THE ZOOCARTOGRAPHIC APPROACH TO ANURAN ECOLOGY

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In the course of collecting material for studying aspects of the development of local *Anura*, notably *Bufo angusticeps*, from 1953 to 1956 in Stellenbosch, it was observed that the sites in which the various anuran species oviposited were very narrowly delimited. Similar observations were made in Natal from 1957 on. In 1959 a request for specimens of *Pyxicephalus adspersus* drew the present author's attention to the peculiar distribution of this species, viz. its absence from a considerable area around Pietermaritzburg. Dr. J. C. Poynton, at that time having recently begun a review of the southern African *Anura*, kindly confirmed that he had encountered few records of this species in Natal or the Pondoland region. The known distribution of *Pyxicephalus adspersus* was compared with a geological map, in view of the burrowing habit of the species, but no correlation could be found. With the publication by the Weather Bureau of W.B. 28 in 1965 a possible explanation became apparent, viz. that the species is uncommon in areas characterised by high humidity, cloudiness and an annual rainfall of more than 800 mm – see later, Figure 3. Between the time the problem was encountered and a possible explanation obtained, i.e. between 1959 and 1965, a number of publications dealing with southern African *Anura*, notably those of Dr. J. C. Poynton of the University of Witwatersrand, have included, or been devoted to, an approach which may be termed zoocartographic (or zooecocartographic). In this approach the data on distribution of species (or subspecies) are plotted on maps and correlations with variables are then sought, for instance correlations between the limits of the ranges of the species and the 13°C and 18°C Mean July Surface Isotherms as plotted by Poynton (1964a, 1964b, and earlier papers listed in 1964a). The general conclusions reached in these publications could not be accepted because they did not explain the distribution of *Pyxicephalus adspersus* nor did they accord with the marked preferences shown by frogs and toads in choosing ovipositional sites. Thus the following statement could not be accepted: "As pointed out above, thermal conditions appear to act directly on amphibian distribution, while rainfall appears to act indirectly through its effect on the habitats of the amphibians." (Poynton 1964b, p. 213.) The present paper attempts to determine whether, if the published zoocartographic conclusions are faulty, this can be ascribed to hazards inherent in the zoocartographic approach, largely because distribution maps are essential to the approach. Since Poynton has recently extensively revised the synonymies of southern African *Anura* and plotted the distributions of the anurans defined according to these synonymies and, as mentioned above, related these distributions to isotherms which he has plotted, the zoocartographic approach would most effectively be examined by examining Poynton's work with respect to the synonymies recognised, the distributions plotted or the isotherms plotted. A critical examination of Poynton's work thus becomes the main proximate aim of this paper, the ultimate aim being to assess the limitations of the whole approach and also, in doing this, to show how zoocartographic correlations can be checked by a more direct method of correlation of variables and locality records. It can be stated at the outset that the chief disadvantage of the zoocartographic approach is considered to be that it involves the manipulation of a mass of data with frequent opportunities for error, and that even minimal errors tend to render conclusions questionable.

Reliability of Locality Records and Identifications

Since locality records form the basis of the zoocartographic approach, mis-identification of some of the specimens on which the locality records are based constitutes a great potential hazard in this approach, a single mis-identification of a specimen or a batch of specimens from one locality may require the reappraisal not only of the distribution, and hence the ecological correlations of the species to which the specimen was or specimens were incorrectly assigned, but also of the species to which they actually belong. Further, a detected mis-identification casts doubt on all the identifications of the species confused, and detected mis-identifications in a number of species pairs or groups must raise doubts about all the identifications, hence about all the locality records and hence all the correlations at specific level. By contrast the value of direct observations on the ecology of a single community of a species, or on a number of communities within a limited portion of the range of the species, may not be affected at all by a mis-identification – the observations may simply refer to a different species or both (or all) of the confused species. Thus Wager's observations on the tadpoles of *Hyperolius marmoratus* (*Rappia marmorata*) actually referred to *Phrynomerus bifasciatus* (Wager 1926, pp. 170–174; Wager 1929, pp. 125–126), and his observations on *Cacosternum nanum* in his recent book (Wager 1965) either refer to *Cacosternum boettgeri* only (as appears to be the case for the tadpoles) or refer to both of these *Cacosternum* species. Fortunately Wager included good photographs of specimens which made the mis-identification immediately apparent. When the locality records for *Cacosternum nanum* given by Poynton (1964a) are compared with the W.B. 28 map of annual rainfall, the species appears to occur mainly in the 801+ mm per annum area – see later, Figure 6. However, there is reason to suspect that some of these locality records may be attributable to *C. boettgeri* since Dr. Poynton commented on the mis-identification of *Cacosternum boettgeri* as *C. nanum* in Wager's book and Dr. Wager, in a letter to the reviewing journal, wrote as follows: 'Thirdly, he says, "The illustrations said to be *Cacosternum nanum* on page 151 are in fact *C. boettgeri*." Poynton appears to have forgotten that he himself identified these particular frogs as *C. nanum*. They were photographed, preserved and numbered (so that the photographs could not subsequently be confused), and along with a long series of specimens of both species from many localities in the Transvaal, O.F.S., Zululand, Natal, Pondoland and E. Cape, were all examined and identified and subsequently rechecked by Poynton.' (Quoted from a copy with Dr. Wager's permission.) It must be emphasised that some species of frogs are not easily identified from preserved specimens and it is not unusual that identifications from such material are inconsistent. In such circumstances only identifications from fresh specimens would be acceptable for locality records for zoocartography.

Hylambates (*Kassina*) *wealei* also appears to be found mainly in the 801+ mm rainfall per annum areas – see later, Figure 8. However, a problem of identification may be presented by the genus (or subgenus) *Kassina*, of which Poynton (1964a) recognises two species in southern Africa, *K. senegalensis* and *K. wealei*, regarded as "tropical" and "Cape" species respectively. Distinct *K. senegalensis* and *K. wealei* tadpoles have been described and the calls of the adults are quite distinct according to Poynton (1964a), that of *K. senegalensis* being described as "a loud explosive 'boip' resembling the bursting of a large bubble" (p. 177) and that of *K. wealei* "being a creaking noise similar to that produced by turning a cork in a bottle" (p. 179). Fitzsimons (1946, p. 373), referring to *Kassina wealii wealii* from Grootvadersbosch (near Swellendam), states: "The call of the males is a loud spasmodic, high-pitched 'Plocking', which goes off suddenly like the drawing of a cork; this is quite unlike the call of *K. w. quinquevittata* Hewitt, of the western Cape Province, which Rose (1929, *Veld and Vlei*, p. 36), describes as a 'loud strident creak'." Poynton lists Fitzsimons (1946) in his bibliography (op. cit.) and shows *K. senegalensis* as not occurring within 500 kilometres of Grootvadersbosch in his map of its distribution, therefore it can be concluded that Fitzsimon's specimens are accepted as *K. wealei* although the call described for them is that characteristic of *K. senegalensis*. Whether the call is referable to the specimens actually collected cannot now be ascertained, for the specimens, to quote Loveridge on other series, "maintain a conspiracy of silence".

It may again be mentioned that, in an unpublished thesis, Broadley (1966, p. 483) comments on the "tropical" – "non-tropical" pair *Breviceps mossambicus* – *Breviceps adspersus adspersus* sensu Poynton as follows: "Discussion. Poynton (1964a) has treated *adspersus* as a full species, sympatric with *mossambicus*, distinguishing them largely on dorsal colouration and a difference in call. My impression is that *adspersus* is a western race which has evolved in the Kalahari and spread east into Rhodesia, Transvaal and southern Mozambique, intergrading extensively with the typical form." Some of the specimens from the cool locality Sinoia (Mean July temp. 13·7°C) are placed in the non-tropical *Breviceps adspersus adspersus* (*Breviceps mossambicus adspersus*) by Poynton, but are considered by Broadley (loc. cit.) to be better placed in "tropical" *B. mossambicus mossambicus* (see Table 1). All ecological studies may be disturbed by the discovery, as in the *Cacosternum* and *Kassina* examples, that what was considered to be one species may in fact be two or more species, or by lack of clarity, as in the *Breviceps* example, as to where the limits between two species should be drawn. It should be clear, however, that ecological studies of single populations are less likely to be disturbed than studies based on maps of distribution, and, if the former are disturbed, the disturbance will tend to be of a less profound nature.

Since Stuckenberg, in another paper in this symposium, refers to the distribution of *Hyperolius pusillus*, it may be mentioned that there is evidence that *H. pusillus*, as recognised by Poynton, is composite. Series of *Hyperolius pusillus* and *H. nasutus* specimens kindly furnished by Dr. Poynton included one specimen identified as *H. pusillus* (Poynton's No. 1069) which proved to have a skeleton outside the range of the rest of the *H. pusillus* specimens and outside the range of a long series subsequently collected. (Confusion with *H. nasutus* specimens was not possible as there were the correct number of these.) Dr. Poynton re-examined the specimen at the time and confirmed that it was *H. pusillus*. Doubts must be entertained about the relegation by Poynton (1964a, pp. 192–193) of *H. poweri* Loveridge to the synonymy of *H. nasutus*.

TAXONOMIC QUESTIONS AND LOCALITY RECORDS

Naturally, questions of synonymy and affinity are crucial to zoocartographic methods. The distribution of a taxon must depend on how that taxon is defined, i.e. how it is delimited from other taxa. Where there are comments on the bases of definition of the taxa these should carefully be assessed. Recent anuran zoocartographic work in southern Africa, by Poynton and others, has relied on Poynton's revision (1964a) of the group, and it may be expected that this will continue to be the case for some time. The number of species recognised in this revision represents a considerable reduction (largely correctly, the present author believes—and hopes for the sake of simplicity). Poynton, discussing internal features as taxonomic "characters", comments: "A reassessment of the degree of variation occurring within each form is the chief reason for so many names being relegated to the synonymy in this revision." (1964a, p. 13.) Poynton appears to claim to have made a careful study of internal features, hence zoocartographers using Poynton's synonymies should be alert to any potential errors in respect of internal features, such as inconsistencies of nomenclature. Thus Poynton uses two different nomenclatures for the pectoral girdle indiscriminately, for instance that of Ecker, Gegenbauer, Gaupp and De Villiers on page 154 ("the bony clavicle extends along the whole length of the procoracoid bar") and that of W. Parker, Fürbringer and Broom on page 124 (". . . unossified anlagen of the procoracoid.") He appears to equate alizarin staining with the presence of bone (p. 154 and p. 155). He gives some descriptions which are either very imprecise or wrong, in at least one case despite the fact that a specific accurate description existed, Fitzsimons correctly having noted the presence of a procoracoid cartilage in female *Arthroleptis* (Fitzsimons 1947, p. 124), while Poynton (p. 159) states: "Procoracoid-clavicular bar fully ossified." (Poynton lists Fitzsimons' paper in his bibliography.) It is possible that imprecisions or inaccuracies relating to internal features may not result in errors in delimitation of taxa, and it is to be hoped that this will prove to be the case with Poynton's synonymies. At generic level Poynton has been able to draw on the detailed studies of internal anatomy, particularly cranial anatomy, from the Stellenbosch school of zoologists, and most of his conclusions therefore appear to be soundly based. In one case of great zoocartographic import, viz. the position of *Heleophryne*, Poynton rejects the conclusions of Du Toit (1934) without producing any evidence either in conflict with the observations made, or to support his statement that Du Toit was influenced by an earlier study of a specimen thought incorrectly to be a *Heleophryne* or that Du Toit's Heleophrynidae was "a family which in any case was erected on a fictitious animal". (Poynton 1964a, p. 37.)

In many other judgments with direct bearing on zoocartography or more directly on ecology, Poynton offers either no evidence or evidence which examination of the literature would have shown to be questionable. For example, he states of *Pyxicephalus adspersus:* "In central Africa the Africans themselves are substantial predators, which might account for Loveridge's inaccurate conception of the size of this form." (Poynton 1964a, p. 95.) Poynton does not refer to all Loveridge's early work, otherwise he might have been more hesitant about referring to "Loveridge's inaccurate conception", nor does he refer to Boettger (1887), who found large specimens where they were also an important food (p. 137); Boettger also, incidentally, is one of the authors – Pfeffer (1893) and Bocage (1895) are others

– who relegated *P. edulis* to the synonymy of *P. adspersus* (*Rana adspersa*), Poynton describing this synonymy as "New synonymy" in his 1964 revision. As mentioned earlier (in the first paragraph), the distribution of *Pyxicephalus adspersus* is a matter of importance; thus the possibility of *P. edulis* being distinct, and not juvenile *P. adspersus* as Poynton concludes, is of concern to zoocartographers. This is particularly so in view of the possibility that the specimens recorded in the St. Lucia area, which is wetter than the rest of the recorded range of *P. adspersus* south of the Limpopo (Fig. 3), may not be typical *P. adspersus*. Poynton remarks "Juvenile and half-grown bullfrogs are more commonly encountered than fully grown specimens. Juveniles have been known to form swarms in some localities." (1964a, p. 95.) Poynton does not list the localities involved, nor does he say on what criteria the specimens were judged juvenile, or whether specimens judged as adults are known in the same localities. Dr. J. A. Pringle of the Natal Museum observed swarming of bullfrogs smaller than typical *P. adspersus* in the Mtubatuba area (personal communication), i.e. in the region where *P. adspersus* would not be expected if they are restricted to areas with annual rainfall of 800 mm or less. The apparent absence of large specimens in the swarms suggests that the specimens represent the maximum size attained in the area at the time. It should be obvious that Poynton's distribution data are unhelpful in this matter, and also that a zoocartographer anxious to interpret rainfall as a determining factor of distribution might be tempted to recognise *P. edulis* as a different species if this excluded *P. adspersus* from the wetter areas. The result would be a tautology.

RELIABILITY OF RANGES

The ranges on which zoocartographic comments on Southern African Anura have been based are derived almost exclusively from post-metamorphic material, although tadpoles offer a better means of establishing the range of most species (Van Dijk 1961, pp. 44–45). Collecting is also biased to particular areas (cf. comments on Twinstreams below), while the possible influence of this on zoocartographic ideas has not received much attention. There are important records which have not been mentioned (as far as can be ascertained) in any zoocartographic work, either as records or as mis-identifications. Bocage (1895, p. 184) reports *Hemisus guttatum* (as well as *H. marmoratum*) in central Angola, which, if the specimens are correctly identified and localised, considerably extends the range based on the eleven specimens examined by Poynton (1964a) and three other records he mentions (op. cit. p. 166) all located between Durban and Cato Ridge in the south and Piet Retief in the north. Conclusions on ecology derived from distribution data may have to be altered more or less radically.

LIMITING FACTORS AND CORRELATIONS WITH THESE

A. *Reliability of Published Isotherms*. Limits of cartographic faunal divisions (e.g. isotherms) must be based on accurate and sufficient data. Poynton has used isotherms as the limits of his cartographic faunal divisions. Clearly, the first essential is to make sure that these isotherms are accurately placed. Poynton's 18°C Mean July Surface Isotherm follows the eastern boundaries of Swaziland and Transvaal so closely that a causal relationship must be

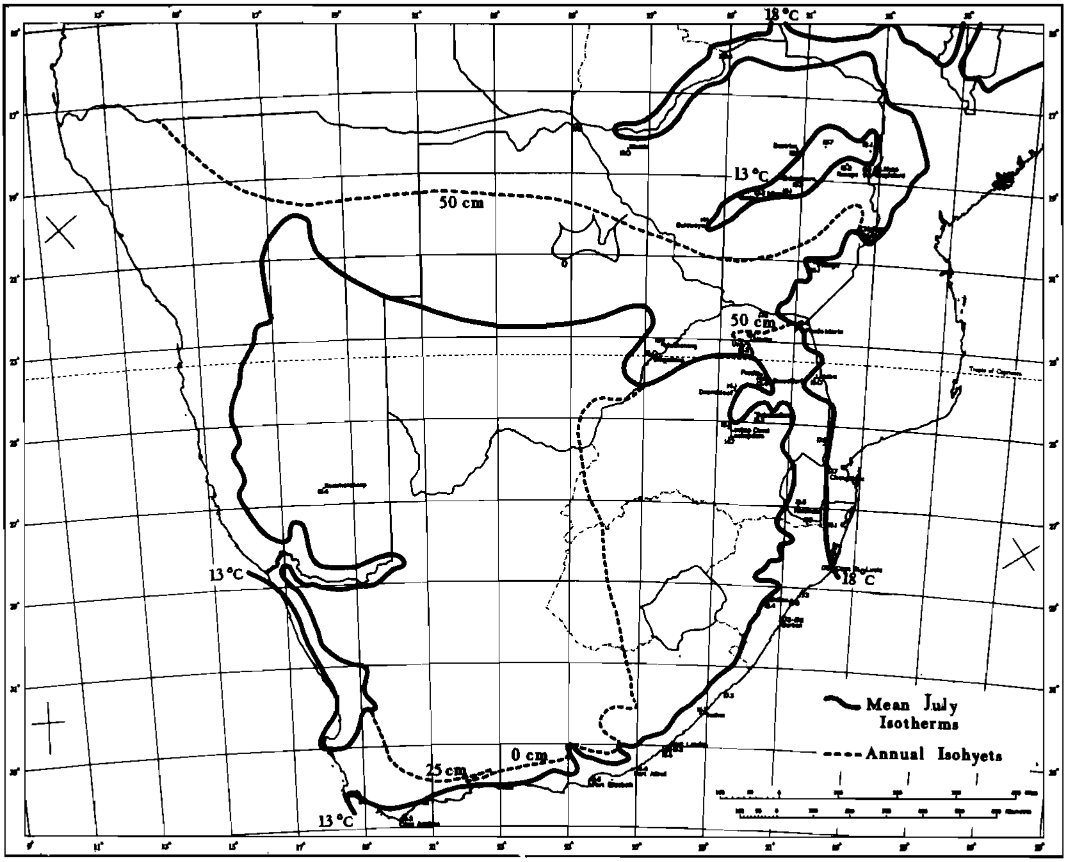

FIGURE 1
Mean July Surface Temperatures of selected stations compared with 18° C and 13° C Mean July Surface Isotherms after Poynton (1964a, Map 3). Data from W.B.19 and the Rhodesia Climate Handbook Supplement 1. All stations with mean July temperature 17·0° C or over, and all Rhodesian stations with mean July temperatures 13·0° C or less are shown. Where Poynton's isotherms appear to be incorrectly placed in relation to particular weather stations, the names of the stations are given. The coastal weather stations used to obtain the scale for Fig. 2b from that for Fig. 2a are shown.

sought, and the hypothesis that both are determined by topography suggests itself. It is not clear how Poynton arrived at his line from his earlier papers, but it is legitimate to assume that he would have mentioned any data used besides the Weather Bureau Statistics available in W.B. 19 and the Rhodesian Climate Handbook Supplement 1 mentioned in the caption of Figure 2 in his 1964b article. W.B. 19 contains only two points above 18°C and nine between 17·0° and 17·9°C, while the Rhodesian Handbook shows no station with a July mean between 17·0° and 18·9°C and only two points from 19·0°C upwards. Clearly the same physical features which determine the eastern political boundaries of Transvaal and Swaziland are used to interpolate between the two points in W.B. 19. It is clear that the limit of this isotherm in the south must be extremely difficult to determine as there are no physical features in the south as clearly defined as those to the west of the Moçambique plain. The Weather Bureau's publication W.B. 28 (apparently first published in 1965 and hence not seen by Poynton) gives the 17·5°C mean July isotherm as reaching the coast in the region of St. Lucia mouth, the point at which Poynton places his 18°C equivalent, and it is this region which features so prominently in Poynton's publication. The station Dukuduku, which lies close to Poynton's line, has a mean July temperature of 16·8°C over the period 1933–1940 (W.B. 19). This clearly suggests that the 18°C mean July isotherm should be placed further north than shown by Poynton (1964a, p. 260; 1964b, Figs. 1–3).

Poynton's 18°C mean July isotherm is placed by him on the wrong side (west) of weather stations with mean July temperatures below 18°C, viz. Letaba (Mondswani) 16·0°C and Triangle 16·1°C, and on the wrong side (east) of weather stations with mean July temperatures above 18°C, viz. Punda Maria 18·4°C and Wankie 19·0°C (Fig. 1). Poynton's 18°C isotherm also passes over Changalane 17·7°C, and just on the correct side of Chipinga 14·6°C, obviously too close to both of these stations. There are insufficient stations with mean July temperatures between 12·5°C and 13·5°C to make the drawing of a 13°C mean July isotherm an easy matter. It is, however, a simple matter to show that Poynton's 13°C isotherm has not been drawn with care, for the area in Rhodesia enclosed by the 13°C mean isotherm should include all the stations with July mean temperatures below 13·0°C and it in fact excludes four of the six – Beatrice 12·7°C, Rusape 12·2°C, Stapleford 9·2°C and the important locality Mount Nuza 8·9°C. This gives the impression that July temperatures in Rhodesia are higher over parts of the highlands than they in fact are. Inyanga 12·1°C and Marandellas 12·7°C lie within the area enclosed by the 13°C isotherm, which is correct; but Gwelo 13·2°C, Mtao 13·1°C and Enkeldoorn 13·3°C also lie within this area, which is incorrect. The area should thus be less extensive southwards and more extensive south-eastwards. The 13°C isotherm in Rhodesia also passes over Bulawayo 14·1°C mean July temperature.

Poynton's 18°C and 13°C mean July isotherms are thus placed on the wrong side of 8 of the 39 weather stations in Rhodesia, while the 18°C isotherm is clearly too close to Chipinga and the 13°C isotherm too close to Bulawayo on available evidence. Stations of interest in assessing the 13°C mean July isotherm outside Rhodesia have been named in Figure 1 and their mean July temperatures given. Some stations of interest, such as Ofcolaco and Mamathole, have been omitted. It may be concluded that the 18°C mean July isotherm in southern Africa cannot be plotted with sufficient accuracy to be useful as a zoocartographic correlate, and this applies also to the 13°C mean July isotherm in Rhodesia (as well as in the west of the subcontinent).

B. *Reliability of Correlation between Isotherms and Distribution*. Temperature is the main variable considered in Poynton's zoocartographic papers. The 18°C mean July isotherm (July being taken to be the coldest month) is used to define tropical species of Anura: "A tropical form is here taken to be a form at least a substantial part of whose range is included in an area experiencing a tropical climate as defined by Köppen, i.e. in which the coldest month has a mean temperature of over 18°C (64·4°F)." (Poynton 1964a, p. 223.) Poynton lists 41 "forms" which he considers tropical (p. 223) and comments (p. 224): "Only six of the tropical forms do not extend beyond the tropical limits in Southern Africa, namely *Xenopus muelleri*, *Bufo t. beiranus*, *Hylarana galamensis bravana*, *Ptychadena floweri*, *Phrynobatrachus* *acridoides* and *Hyperolius argus* . . . The Tropical subtraction margin contains a number of characteristic patterns (Poynton 1962c) . . . These patterns are presumably the result of the various forms avoiding the arid Kalahari and the cool highveld, but being able to follow tongues into South West Africa, along the Limpopo basin towards Griqualand West, and along the eastern coastal lowlands." In Table 1, based essentially only on Poynton's distribution data, it can be seen that the temperature tolerance of these "tropical" species does not suggest that low temperatures are avoided if July mean temperatures are good criteria. (The data are taken to apply throughout a quarter-degree square, as usual in zoocartographic works.) It can be seen that *Xenopus muelleri* tolerates mean July temperatures below 18°C, in contrast to Poynton's quoted statement. Poynton goes on to state that "subtraction of the tropical fauna also takes place southwards along the Natal coastal lowlands. Figure 123 gives a graphical picture of this subtraction. The figure shows that an almost precipitous subtraction of the tropical fauna takes place on the southern portion of the Mozambique plain, particularly in the region of Lake St. Lucia. This spectacular subtraction is all the more remarkable because the area in which it occurs shows no pronounced physiographical climatic or ecological changes. The 18°C July isotherm does indeed cut across the lowlands in this region, but as the temperature gradient is so very gradual, it is difficult to see how the temperature conditions are directly responsible for this headlong subtraction. Moreover, amphibians tend to be concealed and protected in hibernation at this time of the year. Nevertheless, the limits of the main concentration of the tropical amphibians, both western and southern, coincide with the course of this isotherm, which runs along the western edge of the Mozambique plain and then traverses the plain at about 28°S. Pienaar (1963) has confirmed the correlation between this isotherm and the main limitation of the tropical fauna in the Kruger National Park" (pp. 224–225). (Pienaar took his isotherm from Poynton, 1961 – personal communication. As mentioned above, Letaba at 16·0°C is on the wrong side of the 18°C isotherm.) Figure 2a shows that the subtraction is not as sudden as Poynton suggests, and that the main subtraction is not in the region of St. Lucia but further south, at 29°S (as Poynton himself observes on page 211 of his 1964b paper), while Figure 2b, derived from Table 1, shows how far the various species would be expected to extend along the Natal coast if temperatures of neighbouring weather stations (in the same quarter-degree square) were valid measures of temperature. Data for *Hyperolius argus*, *Bufo taitanus*, *Hylarana galamensis*, *Abrana floweri*, *Leptopelis flavomaculatus*, *Phrynobatrachus acridoides* and *Ptychadena taenioscelis* are not available as they do not occur in any 1/4° square with a weather station (see Table 1). From Figure 2 it is clear that, with the single exception of *Hyperolius pusillus*, all the Anura listed in Table 1 for which there are data, occur, somewhere in their range, in 1/4° squares with recorded mean July temperatures below those which Poynton considers limit their southward coastal distribution. Besides *Hyperolius pusillus* there are four species which do not appear to occur where July temperatures are more than a degree lower than those experiences at the southernmost limit of their distribution on the coast. These species are: *Hylambates maculatus*, *Hyperolius p. puncticulatus*, *Afrixalus fornasinii* and *Hyperolius tuberilinguis*. It is significant that these are all leaf-frogs confined in southern Africa to the coastal plain. The decreasing width of the coastal plain southwards offers an obvious explanation for the reduction of the number of species confined to the

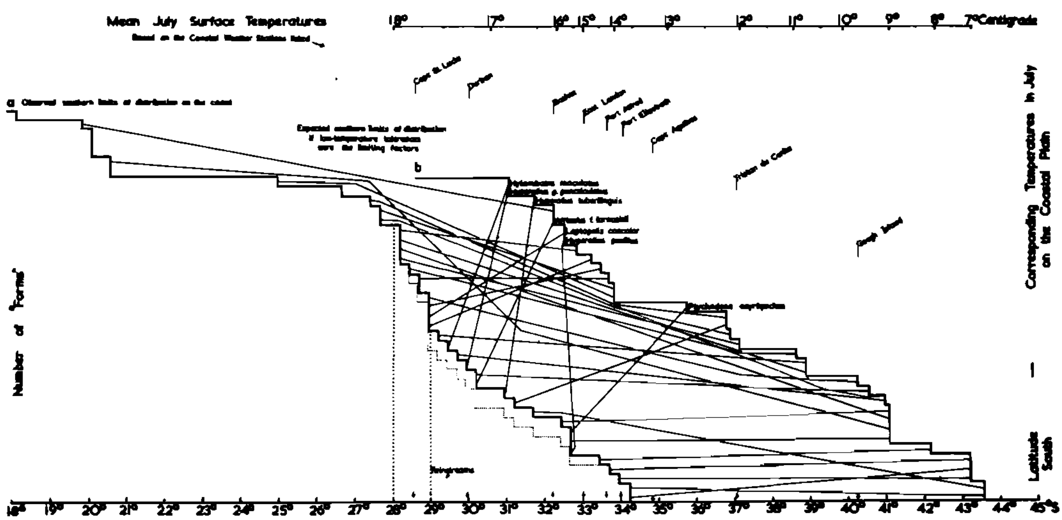

FIGURE 2

Southward reduction in "tropical forms" along the east coast. The latitudinal positions of major coastal weather stations are shown. (*a*) On the left; the southern limits are based on Poynton's data, with few additional records (e.g. *B. garmani* subsequently recorded south of 28° S, at Pietermaritzburg.) The dotted graph indicates how the graph would have to be modified if account were taken of the absence of *Pyxicephalus adspersus* and *Tomopterna delalandei cryptotis* from part of the coastal region (*b*) Southward reduction as it would be expected, from Table 1, to occur if it occurred in response to decreasing mean July temperatures as recorded at the coastal weather stations listed. The temperatures are the coldest mean July temperatures experienced by the animals anywhere in their ranges. The dotted line represents the change which one record of *B. pusillus* by Broadley would make necessary. The lines between graphs (*a*) and (*b*) indicate changes for individual species, which can be identified from Table 2.

coastal plain. This is beautifully illustrated in Stuckenberg's paper in this symposium (1969, pp. 153–157). *Leptopelis concolor*, also a leaf-frog and confined to the coastal plain and the Transvaal lowveld, and *Ptychadena oxyrhynchus*, which is only confined to the coastal region in the southern part of its distribution, are the only other species with apparent mean July temperature tolerances less than 3°C lower than suggested by their coastal distribution. It should be mentioned that the vicinity of Twinstreams, south of the Umlalazi River (Fig. 2), marks the present known southern limit of some species for a reason which is not far to find in the person and property of Mr. Ian Garland, who has preserved some habitats on his own land, has been an active collector, and has made the region accessible to other collectors by his hospitality.

NEW APPLICATIONS OF ZOOCARTOGRAPHIC TECHNIQUES TO SOUTHERN AFRICAN *Anura*

From the foregoing it may be seen, firstly, that published distributions used in zoocartography should be regarded with circumspection, and secondly, that 18°C and 13°C Mean July Surface

Isotherms are both difficult to delineate in southern Africa and apparently do not correspond closely to limits of distribution of anurans. Nevertheless, the zoocartographic technique can serve the function of directing attention to problems and to possible lines of further investigation. A brief account of some zoocartographic observations will illustrate the uses, and the accompanying hazards, of the approach.

Besides the reference, in the first paragraph, to the absence of *Pyxicephalus adspersus* from a considerable area around Pietermaritzburg, reference was also made to a peculiarity of the distribution of both *Pyxicephalus adspersus* and *Tomopterna delalandei cryptotis* in the caption to Figure 2 under a, viz. that these animals are absent from the coast from northern Natal to East London and Port Elizabeth respectively. As these are burrowing frogs, soil conditions suggested themselves as possible factors, as mentioned for *Pyxicephalus adspersus*, but nothing significant could be noticed on a geological map. The Weather Bureau publication WB. 28 was examined, as mentioned, and a number of suggestive patterns were observed, the figure relating to Average Annual number of Days with No Sunshine (Fig. 24) being one of the first to be noticed. Since the figures concerned, Figures 24 to 27, and also the larger figure of Average Annual Duration of Sunshine, Figure 20, were too small for meaningful zoocartographic work, attention was transferred to rainfall, which might be expected to relate to cloud cover. The 801+ mm per annum rainfall area seemed to correspond reasonably well to the region from which the anurans in question were absent, and large versions of Poynton's distribution maps were therefore matched to the 1 : 500 000 rainfall map in W.B. 28. The results were sufficiently encouraging to warrant redrawing of the 801+ mm per annum area on to a map blank with a ¼° grid, similar to that used by Poynton (1 : 400 000). The described distributions of various anurans were then matched to this template (Figs. 3–14). It will be noticed that subjectivity in plotting of both the climate factor (rainfall) and the distributions is avoided because existing maps were used.

Certain anurans appeared to be more or less confined to the 801+ mm per annum regions in the east, but several also extended westward in the south, close to the regions of 801+ mm per annum rainfall areas, i.e. the Cape Mountains. The general pattern thus observed was closest, in the east, to the line indicating 100 days per annum with 0·25 mm or more rain in Figure 144 of W.B. 28, and closest in the west to the corresponding 80 days per annum line. Correspondence was noticed to the line in Figure 120 indicating 60" (1 524 mm) per annum evaporation from Symon's pans, and in Figure 121 to the line indicating 70" (1 758 mm) per annum evaporation from Class "A" pans. As rainfall is the only factor plotted with sufficient accuracy in W.B. 28, only consideration to this will be given; from the foregoing it should be clear that it is not thereby implied that rainfall directly determines distribution. It should be noted that local relief could increase rainfall considerably, or could decrease it in the case of rain shadows. The present author is indebted to Mr. R. S. Crass for a reminder that rain forest occurs at Victoria Falls and to Mr. B. R. Stuckenberg for suggesting the usefulness of the distinction between orographic and cyclonic rain.

Table 3 summarises the correspondence between locality records of southern African anurans and ¼° squares with 801+ mm rainfall per annum over more than half of the square, with 801+ mm somewhere in the square, and with less than 801 mm throughout the square. The areas south of 22°S, i.e. just north of the Limpopo (and hence the northern

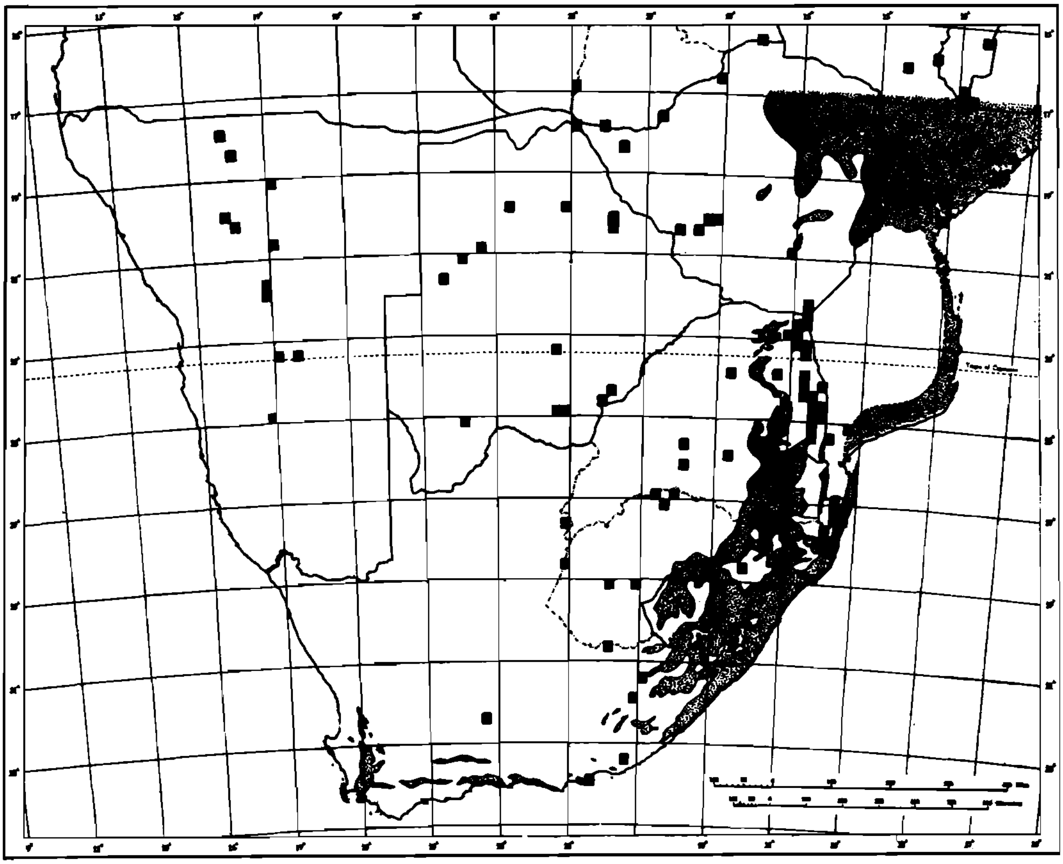

FIGURE 3
Pyxicephalus adspersus.

limits of the Republic of South Africa), and between 22°S and the northern limits of the rainfall map at about 17°S, are recorded separately. It will be noticed that clear patterns in the south are only occasionally as clear north of 22°S. In examining the maps corresponding to the Table (Figs. 3 et seq.) the area south of 22°S should first be examined alone, preferably by covering the upper part of the map.

It will be noticed in Figure 3 that *Pyxicephalus adspersus* occurs south of 22°S in only six ¼° squares which appear to be within the 801+ mm area (all marginal). One of these squares has the weather station Wakkerstroom in it, where 759·7 mm per annum is the mean figure recorded, while two of the other squares are also exceptions in other cases, viz. Van Reenen and Lake St. Lucia. The coast from Kosi Bay to Port Durnford (containing the stations Mseleni, Ntsengwane and Mosquito Hill, Cape Vidal, St. Lucia Eastern Shores and Village and Estuary, Sibuluwane, Kwa-Mbonambi, and Richard's Bay) is likewise an area where other anurans otherwise largely restricted to the less than 801 mm regions occur,

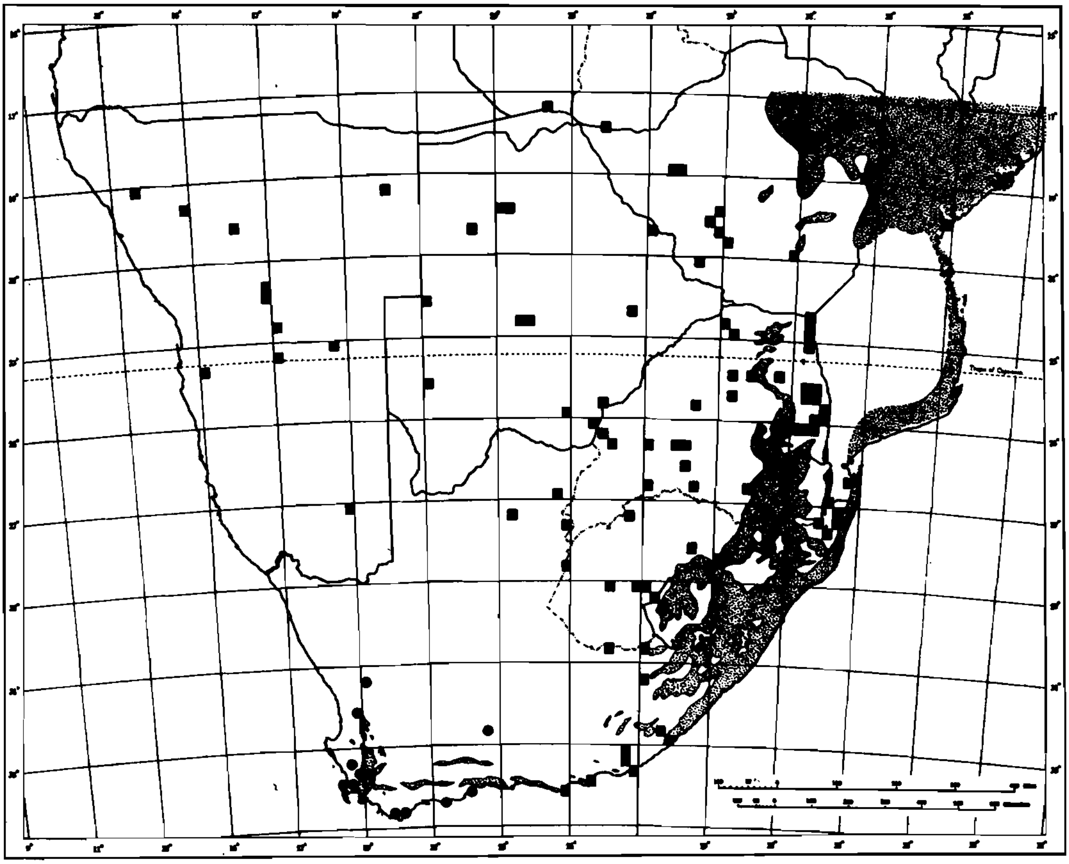

FIGURE 4
Tomopterna (*Pyxicephalus*) *delalandei cryptotis.*

and *P. adspersus* occurs at Mseleni and Port Durnford. *Tomopterna* (*Pyxicephalus*) *delalandei cryptotis* (Fig. 4) occurs in only three ¼° squares which appear to be within the 801+ mm area. These are all close to the margins of the area and represent the localities Morija (Lesotho), Nkandhla, and, again, Van Reenen. Nkandhla has 882·0 mm per annum mean rainfall, but the forest floor is exceptionally steep and well-drained, with water only at the bottom of very deep gorges, the name, which signifies "The place of exhaustion", referring to the steepness. *Tomopterna natalensis* (Fig. 5) shows a distribution roughly complementary to that of *T. delalandei cryptotis*, being found mainly in the areas with 801+ mm rainfall per annum, while *T. tuberculosa* (Fig. 5) is found in the 801+ mm region north of 22°S. Neither *P. adspersus* nor *T. delalandei cryptotis* show a pattern of avoidance of high rainfall areas north of 22°S in Rhodesia and Moçambique.

Cacosternum nanum (Fig. 6), as recorded by Poynton, closely follows the 801+ mm

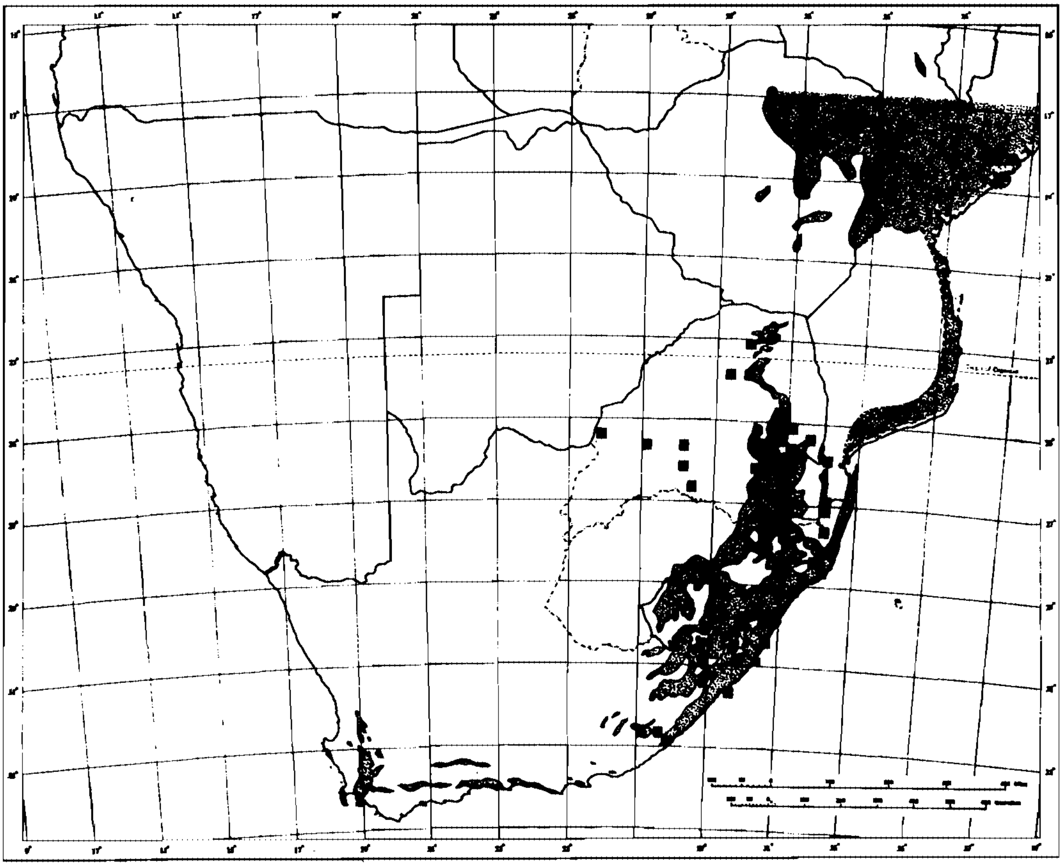

FIGURE 5
Black squares: *Tomopterna (Pyxicephalus) natalensis*; black circles: *T. (P.) tuberculosa.*

per annum area except at Mossel Bay, Cape St. Francis, Grahamstown and Port Alfred. The Grahamstown–Port Alfred area is highly variable, while Cape St. Francis is adjacent to a coastal 801+ mm area, and the north shore of Mossel Bay is close to 801+ mm areas in adjacent ¼° squares northwards and eastwards. Table 4 analyses the known rainfall figures for stations in the ¼° squares in which *C. nanum nanum* and *C. nanum parvum* are recorded. In cases such as Port Alfred and Grahamstown the figures elsewhere in the same ¼° square may be considerably different. Where there are no weather stations with rainfall data in the ¼° square, the data of the rainfall map are more fully recorded. There are apparently errors, marked by asterisks in Table 4, in the localities in the map, but these are not important except in that the reliability of all the maps becomes suspect. It should also be remembered that evidence was quoted suggesting that *C. boettgeri* has sometimes been identified as *C. nanum*. *Cacosternum boettgeri* (Fig. 7) has a distribution mainly in the areas with less than

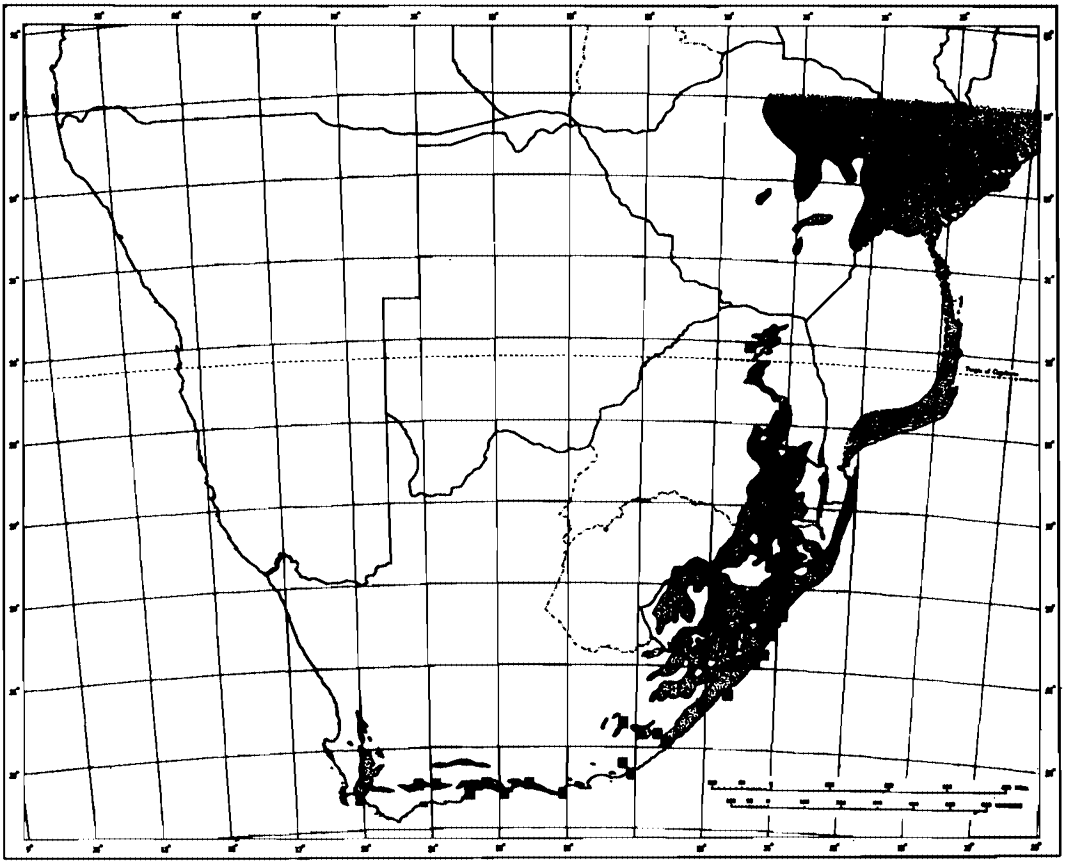

FIGURE 6
Black squares: *Cacosternum n. nanum*; black half squares: *C.n. parvum.*

801 mm rainfall per annum, both south and north of 22°S. *C. boettgeri* lives in short grass, or *Restio* stands in the Cape, in open sunny places, and breeds in flooded meadows or pools with grassy (or *Restio*) verges, whereas *C. nanum* lives and breeds in more shady places, such as reed-beds and pools in bush. The type of habitat favoured by *C. boettgeri* is very rare in undisturbed areas with a rainfall of more than 801 mm per annum, but occurs wherever bush has, or reeds have, been cleared and short grass has been planted.

In Figure 8 and Table 5 it will be seen that *Hylambates* (*Kassina*) *wealei*, as recorded by Poynton, is mainly in the 801+ mean rainfall areas and does not extend far from such areas. The problem raised by the specimens at Grootvadersbosch (3320Dc) was referred to above. The record for Lidgetton (2930Ac) is apparently misplaced in the map, but this is not directly important. *Hylambates senegalensis* is common in the drier areas, but is found in many of the localities with more than 801 mm of rain per annum. What was said of *C.*

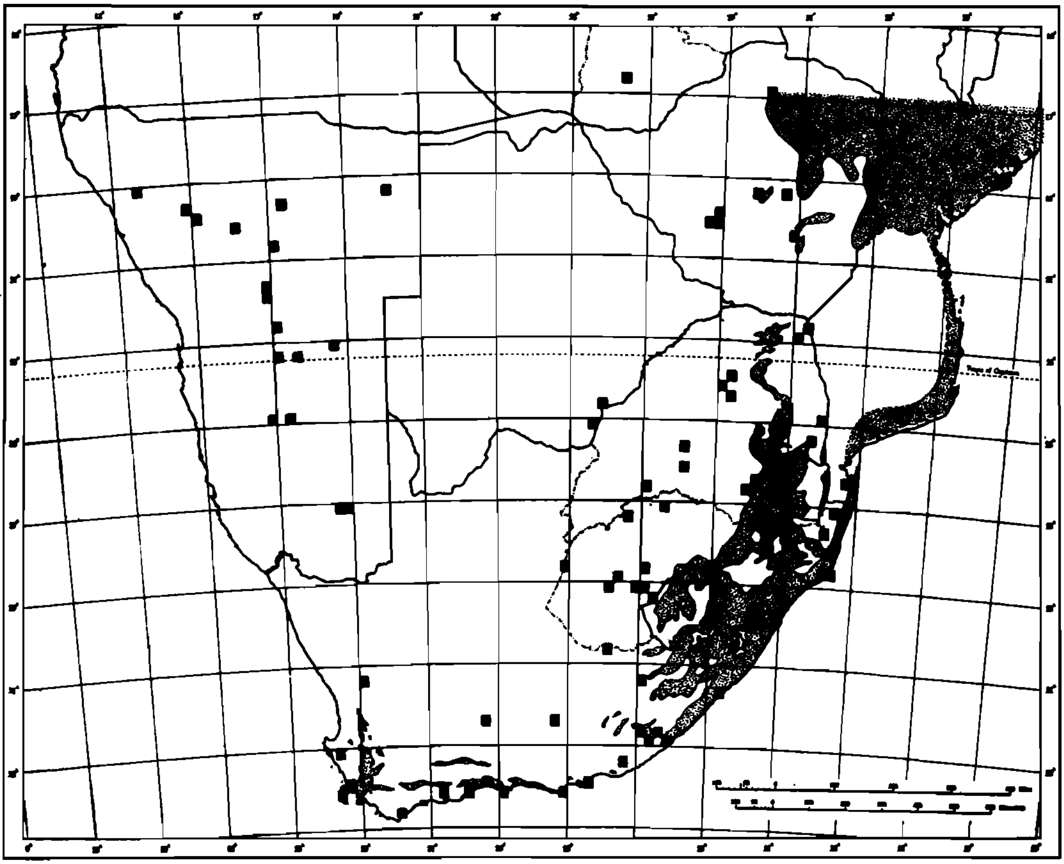

FIGURE 7
Cacosternum boettgeri.

boettgeri habitats above is also applicable to *H. senegalensis,* except that deeper water with considerable aquatic vegetation is required for breeding.

Reference was made to the possibility that *Hemisus guttatum* occurs in Angola. In southern Africa the species is only known from areas with 801+ mm rainfall per annum (Fig. 9). *Hemisus marmoratum* (Fig. 10) is recorded south of 22°S from localities with less than 801 mm rainfall per annum, except for the localities Hluhluwe and Lake St. Lucia, which are exceptions in several other cases. It will be noticed that, as in the cases of *Pyxicephalus adspersus* and *Tomopterna delalandei cryptotis,* north of 22°S no rainfall-related pattern can be observed. The factors operative may also be operative all the way along the Moçambique plain and so may account for the records in areas with high rainfall along the coast to about 29°S of anurans otherwise more or less confined to areas with less than 801 mm rainfall per annum.

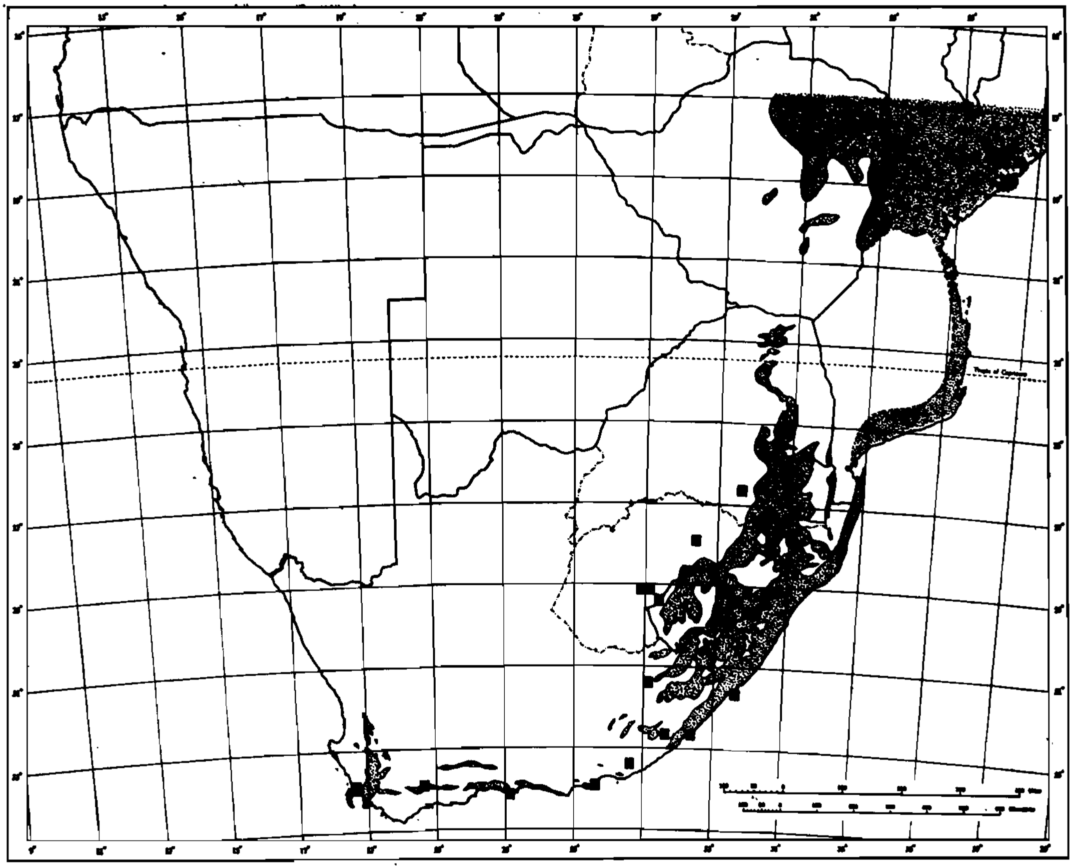

FIGURE 8
Hylambates (Kassina) wealei.

Strongylopus (Rana) fasciatus (Fig. 11) is recorded mainly from localities in areas with 801+ mm rainfall per annum both south and north of 22°S. Since *S. fasciatus* is a winter-breeding frog (at least in the summer-rainfall area), it is interesting that a similar pattern is observed to that seen in rainy-season breeders. *Strongylopus (Rana) grayi* (Fig. 12) is likewise recorded mainly from localities in areas with 801+ mm rainfall per annum, but it is also recorded from dry localities, including Kuboos (less than 100 mm), Mariental (101–200 mm), Vosburg (188·5 mm), Touwsriver (210·6 mm) and Van Rhyn's Pass (401–500 mm). Without these five localities, the species would appear on a map to show good correlation with high rainfall, thus illustrating very well the hazards of conclusions drawn from a map alone. *S. grayi* has adapted itself well to living and breeding in wattle and poplar plantations, and poplars are often seen on Karroo farms where there is sufficient borehole water, but how the species could spread to isolated farms is difficult to conceive.

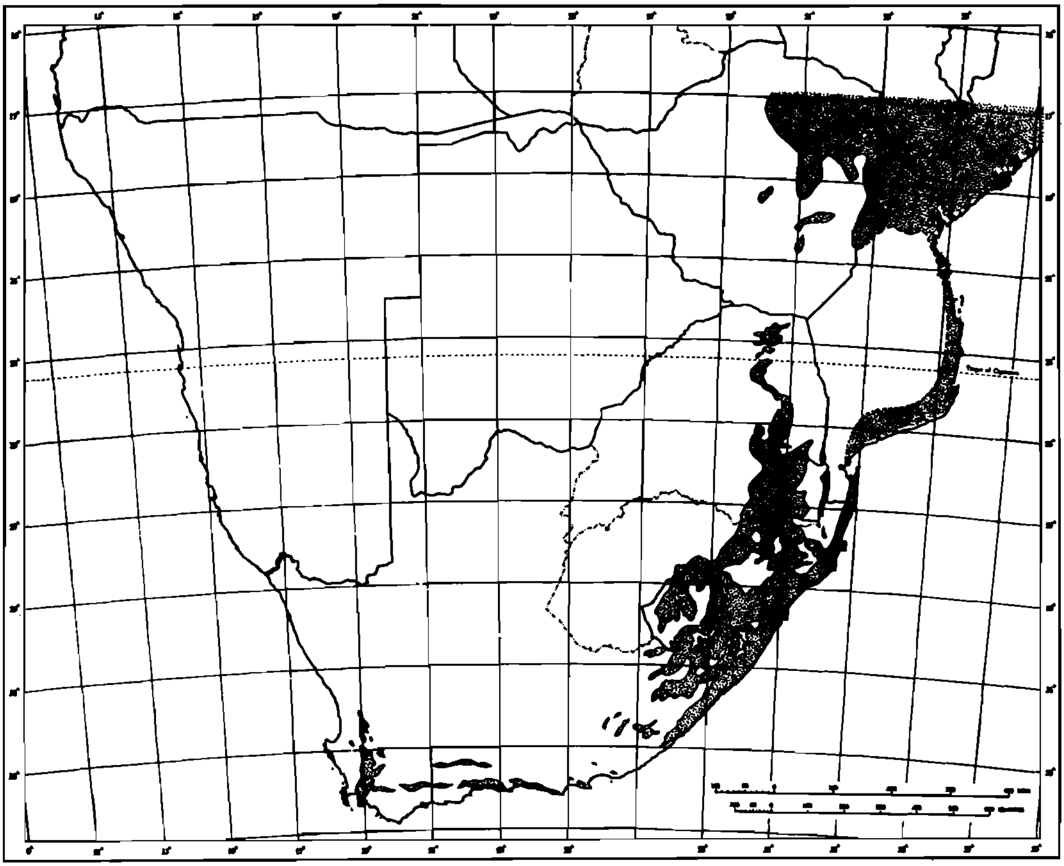

FIGURE 9
Hemisus guttatum.

Ptychadena porosissima (Fig. 13) appears to follow the ¼° squares with 801+ mm mean rainfall per annum very closely, both south and north of 22°S, being recorded in only two ¼° squares which lie wholly outside the 801+ mm areas. Of these two records one refers to Rustenburg, where there is a weather station at which the mean annual rainfall is recorded as 670·0 mm. The 700 isohyet, however, passes close to Rustenburg, and the rainfall in Rustenburg Kloof may be expected to be considerably higher than that of the surroundings, hence accounting for it being known as a beauty spot. (The Rustenburg ¼° square is also a locality of *Tomopterna natalensis*, see Figure 5.) The other apparently aberrant record is marked as 1726Dd on the map, but this does not appear to correspond to any of the localities at which the species is recorded. There is a record listed of occurrence of the species at Victoria Falls, 1725Dd, i.e. one degree to the west of 1726Dd, and this is not plotted on the map, therefore the record 1726Dd is presumed to be a mistake. (A locality corresponding to 1726Dd could

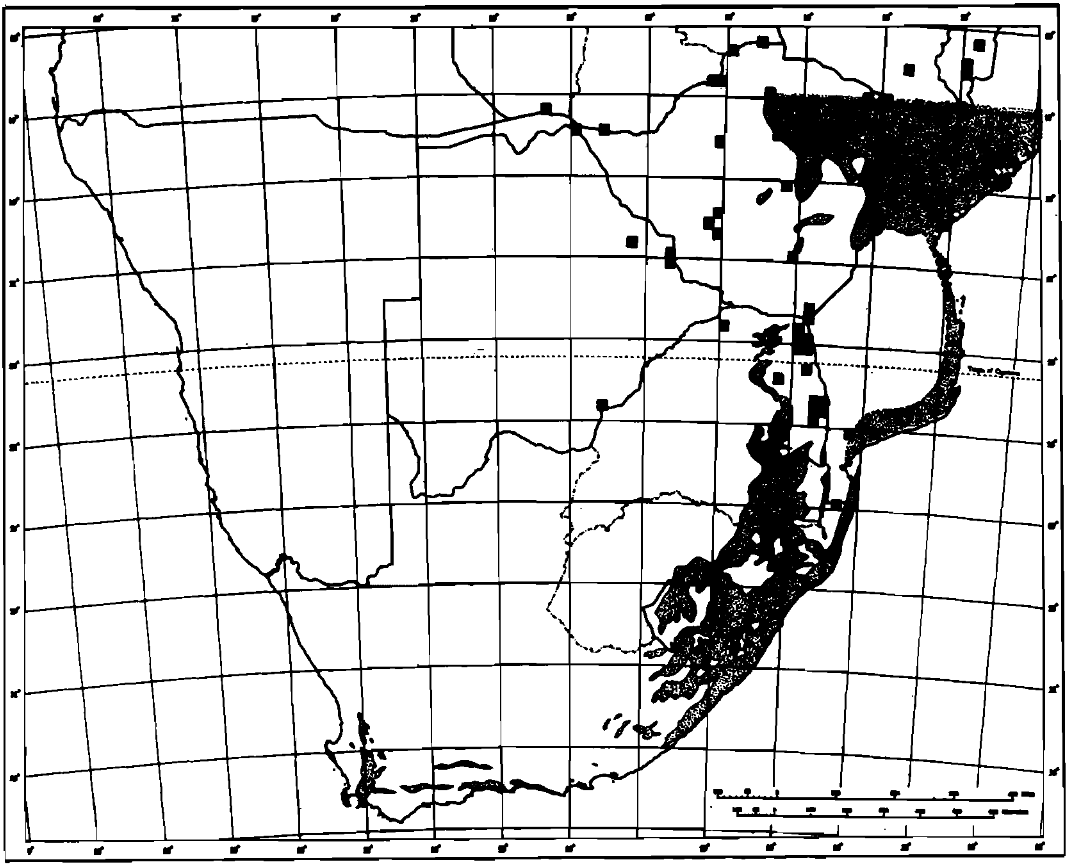

FIGURE 10
Hemisus marmoratum.

not be traced in the Gazeteer, although a cross appears in this square in Poynton's Map 1, showing distribution of collections. The square was found to be marked in the distribution maps of *Phrynomerus bifasciatus*, *Hylarana darlingi*, *Ptychadena anchietae*, and *Ptychadena subpunctata*, while 1725Dd was not marked although Livingstone was listed as a locality in the case of the first three of these species and Victoria Falls in the case of the third and fourth, these localities being the only ones unaccounted for in each case.) Rain forest is present in the spray zone of the Victoria Falls and it would not be surprising to find *Ptychadena porosissima* there if high rainfall was the main factor involved in determining suitable habitats. The distribution of *Pt. mossambica* is approximately complementary to that of *Pt. porosissima* south of 22°S.

In Figure 14 it will be seen that *Strongylopus* (*Rana*) *hymenopus* is shown as occurring

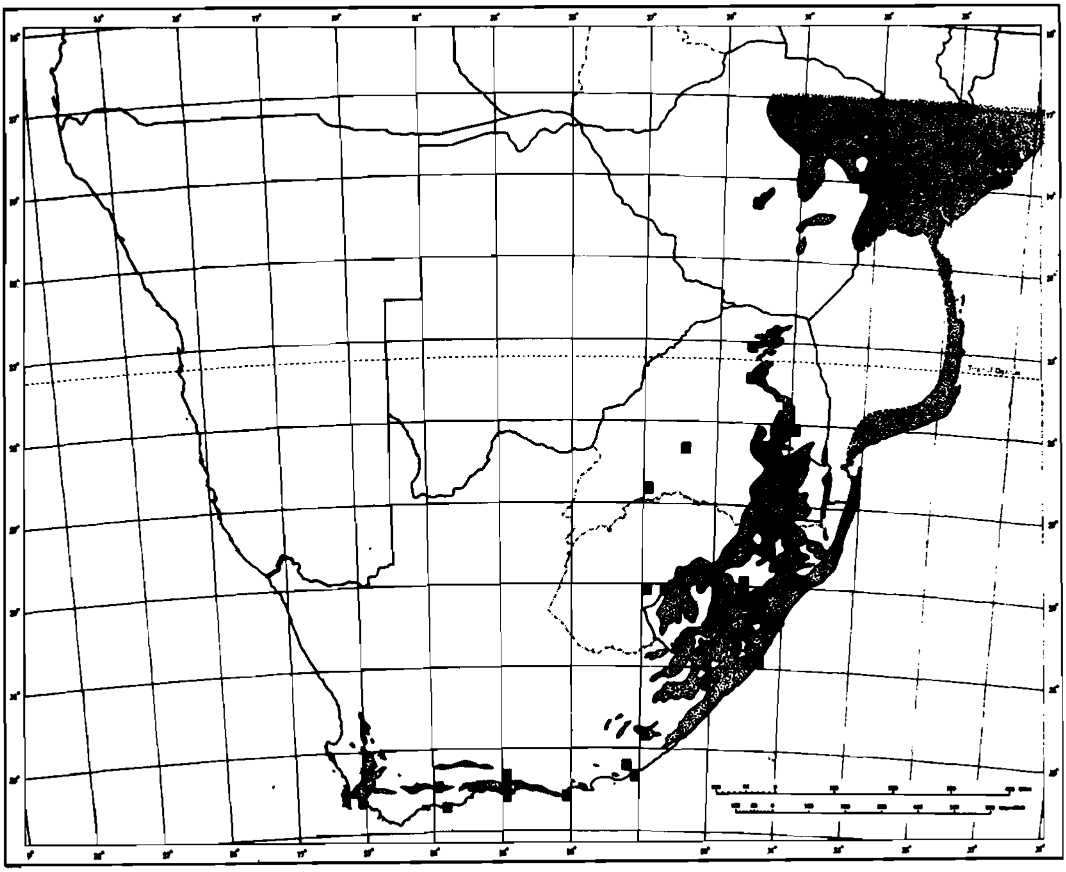

FIGURE 11
Black squares: *Strongylopus* (*Rana*) *f. fasciatus*; black half squares: *S.* (*R.*) *f. montanus*.

in one ¼° square, 2926Bb, in which the rainfall is apparently nowhere more than 801 mm per annum, although no listed locality of the species appears to fall in this square. The locality record Thaba Putsua, 2927Dd, however, is listed, but not plotted, and it is therefore reasonable to conclude that Thaba Nchu, 2926Bb, has been plotted instead of Thaba Putsua, 2927Dd. (Nemahedi Camp is listed as a locality, but does not appear in the Gazeteer in which all localities for all species should be listed. Many other localities listed do not appear in the Gazeteer, although some of them have apparently been plotted, e.g. Lake Sibayi.) The record 2926Bb was considered suspect not only because of the lower rainfall than at the other localities, nevertheless, the discrepancy in regard to rainfall did draw attention to this apparent error, and the hypothesis that distribution correlates (not necessarily directly) with rainfall has apparently proved to have a value in predicting the presence of an error,

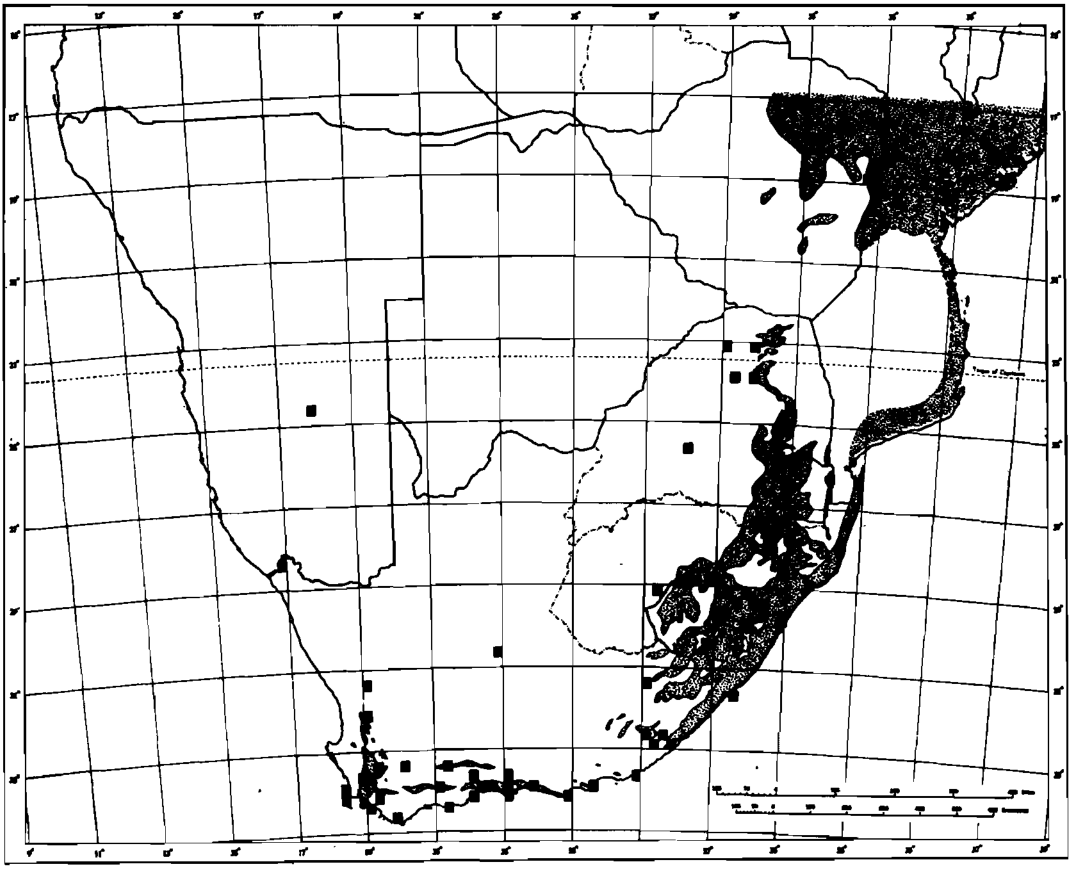

FIGURE 12
Black squares: *Strongylopus* (*Rana*) *g. grayi*; black half squares: *S.* (*R.*) *g. rhodesianus.*

i.e. the hypothesis has, in this case, been weighed in the balance and not found wanting.

From the above it will be seen that the zoocartographic approach has, despite its limitations, some value, for instance in directing attention to possible factors which render such localities as Victoria Falls peculiar. It will also be clear that apparent good fits to particular values of a parameter (mean annual rainfall) south of 22°S, are not necessarily associated with good fits to the same value of the parameter north of 22°S, although latitude sometimes appears to have no effect. This, together with other considerations, including the apparent unreliability of some published distributions, and hence all others from the same work unless checked, make it plain that zoocartography, as an autonomous procedure, is hazardous. The present author considers that rate of change of altitude, i.e. slope, is the most important variable related to anuran ecology, and that this variable must be considered

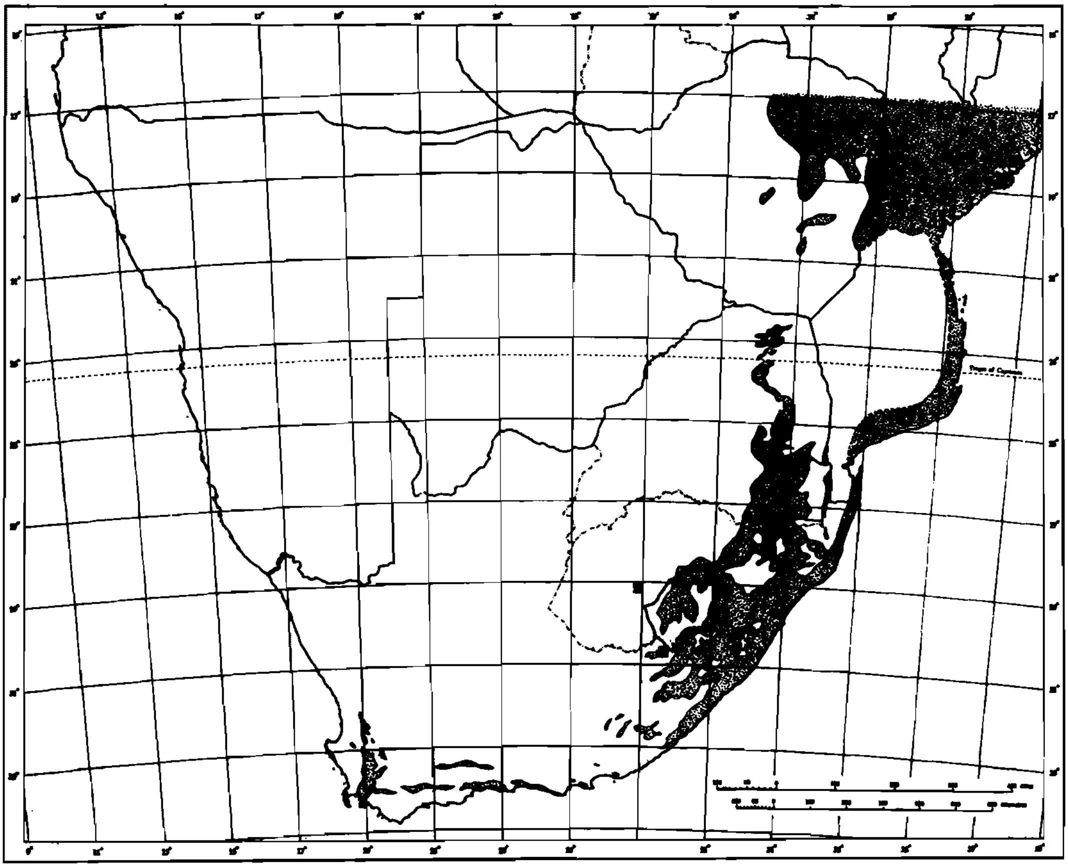

FIGURE 13
Ptychadena porosissima.

in relation to aspect, including absolute altitude and altitude in relation to the surrounding areas, distance from the sea, and latitude (which determines prevailing winds, and also day length and zeniths). The anurans *Heleophryne spp*, *Strongylopus hymenopus* and *S. wageri*, *Rana vertebralis*, and others, are more or less confined to the 801+ mm mean annual rainfall areas, not only because of the high rainfall, but also because the high rainfall is associated, south of 22°S, with high slope (except at the coast). Dr. Olive Hilliard, of the Herbarium, University of Natal, Pietermaritzburg, has pointed out (personal communication) that the distribution of the 801+ mm mean annual rainfall areas is familiar to her from the distribution of some species of the angiosperm *Streptocarpus*, and that species of this genus extending outside the 801+ mm areas are associated with broken ground. Within the 801+ mm mean annual rainfall areas some anuran species, such as *Hyperolius*

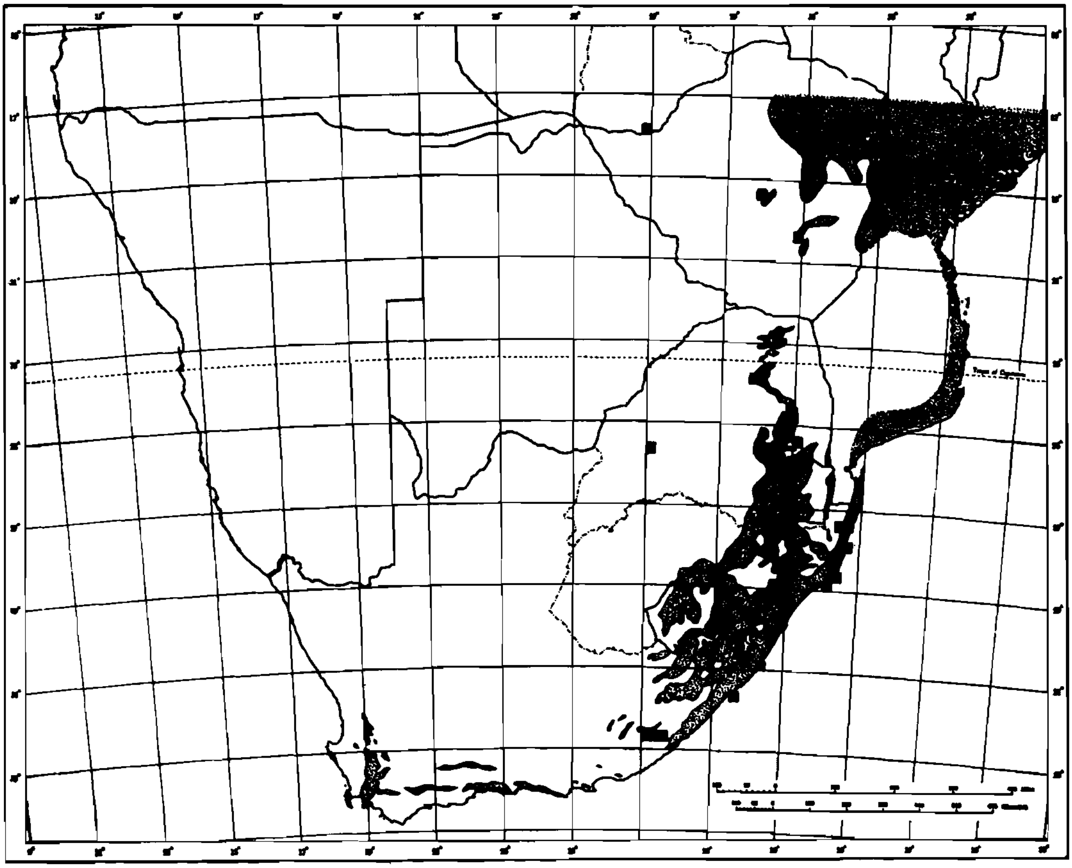

FIGURE 14
Strongylopus (Rana) hymenopus.

tuberilinguis and *Hylambates maculatus*, appear to be confined to the coastal plains.

It will be noticed that the above zoocartographic exercise tends to lead back to direct consideration of the autecology of each species, notably in attempting to understand apparently aberrant localities.

Mean Annual Rainfall and Anuran Distribution

Areas with more than 801 mm Mean Annual Rainfall after W.B. 28 are represented by Shading Superimposed on Maps of Distributions of southern African *Anura* after Poynton from Annals of the Natal Museum, Volume 17, 1964, by kind permission of the editors.

CONCLUSIONS

Summarising, it may be said that the zoocartographic approach may be legitimate when correlations are sought between distributions and variables which can reasonably be expected to have ecological implications – such as *effective temperature* (cf. Stuckenberg in this symposium) – but any attempt at finding variables of ecological significance by reference to distribution maps alone is fraught with danger. Further, the zoocartographic approach to ecology presumes meticulous attention to synonymy and affinities with particular attention being paid to a clear statement (not necessarily in the same publication) of the number of specimens examined at each station, the sexes and states of maturity as well as the dates (or ranges of dates) of collection of specimens, the ranges of size of both males (usually smaller) and females (usually much less commonly collected), by whom identified, whether identified when alive, freshly dead or preserved, and other data which could give insight into the reliability of each locality record. All taxa should be defined with use of means and standard deviations for substantial samples for each numerical criterion and with details of the number of specimens, at which localities, which are distinct or overlap in phenoscopic characters where these observations are used for taxonomic changes. Records in the literature must be exhaustively collected and analysed and improbabilities should be checked as far as possible. This all amounts to saying that the identifications, synonymies and locality records should be expressed as far as possible by a presentation of data which the reader can assess for validity himself, rather than forcing him to rely on the judgments of some other investigator, however reliable that investigator may be.

It is concluded that these conditions can rarely be realised, and that the zoocartographic approach can therefore as rarely be legitimately applied as an autonomous procedure. It is believed that zoocartographic studies may serve a purpose in suggesting further lines of more rigorous investigations, but that the correlations indicated by zoocartographic techniques should always be checked, if this is possible, by direct correlations of the variables with locality records. It is considered that the objections to the zoocartographic approach can largely be circumvented by substituting for such studies, or complementing them with, direct correlations of variables with locality records, as exemplified by Table 1.

ACKNOWLEDGMENTS

I wish to express my appreciation to Mr. B. R. Stuckenberg for many stimulating discussions. I wish also to thank him, Professor A. D. Harrison, Mr. R. S. Crass and Dr. J. C. Poynton for reading the manuscript and making valuable comments.

TABLE 1: MEAN JULY TEMPERATURES (° CENTIGRADE) AT WEATHER STATIONS IN ½° SQUARES

6,0	7,0	8,0	9,0	10,0	11,0	12,0	13,0
			9,2 *Stapleford*			12,1 Inyanga	13,8 Salisbury
			9,0 Rabonie Ranch	10,7 Lobatsi	11,3–11,9 Brits	12,1 Inyanga	13,8 Sinoia
6,8 Harrismith	7,7 Maseru	8,2 Carolina	9,5 Potchefstroom	10,7 Lobatsi	11,0 Pietersburg	12,7 Marandellas	13,8 Salisbury
				10,7 Lobatsi	11,0 Pietersburg	12,1 Inyanga	13,8 Salisbury
			9,5 Potchefstroom	10,4–10,8 Woodbush	11,5 Nylstroom	12,0 (11,7) Gaberones	13,7 Sinoia
							13,7 *Sinoia*
		8,2 Carolina		10,4–10,8 Woodbush	11,0 Pietersburg	12,8 Zebedela	13,7 Sinoia
			9,3 (9,7) Vryburg	10,4–10,7 Kimberley	11,0 Pietersburg	12,8 Palapye Road	13,8 Salisbury
		8,9 Mt. Nuza	9,2 *Stapleford*				13,8 Salisbury
		8,9 Mt. Nuza					
					11,6 Cedara		
		8,9 Mt. Nuza		10,9 Onderstepoort		12,1 Inyanga	13,8 Salisbury
	7,1 Imperani	8,7 Vereeniging	9,5 *Potchefstroom	10,7 Lobatsi	11,0 Pietersburg	12,8 Zebedela	13,4 Fort Victoria
	7,1 Wakkerstroom	8,3 Bloemfontein	9,3 (9,7) *Vryburg	10,7 Lobatsi	11,6 Grahamstown	12,3 Kanye	13,8 Salisbury
	7,1 Wakkerstroom	8,3 Middelburg (Tvl.)		10,4–10,7 Kimberley	11,0 Pietersburg	12,3 Mochudi	13,8 Salisbury
							13,7 Sinoia
						12,7 Marandellas	
		8,2 Carolina		10,9 Onderstepoort	11,2 Rustenburg		13,9 Louis Trichardt
6,8 Harrismith	7,7 Maseru	8,3 Bloemfontein	9,5 Potchefstroom	10,7 Lobatsi	11,0 Pietersburg	12,8 Zebedela	
							Between
						12,7 Marandellas	13,7 Sinoia
				10,7 Lobatsi	11,0 *Pietersburg	12,8 (10,1) Twinthorns	13,1 Mahalopyo

WHERE ANURAN SPECIES ARE RECORDED EXCEPT WHERE INDICATED BY • THE SPECIES ARE "TROPICAL"

14	15,0	16,0	17,0	18,0
	15,1 Mtoko			
	15,6 Nuanetsi 15,6 Emmett		17,5 Komatipoort	*Xenopus muelleri.*
				Bufo taitanus beiranus. Not in any ¼° square in which there is a weather station.
14,0 (12,8–14,3) Pusella	15,5 Skukuza	16,0 Letaba	17,5 Komatipoort	*pusillus*
14,1 Bulawayo	15,3 Maun	16,4 Beitbridge	17,5 Komatipoort	*garmani.*
14,1 Bulawayo	15,1 Mtoko	16,2 Livingstone	17,9 Cape St. Lucia	*regularis*
14,9 (13,7) Umtali	15,1 Mtoko	16,0 Letaba		•*Bufo vertebralis fenoulheti.*
14,1 Bulawayo	15,0 Nelspruit	16,4 Beitbridge	17,5 Komatipoort	*Schismaderma carens.*
14,1 Bulawayo		16,6 (15,6) Maboki		*Breviceps mossambicus.* Also between Bulawayo (14,1) and Inyati (13,9). Only 10 ¼° squares are occupied.
14,1 Bulawayo	15,3 Maun	16,1 Eshowe		•*Breviceps a. adspersus.*
14,1 Bulawayo	15,0 Shabani	16,9 Thankerton	17,9 Cape St. Lucia	*Phrynomerus b. bifasciatus.*
14,9 (13,7) Umtali	15,9 Gokwe			*Arthroleptis stenodactylys.* These are the only ¼° squares with weather stations in which the species is recorded.
14,9 (13,7) Umtali				*x. xenodactyloides.* These are the only ¼° squares with weather stations in which the species is recorded.
14,3 Mfongosi		16,1 Eshowe	17,9 Cape St. Lucia	•*wahlbergi.*
				Phrynobatrachus acridoides. Not recorded in any ¼° square with a weather station. *The locality Nyamakari is adjacent (SE) to Umtali* 14,9 (13,7).
14,6 Chipinga	15,5 Skukuza	16,3 Figtree	17,8 Stanger	*ukingensis mababiensis.*
14,1 Bulawayo	15,1 Mtoko	16,2 Goodville	17,7 Changalane	*natalensis.*
14,1 Bulawayo	15,1 Mtoko	16,9 Thankerton	17,5 Komatipoort	*Rana angolensis.*
14,7 Plumtree	15,3 Maun	16,2 Livingstone		*Pyxicephalus adspersus.*
14,9 (13,7) Umtali	15,1 Mtoko	16,2 Livingstone		
	15,6 Skukuza	16,9 Thankerton		*Tomopterna marmorata.* These are the only ¼° squares with weather stations in which the species is recorded.
	15,9 Gokwe			
	15,1 Mtoko			•*Tomopterna tuberculosa.* These are the only ¼° squares with weather stations in which the species is recorded.
14,4 (12,5, 12,1) Bergvliet	15,6 Emmett	16,9 Thankerton	17,3 Port St. Johns	•*Tomopterna natalensis.* Also adjacent to Heidelberg (Tvl.) 7,7
14,1 Bulawayo	15,1 Mtoko			*Tomopterna delalandei cryptotis.*
				Ptychadena taenioscelis, Not recorded in any ¼° square with a weather station.
		16,2 Livingstone		*chrysogaster guibei.* This is the only ¼° square with a weather station in which the species is recorded. Also adjacent to Mt. Nuza 8,9 and Umtali 14,9 (13,7).
(Ghanzi 13,5 and Maun 15,3)		16,7 (16,9) Empangeni	17,9 Cape St. Lucia	*m. mascareniensis.* These are the only ¼° squares with weather stations in which the species is recorded.
14,4 *Hartley*	15,6 Emmett	16,8 Dukuduku	17,9 Cape St. Lucia	*oxyrhynchus.*
14,7 Plumtree	15,5 Skukuza	16,0 Letaba	17,5 Komatipoort	*anchietae.*

		10,7 Lobatsi	11,2 Kalkfontein	12,0 (11,7) Gaberones	13,8 Salisbury
8,9 Mt. Nuza		10,4–10,8 *Woodbush	11,5 *Little Quendon	12,1 Inyanga	13,2 Gwelo
8,9 Mt. Nuza	9,2 *Stapleford*			12,1 Inyanga	13,8 Salisbury
				12,7 Marandellas	13,8 Salisbury
					13,8 Salisbury
					13,7 Sinoia
			12,0–11,7 Gaberones		13,8 Salisbury
		10,9 Mafeking	11,0 Pietersburg	12,0 (11,7) Gaberones	13,4 Fort Victoria
					13,8 Salisbury
8,3 Bloemfontein	9,3 (9,7) Vryburg	10,7 Lobatsi	11,0 Pietersburg	12,8 Zebedela	13,4 Steynsdorp
				12,1 Inyanga	13,1 Mtao
				12,1 Inyanga	13,8 Salisbury
				12,7 Marandellas	
				12,4 (11,7) Mbabane	13,9 White River

Data after Poynton (1964a) except for records in italics from Broadley (1966).

14,1 Bulawayo	15,6 Nuanetsi	16,2 Livingstone		*mossambica.*
14,3 Mfongosi		16,9 (16,4) Hillary	17,3 Port St. Johns	*porosissima.*
	15,3 Maun		17,5 Kasane	**Ptychadena subpunctata*. These are the only ¼° squares with weather stations in which the species is recorded.
14,6 Chipinga				**Ptychadena uzungwensis*. These are the only ¼° squares with weather stations in which the species is recorded.
				Abrana floweri. Not recorded in any ¼° square with a weather station.
				Hylarana galamensis bravana. Not recorded in any ¼° square with a weather station.
14,7 (13,7) Umtali				**Hylarana darlingi.*
	15,1 Mtoko	16,5 (15,2, 15,8) Leydsdorp		*Hildebrantia o. ornata.*
14,9 (13,7) Umtali	15,5 Skukuza	16,5 (15,2, 15,8) Leydsdorp		*Hemisus marmoratum.*
14,7 Plumtree	15,1 Mtoko	16,3 Figtree	17,5 Komatipoort	*Chiromantis xerampelina.*
				Leptopelis flavomaculatus. Not recorded in any ¼° square with a weather station. Four of the five occupied ¼° squares are adjacent to squares with stations with temperatures below 15°C.
	15,6 Emmett	16,5 (15,2, 15,8) Leydsdorp	17,9 Cape St. Lucia	*Leptopelis concolor.*
14,9 (13,7) Umtali ,	15,1 15,9 Mtoko Gokwe			**Leptopelis bocagei*. These are the only ¼° squares with weather stations in which the species is recorded,
	15,6 *Nuanetsi* (Majinji)	16,7 (16,9) Empangeni	17,8 17,7 Stanger Changa- lane 17,9 Cape St. Lucia	*Hylambates maculatus*. These are the only ¼° squares with weather stations in which the species is recorded. Also adjacent (SE) to Umtali 14,9 (13,7) (Vumba Mts.)
14,4 (12,5, 12,1) Bergvliet	15,5 Skukuza	16,5 (17,3, 17,5) Durban	17,3 Port St. Johns	*Hylambates (Kassina) senegalensis*. Also in ¼° squares adjacent to Maseru 7,7 and Harrismith 6,8.
		16,2 Umbogintwini	17,9 Cape St. Lucia	*Afrixalus fornasinii*. These are the only ¼° squares with weather stations in which the species is recorded.
14,6 Chipinga 14,9 (13,7) Umtali	15,6 Emmett 15,5 Skukuza		17,7 Changalane 17,5 Komatipoort	*b. brachycnemis*. These are the only ¼° squares with weather stations in which the species is recorded.
				Hyperolius argus. Not recorded in any ¼° square with a weather station.
		16,7 Mt. Edgecombe 16,8 Pennington	17,8 Stanger	*tuberilinguis*. These are the only ¼° squares with weather stations in which the species is recorded. Also adjacent to Chipinga 14,6.
		16,8 Dukuduku	17,3–17,5 (16,5) Durban	*p. puncticulatus*. Also occurs in the ¼° square between Empangeni 16,9 (16,7) and Eshowe 16,1.
	15,6 Emmett			
	15,6 *Nuanetsi*	16,7 (16,9) Empangeni	17,7 Changalane	*pusillus.*
14,9 (13,7) Umtali	15,1 Mtoko	16,7 (16,9) Empangeni	17,9 Cape St. Lucia	*n. nasutus.*
	15,1 Mtoko			*marmoratus broadleyi*. These are the only ¼° squares with weather stations in which the species is recorded
14,0 (12,8–14,3) Pusella	15,0 Nelspruit	16,4 Beitbridge	17,5 Komatipoort	*marmoratus taeniatus.*
			16,2 Livingstone	**Hyperolius aposematicus*. There are only two other ¼° squares in which the species is recorded, neither with weather stations.

* Signifies possibly not in localities with July mean over 18°C.

TABLE 2

SOUTHWARD REDUCTION OF "TROPICAL FORMS" ALONG THE EAST COAST
(*Compare Figure* 2)

Hyperolius argus
18°
Ptychadena chrysogaster
Bufo taitanus
Hylarana galamensis
Abrana floweri
20°
Arthroleptis x. xenodactyloides
Leptopelis flavomaculatus
21°

Hildebrantia o. ornata
25°
Phrynobatrachus acridoides
27°
Bufo pusillus

Tomopterna marmorata
Hyperolius marmoratus taeniatus
28°
Xenopus muelleri
Ptychadena mossambicus
Arthroleptis stenodactylus
Hemisus marmoratum

Chiromantis xerampelina

Breviceps mossambicus
Ptychadena taenioscelis

Phrynomerus b. bifasciatus
Ptychadena m. mascareniensis
Leptopelis concolor
Afrixalus b. brachycnemis

29°
Ptychadena anchietae

Hylambates maculatus

Bufo garmani

Hyperolius p. puncticulatus
30°
Schismaderma carens
Afrixalus f. fornasinii

Hyperolius tuberilinguis
31°
Hyperolius nasutus

Bufo regularis
32°
Phrynobatrachus ukingensis mqbabiensis

Ptychadena oxyrhynchus
Ptychadena porosissima
Hyperolius pusillus
33°
Hylambates senegalensis

Phrynobatrachus natalensis

Pyxicephalus adspersus
34°
Tomopterna delalandei cryptotis
Rana angolensis

35°

TABLE 3

NUMBER OF ¼° SQUARE LOCALITY RECORDS OF VARIOUS SOUTHERN AFRICAN *Anura*, WHERE THE MEAN ANNUAL RAINFALL IS RESPECTIVELY MAINLY 801+ MM, SOMEWHERE IN THE ¼° SQUARE 801+ MM, AND WHOLLY LESS THAN 801 MM (DATA AFTER POYNTON 1964a AND W.B. 28)

	South of 22°S			*North of 22°S*		
	Mainly 801+ mm	*Somewhere 801+ mm*	*Less than 801 mm*	*Mainly 801+ mm*	*Somewhere 801+ mm*	*Less than 801 mm*
Xenopus muelleri	2	4	21	5	1	3
laevis	15	13	28	18	1	12
gilli	—	2	2			
poweri				—	—	2
Bufo rosei	3	8	1			
amatolica	—	1	—			
angusticeps	4	3	3			
g. gariepensis ..	5	5	41			
g. nubicola	2	—	—			
g. inyangae				1	—	—
pusillus	1	5	6	13	3	14
regularis	23	9	21	25	3	12
garmani	6	7	39	3	2	25
rangeri	18	21	26			
pardalis	—	7	4			
ngamiensis				—	—	1
v. vertebralis ..	—	—	12			
v. fenoulheti ..	1	4	15	8	3	8
v. grindleyi ..				1	—	—
v. jordani	—	—	1			
v. hoeschi	—	—	5	—	—	3
v. dombensis ..				—	—	3
beiranus taitanus ..				3	—	—
anotis				1	—	—
Schismaderma carens ..	13	6	19	4	3	11
Heleophryne rosei ..	—	1	—			
p. purcelli ..	4	1	—			
p. depressa	—	—	1			
p. orientalis	—	1	—			
p. regis ..	1	3	1			
natalensis ..	10	1	0			

(Continued on next page)

(Table 3 continued)

	South of 22°S			North of 22°S		
	Mainly 801+ mm	Somewhere 801+ mm	Less than 801 mm	Mainly 801+ mm	Somewhere 801+ mm	Less than 801 mm
Breviceps verrucosus ..	15	—	—			
tympanifer ..	—	4	2			
maculatus ..	2	—	—			
acutirostris ..	1	1	—			
gibbosus ..	—	2	—			
fuscus	2	5	—			
s. sylvestris ..	1	1	—			
s. taeniatus ..	—	1	—			
montanus ..	3	1	1			
r. rosei ..	—	1	1			
r. vansoni ..	—	—	2			
namaquensis ..	—	—	3			
macrops ..	—	—	2			
a. adspersus ..	13	10	24	8	4	18
a. pentheri ..	7	1	—			
mossambicus ..	4	3	1	—	—	2
poweri				—	—	3
Phrynomerus bifasciatus ..	5	8	26	8	3	13
affinis ..				—	—	1
annectens ..	—	—	3	—	—	8
Pyxicephalus adspersus ..	6	6	46	8	1	23
Tomopterna d. delalandei	1	4	7			
d. cryptotis ..	3	11	58	3	2	18
natalensis ..	19	16	7			
tuberculosa ..				7	—	—
marmorata	—	3	4	4	1	8
Rana angolensis	36	24	36	21	4	4
fuscigula	14	21	41			
vertebralis	4	1	—			
Strongylopus f. fasciatus	18	10	10	6	3	—
f. montanus ..	2	4	1			
g. grayi ..	23	20	16			
g. rhodesianus				6	1	—
wageri ..	5	—	—			
hymenopus	5	1	See Text			
Hylarana darlingi ..				10	2	2

(Continued on next page)

(Table 3 continued)

	South of 22°S			North of 22°S		
	Mainly 801+ mm	Somewhere 801+ mm	Less than 801 mm	Mainly 801+ mm	Somewhere 801+ mm	Less than 801 mm
galamensis bravana				2	—	—
Hildebrantia o. ornata ..	—	—	9	8	1	3
Ptychadena oxyrhynchus ..	21	4	3	14	3	6
porosissima ..	18	7	1	5	2	1
mossambica ..	1	1	25	5	1	10
anchietae ..	9	12	37	9	2	13
taenioscelis ..	4	1	—	—	—	3
subpunctata ..				—	—	10
uzungwensis ..				10	1	—
m. mascareniensis ..	9	1	1	1	—	4
chrysogaster guibei				3	—	—
Abrana floweri				4	—	1
Phrynobatrachus ukingensis mababiensis	15	8	17	28	2	12
natalensis	26	20	45	22	6	20
acridoides	4	1	1	13	—	—
Microbatrachella capensis	—	—	1			
Cacosternum boettgeri ..	9	12	44	3	2	13
n. nanum ..	16	11	4			
n. parvum	7	4	—			
namaquense	—	—	7			
capense ..	1	1	2			
Arthroleptella lightfooti ..	4	2	1			
hewitti ..	15	—	—			
Anhydrophryne rattrayi ..	—	2	—			
Arthroleptis wahlbergi ..	19	—	—			
troglodytes ..				1	—	—
xenodactyloides				10	—	—
stenodactylus	4	—	—	19	2	1
Hemisus marmoratum ..	2	1	16	10	2	11
guttatum ..	9	—	—			
Natalobatrachus bonebergi	6	—	—			
Cihromantis xerampelina ..	6	9	30	8	3	13

(Continued on next page)

(Table 3 continued)

	South of 22°S			North of 22°S		
	Mainly 801+ mm	*Somewhere 801+ mm*	*Less than 801 mm*	*Mainly 801+ mm*	*Somewhere 801+ mm*	*Less than 801 mm*
Leptopelis concolor ..	5	7	10			
natalensis ..	14	—	—			
bocagei ..				5	3	4
xenodactylus ..	1	—	—			
flavomaculatus				5	—	—
Hylambates maculatus ..	10	3	7	5	—	—
(Kassina) senegalensis	19	11	33	16	3	19
wealei ..	13	5	8			
Hyperolius horstocki ..	—	4	2			
semidiscus ..	10	3	1			
p. puncticulatus	9	2	2	2	—	—
pusillus ..	11	4	9	3	—	1
nasutus ..	12	2	—	18	2	6
tuberilinguis ..	12	7	1	14	—	—
argus				3	—	—
m. marmoratus	14	2	—			
m. verrucosus	5	4	5			
m. taeniatus ..	7	10	23	12	2	5
m. broadleyi ..				15	1	2
m. marginatus				1	—	—
swynnertoni ..				2	—	—
rhodesianus ..				—	—	2
aposematicus				—	—	2
angolensis ..				—	—	1
Afrixalus b. brachycnemis	6	5	8	16	2	—
b. knysnae ..	11	4	—			
spinifrons ..	4	—	—			
f. fornasinii ..	9	2	2	11	—	—

TABLE 4
MEAN ANNUAL RAINFALL (MM) OF LOCALITIES AT WHICH
Cacosternum nanum IS RECORDED BY POYNTON 1964A
(Rainfall data after W.B. 19, 20 and 28)

Cacosternum nanum nanum

Mossel Bay	Cape St. Francis	Garcia Pass	Louws Creek	Hogsback
401–700	640·3	601–801+	701–1 001+	601–1 251+
	Port Alfred	Grootvadersbos	Knysna	Umhlali
	660·3	701–801+	701–1 001+	1 001+
	Louis Trichardt	Katberg	Noetzie Bay	Amanzimtoti
	680·4	701–801+	701–1 001+	1 001+
	Grahamstown	Umfolosi	Wilderness	Uvongo
	697	701–801+	701–1 001+	1 001+
		East London	Krantzkloof	Hibberdene
		771·9	801–1 001+	1 001+
		Hluhluwe	Botha's Hill	Port St. Johns
		794·0	801–1 001+	1 001+
			Mariannhill	Mquanduli
			801–1 001+	1 001+
			*Dullstroom	Loteni
			801·3	1 001+
			Kei Road	*Bulwer
			803·5	1 095·0
			Piet Retief	Stormsriver
			912·6	1 046·3
			Pietermaritzburg	Port Shepstone
			922·4	1 114·3
				Durban
				1 159·6

Cacosternum nanum parvum

Lydenberg	Matatiele	Van Reenen	Champagne	Jambili Forest
645·3	701–800	801+	Castle 1 001+	1 251+
		Mooi River	Cathkin	Woodbush
		801+	1 001+	1 741·7
		Royal Natal		
		National Park	Sabie	
		801+	1 113·9	
		Drakensberg		
		Gardens		
		801+		
		Cathedral Peak		
		801+		
		Haenertsburg		
		853·2		

TABLE 5

MEAN ANNUAL RAINFALL (MM) OF LOCALITIES AT WHICH HYLAMBATES (KASSINA) WEALI IS RECORDED BY POYNTON 1964A (Rainfall data after W.B. 19, 20 and 28)

Near Cape Town 576·9, 545·6. Port Elizabeth 588·6.

Tweespruit 601–700. Thaba Nchu 601–700. Dordrecht 602·1. Near Maseru 687·1. Grahamstown 697.

Morgenzon 701–800. Reitz 704. Grootvadersbos 701–801+. Kei Road 803·5. Royal Natal Nat. Park 801+. Merthley Dam 801+. Boston 801+. Fouriesburg 801+. Underberg 801+. Kei Mouth 801+. Inhluzane 801+. Mooi River 801+. Knysna 701–1 001+.

Champagne Castle 1 001+. *Lidgetton 1 001+. Port St. Johns 1 001+. Loteni 1 001+. Sabie 1 113·9.

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