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Subspeciation, clines and contact zones in the southern Afrotropical avifauna

by P. A. Clancey

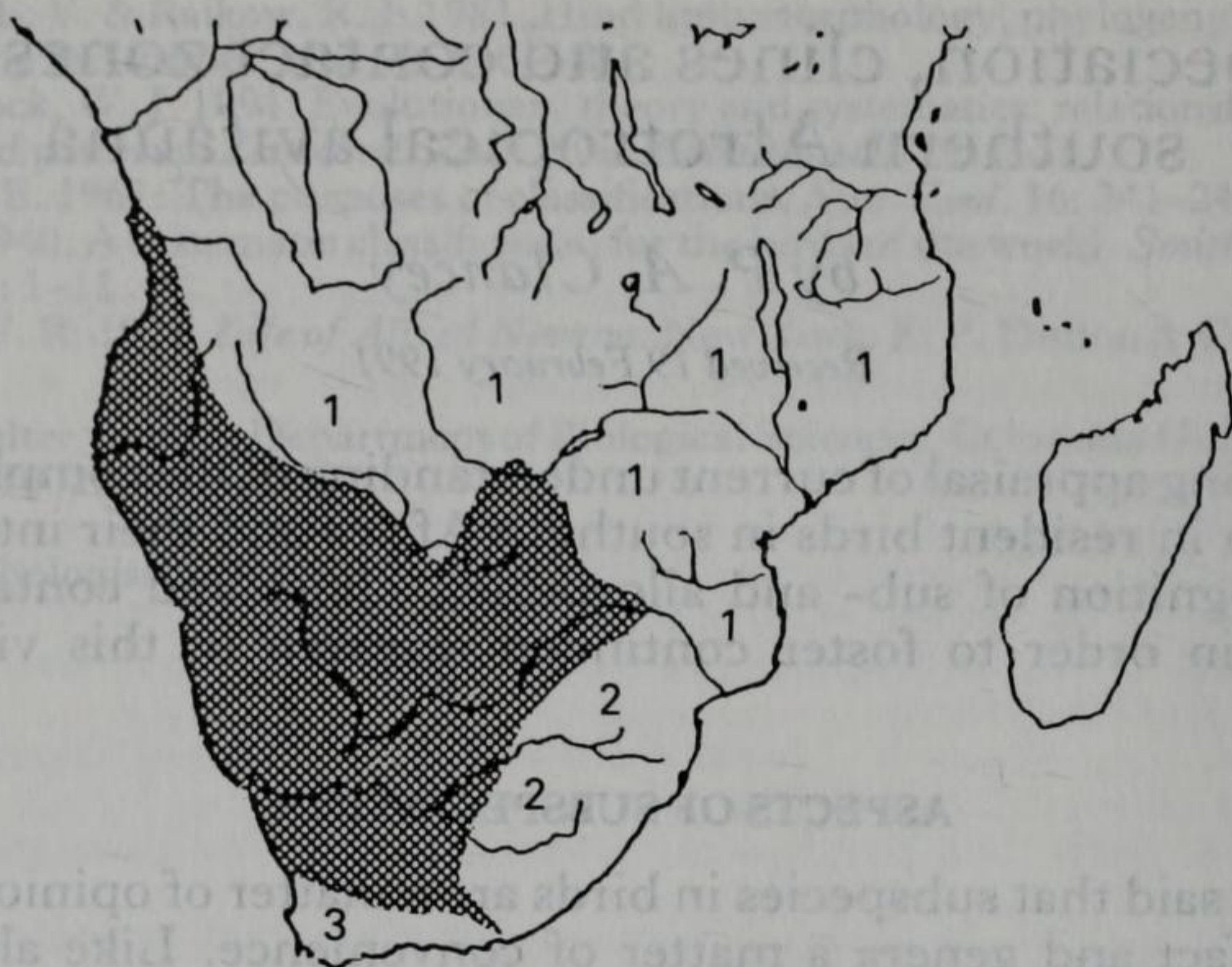
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The following appraisal of current understanding of the complex patterns of variation in resident birds in southern Africa and their interpretation in the recognition of sub- and allospecies, clines and contact zones is presented in order to foster continued research in this vital field of enquiry.

ASPECTS OF SUBSPECIATION

It has been said that subspecies in birds are a matter of opinion, species a matter of fact and genera a matter of convenience. Like all such trite comments, the views expressed are only true in part, but, nevertheless, they correspond with those held by many non-systematists. With effective research, given the requisite material and time to investigate the issues in depth, a conclusion on the desirability of subspecific recognition can assuredly be a statement of fact. The subspecies, albeit sometimes used with a measure of diffidence, will maintain its vital status as the lowest taxonomic category recognised in nomenclatural terms by the International Commission's *Code of Zoological Nomenclature*. It fulfils an integral role in the naming of discrete populations and complexes of distinguishable forms of polytypic species, enabling circumvention of most of the contentious issues encountered by earlier workers who pinned their faith in the maintenance of rigid binomialism. That vertebrates (and others organisms) varied geographically was indeed appreciated by many early taxonomists, who were disposed to rank such variants as full species. Formulation of the subspecies concept dates from about the time of C. W. L. Gloger (1803–1863) and the contemporary publications on evolutionary theory by Charles Darwin.

The effective study of subspeciation in species with largely continuous continental ranges demands ready access to an extensive volume of material, generally far in excess of that held by the largest of museums. In Africa such research is handicapped by the distant siting of basic collections of the continent's birds in European and North American centres, making access difficult and expensive, while in the case of the vital East African sector, virtually all the well-prepared collections formed since the 1939–1945 war are remotely housed in the United States. Conversely, the copious South African and Zimbabwean material brought together since the early 1950s is available in the Southern African Subregion's major museums, and has figured extensively in the research on the avifauna of the south-central, eastern and southern Afrotropics by local ornithologists. In the following discussion I draw freely on data from this research carried out in the south of the continent and to be found in journals of mainly African museums and ornithological societies published between 1950 and 1991.



Map 1. The Afrotropical Region showing the distribution of the South West Arid Zone (shaded) and adjacent environments. 1 = savanna woodlands (mainly Miombo); 2 = mixed forest bushveld and grassland-types; 3 = Cape Fynbos (macchia) and temperate forest.

Variation in the South West Arid Zone

The geographical variation patterns displayed by birds—their races or subspecies—in south-central and southern Africa are in the main prescribed by the disposition of the major plant communities of the South West Arid Zone, which covers rather more than 50% of the Afrotropics south of 16° S. Also influential in this regard are the woodlands of the so-called Miombo savanna juxtaposed to the north and northeast of the said zone, south to the arid valley of the Limpopo R., where the savanna type terminates, these playing a like but rather more restrictive role in the determination of racial range patterns. To the south of these dominant biotic sectors, a mosaic of veld-types, ranging from upland to even alpine grassland, bushveld and, to a limited extent, evergreen forest, both coastal and montane, exert a not indecisive influence in the marked subspeciation of many plastic species.

In a recent study into endemism levels in birds of regions south of 16° S in Africa, but mainly in the South West Arid Zone, c. 70% of the some 170 regional endemics were found to be peculiar to desertic country, a finding supporting the view that this xeric avifauna had remained largely unaffected by the climatic and biome oscillations of the Pleistocene and immediate subsequent times. In contrast, the eastern and southern veld-types present to the south of the Miombo savanna woodlands (which support an interesting range of endemics) are poorly endowed with species peculiar to them, this being the outcome undoubtedly of the ecological history of such habitats stemming from the disturbing expansions and contractions of the Lower Guinea Forest. Such major disruptions affected savanna bird species in particular, leaving to this day their indelible imprint stratified west to east and in the ripple-like configuration revealed in the range-maps of many species and

species-groups. In such situations, the remnant form derived from the primal colonization—now at the level of a discrete species—is confined to a narrow range in the southwestern corner of Africa, with the descendants of later expansionary thrusts lying stratified and at differing stages of evolutionary development disposed to its north and northeast. That the ranges of the individual forms are not infrequently wholly or partially interlarded by untenanted tracts of country is of no small biogeographical significance. This is lucidly demonstrated in the barred bush warblers of the genera *Calamonastes* and *Euryptila* (Clancey 1986, esp. Fig. 3, p. 258).

The broad pattern of savanna species distribution reveals a pronounced continental bias from the northeast to the south in species recruitment, and surprisingly little in the reverse direction. That such southward oriented augmentation is not a thing of the past is clearly illustrated in the increasing occurrence of the Golden Pipit *Timetothylacus tenellus*—an endemic characteristic of the North Eastern Arid Zone—in the northeast of southern Africa from Zimbabwe to the plateau of the Transvaal. Analogous situations exist in some species which extend far beyond the Afrotropics, as instanced by the Long-billed Pipit *Anthus similis*, which extends from the desertic south of the central Palaeartic and northwestern Indomalaya to the northeastern and southwestern drier country of the Afrotropics. These 2 Afrotropical population groups are separated from one another by intrusive elements of the confusingly similar Wood Pipit *Anthus nyassae*, a pipit of the Miombo biome of south-central Africa and discrete from *similis* in both morphology and ecology, which derives from a like but earlier lineage to that of the contemporary *A. similis* (see especially Clancey 1985). The occurrence of *similis* in the southern parts of Africa was seemingly accomplished by leap-frog colonization across unsuitable country and the savanna woodlands inhabited by *nyassae* subspp.

The broad spectrum of the Palaeartic/Afrotropical bird migration system also furnishes instructive similarities, especially so in the cases of northern species which, through the millenia, have founded colonies in Africa, again in the east and south of the continent. Noteworthily, these again are birds of largely open country environments, particularly savanna types, and not of heavy forest. These colonizations tend to underscore the overriding ecological impact which the seasonal unsuitability of the northernmost sector of the Eurasian landmass has for long exerted in the development of survival strategies in many birds; whereas comparable conditions in the southern hemisphere are only to be found to a limited extent in the south of South America and still less so in southern Australasia.

The broad patterns of geographical variation in southern African birds and their taxonomic interpretation are closely correlated with major vegetational facies and precipitation gradients, conforming closely with those found elsewhere in the world where habitats range sequentially from hygic forest, moist and dry savanna to near absolute desert. In species characteristic of the South West Arid ecosystem, mensural variation is circumscribed in inhabitants of savanna woodland-types, but is pronounced in terrestrial feeders such as larks, in which the length and mass of the bill may visibly increase in clear reaction to the hardness of the

substrate. For example, there is a marked increase in the bill-mass in 2 karoooid races of the Sabota Lark *Mirafra sabota* (*M.s. bradfieldi* and *herero*) compared with its other subspecies, of which there are 8, and which are relatively slender billed by comparison. Substrate-related variation in bill-form also occurs in forms of *Certhilauda* spp., especially in the Long-billed Lark *C. curvirostris* and the isolated Red Lark *C. (erythrochlamys) burra*, which hybridizes on its periphery with the more slender-billed Karoo Lark *C. albescens*. Just to complicate matters, there is a marked difference in bill-length and profile between the sexes in certain of the *Certhilauda* taxa, yet, interestingly enough, such plasticity in bill-facies is not evident in nearly all other sympatric alaudids.

The plumage of larks, perhaps more so than other terrestrial birds, also varies with local shifts in ground-colour as well as texture (as clearly shown by Hoesch & Niethammer 1940), yet their overall variation patterns are concordant in many respects with those of polytypic species not overtly affected by edaphic factors, such as the equally terrestrial pipits (*Anthus* spp.). Response to local changes in soil-colour reaches its extreme in the mosaic of subspecific forms in the Spike-heeled Lark *Chersomanes albofasciata*, which highly variable species is centred on the arid zone, but which extends in to country to the southeast and north of its core, and has even founded a distant isolate population in northern Tanzania. Despite the high measure of purely localized response to soil-colour change, the overall pattern in *C. albofasciata* is in line with the norm, in that the more deeply coloured races are found in the mesic south and southeast and the palest along the xeric edge of the Namib in northwestern Namibia. The change from dark to light is a progressional or clinally stepped mosaic-cum-gradient. Fourteen subspecies of *C. albofasciata* are admitted in the 1980 *S.A.O.S. Checklist* for the Southern African Subregion alone, while yet others have been proposed.

In moderately polytypic species other than larks centred on the arid zone, relevant taxonomic variation is generally accommodated by the formal recognition of 4 or more subspecies on characters analogous to those just outlined for austral African larks. In considering other instances of edaphic and phenotypic reaction, the status of both localized and widely fragmented populations breeding on the glaring substrate of saline pans in the interior of northern Namibia and the Kalahari region of Botswana, northeast to northwestern Zimbabwe requires to be mentioned, since more than just larks are affected. These interior localized saline pans are tenanted, often seasonally, by very pallid forms of francolin (*Francolinus levaillantoides* subspp.), sandpipers *Charadrius* spp., coursers *Cursorius* & *Rhinoptilus* spp., sandgrouse *Pterocles* spp., small nomadic larks of the genera *Calandrella*, *Spizocorys* and *Eremopterix*, and pipits *Anthus* spp. Environmental glare and not soil-colour is seen as the deciding factor in determining the colouration of such salt-pan forms.

Variation in the mesic sectors

In the wide range of moister habitats arcing round the arid sector on 3 sides, conditions for extensive subspeciation among savanna breeders

exist, yet, significantly enough, these same habitats carry many fewer endemics. This is an outcome of the dynamics of the biota's Quaternary past. Study of some of the relicts reveals they have responded to the interplay of local ecological factors, for example in both the localized Ground Woodpecker *Geocolaptes olivaceus* and the Knysna Woodpecker *Campethera notata*. *G. olivaceus* is an aberrant eurytopic picid of both Karoo and Afro-montane grassland types, and at some stage in its evolutionary history its range was split and polarized in western and in eastern refugia, the 2 populations later meeting in a zone of secondary contact in the eastern Cape Province (see Clancey 1988). Recent study has confirmed that 3 races are admissible and that an earlier recommendation that the variation was clinal and the species monotypic was unjustified (*pace* Earlé 1986). Regional variation in the forestal *C. notata* pursues a different course, its disposition and morphology being dictated by the nature of its woodland niche, with one race centred on stands of *Euphorbia* and dry bushveld and the other on coastal evergreen rain-forest and its remnants. Its phylogenetic status is somewhat clearer than that of *G. olivaceus*, as its general colour saturation, green colouration and heavy black ventral spotting connote a relationship with contemporary equatorial forest woodpeckers.

In some complexes of what may be termed residual relicts, i.e. relict species without verifiable extinct or surviving relatives, the ancient splitting of the deep southern Afrotropical avifauna into 2 small refugial areas at one stage furnished the isolating mechanism basic to the development of allospecific pairs in the region, as in the sugarbirds *Promerops cafer* and *P. gurneyi*, the rockjumpers *Chaetops frenatus* and *Ch. aurantius* and in the siskins *Pseudochloroptila totta* and *Ps. symonsi*. These allospecific pairs are narrowly distributed west to east in association with the main mountain ranges from the western Cape to the Drakensberg complex in the east, though in each instance the individual species of the pairs are spatially segregated in the critical eastern Cape region (the putative site of the ancient refugial rift). In the case of *P. gurneyi*, a major range extension must have occurred at some stage to found the population present in the eastern Zimbabwe frontier mountains (*P.g. ardens*), and similarly in the endemic bush shrike *Telophorus zeylonus*.

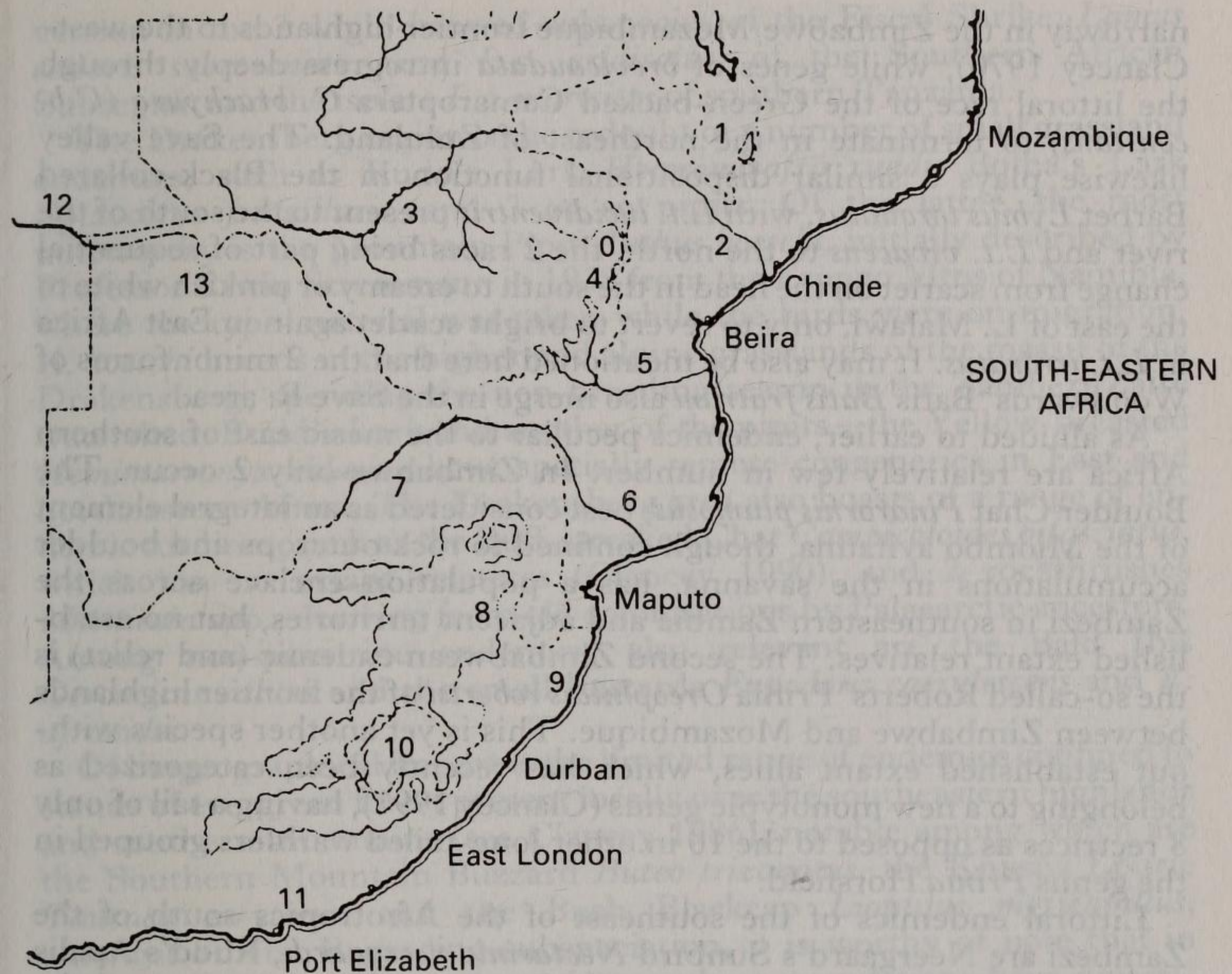
A singularly important faunal area is that of the ecotone which separates the *Fulbernardia/Brachystegia* woodland savanna (Miombo) of south-central Africa from the *Acacia* and associated dry-country vegetation to its south, and which is distributed from southern Angola and northern Namibia eastwards. Here the geographical variation in many birds is in the form of a marked increase in overall size together with the assumption of greyer colouration over the upper-parts, and in some there is a decided thickening of the bill, for example in the race of Red-eyed Dove *Streptopelia semitorquata maxima* and that of the Thick-billed Weaver *Amblyospiza albifrons maxima*; the latter, significantly, parallels a comparable increase in bill-mass in the races of the Yellow-rumped Bishop *Euplectes capensis* in the Cape's Winter Rainfall District. The ecological basis of the increase in size and colour modification in such residents of the southern Angola/northern Namibia ecotone is currently obscure.

The avifauna of the mid-Kunene R. to the west of the ecotone has its composition effectively modified by the ambient aridity of the rivercourse as it transects the Namib. On the other hand, the Okavango R. to the east, which flows through the same ecotone, supports an essentially riverine avifauna, which is disparate yet richer in its species composition. This results from the river's flanking vegetation permitting several forms from the hygic parts of central and northern Angola to penetrate the northeast of the South West Arid Zone. Nevertheless, the vegetation of the mid-Kunene also facilitates some southward range extension in species with equatorial but rather more western affinities. For example, the Kunene race of *S. semitorquata* is the nominate, with *S.s. maxima* (see above) replacing it along the Okavango (Clancey 1986a, 1989b); in the Green Pigeon *Treron calva*, *T.c. ansorgei* is replaced by *T.c. damarensis* along the mid-Okavango. This same pattern is evident in a wide range of other polytypic species, including the woodhoopoes *Phoeniculus damarensis* (in the west) and *P. purpureus angolensis* (in the east), and the Long-tailed Glossy Starling *Lamprotornis mevesii* with *L.m. violacior* and *L.m. benguellensis* in the west and nominate in the east (Clancey 1973). Of moment from the ecological standpoint is the parallel bronzing in the plumages of *P. damarensis* and *L.m. benguellensis*, which are sympatric in the southwest of Angola.

Over the plateau of Zimbabwe and adjacent Mozambique, thence extending on to the littoral plain, is the southeastern terminal block of the Miombo savanna, which is effectively sundered from the main stand lying to the north by the dry Zambezi and Luangwa valleys. This partial isolation is reflected in the presence of a range of Zimbabwean races of species either endemic to or closely associated with the plateau sector of the Miombo savanna. However, in the eastern lowlands the influence of any rivercourse sundering of the environment is minor, as the woodlands are continuous, and, strangely enough, the wide lower reaches of the Zambezi and its flood-plain in Mozambique do not form a functional faunal barrier; more or less continuous populations of a species present both to the north and south of the Zambezi frequently do not differ at all racially. Such influence as the west/east faunal divide of the Rift exerts in the distribution of taxa at this latitude in the Afrotropics also appears circumscribed, except in cases such as the turaco (lourie) forms *Tauraco livingstonii* and *T.(l.) schalowi*, and, again, in the savanna barbets *Stactolaema whytii/sowerbyi*, which may or may not be conspecific, as frequently treated.

It has not been generally appreciated by those interested in zoogeography that the most effective river faunal divide in the southeast of Africa is that furnished by the mid- and lower Limpopo R., reinforced as it is by the eastward extension of the arid climate of the desertic western and interior landmass of the southern parts of the continent. This last is convincingly shown by the finding of discrete races in the east of Sul do Save, southern Mozambique, of such dry country inhabitants as the small granivores: the Shaft-tailed Whydah *Vidua regia* and the Violet-eared Waxbill *Uraeginthus granatinus*.

The localized Miombo subspecies present on the Zimbabwe plateau are in the main restricted distributionally, while those of the same biome



Map 2. The eastern aspects of the Southern African Subregion showing major geographical features alluded to in the general discussion.

- 1: Rift of Malawi (and Shiré R. valley)
- 2: Lower Zambezi R.
- 3: Mid-Zambezi R. valley
- 4: Zimbabwe/Mozambique frontier highlands
- 5: Save R. (Sabi R. in Zimbabwe)
- 6: Limpopo R. (and terminal limit of the Miombo savanna)
- 7: Upper Limpopo R. valley
- 8: Transvaal Drakensberg Mtns
- 9: Lake St Lucia region
- 10: Drakensberg massif
- 11: Great Fish R.
- 12: Okavango R.
- 13: Okavango R. delta and swamp

in the eastern lowlands normally range well to the north of the Zambezi, as in such forms as the Mashona Hyliota *Hyliota australis inornata*, the Red-faced Crombec *Sylvietta w. whytii*, and the Mozambique Batis *Batis soror*. The Save R., interposed in Mozambique between the Zambezi and Limpopo, forms the contact zone between complexes of some polytypic species; among those which may be mentioned are the boubous *Laniarius ferrugineus* and *L. aethiopicus*, and the camaropteras (bleating bush warblers) *Camaroptera brachyura* and *C. brevicaudata* (which hybridize

narrowly in the Zimbabwe/Mozambique frontier highlands to the west—Clancey 1970), while genes of *brevicaudata* introgress deeply through the littoral race of the Green-backed Camaroptera *C. brachyura* (*C.b. constans*) to terminate in the northeast of Zululand. The Save valley likewise plays a similar dispositional function in the Black-collared Barbet *Lybius torquatus*, with *L.t. lucidiventris* present to the south of the river and *L.t. vivacens* to the north, the 2 races being part of sequential change from scarlet on the head in the south to creamy or pinkish white to the east of L. Malaŵi, only to revert to bright scarlet again in East Africa in *L.t. irroratus*. It may also be mentioned here that the 2 minor forms of Woodward's Batis *Batis fratrum* also merge in the Save R. area.

As alluded to earlier, endemics peculiar to the mesic east of southern Africa are relatively few in number. In Zimbabwe only 2 occur. The Boulder Chat *Pinarornis plumosus*, best considered as an integral element of the Miombo avifauna, though confined to rock outcrops and boulder accumulations in the savanna, has a population enclave across the Zambezi in southeastern Zambia and adjacent territories, but no established extant relatives. The second Zimbabwean endemic (and relict) is the so-called Roberts' Prinia *Oreophilais robertsi* of the frontier highlands between Zimbabwe and Mozambique. This is yet another species without established extant allies, which has recently been categorized as belonging to a new monotypic genus (Clancey 1991), having a tail of only 8 rectrices as opposed to the 10 in other long-tailed warblers grouped in the genus *Prinia* Horsfield.

Littoral endemics of the southeast of the Afrotropics south of the Zambezi are Neergaard's Sunbird *Nectarinia neergaardi*, Rudd's Apalis *Apalis ruddi*, the Lemon-breasted Canary *Serinus citrinipectus* and the Pink-throated Twinspot *Hypargos margaritatus*, currently under threat of extinction from the continuing expansion of its close relative *H. niveoguttatus* (see Clancey 1986).

Variation in southeastern humid lowland forms is manifest in increased saturation and lipid levels and a reduction in size, in line with both Gloger's and Bergmann's rules, compared with conspecific races occurring over the interior plateau. Diminution in size not only affects wing- and tail-lengths, but also the mass of the bill in some species, as in 2 small hornbills—the Southern Yellow-billed *Tockus leucomelas parvior* and the Red-billed *T. erythrorhynchus degens*.

The region immediately to the south of the Limpopo R. is, in the east, dominated by the Drakensberg montane system and its complex mosaic of grasslands, intrusive bushveld and patches of evergreen forest, the avifaunal composition of which, as previously asserted, bears the imprint of the major climatic and vegetational vicissitudes of the Quaternary.

Apart from the actual composition of the bird-fauna are the large breaks in the ranges of some widely distributed species, the gaps consisting of stretches of what, to human eyes, is eminently suitable terrain lying untenanted. The reason for this is obscure, but presumably some ancient disruption in the pattern of colonization, or the dying out of populations through competition or local disease may have precipitated it. Such range disruptions are found in the Olive Woodpecker *Mesopicos griseocephalus* and the Plainbacked Pipit *Anthus leucophrys*, and in a rather different

version in the 2 white-browed subspecies of the Fiscal Shrike, *Lanius collaris subcoronatus* and *L.c. aridicolus*, of the Southern African Subregion and the isolate *L.c. marwitzi* of southern Tanzania.

The Drakensberg region is the redoubt of a number of small grassland endemics, such as Rudd's Lark *Heteromirafrā ruddi*, Botha's Lark *Spizocorys fringillaris*, and 3 or so pipits. Of the latter, the most noteworthy is the Mountain Pipit *Anthus hoeschi*, initially described by Professor Erwin Stresemann in 1938 from the Erongo Mtns of Namibia, where the type-material was taken while the birds were on migration. *A. hoeschi* breeds in the higher and alpine grasslands of the massif of the Drakensberg, spending the non-breeding season in the Zambezi/Zaire watershed. Rudd's Lark and another of the pipits—the Yellow-breasted *Hemimacronyx chloris*—have spatially remote congeners in East and northeastern Africa. The Drakensberg area also boasts of a range of endemic turdines, such as the Buff-streaked Chat *Campicoloides bifasciatus*, which has no extant relatives (Clancey 1990), and 2 rockthrushes *Monticola* spp., deriving from old colonisations by Palaearctic ancestors. Among non-passerine endemics, also relevant are the Bald Ibis *Geronticus calvus* and the small bustards *Eupodotis caerulescens* and *E. afraoides*.

Of biogeographical import is the limited range of endemics confined to stands of evergreen forest present locally over the southeastern highlands and southern mountains (see Clancey 1986), notable among which are the Southern Mountain Buzzard *Buteo trizonatus*, the Knysna Lourie *Tauraco corythaix* and the Bush Blackcap *Lioptilus nigricapillus*, amongst others. Regarding subspeciation, it is worthy of note that in some characteristic forestal species, southern populations have diversified from restriction to a forest environment and now exploit niches in both mesic and xeric habitats, this translating into the development of dry country subspecies. Such birds are the Olive Thrush *Turdus olivaceus* (with the xeric *T.o. smithi* nearing the level of a full species), the Cape Robin *Cossypha caffra* and the small Lesser Double-collared Sunbird *Nectarinia chalybea*, the extralimital parts of their ranges being tenuous and fragmented compared with what is found in the south of the continent. In the sunbird, close analogues in the sub-genus *Cinnyris* replace it to the north of the Limpopo R. (Clancey & Irwin 1978, Clancey 1986).

What may be referred to as the terminal avifaunal division of the Afrotropics, namely the Winter Rainfall District of the Cape, supports a limited number of endemics restricted to the Cape Fynbos (Macchia) biome, dominated by *Protea* and heath *Erica* spp. Among these are the Cape Sugarbird *Promerops cafer* referred to earlier, Victorin's Scrub Warbler *Bradypterus victorini*, the Orange-breasted Sunbird *Nectarinia violacea*, the Protea Seed-eater *Poliospiza leucoptera* and the Cape Siskin *Pseudochloroptila totta*. The entire region is relatively constricted, being centred on the mountains (and then largely on their seaward facing versants) lying to the south of the South West Arid Zone from the Cape of Good Hope, eastwards to just west of Algoa Bay. Taxonomically relevant variation in local polytypic bird species differs little from that defined above for those present in the east of southern Africa, but on the whole shows an inclination towards a still more saturated and heavily marked

dorsal and ventral plumage. Variation in size is limited, but, as shown earlier, can affect bill-mass, as in the bishop *Euplectes capensis*.

AVIAN CLINES IN SOUTHERN AFRICA

The cline concept as initially proposed by J. S. Huxley (1939) has frequently been misapplied in avian systematics, consistently so by some authors who have found its use advantageous in the disposing of otherwise intractable problems encountered in research into geographical variation.

In the southern third of Africa variation interpretable as clinal *sens. strict.*, is to be found in remarkably few birds. Those so affected are largely centred on arid country, the biota of which, as demonstrated earlier, was much less affected by the disruptive events of the Quaternary. In the case of the mesic north and in the east and south, clinal variation has not been found in the many (polytypic) species closely studied in recent years, this finding being a result of the periodically disrupted pattern of faunal augmentation which characterizes the regions' immediate past history.

Amongst the species of the Arid Zone, mensural variation, which is indubitably clinal in form, affects few species, the most notable of which is the Pale-winged Starling *Onychognathus nabouroup*, an endemic extending narrowly from coastal desert Angola to the Karoo of the Cape, where it meets and interdigitates with the nominate race of the Red-winged Starling *O. morio*. In *nabouroup*, size reaches its maximum in the southern Karoo, declining northwards through Namibia to terminate in southwest Angola, the size gradient not being visibly stepped at any point. However, the starkly whiter webs of the remiges of the northern desertic populations (*O.n. benguellensis*) in newly moulted condition can be invoked in the upholding of the 2 subspecies accepted by most workers (*pace* Craig 1988). In a second case, the extensive range of the nominate subspecies of the Short-toed Rockthrush *Monticola brevipes* extends from the mid- and lower reaches of the Orange R. through Namibia to the coastal desert of Angola. The northern populations of *M.b.brevipes* average slightly paler than the southern ones, while the males of the Angolan coastal deme frequently display a pale central chin-stripe. Study, however, has indicated that subdivision of the nominate race is not justified, as the colour transition is essentially clinal and too slight to warrant nomenclatural recognition, and as for the chin-stripe in males, its limited occurrence in the Angolan coast series available does not merit its use. Accordingly, the proposed northern minor race of *M.b. kaokoensis* is not currently recognised and is treated as part of nominate *brevipes*.

A great measure of so-called clinal colour-variation in dry country birds with an extensive continuum of populations in a continental land-mass is in the form of stepped yet graded mosaic-like progressional change involving either single or combinations (suites) of variables. A tendency to form a clinal disposition may only affect a lone variable in a species and not the other characters. The patterns are normally closely concordant with local precipitation or vegetational (major biome) contouring, and are phenotypically correlated as a result. As mentioned earlier, in the arid country and its periphery, steps and local disruptions

in the various character gradients allow of the recognition of some 3–4 subspecies in moderately polytypic species, the pattern being dark in the south and southeast to a pale extreme in close association with almost absolute desert in the northwest. Size shifts pursue a closely similar pattern, with large elements in the cooler south and smaller sized ones in the northwest. Dismissal of variation as simply clinal, thus denying it any formal taxonomic recognition, is frequently based on study of severely limited material, too often collected in a narrow zone of secondary intergradation or on the step of a gradient. Such, assuredly, does not fulfil the scientific requirements needed for the determination of a true cline as envisaged by Huxley.

SOUTHERN AFRICAN PRIMARY AND SECONDARY CONTACT ZONES

In relation to the above issues, the resident bird fauna of the areas of Africa lying to the south of the Limpopo and Orange Rivers furnishes a lucrative field for investigative research. In his highly instructive paper on hybrid (contact) zones in Australian birds, the late Julian Ford (1987) describes them in his 'Introduction' as "regions of steep genetic and phenotypical intergradation between relatively uniform contiguous populations", going on to state that morphological change across geographical fronts may arise locally through selection by an environmental gradient without the involved populations having been previously isolated. As a result primary and secondary contact zones may be difficult to distinguish. The following includes only some of the contact zones identified more recently in southern Africa.

The White-eye *Zosterops* spp. complex resident in the south of and to the south and east of the South West Arid Zone has, in the western populations in which the ventral yellow is restricted to the throat and under tail-coverts, the mid-ventral surface white tinged laterally with buff or grey. To the east of these elements occur 2 plexuses of birds with the entire under-parts yellow. One of these is morphologically part of the western oriented *Z. pallidus* (the subspecies *Z.p. virens* and *Z.p. caniviridis*), while the other is part of *Z. senegalensis*, which lies spatially removed from *Z.p. virens* and *caniviridis*, though just impinging on the former in lowland Zululand. These last mentioned 2 forms hybridize in depth in a contact zone over the Drakensberg Mtns with the western white-bellied forms. This contact zone derives from an earlier invasive thrust by an ancestor of *senegalensis*, the descendants of which in contemporary mode furnish, as stated, a further secondary but largely detached convergence on the southern African endemic complex of *Z. pallidus*.

An instructive mosaic of secondary contacts between close congeners is that of the tightly-knit South African ranges of *Pycnonotus capensis*, *P. nigricans* and *P. barbatus*, with only limited hybridization between the individual paraspecies at points along their range interfaces. An analogous combination is also furnished by the batis forms *Batis pririt*, *B. molitor* and *B. soror*, which range within current limits from Namibia and the Cape east to Mozambique, replacing one another parapatrically without hybridization where their ranges converge. *B. soror* is a Miombo savanna monotypic endemic, whereas *pririt* and *molitor* are polytypic

species of *Acacia* and bushveld savanna woodlands. Here, it is worth pointing out again the hybridizing of the *Camaroptera* spp. forms in the upper Save (Sabi) R. drainage; and allude to the hybridization between the parrots *Poicephalus cryptoxanthus* and *P. meyeri* from southeastern Zimbabwe to the northeastern Transvaal and adjacent Mozambique (see Clancey 1977). This latter case is of significance as *meyeri* does not hybridize with its western allospecies *P. rueppellii* in Namibia. Among the austral African larks one finds a particularly interesting instance in the Dune Lark *Certhilauda erythrochlamys* of the dunes of the Namib Desert in Namibia, which at some stage expanded its range into the extremely arid lower Orange R. basin. The subspecies (or near species) so formed, namely *C. (e.) burra*, the so-called Red Lark, now hybridizes on its range periphery with the Karoo Lark *C. albescens*, which latter even intrudes between *burra* and the Namibian forms of *erythrochlamys* (see Clancey 1989b).

A re-examination of the variation in the southern populations of the Cape Turtle Dove *Streptopelia capicola* (Clancey 1989a) determined that 2 of the local races were derived from longstanding and now consolidated hybridizing events, both races being distinguishable from either of the parental forms.

In the subspecific interpretation of variation in the Ground Woodpecker *Geocolaptes olivaceus* mentioned earlier, this resulted from early splitting of populations between western and eastern faunal refugia, occasioned by the spread of aridity during the Quaternary. The descendants now meet in a broad zone of secondary contact in the eastern Cape.

In cases of what is in effect secondary contact, the contending taxa may not necessarily be physically contiguous, being segregated by an intrusive stretch of untenanted terrain, well shown in the range map of the 2 allospecies of Black Korhaans *Eupodotis afra* and *E. afroides* (see Clancey 1989). In such cases it seems as if the descendants of the initial colonization have withdrawn in the face of the expanding and dynamic secondary colonist. On the other hand, such a range hiatus may have resulted from selection against the resulting hybrids from direct physical contact at an early stage. Further and more detailed investigative research into this detached form of contact by closely allied taxa, of which several others have so far been identified, may help shed some additional light on the possible evolutionary mechanisms involved in their formation.

CONCLUSIONS AND SUMMARY

The Southern African Subregion with its involved mosaic of mesic habitats distributed to the north, east and south of an extensive arid zone, which varies from dry savanna and steppe-like conditions to near absolute desert along the western seaboard, supports a large and varied avifauna, of which some 70% of the 170 determined endemics of the entire subregion are peculiar to the arid sector, namely the South West Arid Zone. Many of these have radiated subspecifically in response to the long-term environmental stasis of this dry region. The mesic environments arcing round this arid sector have by contrast many fewer endemic species; yet the mesic avifauna is both integrally varied and rich. The

TABLE 1
Subspeciation in some Southern African Subregion families

Family	Total of species	No. of subspecies	No. of monotypic species	No of taxa below generic level
Phasianidae	15	39	1	40
Otididae	11	14	3	17
Columbidae	13	30	nil	30
Lybiidae	10	23	nil	23
Picidae	9	25	nil	25
Alaudidae	23	92	6	98
Turdidae	40	97	8	105
Sylviidae (excluding the Cisticolidae)	42	123	2	125
Sturnidae	12	17	2	19
Fringillidae (genera <i>Serinus</i> and <i>Poliospiza</i>)	12	35	3	38

Note. Comparable data for other families can be computed from the *S.A.O.S. Checklist of Southern African Birds* (Clancey 1980) and the revisionary updates of 1987 and 1991.

comparative shortfall in endemic species is a result of the major climatic and vegetational events of Quaternary times.

The magnitude of the resident bird fauna of the Southern African Subregion and its wide range of environments translate into a wealth of subspeciation, as shown in examples in Table 1. Comparable data for other families can be computed from the *S.A.O.S. Checklist of Southern African Birds* (Clancey 1980) and the revisionary updates of 1987 and 1991.

Clines (*sens. strict* Huxley 1939) affecting both mensural and colour variables have been found to be limited in the avifauna present south of 16° S in Africa, and restricted to the South West Arid Zone. No cases have been found among residents in the various mesic vegetational types distributed peripherally to the arid country, assuredly due to the fundamental climatic shifts during the Quaternary and attendant subsequent vegetational and other ecological changes.

Variation, often interpreted as on a cline, may, on critical study, be found to consist of a suite of variables rather than a single one, and disposed mosaically through the entire plexus of populations. In such instances, a clinal style of progressional character shift will normally only affect a single criterion, which, unless stepped at some point, may be disregarded for formal taxonomic purposes.

In examples of primary and secondary contact zones south of 16° S, most of them researched in depth, so far occur in the southeastern lowlands, with some clearly linked to the termination of the *Julbernardia/Brachystegia* (Miombo) savanna on the Limpopo. Most are seemingly cases of primary contact. The Cape Province boasts of a range of secondary contacts, as in the Ground Woodpecker *Geocolaptes*, while among the 3 *Pycnonotus* bulbuls, the paraspecies clearly furnish an example of

secondary contact with minimal hybridization at the interfaces of the ranges. In yet other instances, the taxa are in close geographical but not direct physical contact, and are effectually allospecies, narrowly segregated from one another by untenanted country. The reasons underlying this latter aborted type of contact are as yet only speculative.

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Note: An extended list of additional references dealing with subspecific variation and particularly endemicity in southern African birds may be found in Clancey (1986).

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