. Similarly *Xenopus* sp. and *Bufo pardalis* were observed breeding at the same time of the year in rock pools at Betty's Bay (December 1966–January 1967); according to Dr M. E. Malan (personal communication) this is a rare occurrence; presumably good rains in the spring resulted in seepage of fresh water into the pools and good weather reduced influx of salt water. Gradual extension of the range of *B. pardalis* along the coast could have occurred as a result of occasional favourable seasons which permitted use of supratidal rock pools (Figure 3).

The breeding season of a taxon in any area must be considered in relation to those of possible competitors, notably other species of the genus. Thus *Bufo rangeri* breeds from August in Pietermaritzburg, starting before *B. regularis*, while it breeds later than *B. pardalis* in the eastern Cape: 'The first appearance of *pardalis* in August is made by numerous individuals all at once; but *rangeri* does not appear in equally large gatherings at the dams until late in the season – November' (Ranger in Hewitt 1937:87). In studying dispersion it is necessary to map related species, or taxa with similar habitats, on the same map (cf. Figure 3, in which *Bufo rangeri* is shown with other members of the *B. regularis* group). The study of relationships by serological, karyotypic and detailed anatomical methods is a necessity for future work.

HABITATS AND DISJUNCT DISTRIBUTION

Specific habitats are related to disjunct distribution. This is illustrated by *Heleophryne* (Figure 1) and *Arthroleptella* (Figure 7), and less obviously by *Breviceps* (Figure 2) and *Strongylopus* (Figure 5). *Heleophryne* occurs in association with torrents and *Arthroleptella* with steeply sloping terrain, typically forested, where the eggs can develop on moss kept damp by seepage. (In the Cape Peninsula *Arthroleptella* also occurs on the top of the mountains and in areas which are no longer forest). *Strongylopus* shows association with regions of high rainfall (or associated parameters) and in particular with fast-flowing water in the cases of *S. wageri* and *S. hymenopus*. In the cases of *Heleophryne* and *Arthroleptella* the distributions accord with those of 'the montane palaeogenic element in the South African invertebrate fauna' described by Stuckenberg (1962), and indicate their occupation of relict habitats from a more continuous distribution during the last hypothermal, centred in the south of the continent. In the case of *Heleophryne* Gondwana relationships are indicated, the genus being apparently related to the leptodactylids, at present centred in South America and Australia. In the case of *Arthroleptella* and *Strongylopus* the relationships are with ranids from the north, but these genera appear to have had their origin in the south, whether in the western Cape or the eastern highlands. Unlike *Heleophryne* and *Arthroleptella*, *Strongylopus* is less restricted in habitat and is more widespread, having extended beyond the dry Limpopo River barrier, and has occupied an area in Rhodesia around that indicated by Stuckenberg (1962) as being similar to those areas occupied by montane palaeogenic elements south of the Limpopo. Stuckenberg (1969) discusses conditions in the Limpopo valley during the last hypothermal.

Breviceps (Figure 2) appears to have had its origin north of the Limpopo River, probably north of the Zambezi River, as indicated by the present distribution of *Probreviceps* mainly north of the Zambezi. It appears to have spread while essentially sylvicolous, the extra-aquatic mode of development having evolved in response to lack of suitable water for breeding in forests (Van Dijk 1971b). Reduction of forest and inability to compete with anurans with aquatic breeding in the intervening areas has resulted in isolation of the genus in a number of areas, with resulting speciation. Only *B. adspersus* has achieved wide distribution. The Zambezi River appears to be a more or less effective barrier southwards to the *B. poweri* genes.

Dispersal southwards and subsequent isolation in high moisture areas in Rhodesia and south of the Limpopo is indicated in *Ptychadena porosissima* (Van Dijk 1971a).

NORTHWARDS EXTENSION FROM THE SOUTH WESTERN CAPE REGION

Stuckenberg (1962) maps the seemingly anomalous presence of a dipteran (Blepharoceridae) with a torrent-dwelling larva to the north (NNW) of the Cape Fold belt in the west. There are species of *Breviceps* (Figure 2) and a species of *Cacosternum* (Figure 6) which similarly extend north-north-westwards from the Cape Fold belt in the west, but they extend considerably further. These extensions can be attributed to northwards movement of the winter rainfall belt in the past (Van Zinderen Bakker 1969). These anurans were independent of streams, being terrestrial (*Breviceps*) and shallow pool-breeders (*Cacosternum*), and they were able to adapt to the increasingly arid climate as the winter rainfall belt moved southwards.

RIVER VALLEYS AS ROUTES AND BARRIERS

The upper Limpopo valley acts as a barrier to the montane palaeogenic invertebrates referred to by Stuckenberg (1962) and also to the corresponding element in the anuran fauna. The dry climate of the west of the subcontinent extends along the upper Limpopo valley and is an effective barrier to anurans, the distributions of which correlate with high rainfall. In Van Dijk (1971a) reference is also made to a difference in rainfall correlation north and south of the Limpopo in many species. Equally the Limpopo valley makes a break in the high rainfall region of the eastern Transvaal and serves as a route into the northern Transvaal for anurans on the somewhat drier coastal plain.

Mention has been made of the Zambezi as a barrier (to *Breviceps poweri*: Figure 2). This valley also appears to be a route between the coastal plain and the Okavango swamps.

The figures in Stuckenberg (1962) show that the distributions of some Cape Fold belt endemics eastwards, as well as some eastern highland endemics south-westwards, cease in the region of the Great Fish River valley. This valley and the Kei valley, with the associated, easily erodable Karroo shale sediments, and the Cape Macchia flora, appear to be effective barriers for some anurans. It is significant that the southern limits of the distribution of the anurans *Phrynobatrachus* and *Ptychadena* lie in the region where grassland gives way to macchia and hence these limits coincide closely with those of the grassland-dependent, cattle-ranching Nguni peoples.

POSSIBLE RECENT EXTENSIONS OF DISTRIBUTIONS

The distribution of *Cacosternum nanum* (Figure 6) correlates quite well with high rainfall (Van Dijk 1971a). *C. boettgeri* occurs in drier areas, but also in some areas which are wet; the author has attributed this to the habitat, i.e. open pool breeding sites resulting from human activities (Van Dijk 1971a); the dispersal mechanism is unknown.

The occurrence of *Strongylopus grayi* (Figure 5) in a few dry localities in the west is deserving of special study to determine the habitats at these localities. The author has suggested association with poplar stands (Van Dijk 1971a). It is conceivable that the eggs, which are laid out of water and frequently in poplar plantations, could have been conveyed with poplar slips, some species of poplar being propagated by slip.

Those anurans which will breed in dams, such as *Xenopus laevis*, *Schismaderma (Bufo) carens* and *Kassina senegalensis*, have probably extended their ranges substantially. Quarries for road-gravel, with their arrangement along roads, often provide breeding sites for these anurans as well as for many others, and roads are probably very important as dispersal routes on this account.

NOTES ON THE MAPS (FIGURES 1-8)

The maps are based on published records, records available from such sources as Broadley (1966) and new records. Unpublished records are shown, where possible, by open symbols (for *Rana*, Figure 4, incomplete symbols are used instead). Care has been taken in plotting the localities to reduce errors to a minimum; the author would appreciate queries about any of the localities considered suspect.

The map blanks were purchased from the Department of Geography, University of Witwatersrand, and were chosen because they form part of a series which covers the whole of Africa and because they permit reference to major towns, rivers and mountains during plotting as these features and a $\frac{1}{2}^{\circ}$ grid are shown in pale blue (which does not reproduce). It may be noted that Grahamstown and East London are questionably situated in relation to the grid. It is considered important, and it is intended, to plot distributions throughout Africa.

Consistency in identification of the various taxa is sometimes difficult to ensure. This particularly applies to the limits between *Breviceps mossambicus* and *B. adspersus* (Van Dijk 1971a). Broadley (1966) regards *poweri*, *adspersus* and *mossambicus* as subspecies. The taxonomy of the southern *Breviceps* and also the southern *Heleophryne* (Visser, this symposium) is likely to change, but the basic distributional facts may not be affected.

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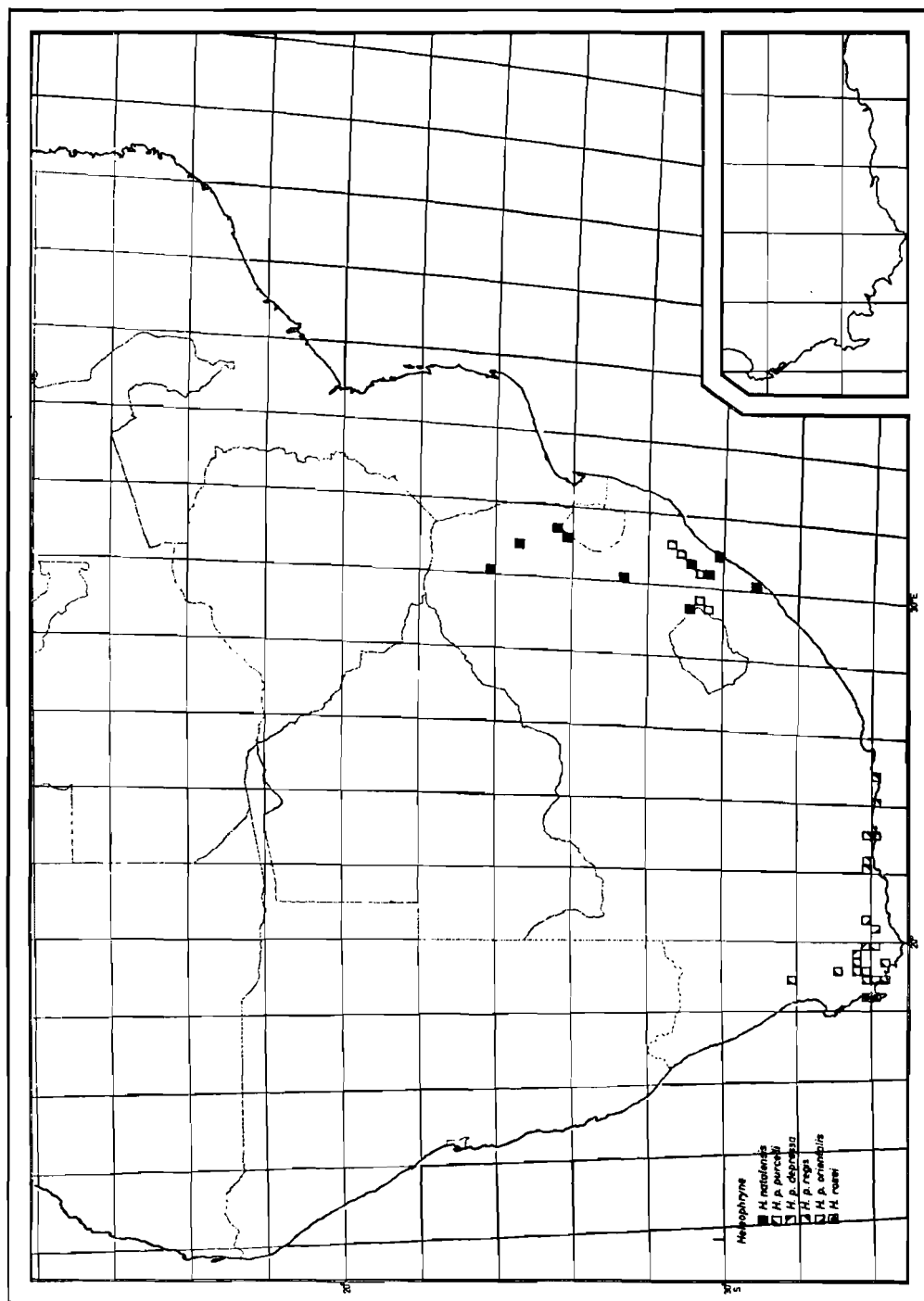


FIGURE 1
Distribution of *Helophryne* in southern Africa.

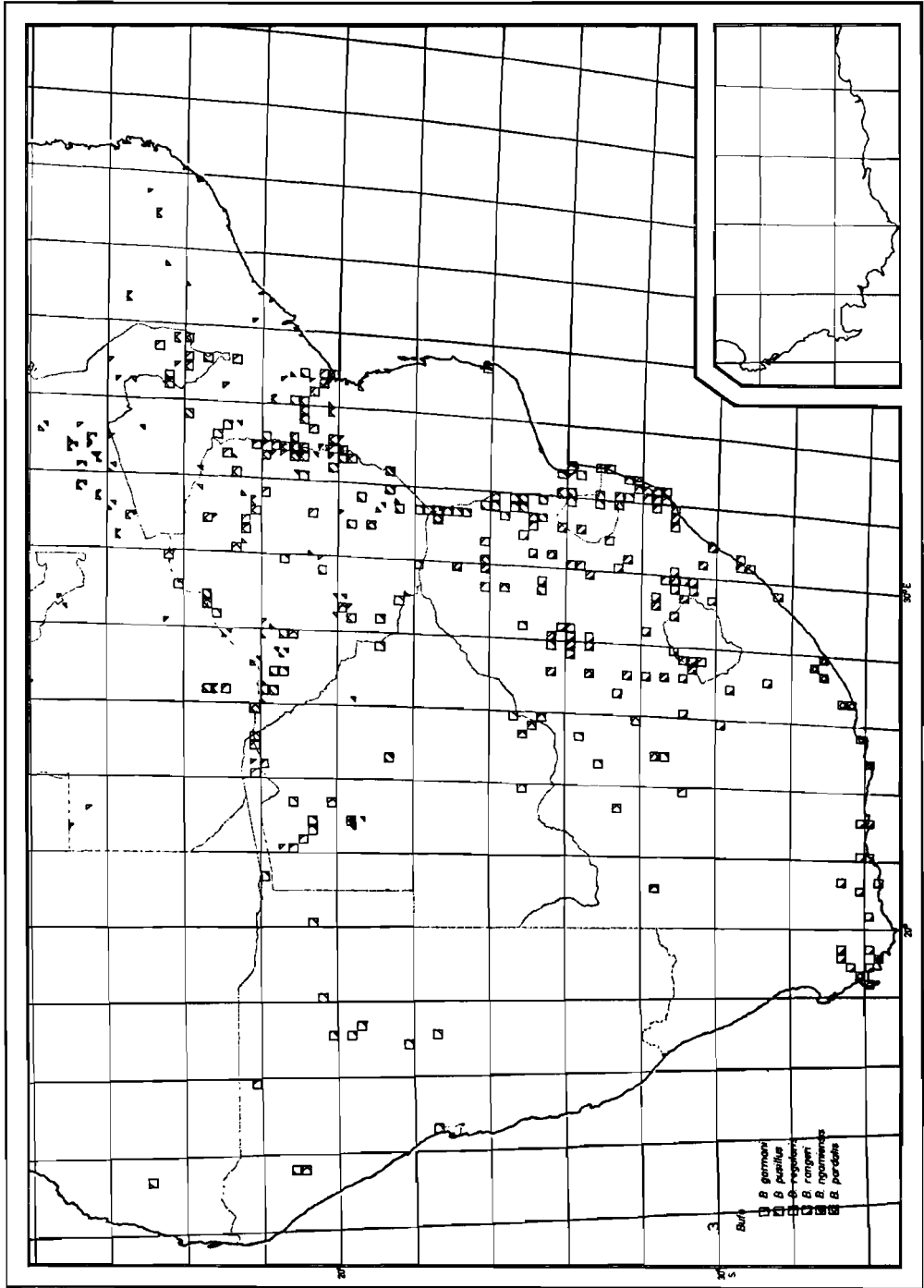


FIGURE 3
Distribution of *Bufo* (*regularis* group) in southern Africa.

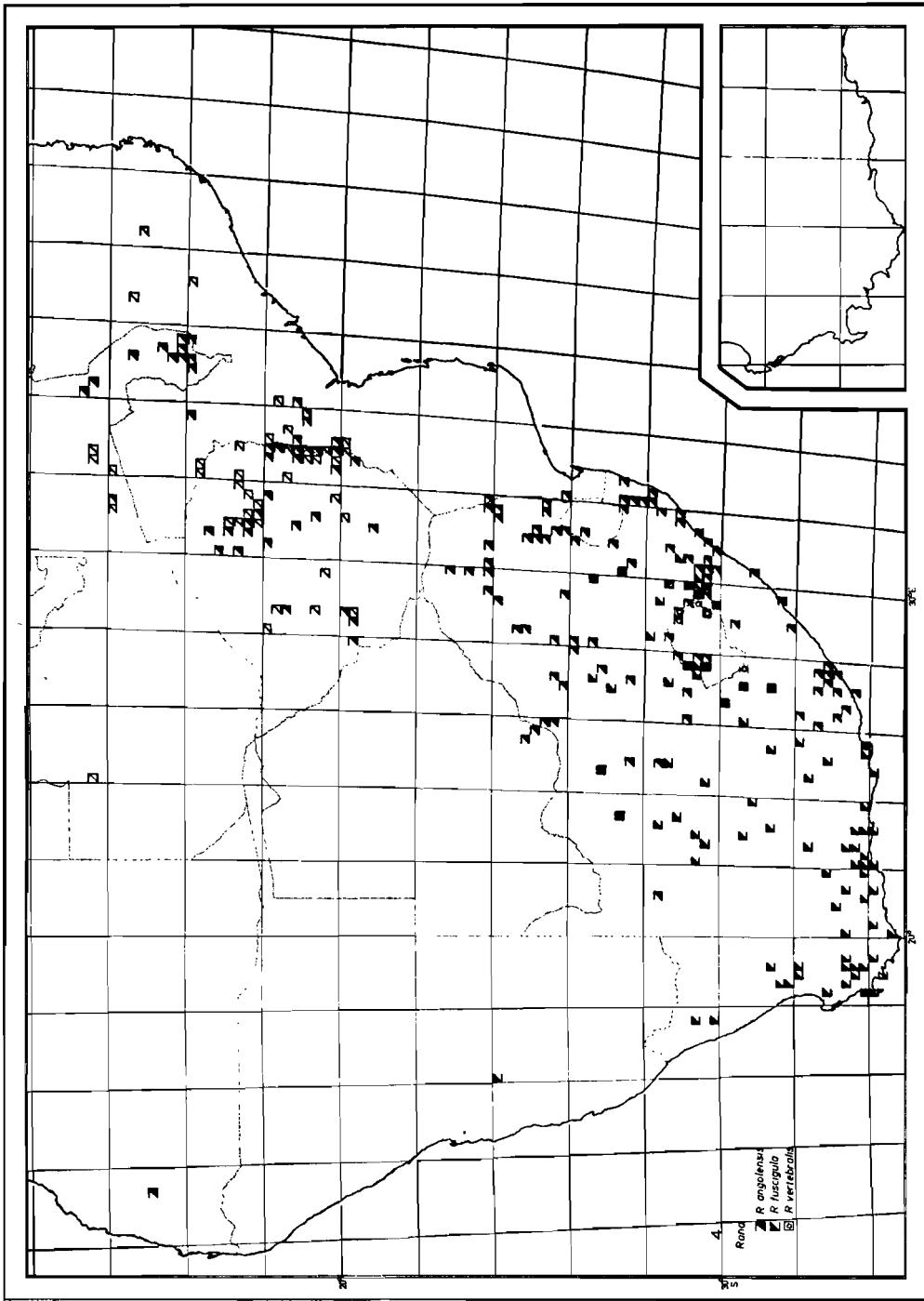


FIGURE 4
Distribution of *Rana* in southern Africa.

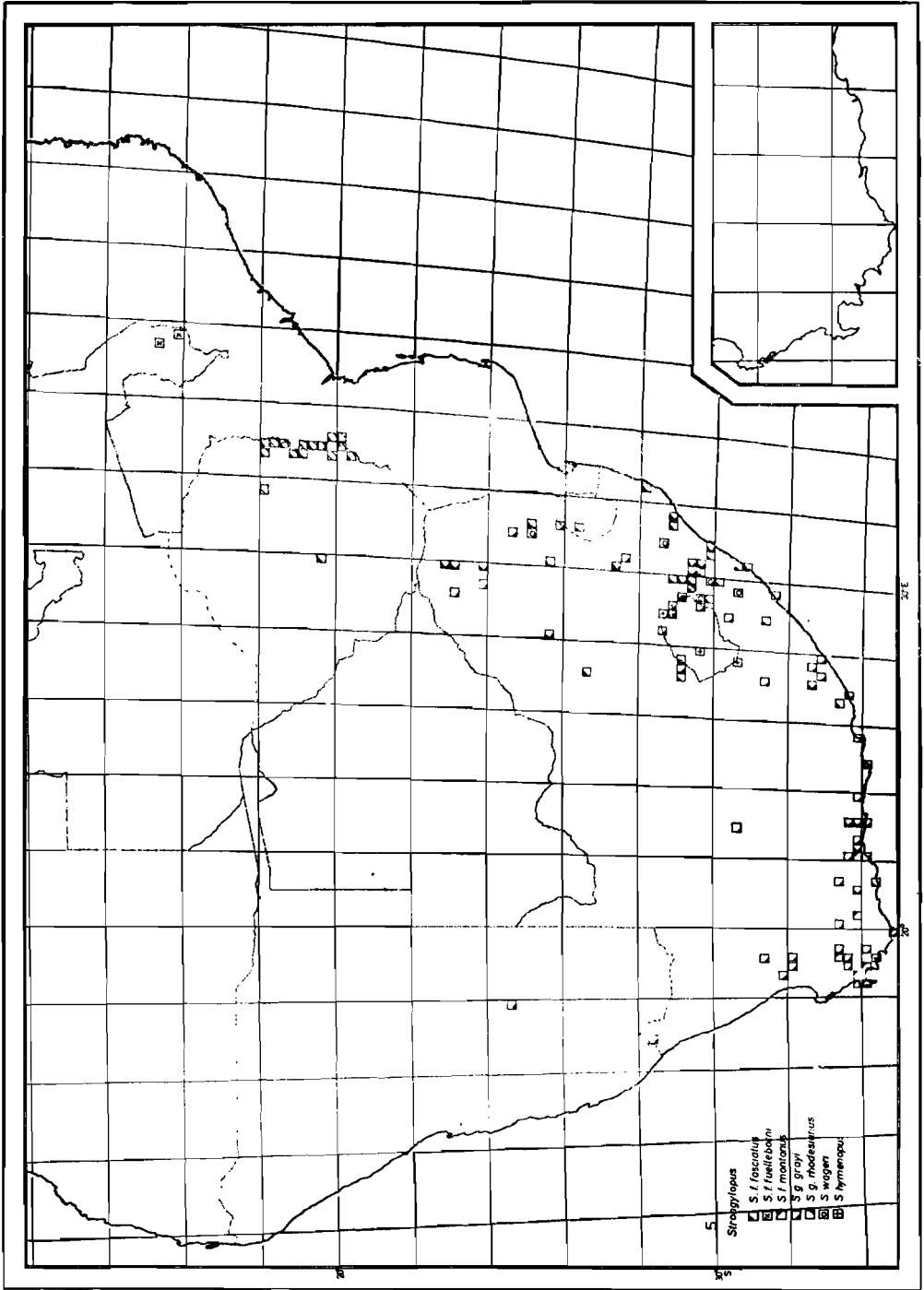


FIGURE 5
Distribution of *Strongylopus* (*Rana*) in southern Africa.

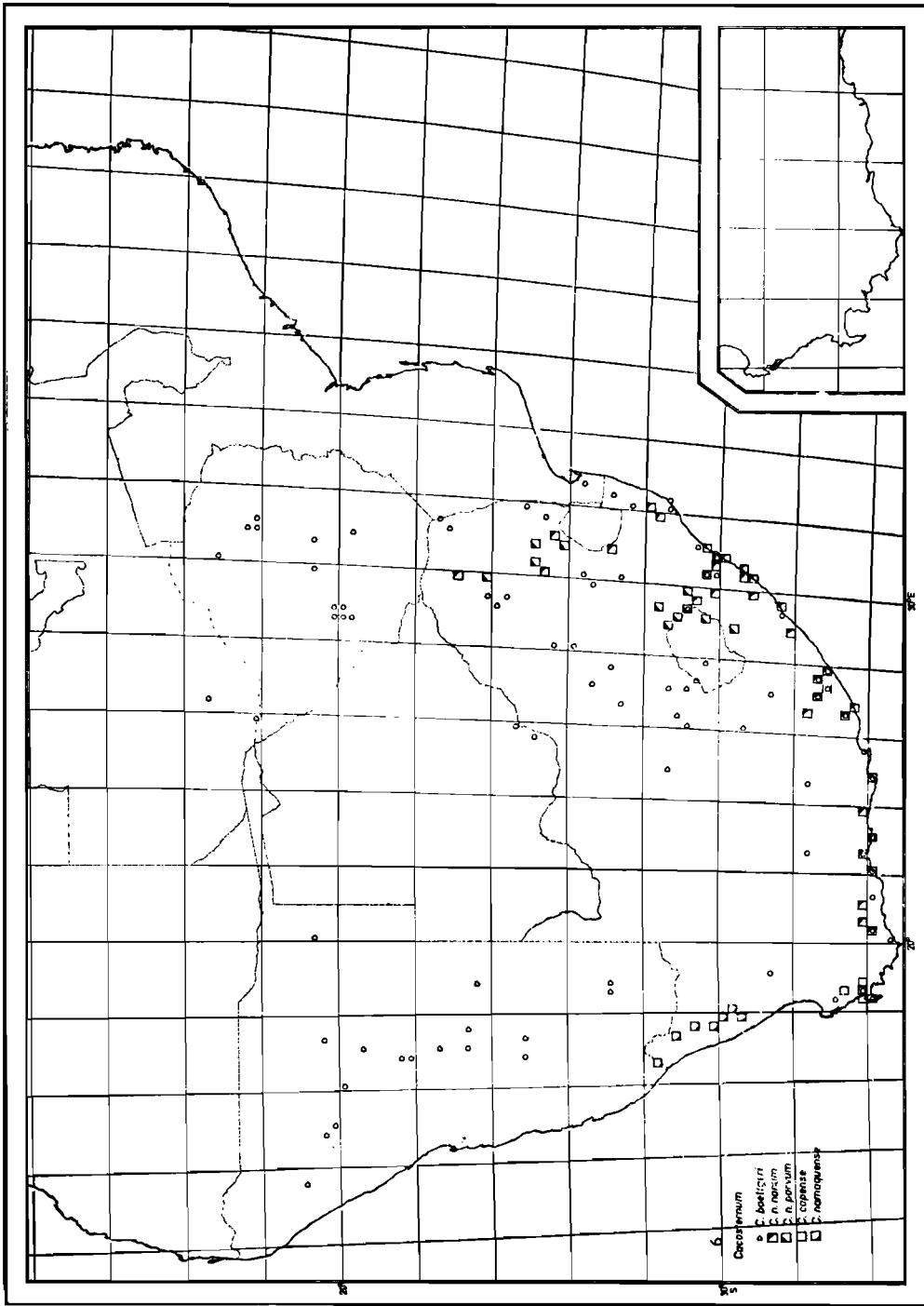


FIGURE 6
Distribution of *Cacosternum* in southern Africa.

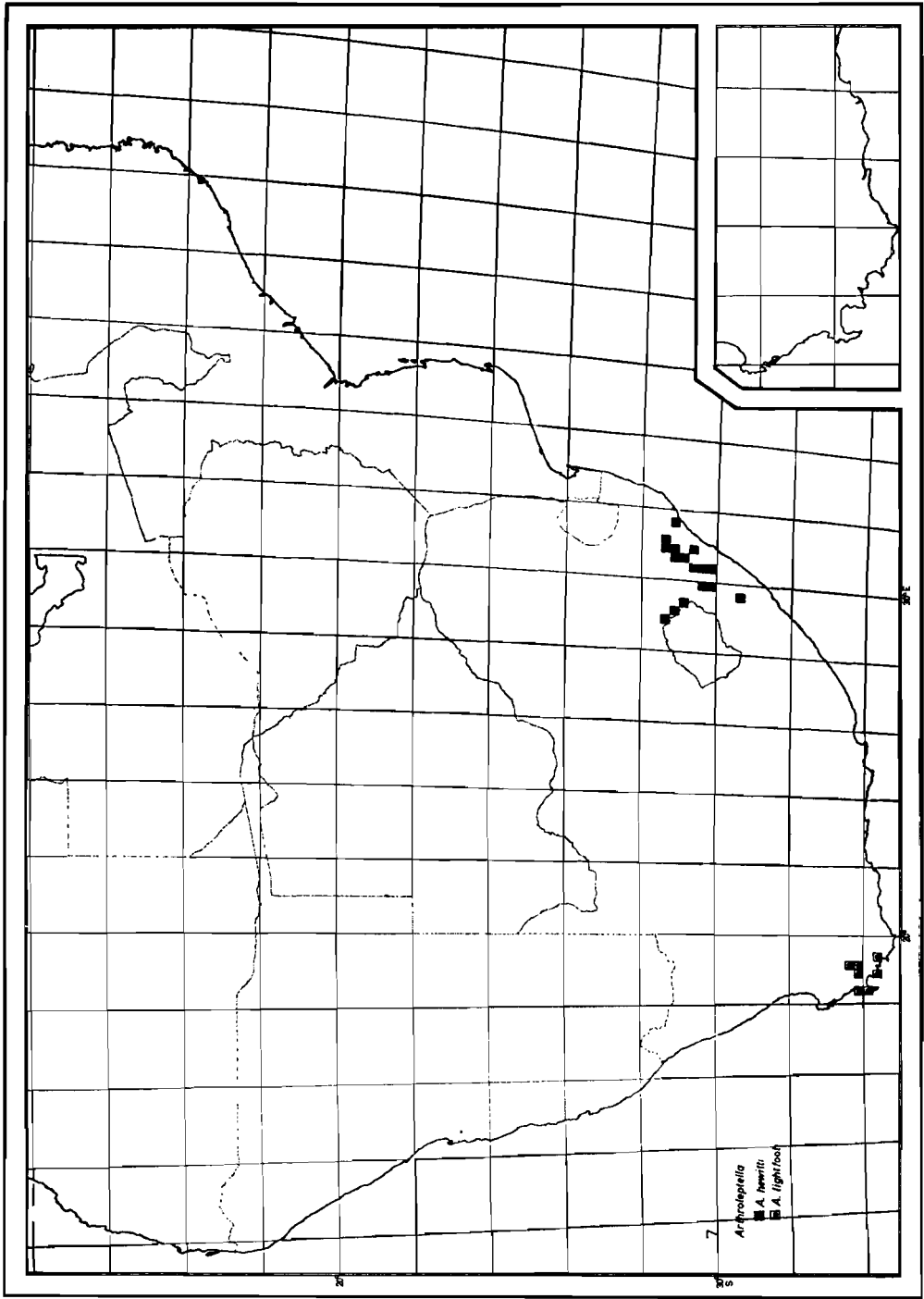
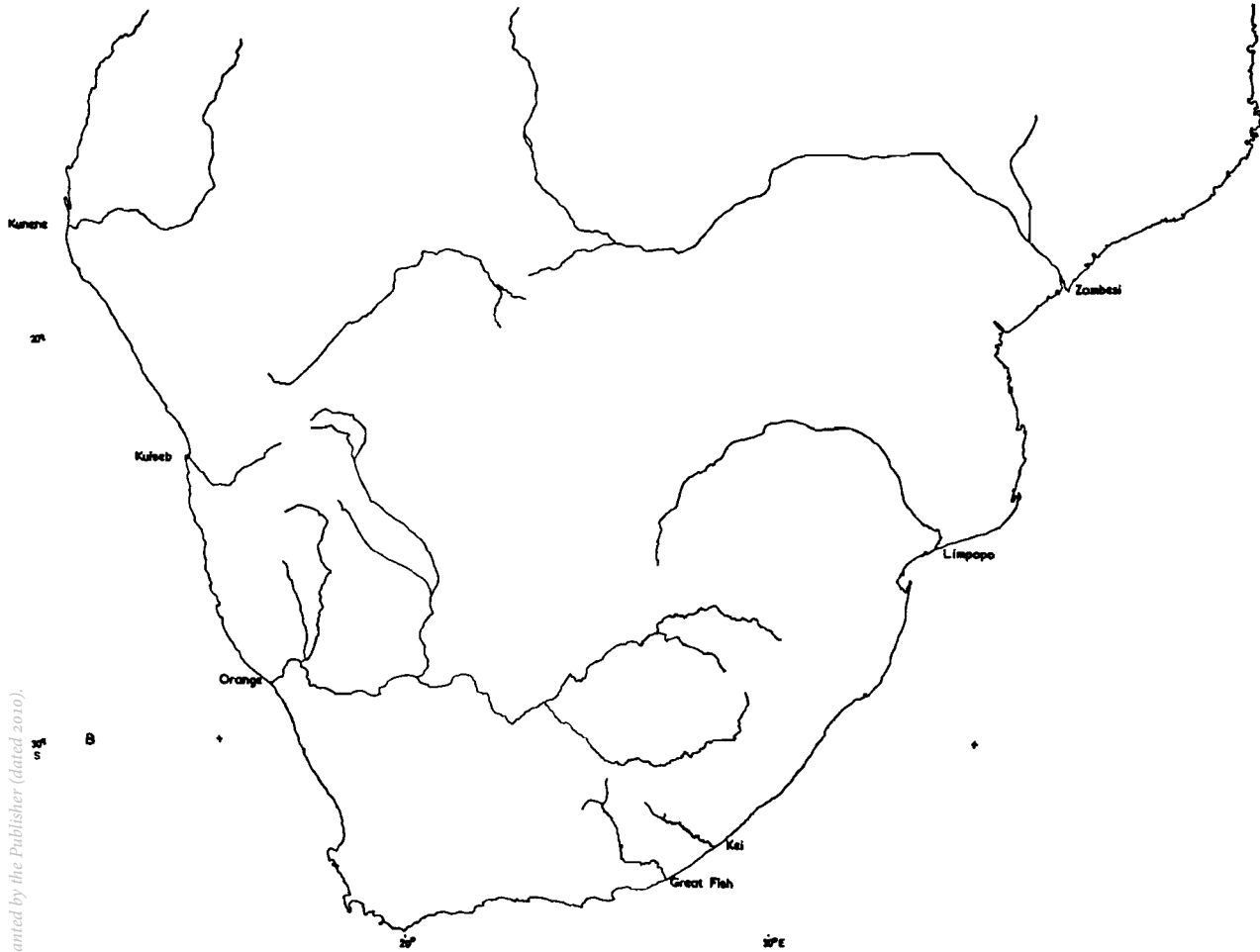


FIGURE 7
Distribution of *Arthropepella* in southern Africa.



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FIGURE 8
Rivers or river-valleys of southern Africa which are significant barriers to, or routes for, dispersal of Anura.