On species pairs among southern African amphibians

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At least five species pairs of southern African anurans show phenetic evidence of widespread sympatric hybridization. One member of each pair can be designated 'nontropical' (in a thermal, not cartographic sense), the other 'tropical'. Climatic fluctuations in the late Quaternary are seen to be involved in the process of speciation. Present altitudinal and latitudinal zonation of temperature seem involved in the maintenance of present range differences between members of pairs. A relatively complex situation is described in *Breviceps*, where, in the region of Zambia, the separation of one pair appears to be maintained by the intrusion of another pair.

S. Afr. J. Zool. 1982, 17: 67 – 74

Ten minste vyf spesies-pare van Suider-Afrikaanse Anura toon fenetiese bewyse van wydverspreide simpatriese verbastering. Een lid van elke paar kan as 'nie-tropies' (in die termiese, nie in die kartografiese sin) beskou word, die ander as 'tropies'. Klimaatskommelinge in die laat-Kwaternêre tydperk blyk betrokke te wees by die proses van spesiasie. Huidige hoogte- en breedtesonasie in temperatuur is blykbaar betrokke by die handhawing van bestaande verskille in verspreidingsgebied tussen lede van pare. 'n Relatief komplekse situasie word beskryf in *Breviceps* waar, in die Zambiese gebied, die skeiding van een paar blykbaar deur die indringing van 'n ander paar gehandhaaf word.

S.-Afr. Tydskr. Dierk. 1982, 17: 67 – 74

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Received 25 September 1981; accepted 12 November 1981

While taxonomic study of the southern African anurans has in many cases not progressed far enough to allow confidence with regard to the recognition of many sister groups and of derived morphological states, several species pairs or clusters seem to be sufficiently recognizable and zoogeographically interesting to be worth reviewing. In this paper, particular attention is given to pairs that indicate hybridization, on account of their specially dynamic interest. Use of the term 'hybridization' follows that of Woodruff (1973), who applied the term 'sympatric hybridization' to 'cases where the two parental types are broadly sympatric' (p. 216), the most complete expression of this being 'widespread sympatric hybridization' in which 'hybrids are found, together with "pure" or "parental" types, throughout the zone of overlap' (p. 216).

The following species pairs, classified according to their degree of sympatry and hybridization, may be listed. Other possible pairs, such as *Phrynomerus bifasciatus* (Smith)/*affinis* (Boulenger) and members of the *Tomopterna* complex, could be included in the list, but their taxonomy is at present too unclear for them to be usefully considered.

(i) Widespread sympatric hybridization
- *Bufo gutturalis* Power/*rangeri* Hewitt (? also *garmani* Meek): sympatric in the Transvaal, Free State, Natal and Transkei.
- *Breviceps mossambicus* Peters/*adspersus* Peters: sympatric in northern Botswana, Zimbabwe, southern Mozambique, eastern Transvaal, northern Natal. A distinctive form of Angolan '*mossambicus*', hybridizing with *adspersus*, is considered in the Discussion.
- *Phrynobatrachus mababiensis* FitzSimons/*parvulus* (Boulenger): sympatric in Angola, Zimbabwe, Zambia, Malawi, Zaire, Tanzania.
- *Hemisus marmoratum* (Peters)/*guineensis broadleyi* Laurent: sympatric in northern Transvaal, Zimbabwe, southern Mozambique.
- *Hyperolius nasutus* Günther/*granulatus* (Boulenger): sympatric in Angola, northern Botswana, Zimbabwe, Zambia, Zaire.

(ii) Narrow zone of sympatry, occasional indication of hybridization
- *Xenopus muelleri* (Peters)/*l. laevis* (Daudin) + *poweri* Hewitt: sympatric along the edge of Mo-

zambique Plain and the Zambesi Basin (few possible hybrids in Botswana).

(iii) Narrow zone of sympatry, no evidence yet of hybridization

Breviceps mossambicus Peters/*poweri* Parker: sympatric in southern Malawi.

Breviceps adspersus Peters/*poweri* Parker: sympatric in extreme south of Zambia (Livingstone).

Phrynobatrachus acridoides (Cope)/*natalensis* (Smith): sympatric along the edge of the Mozambique Plain.

Afrixalus brachycnemis (Boulenger)/*spinifrons* (Cope): sympatric in southern Zululand.

Other herpetologists would probably add or subtract various pairs according to their conception and evaluation of 'sister species' or 'species pairs': one thing they would probably all agree on is that the pairs listed in Group (i) have (not surprisingly) caused exceptional taxonomic difficulties. Every pair in this group has been treated as a single species at some time in the past, which has not been the case with pairs in the other groups.

Bufo gutturalis/rangeri

The first detailed study of a case of sympatric hybridization in southern Africa was reported by Passmore (1972), who worked on three *Bufo* species. Poynton (1964) had noted 'slight intergrading' in dorsal pattern between *rangeri* and *garmani*, but Passmore showed that in both call pulse rate and in call duration, 'intergrades' studied in Pretoria and Johannesburg involved *rangeri* and *gutturalis* (then called *regularis*) rather than *rangeri* and *garmani*. Passmore's figures of both call pulse rate and of duration show a very wide range of variation, so wide as to include the ranges of both 'pure' parental species as recorded in allopatry. This clearly falls within Woodruff's definition of 'hybridization', and further, satisfies the requirement of Schueler & Rising (1976: 284) that 'an increase in variability and intermediacy in concert constitute the only phenetic evidence of hybridization'. The frequency distributions of pulse rate and duration show no strong clustering, indicating 'free hybridization' as defined by Schueler & Rising (1976) ('no impediment to random mating among the phena at least in the hybrid zone').

The case described by Passmore (1972) is typical of what is understood by 'sympatric hybridization' in this paper. An important zoogeographical feature to note is that *B. gutturalis* and *garmani* are both 'tropical' in the sense used by Poynton (1964: 223): 'a form at least a substantial part of whose range is included in an area experiencing a tropical climate as defined by Köppen'. Both are widespread on the Mozambique Plain and the lowlands to the north (Poynton 1964, Map 9). On the other hand, *rangeri* avoids the Mozambique Plain, reaching the coast only to the south of Durban. Yet it is widespread along the cooler eastern and southern Cape seaboard, and extends over the eastern highlands and eastern plateau slopes. This is a distinctive nontropical range ('eastern transitional', Poynton 1964, Map 12). It will be noted that the other species pairs considered in this paper which show evidence of sympatric hybridization also show this zoogeographical pattern: one member of the pair has a widespread 'tropical' distribution pattern, while the other member is also widespread but has a nontropical pattern. In the other species pairs, however, the (climatically) nontropical member of the pair occurs well within the cartographical tropics, a zone only just reached by *B. rangeri* in the uplands of the northern Transvaal.

Breviceps mossambicus/adspersus

Breviceps Merrem is a genus of completely terrestrial burrowing frogs. In southern Tanzania and northern Mozambique, only one form is recognizable. It is characterized mainly by the absence of light patches or spots over the back and sides of the body, and by the presence of a single gular patch, uniformly darkened to marbled. A clear illustration of this form was given by Peters (1882) in his description of the species *mossambicus*. In the same publication, Peters also described *adspersus* from Damaraland and the Transvaal, named on account of a series of light paravertebral patches or spots, a dorsolateral series of light spots, and a light interocular bar. He noted that the gular region in *adspersus* has paired dark markings, in contrast to the undivided gular patch of *mossambicus*. The *adspersus* markings are consistently shown in material from Namibia, Botswana, the Tansvaal apart from the extreme eastern lowlands, and the Natal lowlands south of the Tugela.

The uniformity in northeastern *mossambicus* and southwestern to southern *adspersus* could justify the retention of Peters' two forms, but most authors in the earlier part of this century placed *adspersus* in the synonymy of *mossambicus*. Subsequently, the two forms were treated sometimes as subspecies, sometimes as full species. The taxonomic uncertainty arises mainly from the fact that material from the intervening area between the ranges of 'typical' *mossambicus* and *adspersus*, namely Zimbabwe and the southern half of the Mozambique Plain, shows tremendous variation: any large series is likely to contain a range from the typical *mossambicus* pattern of no light spots to an intermediate pattern in which dorsolateral but no paravertebral spots are present, to the *adspersus* pattern of both paravertebral and dorsolateral spots (Figure 1).

This situation appears to be a case of 'widespread sympatric hybridization' characterized by Woodruff (1973). So far, there are no indications that the intermediate pattern of only lateral spots has become stabilized anywhere to form a distinctive population as has happened in the case of *Rana 'esculenta'*, resulting from hybridization between *R. ridibunda* Pallas and *R. lessonae* Camerano (Günther, Uzzell & Berger 1979). The dorsolateral spots recall the markings of *B. poweri* Parker from Zambia and eastern Malawi, but *poweri* can be separated from *mossambicus-adspersus* intermediates not only by its characteristic urostylar patch, but anatomically by its very short outer digits and fused digging metatarsal tubercles. No strongly marked geographical grading in the proportion of *mossambicus* to intermediate to *adspersus* individuals occurs. Table 1 shows the proportions of the different patterns in six single series (specimens of the series collected at the same time) from Mozambique to central Zimbabwe; it indicates no particular trend except for a relatively higher representation of the *adspersus* pattern to the west.

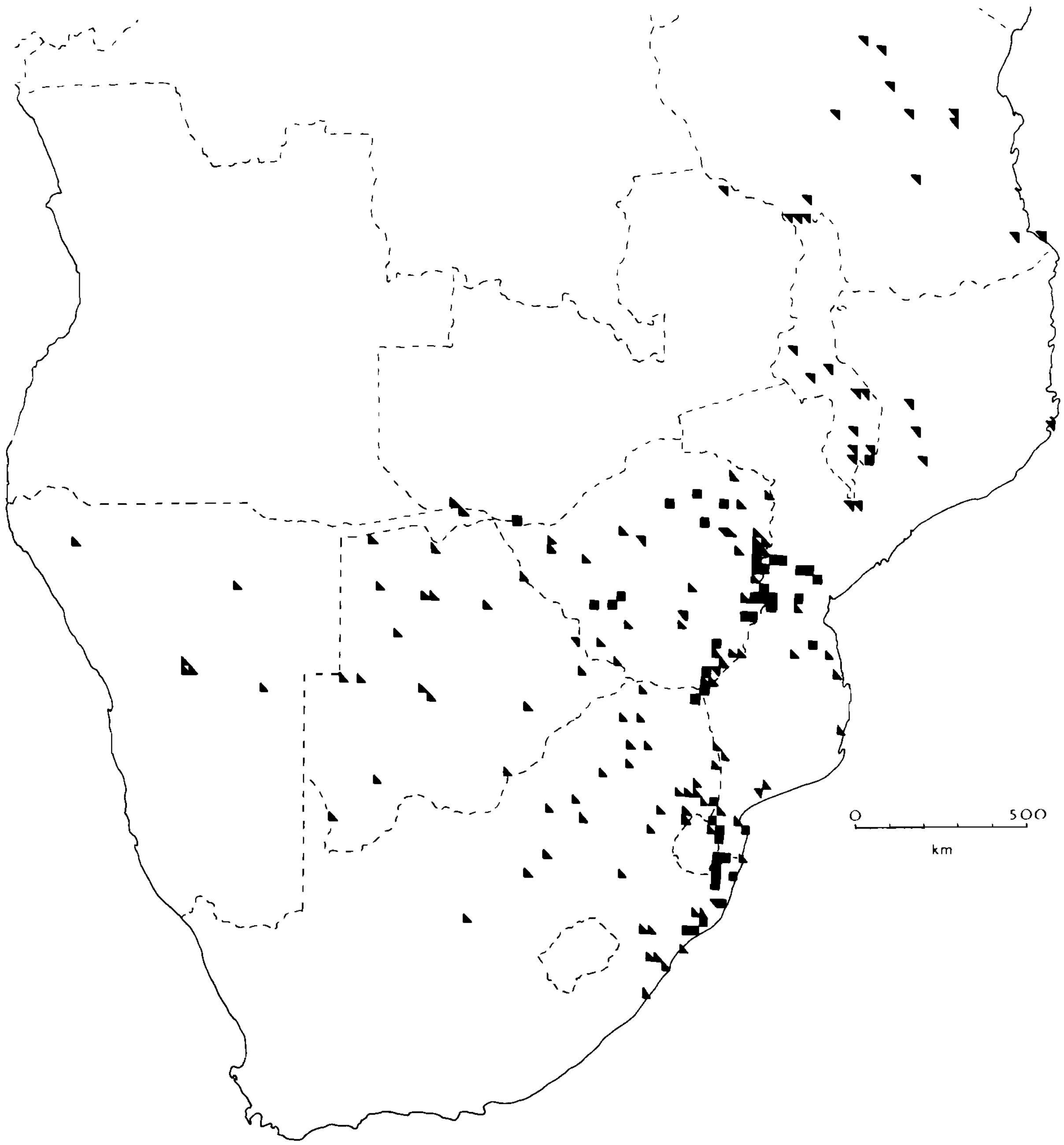

Figure 1 Ranges of *Breviceps mossambicus* ◥, *B. adspersus* ◣, and intermediates ■. West Zambian and Angolan '*mossambicus*', and southern *pentheri*, are not shown.

Table 1 Ratio of *Breviceps mossambicus*, intermediate and *adspersus* patterns in single series (collected at the same time) from various localities. Quarter-degree references are given.

Locality	No. of specimens	*mossambicus* %	intermediates %	*adspersus* %
Mudá — Lamego (1934 A4)	22	14	59	27
Xiluvo (1934 A1)	20	20	55	25
Silverstreams (1932 D3)	8	13	25	62
Nyamwanga (1731 B3)	5	40	40	20
Razi (2030 B2)	6	33	17	50
Umvukwes (1730) B2)	16	13	31	56

Bordering the range of *adspersus*, along the cooler eastern escarpment down to the eastern Cape, is a darkly coloured form (to the extent of being uniformly dark as in *mossambicus*) referable to *pentheri* Werner. The range of this form, perhaps best regarded as a subspecies of *adspersus* (Poynton 1964), is not shown on the map. Angolan material will be considered in the Discussion.

Hemisus marmoratum/guineensis

Hemisus Günther is, like *Breviceps*, a genus of burrowing frogs, but unlike *Breviceps* there is a free-swimming tadpole stage, and digging is done with a hard-tipped snout, not with metatarsal tubercles. Material showing complex variation was referred to a single species, *marmoratum* Peters, by Poynton (1964). Laurent (1972) proposed a new taxon, *guineensis broadleyi*, for some of these specimens. Most available material can indeed be

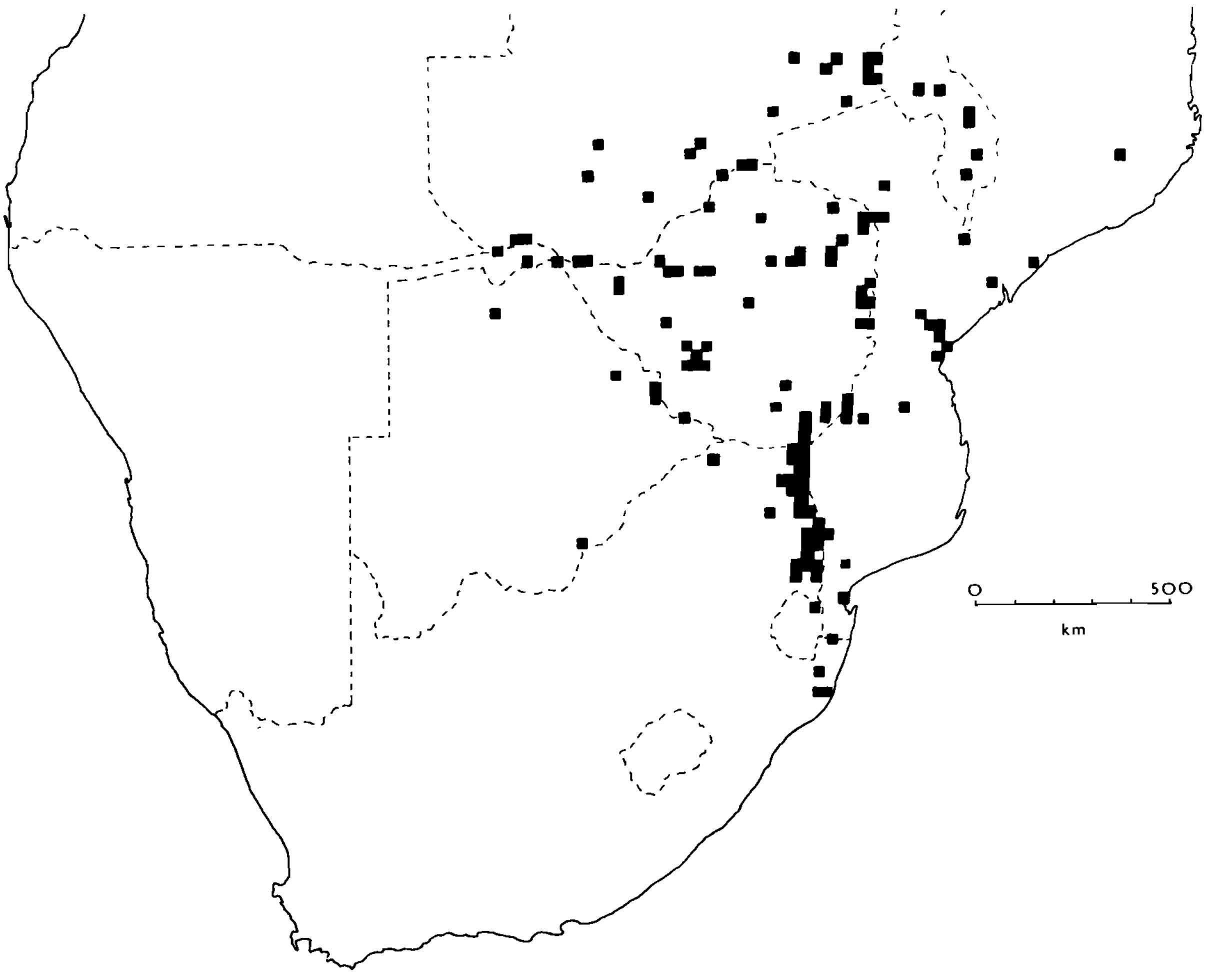

Figure 2 Range of *Hemisus marmoratum* south of 12°S.

separated into *marmoratum* and *g. broadleyi* according to Laurent's criteria, but the criteria fail with some specimens which are not so much intermediate between the two forms as a mosaic of characters from each form. If Laurent is correct in supposing two different species to exist, then the mosaic individuals suggest another case of sympatric hydridization, since they have been collected from scattered points in the common range (Figures 2 & 3). Figure 4 shows the chief characters used by Laurent in diagnosing the two species, and the mixing of these characters in the apparent hybrids, in the form of a hybrid index.

Figure 3 shows *g. broadleyi*, as currently recognized, presenting as decided a 'tropical' distribution as *marmoratum*; however, some differences in markings (presence or absence of light lines) between Mozambique and Zimbabwe material still have to be taken into account taxonomically. Laurent's *g. broadleyi s.s.*, based on a Zimbabwean holotype, may thus turn out to be nontropical.

Hyperolius nasutus/granulatus

In a study of a large collection of reed frogs from the Upemba National Park, Zaire, Laurent (1957) distinguished two species of sharp-nosed reed frogs, although material from four localities presented 'un mélange de caractères'. The two species recognized by him, *H. nasutus* and *H. granulatus*, have been treated as one species by most authors. Recent analysis of southern African material suggests a unimodal rather than a bimodal range of variation in Laurent's chief morphological character, the degree of webbing, and less correlation between webbing and markings than Laurent described. However, plotting the distribution of presumed members of the two taxa and of intergrades or mosaics yields a pattern of distribution suggesting a case of widespread sympatric hybridization.

In preparing the accompanying map (Figure 5), only markings have been used in identifying specimens. Those with a mid-dorsal line of dark spots are referred to *nasutus*; specimens with a pair of light paravertebral bands to *granulatus*. Some specimens show both a mid-dorsal line and paravertebral bands, and these are plotted as intermediates, as also are series where no separation into two taxa seems possible. Specimens showing neither type of marking are plotted as *nasutus*, which is how most herpetologists would identify them. The degree of webbing seems to fail as a diagnostic character: specimens with the *granulatus* type of markings tend more commonly to have more reduced webbing than is shown in specimens of the *nasutus* type, but the range of variation in *nasutus* includes the *granulatus* range.

The resulting distribution pattern (Figure 5) shows the *granulatus* pattern to be present west of the Luangwa Valley and the Zimbabwe escarpment, but not represented in the 'East African' area. In the central and western areas of sympatry, the *granulatus* pattern has been col-

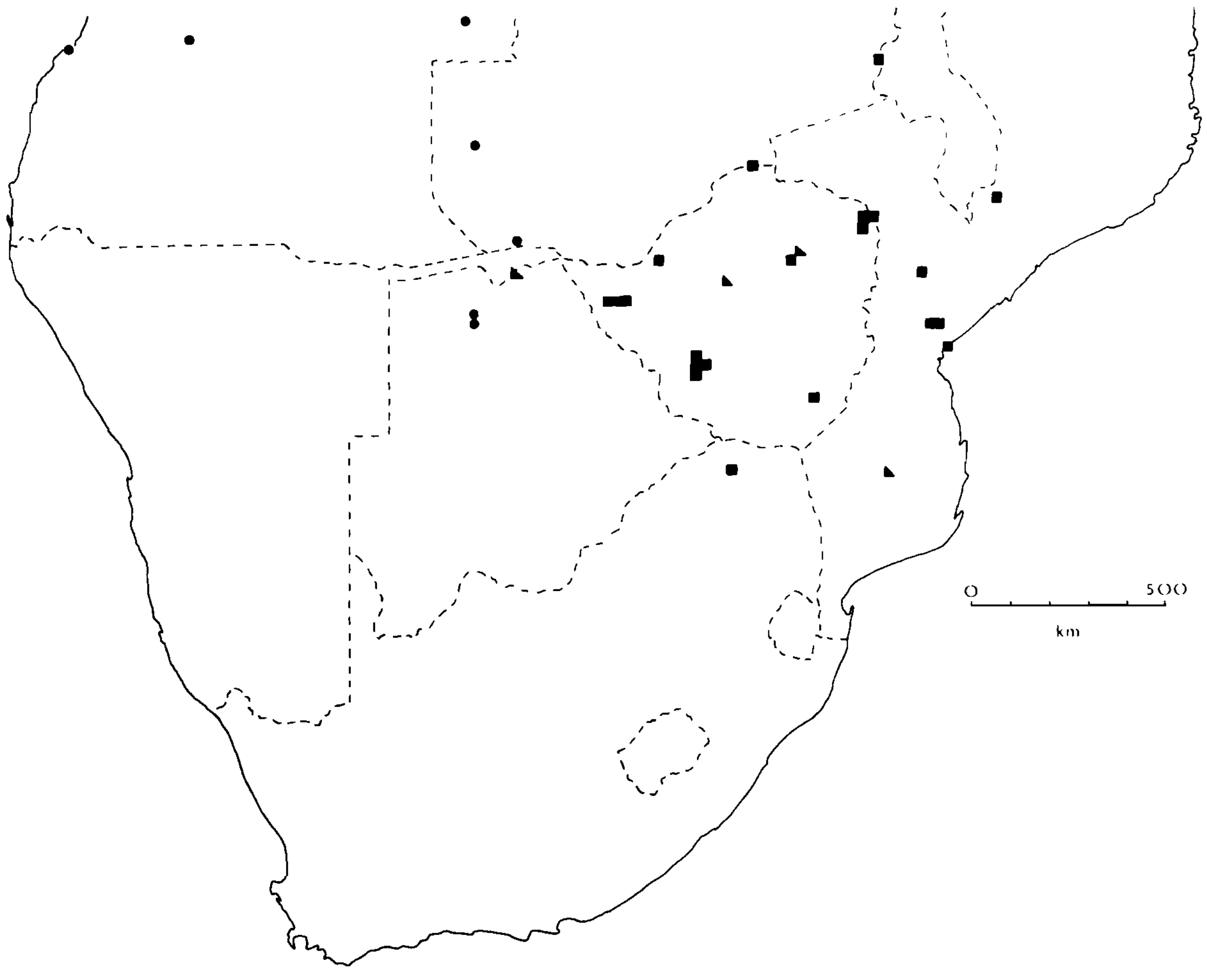

Figure 3 Ranges of *Hemisus guineensis broadleyi* ■, *H. g. microps* ●, and intermediates between *H. g. broadleyi* and *H. marmoratum* ◣.

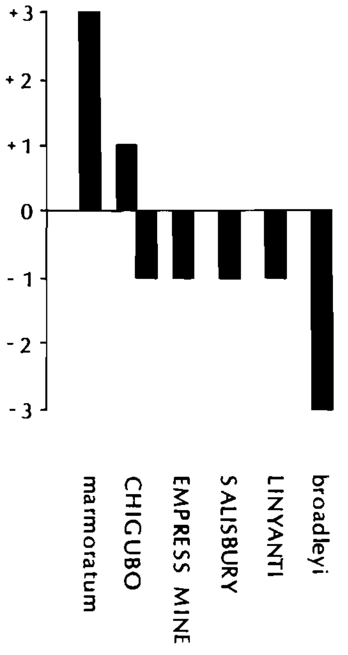

Figure 4 Unweighted hybrid index values of *Hemisus marmoratum* (+3), *H. guineensis broadleyi* (−3), and apparent hybrids from four different localities. Differential characters are: adult size (maximum 30 mm male or 38 mm female = +1; maximum 36 mm male or 46 mm female = −1), 5th toe/length inner metatarsal tubercle ratio (77−160% = +1; 46−77% = −1) and markings (marbled = +1; not marbled, light mid-dorsal line = −1).

lected at only half as many localities as the *nasutus* pattern, and gives some indication of being more common on higher, cooler ground.

Phrynobatrachus mababiensis/parvulus

The pattern of distribution of these two species of dwarf puddle frog is similar to the pattern shown by *Hyperolius nasutus* and *granulatus*. *P. parvulus* is a highland form in East Africa; it is restricted to a higher altitude than *mababiensis* in the Upemba National Park (Schmidt & Inger 1959), and it occurs as an upland species in Zimbabwe. *P. mababiensis* is much more widespread, and it occurs to the apparent exclusion of *parvulus* on the Mozambique Plain, the Limpopo Basin and probably the Mababe Flats. *P. parvulus* shows a tendency to enter forest, which is not shown by *mababiensis*, but both species have been collected in the same dam or vlei in various localities.

The two species have been confused, or at least not consistently separated, by most authors, although Schmidt & Inger (1959) recognized these two species in the large Upemba collection (creating the synonym *cryptotis* for *mababiensis*). As Laurent (1964) has noted, variation and indefiniteness of 'characters' often make separation uncertain, with the result that it is unclear whether phenetically 'intermediate' individuals are true hybrids or not. At least one large series indicates hybridization: a Zimbabwe Museum series of 54 specimens from the Nyika Plateau (Zambia) has some

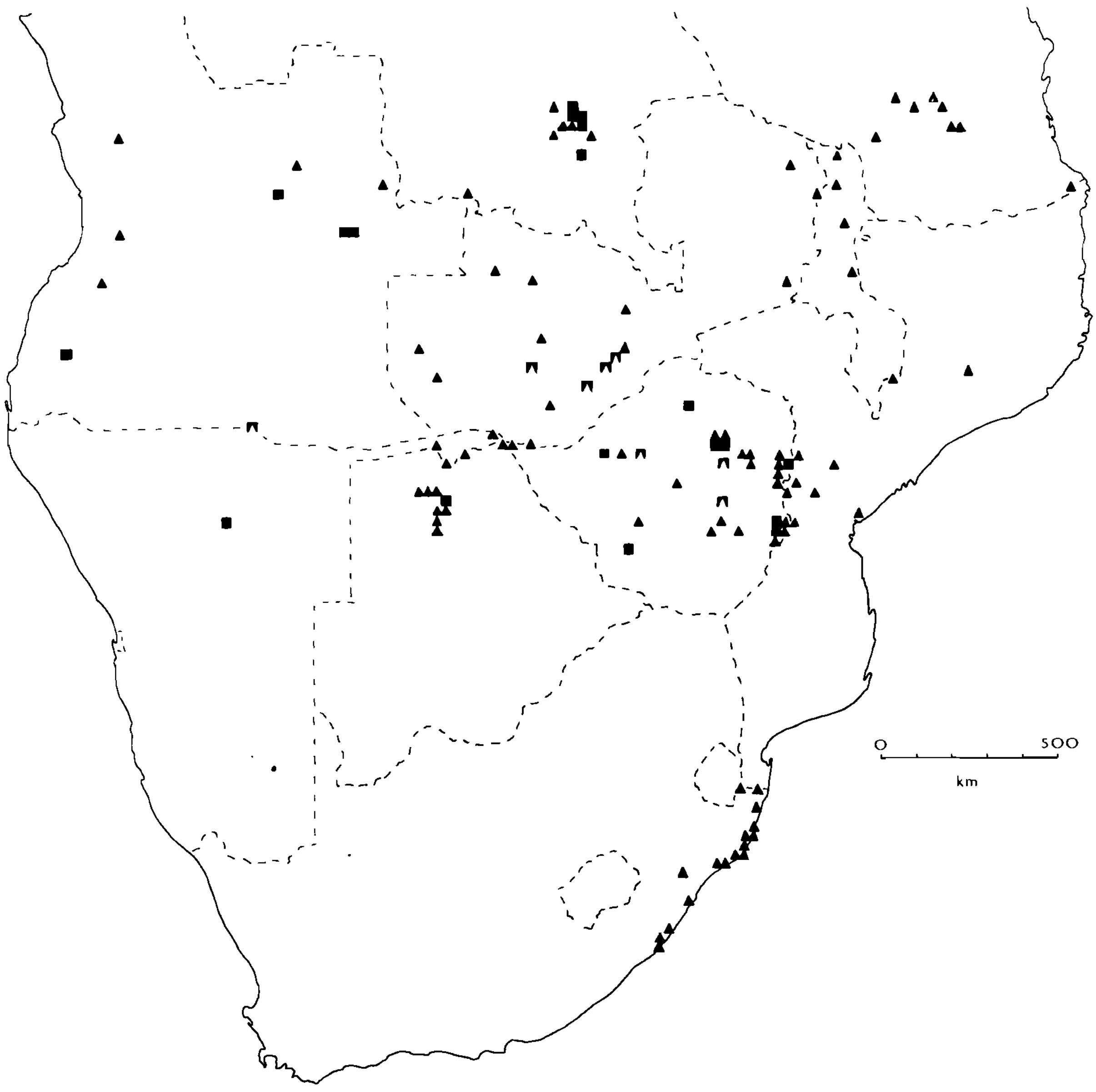

Figure 5 Ranges of *Hyperolius nasutus* ▲, *H. granulatus* Π and intermediates ■ south of 8°S.

specimens that can be selected as 'typical' *parvulus* or *mababiensis*, yet as a whole the series shows apparent independent assortment and intergrading of the characters used by Schmidt & Inger (1959) to separate the two forms.

Discussion

Field data, biochemical analyses and karyological data are lacking in this study, and it can be no more than an assumption that the morphological 'characters' used are acceptably reliable, as they have proved to be in studies on *Rana 'esculenta'* and its parent species (Uzzell & Hotz 1979; Günther, Uzzell & Berger 1979). This assumption has to be made in the face of the fact that some morphologically similar species are quite distinct genetically, while other genetically similar species have quite distinct morphologies (Levinton & Simon 1980). It is also assumed in this paper that cases suggesting hybridization are not primarily the result of habitat alteration following human settlement, since series of apparent hybrids have been collected in minimally altered localities.

If the cases considered here have indeed more significance to zoogeography than simply an array of artifacts, what is suggested by them? In a review of the different forms of the common lizard *Mabuya striata*, Broadley (1977) shows *s. striata* (Peters) to be distributed over the eastern lowlands as far south as Natal, and extending westwards into Malawi and along the Limpopo Basin to Botswana. It intergrades with *wahlbergii* (Peters) and *punctatissima* (Smith), which are distributed in areas to the west and south, with some disjunct highland populations. This pattern recalls features of the anuran patterns just considered. Broadley (1977) states that *striata* 'probably evolved on the East African coastal plain, extended its range to the west coast during a pluvial, and was then split into eastern and western populations during the next interpluvial' (p. 75). Sympatry has resulted from 'subsequent recolonization of the central areas'.

In the case of *punctatissima*, the designation 'western populations' could be 'western and southern', since the range extends south of the *striata* range into the Transkei. A southern component is even more extensively developed in *Breviceps adspersus* (Figure 1), and the same 'western and southern' pattern is shown in the pairs *Xenopus muelleri/laevis* and *Phrynobatrachus acridoides/natalensis* (Poynton 1964, Maps 4 & 47). The southern component could have vicariated as a result of isolation caused by aridification along the Limpopo Basin, separating 'East African' populations from those to the south; but the 'western and southern' ranges also agree with the thermal pattern, since they cover cooler lowland south of the 'East African' coastal region as well as cooler upland to the west, sometimes with disjunct populations on isolated highlands. The designation 'non-tropical' (in a thermal, not a cartographic sense) is therefore suitable for 'western and southern' ranges, although some more comprehensive term may be preferable to emphasize that a whole climatic complex needs to be taken into account when considering the splitting and subsequent interactions of populations.

In the part of Africa being considered, indications are that aridification and hypothermal conditions have tended to be coincident during the Quaternary (van Zinderen Bakker 1978). The joint effect of lowered rainfall and temperature could have been to split ranges in the way envisaged by Broadley for *Mabuya striata*, at the same time selecting for greater cold tolerance in the western and southern populations. An interglacial phase could lead to 'subsequent recolonization of central areas', as suggested by Broadley; but the two daughter species (eastern and western-southern) could well have developed different temperature preferences and tolerances, which would tend to maintain range differentiation in accordance with the altitudinal and latitudinal zonation of temperature. This situation is suggested by all the anuran species pairs considered in this paper, allowing for the taxonomic lack of clarity in the *Hemisus* pair.

The occurrence of hybridization between several pairs suggests that their differentiation has been fairly recent; it could well have occurred during the last glacial period. If this is the case, then the whole process of vicariation and subsequent partial sympatry could have occurred within the last 30 000 years or so.

The vicariance biogeography of Croizat, Nelson & Rosen (1974) would be critical of attempts to explore the situation prior to these events, yet to pass over the dispersal of populations prior to splitting and to evade questions concerning areas of origin is, as Brundin (1981) has recently argued, the result of an unduly restrictive attitude. Broadley (1977), as already noted, has suggested that *Mabuya striata* 'probably evolved on the East African coastal plain' before it 'extended its range to the west coast . . . and was then split into eastern and western populations'. Something comparable is indicated by members of the genus *Breviceps*. This genus shows an ecological and morphological spectrum from sylvicolous species with relatively weakly flanged metatarsal digging tubercles and long toes, to savanna-living species with strongly flanged metatarsal tubercles and reduction in the length of the outer digits (Poynton & Pritchard 1976).

Species represented north of the Limpopo all belong to the latter part of this spectrum. The few collected specimens of Angolan *Breviceps* have all been referred to *mossambicus* (e.g. Parker 1934), but a tendency towards dark lateral banding and dorsal speckling indicates some differentiation from eastern populations. These markings appear to be derived characters relative to the more uniformly coloured eastern *mossambicus*, and the Angolan form could thus represent an 'extension' of eastern *mossambicus* which has become separated along the lines suggested by Broadley (1977) for *Mabuya striata*. Yet, unlike the *Mabuya* case, there has been no 'subsequent recolonization of the central areas': the eastern and western populations are separated from each other by *poweri* of Zambia (excluding the extreme west). It appears that *poweri* is derived from *adspersus* stock to the south; *poweri* shows the greatest development of the metatarsal digging flange (the two tubercles are usually fused into a single spade-like structure) and also the greatest reduction in the length of the outer digits shown in the genus. Botswana-centered *adspersus* is penultimate in these features (Poynton 1964). The Zambesi was presumably a factor in the differentiation of these two species of non-swimming frog, but the presence of both species in Livingstone (Livingstone Museum collection) suggests a complex of factors.

The 'western *mossambicus*' – *mossambicus s.s.* pair and the *adspersus* – *poweri* pair are, geographically speaking, set at right angles to each other; it would seem that *adspersus-poweri* exploited, during one or more periods of aridification or soon after remission, the 'drought corridor' that extended up Botswana and Zambia to Somalia (Balinsky 1962; van Zinderen Bakker 1978), and in doing so tended to maintain the separation of eastern and western *mossambicus s.l.* Nevertheless, substantial movement in latitudinal directions must have occurred, as indicated by *mossambicus* and *poweri* becoming sympatric in Malawi (apparently without hybridizing) and the more similar *mossambicus* and *adspersus* becoming sympatric in Zimbabwe and southern Mozambique, with free hybridization. Specimens from Kalabo and Lukano (Field Museum collection), west of the Zambesi in Zambia, show mixed features such as 'western *mossambicus*' lateral and dorsal markings combined with *adspersus* gular markings, suggesting latitudinal movement in this area as well, with at least some degree of hybridization.

Many of these events are consonant with the differentiation of *Mabuya striata* and *wahlbergii* as proposed by Broadley (1977). But the *mossambicus/adspersus* differentiation, involving the extensive southern range of *adspersus*, calls for a fuller explanation than the idea of a simple — or, as in *Breviceps*, even a complex — east-west 'split'. This is true of other pairs considered in this paper, including the *Mabuya striata/punctatissima* pair, and a very wide field of zoogeographical investigation is indicated.

Acknowledgements

This paper is based on data contributing to a projected *Amphibia Zambesiaca* undertaken with Dr. D.G. Broadley, and I am grateful to him for giving me full access to the National Museums of Zimbabwe collections and for help in many directions. I am also grateful to Mr. W.D. Haacke for allowing me access to the Transvaal Museum collections. Work on this project has been done mainly in the Natal Museum, and I gratefully acknowledge the full range of facilities given me. I am grateful for generous loans of material from the Livingstone Museum, the collection of Mr. A.J. Lambiris, the British Museum (N.H.), the Museum of Comparative Zoology, Harvard, the American Museum of Natural History and the Field Museum of Natural History. Mr. L. Raw has been of assistance regarding literature on hybridization. Professor J.A.J. Meester, Dr. D.G. Broadley and Dr. N.I. Passmore have critically read a draft of this paper; illustrations are largely the work of Mrs. M.W. Poynton and Mr. D.M. Dlamini.

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