

# Combined biogeographic role of river valleys and aridity in Southern African bird distribution

P.A. CLANCEY

Research Associate, Durban Natural Science Museum, PO Box 4085, Durban 4000.

## Summary

Clancey, P.A. 1994. **The combined biogeographic role of river valleys and aridity in Southern African bird distribution.** *Durban Museum Novitates* 19: 13-29. Most endemic bird species in Southern Africa occur in the South West Arid Zone. A smaller number of endemic species occurs east and south of this region, where the avifauna is considerably richer, mainly comprising congeners and subspecies of wide-ranging Afrotropical taxa. More than 490 species with extensive extralimital ranges are involved, reaching southern Africa in the mesic eastern regions. Individual species drop out of the avifauna south of the Zambezi Valley to the Cape Peninsula. The rate of species subtraction is affected by the sundering effects of large rivers on major biomes. In the east, four major river systems have biogeographic relevance, their effectiveness as barriers being enhanced by the aridity of the surrounding terrain. Species subtraction rates vary markedly, 80 dropping out between the Zambezi and Limpopo Rivers, 156 between the Limpopo and Umtamvuna Rivers, and 70 between the Umtamvuna and the Sundays and Great Fish Rivers. The stepped decline in numbers continues to the Cape Peninsula. The Orange River is unimportant as a barrier, though separating subspecies along its lower reaches. In the northern parts of the Subregion, the Kunene, Okavango and mid-Zambezi Rivers enable the southward thrust of tropical species and subspecies in the riverine vegetation into relatively inhospitable habitats.

**KEYWORDS:** *aridity, biogeography, birds, faunal barriers, river valleys, Southern Africa, subtraction rate.*

## Introduction

Most of the 170 species of birds endemic to the Southern African Subregion are restricted to the South West Arid Zone (Clancey 1986a, 1989a, 1992). Over the moister east and south of the Subregion, endemism in the substantially larger bird fauna is markedly less evident, because of its more dynamic immediate past than that of the xeric avifauna with its established longterm environmental stability. The smaller number of endemics in the south and east of the Subregion is attributable to the major climatic oscillations of the Pleistocene, and particularly the interglacial of about 10 000 years BP, with their alternating wet and dry periods and associated forestal changes. Range maps in Hall and Moreau (1970) and (Snow 1978) demonstrate the north-south recruitment of bird species to the avifauna over the east of the Subregion, and the ripple-like nature of the broken range patterns resulting from changing limits in the east of the Lower Guinea Forest to the north. The climatic shifts effectively modified the extent and nature of evergreen forest (both montane and lowland) and plateau grassland and the disposition of their respective bird communities, dry phases facilitating the spread of savanna woodland at the expense of forest and, as a corollary, the radial expansion of savanna-based bird forms both on a north-south and a south-north basis.

Expansion and contraction have occurred as the avifauna evolved in response to recurring habitat changes, this frequently resulting in a compression of the habitat available to a species and even its withdrawal to a refugium. For an indepth consideration of these and like biogeographical issues in the Afrotropics, see Crowe and Crowe (1982).

## Materials and Methods

The bird species and their nomenclature dealt with in the present communication are those listed in Clancey *et al.* (1980, 1987, 1991). The conclusions reached on species ranges and taxonomic status are based on a voluminous literature, much of it reflecting my own personal research on the southern and eastern African avifauna, but also embraces data derived from contributions by colleagues on local bird distribution. Most of the supportive data was published from about 1951 in the *Annals of the Natal Museum*, *Durban Museum Novitates*, *Arnoldia Rhodesia*, *Bulletin of the British Ornithologists' Club*, *Ibis*, *Ostrich* and various other publications. Because of the volume of titles involved, these are not enumerated in the "References" section. Focus on issues germane to the present enquiry, such as those of species relationships and limits, distribution, migration patterns and geographical variation was enhanced heuristically by personal involvement in the extraction of data from collections of specimens and the literature for Hall and Moreau (1970) and Snow (1978).

Other relevant research of mine involved an indepth study of geographical variation in the majority of polytypic species, both resident in and as migratory visitors to the southern half of Africa, the description of a large number of previously undescribed taxa, in a major revision of the regional avifauna following the death of Dr Austin Roberts in 1948. In singularly involved cases of status in terms of the limits dealt with in this field of enquiry, guidance was readily sought in the reports on avifaunas in other parts of the world where there are similar combinations of both arid and moist climatic zones.

The present communication is a contribution to a highly

involved and complex field of enquiry, but I trust that it will lead to further work by others in this fundamental aspect of ornithological research.

### Discussion

Apart from the role played by climatic and vegetational vicissitudes in Africa since the Pleistocene in the present composition of the avifauna, that of putative minor zoogeographical barriers and other range modifiers, such as desertification attendant on short-term climatic irregularities and human agricultural activities, require to be addressed. Benson *et al.* (1962) investigated the role of river valleys as avifaunal barriers, in the case of the Zambezi and Limpopo Rivers through their sundering of tracts of evergreen and largely montane forest, savanna woodland types and grassland biomes; none is sufficiently wide to constitute an impediment to gene-flow on its own, as in the case of major north and south tributaries of the Amazon River in South America, which segregate subspecies, allospecies, species and even genera in a stable forest environment (Capparella 1991). Louette (1992) deals briefly with this issue as it effects major forested rivers in Zaire, central Africa, but found that mainly coucals (*Centropus* spp. and gallinaceous birds (guineafowl and francolins) were overtly affected. Interestingly, major rivers in the equatorial rainforest belt in Africa play a more important role in primate geographical variation patterns and distribution.

In my study of the part played by river valleys in southern Africa, I have extended the field of enquiry to embrace all the more important subregional rivers and have concluded that they are effective inhibitors of gene-flow only when they are sufficiently wide, lowlying and seasonally extremely torrid, and above all, consistently arid or relatively so. Such a combination of environmental factors is present in the mid-Zambezi Valley along the frontier between Zambia and Zimbabwe east to the Tete district in Mozambique, the middle reaches of the Limpopo River between Zimbabwe and South Africa and the Sundays and Great Fish Rivers in the eastern Cape. Elsewhere in southern Africa, rivers are in the main ineffective as modifiers of range distribution in birds. Data reinforce the conclusion that the middle stretches of the valleys of the Zambezi and Limpopo have varied at times in their efficacy as barriers in tandem with expansions and declines in subregional aridity levels over the millennia, as demonstrated in respect of the Dahomey Gap in West Africa (Moreau 1966), and that the Limpopo Valley is the more zoogeographically significant of the two presumably as its middle reaches abut on the South West Arid Zone. In contrast, the Tugela Valley, of the mesic Natal region, lacking significant aridity in its valley, plays a limited role in bird distribution.

Over the mesic eastern and southern parts of the Subregion forest endemics above the level of allospecies are few in number, the only representatives being the Bush Blackcap

*Lioptilus nigricapillus*, Chorister Robin *Cossypha dichroa*, Brown Robin *Erythropgygia signata* and Knysna Warbler *Bradypterus sylvaticus*. Endemics of other biomes are the Bald Ibis *Geronticus calvus* and members of the Alaudidae and Motacillidae restricted to high-altitude southeastern grasslands. In undistinguished bushveld tracts along the southeastern littoral, five other small passerine endemics occur, these being Rudd's Apalis *Apalis ruddi*, Woodward's Batis *Batis fratrum*, Neergaard's Sunbird *Nectarinia neergaardi*, Pinkthroated Twinspot *Hypargos margaritatus* and Lemonbreasted Canary *Serinus citrinipectus*. Other species, whether forest or savanna, are seen as allospecies of wide-ranging complexes. Between the Limpopo and Zambezi Rivers, there are three endemics: Boulder Chat *Pinarornis plumosus*, Chirinda Apalis *Apalis chirindensis* (perhaps deriving from the Blackheaded Apalis *A. melanocephala*) and Brier Warbler *Oreophilais robertsi*, the first and last without extant relatives and assuredly relict.

In the present study, I recognize portions of three valley systems as major barriers, two as partially effective barriers, and two as distributional salients where they transect otherwise unsuitable country such as absolute desert, or ecotone, as in the cases of the Kunene and Okavango Rivers. Each case is discussed and its relevance analyzed in so far as the present data permit, while the species and subspecies involved are listed in each sector summary. The subtraction rate, in terms of which species with extensive continental representation reach the southern limits of their range and drop out of the subregional avifauna, is dealt with in association with the barriers and other distributional factors identified here (Table 1).

Of the 156 species listed for the Limpopo and Umtamvuna Rivers, all but 19 range to Natal and Zululand as breeders within the southern subtropical limits. With the part aridity plays in the formation and sustaining of faunal barriers in southern Africa to the east and south of the steppe and desert western parts, aridity is not an overt factor in the barrier status of the Umtamvuna River. This is effected instead by the proximity of the Drakensberg massif to the coast at this point, and the resultant constriction or loss of some important habitats, compounded by the thrusting east of the Karoo ecosystem, from Algoa Bay northeast to the karroid summit of the Drakensberg Range. The zoogeographical importance of the Umtamvuna Valley is underscored by the finding in recent botanical surveys that many plants reach the termination of their ranges at this point, confirming the long standing existence of this river valley and adjacent regions of eastern Transkei and southwestern Natal as a significant centre for biotic change and endemism (van Wyk 1990a and b).

In identifying a biome frontier as an effective range modifier in the area of the Transkei, confirmatory evidence is available from a little further north where, along the lower reaches of the Limpopo River the barrier effect of the xeric river valley is enhanced by the termination of a major savanna

**TABLE 1.** The graduated drop in number of bird species (subtraction scores) for various river systems in the east and south of southern Africa.

Barrier	Non-passerines		Passerines	
	n	%	n	%
Zambezi/Limpopo Rivers	23	8,7	57	24,6
Limpopo/Umtamvuna Rivers	79	29,9	77	33,1
Umtamvuna/Sundays and Great Fish Rivers	23	8,7	47	20,3
Sundays and Great Fish Rivers to Cape Peninsula	139	52,7	51	22,0

woodland biome—the *Brachystegia* woodland (Miombo) ecosystem—on the north bank.

The fourth avifaunal valley barrier is the lowlying country extending from the Umtamvuna River to the Great Fish River/Sundays River region in the eastern Cape, where a tongue of arid Karoo thrusts to the coast and allied karroid vegetational associations extend inland to reach the alpine zone of the Drakensberg Range to the northeast. This complex habitat mosaic terminates the ranges of 70 species with extensive extralimital African ranges. The Great Fish/Sundays Rivers barrier also marks the eastern limits of virtually all avian taxa endemic to the Winter Rainfall District and its fynbos flora. To the west of the Sundays River no valley forms a meaningful barrier, species with tropical origins terminating their ranges in direct response to the rapid decline in suitable forest and forest-edge habitats to the west of George, and perhaps in association with the lower daytime temperatures and reduction in insect food in the interiors of forest remnants.

In the Cape Province, the ecological divergence of essentially stenotopic and wide-ranging continental forest species, has resulted in their subspecific extension into relatively arid country in response to radical past habitat change. In both the Olive Thrush *Turdus olivaceus* (Clancey 1982a) and the Cape Robin *Cossypha caffra* (Clancey 1981), widely distributed dry-country subspecies have evolved as a result of these species' ability to adapt to Karoo and dry riverine *Acacia*, the populations occurring to the south, east and north of the Karoo again associated with forest. The Lesser Doublecollared Sunbird *Nectarinia chalybea* has an arid western and interior race (*N. c. albilateralis*), which extends from Little Namaqualand and the valley of the lower Orange River to the southeastern Cape in the eastern parts of the Little Karoo (Clancey and Irwin 1978). In contrast to this, the Malachite Sunbird *Nectarinia famosa* has adapted its ecology to colonise arid areas such as Little Namaqualand, the lower Orange River and southern Namibia, its normal habitat being the protea zone of relatively mesic highlands. In this instance, however, there is no tendency for the population inhabiting the dry country to subspeciate.

These cases demonstrate that, when confronted with radical habitat alteration or even loss through climatic change, many birds can modify their basic ecological requirements. In so doing they may adapt to the new conditions and locally expand rather than contract distributionally. *Turdus olivaceus* populations of the dry interior of southern Africa (*T. o. smithi*) have virtually attained specific status, with limited direct contact between *T. o. smithi* and nominate *T. o. olivaceus* restricted locally to the southeastern extension of broken-veld types in the southeastern Cape.

Unlike major eastern rivers, the valley of the Orange River is of minor avifaunal import, as it does not represent a range barrier to any full species in this part of the Subregion, but riverine farming and fruit cultivation have added to its habitat diversity. The valley west of Upington and some distance to the south of the Orange, in what is generally referred to as Bushmanland, and classed as Namaqualand Broken Veld (Acocks 1988), is, however, relevant in so far as subspecies are concerned. Several well marked xeric subspecies extend south from Great Namaqualand to reach their southern range limits in Bushmanland in association with low rainfall (below 120 mm p.a.), and in this respect the high level of local variation in populations of some larks of the genera *Certhilauda* and *Pseudammomanes* centred on a zone of evolutionary radiation may be mentioned. The valley of the Orange River also marks the divide between the plain and whitebrowed subspecies (*L. c. subcoronatus*) of the Fiscal

Shrike *Lanius collaris*, which however, show in part the west-to-east rather than south-to-north orientation of subspecies normal in the northwestern Cape in concordance with isohyet contours.

The continuity of the Namib Desert fauna from about the mouth of the Orange River to the coast of Angola as far north as Luanda exhibits only one minor variational gradient step in association with the termination of the sand seas on the Kuiseb River. This is reflected in the ranges of some avian subspecies but not of any full species. Transecting the Namib on the border between Namibia and Angola is the Kunene River, which, in the desert, is of no avifaunal significance, yet the occurrence of riverine woodland upstream from about the Ruacana Falls provides suitable habitat for at least two species not found elsewhere in the Subregion: Rufoustailed Palmthrush *Cichladusa ruficauda* and Cinderella Waxbill *Estrilda thomensis*. Some of the Angolan desert subspecies also penetrate present limits in association with the Kunene drainage. In this instance—but to a much smaller extent than in the wooded valley of the Okavango River—the river valley does not constitute a barrier, but its riverine vegetation acts as a conduit by which some species extend well south of their main ranges into country which is otherwise inhospitable. While the full species composition of the mid-Kunene and mid-Okavango catchments differs only moderately, the races inhabiting the rivers differ markedly; this a correlate of the more arid nature of the country through which the middle and lower Kunene flows.

The zoogeographical significance of the Okavango was highlighted in Clancey (1980, 1992). The riparian woodland of this system is an ecological extension permitting *Brachystegia* endemics and central Angolan mesic and hygic bird taxa to extend well south of their centres of abundance to transect the ecotone between the major stands of *Brachystegia* woodland in Angola and contiguous territories and the dry *Acacia* steppe of the South West Arid Zone. To the southwest of this, the Okavango debouches in a delta-like papyrus-swamp complex into the sands of northwestern Botswana.

While the Okavango does not, in conformity with the Kunene delta dealt with earlier, constitute a zoogeographical barrier, its riparian woodland fringe and remnants also provide a corridor by means of which many northern-based taxa occur within present limits juxtaposed to South West Arid forms. Geographical variation of polytypic species in this riparian woodland and contiguous ecotone affects size and coloration relative to adjacent conspecifics. In the case of the Redeyed Dove *Streptopelia semitorquata maxima*, the bill is markedly more robust, suggesting a difference in diet, yet it occurs in close spatial relationship to the much smaller-billed and shorter-winged *S. s. australis*.

No bird species is endemic to the Okavango system (Clancey 1980), which presupposes that the present environmental mosaic of marshes and dryland habitats is of no great antiquity. While the Kunene and Okavango Rivers have closely contiguous catchments draining the highlands of Huambo and Bié in Angola, the composition of their bird communities downstream differs substantially. As commented earlier, this divergence appears to be a correlate of the drier conditions in the country through which the Kunene flows. Nevertheless, high-rainfall (hygic) forms do thrust south to at least Namibian limits on the Kunene, such as *Streptopelia semitorquata semitorquata*, *Treron calva ansorgei*, *Halcyon senegalensis fuscopileae*, *Cichladusa ruficauda*, *Estrilda thomensis* and others.

Consideration to the subtraction rate may now be given, in which wide-ranging Afrotropical bird species present over

the eastern aspects of the subregion reach their terminal points of range. Few meaningful and definitive lists of relevant species have seemingly been prepared and published. Tables 2-10 address this need.

Of the more than 490 wide-ranging Afrotropical species which enter Southern Africa from the northeast, no fewer than 236 (of which 80 drop out to the north of the Limpopo River) range no further south than the country lying between the lower Limpopo River and the Umtamvuna River (constituting the Limpopo/Umtamvuna interfluvium); this is by far the largest number of species to terminate their southern range limits in an interfluvium. This high dropout rate is coincident with subtropical climatic limits likewise terminating in the same general region. The greatly reduced number of 'tropical', forest birds reaching as far south as the southern and southwestern Cape are either allospecies or subspecies of forms which are largely montane and equally temperate further north in Africa.

### Regional Summaries

#### 1. Mid-Zambezi—Limpopo Rivers

The northern and southern limits of this interfluvial sector were formed by large-scale crustal faulting in the Zambezi

Valley in the north and the Limpopo Valley in the south (Irwin 1981). Both valleys are situated in regions of relatively low rainfall, that of the mid-Zambezi about 600 mm a year (Benson *et al.* 1971), but subject to much annual and cyclical variation. The middle and lower Limpopo sectors are even drier, with an annual rainfall of about 400 mm, with an even higher variation, exacerbated frequently by severe droughts. Altitude, in addition to precipitation levels, results in a tongue of arid lowland extending well to the northeast of the Zambezi River in the Luangwa Valley, which distorts the distribution of the main avifaunal habitats in Zambia, thereby heightening the influence of the dry mid-Zambezi Valley as a major range modifier along the northeastern borders of the Southern African Subregion. Further east, the moist southern-highland system of Malawi and the contiguous lowlands of Moçambique to the Zambezi delta reduce the impact of the mid-Zambezi Valley through the largely continuous savanna woodland of the region. *Brachystegia* woodland reaches its southern limits on the northern bank of the Limpopo River in Moçambique, but does not extend so far south in Zimbabwe, where, in the Limpopo Valley, its place is taken by a deciduous savanna, with Mopane *Colophospermum mopane* dominant and many Baobabs *Adansonia digitata*.

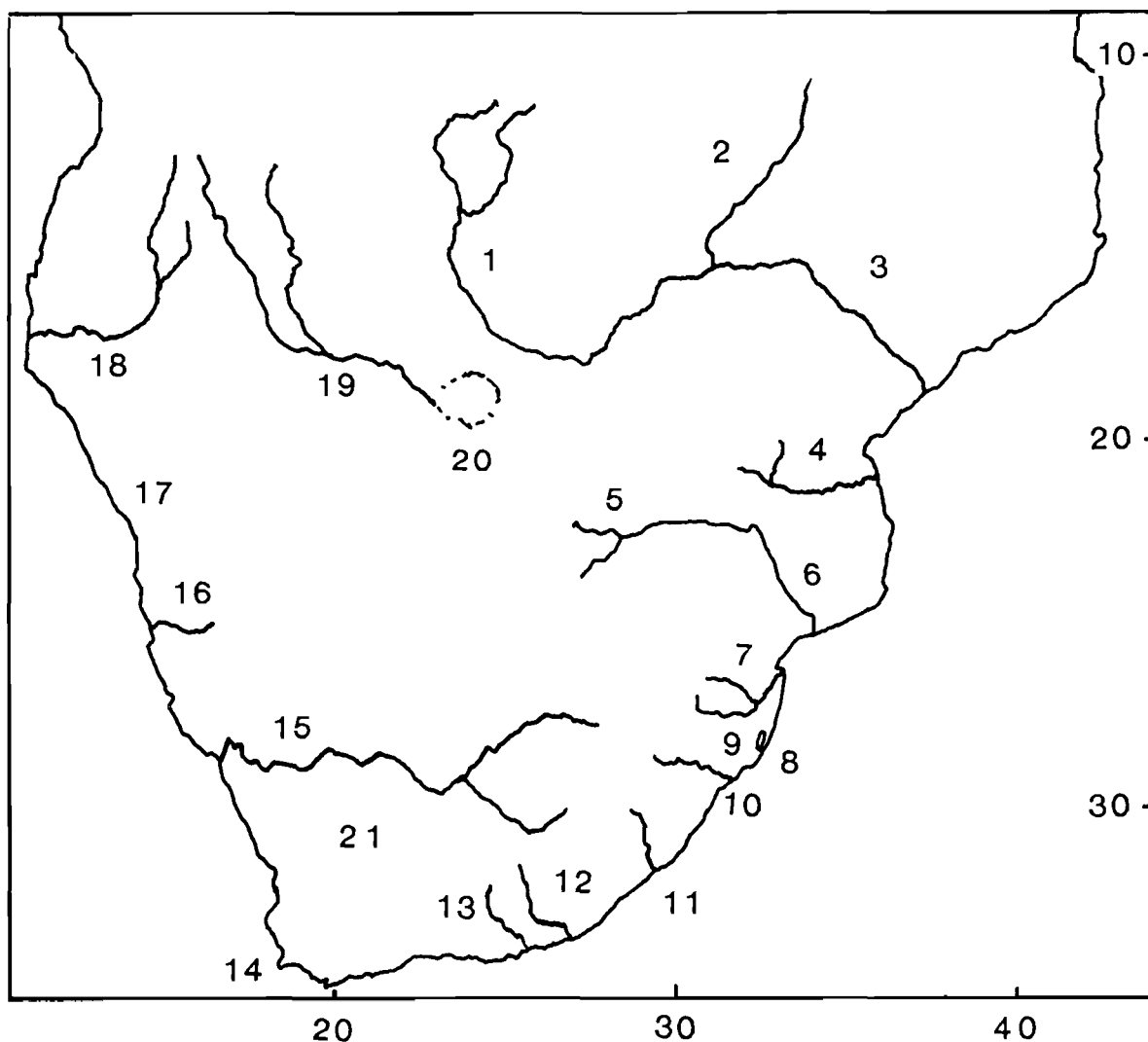


Fig. 1—The Southern African Subregion showing (by numbers) rivers and other topographical features referred to in the text: 1 Mid-Zambezi River, 2 Luangwa Valley, 3 Lower Zambezi River, 4 Save River, 5 Upper Limpopo River, 6 Lower Limpopo River, 7 Pongolo River, 8 Lake St Lucia, 9 Ngoye forest, 10 Tugela River, 11 Umtamvuna River, 12 Great Fish River, 13 Sundays River, 14 Cape Peninsula, 15 Lower Orange River, 16 Kuseb River, 17 Namib Desert, 18 Lower Kunene River, 19 Okavango River, 20 Okavango Swamps and 21 Karoo.

The virtual isolation of the Zimbabwe *Brachystegia* savanna from that of Zambia and Angola is reflected in the presence of a range of well marked subspecies (Table 2). Comparable patterns are found in the case of evergreen-forest and grassland birds, different races occurring both to the north and south of the dry mid-Zambezi barrier. In contrast, over the eastern low country, in line with the absence of any major break in the savanna vegetation, subspecific differentiation is structured in conformity with the uniform nature of the biotope, many subspecies extending from the region of the lower Limpopo Valley to the southeastern parts of Tanzania.

Within Zimbabwe, close to 80 species of birds centred on East Africa reach their southern range limits (Table 3). This sector also marks the southern range limits of several well marked subspecies, and is also a region of limited hybridization through parapatric and secondary contacts (Table 4). Table 5 enumerates the species deriving from deep southern African evolutionary radiations which have expanded as far north as Zimbabwe. Several wide-ranging species are absent from suitable expanses of habitat within Zimbabwe, although they occur immediately north of the Zambezi River and south of the Limpopo River (Table 6). The causal factors underlying these absences are unknown. Aridity is therefore a range determinant only on the interior plateau of the subcontinent, and the overall zoogeographical significance of the mid-Zambezi/Limpopo interfluvium is effected by the detached southern block of *Brachystegia* savanna and its endemic avian species, the distributions of which end on the littoral plain north of the Limpopo River. The termination of the littoral *Brachystegia* savanna at this point renders the middle and lower Limpopo River of more avifaunal distributional significance than the Zambezi River.

Why so many niches in evergreen forest and high-level grassland over the plateau between the Zambezi and the Limpopo Rivers remain largely unexploited or recolonized by congeners is in need of research. For example, in Zimbabwe and adjacent Mozambique there is no ruficolous rockthrush,

the Miombo Rockthrush *Monticola angolensis* being a woodland species confined to *Brachystegia*, yet absent from the eastern humid lowlands. There is also no montane Longbilled Pipit *Anthus similis*, its place being taken by a *Brachystegia*-based analogue, the Wood Pipit *Anthus nyassae* (Clancey 1985). Again the open rocky-country niches favoured elsewhere by other terrestrial birds remain unexploited. One such absentee is a rock-frequenting wheatear *Oenanthe* sp., while the region lacks a forest woodpecker (such as the Olive Woodpecker *Mesopicos griseocephalus*) and a forest-interior canary, such as the Forest Canary *Serinus scotops*, both of which occur in the Soutpansberg, Transvaal, immediately to the south. The woodpecker occurs again from the Zambezi River northwards, but the canary is there replaced by close analogues (Table 6).

Reverting to interspecific hybridization and secondary contact zones between well differentiated subspecies, the Zimbabwean interfluvium has more examples of both phenomena than the other three zoogeographical sectors identified in this paper. While not strictly comparable, the southern third of Africa has some broad similarities to Australia, with its extensive interior desert and steppe habitats, disruptively surrounded by moist uplands and mountains, often with tropical and subtropical forests (Ford 1987a and b), but unlike in Australia, hybridization between bird species south of the Kunene-Okavango-Zambezi line is severely restricted over the east and south. This may have been occasioned by the longterm homeostasis of the South West Arid Zone and the immediate dynamic past of the eastern and southern mesic avifauna.

Both interspecific hybridization and secondary contact between well differentiated subspecies are most in evidence in the mid-Zambezi-Limpopo sector, but even then is remarkably limited. The established cases are given in Table 4. Here I have deliberately omitted mention of the irregular hybridization between sympatric *Francolinus* spp.—namely, the Natal Francolin *F. natalensis*, Rednecked Francolin *F.*

**TABLE 2.** Subspecific differentiation (or absence thereof) north and south of the mid-Zambezi River. Subspecies of endemic and other species of, or associated with, *Brachystegia* savanna and their analogues north of the Zambezi in western and northern Zambia. In the case of species marked \* the two regions share the same subspecific taxon. The list is not exhaustive.

Zimbabwe	Western and northern Zambia
<i>Lybius torquatus lucidiventris</i>	<i>L. t. bocagei</i> and <i>L. t. congicus</i>
<i>Stactolaema whytii sowerbyi</i>	<i>S. w. buttoni</i> and <i>S. w. stresemanni</i> (? also <i>S. w. angoniensis</i> )
<i>Campethera bennettii bennettii</i>	<i>C. b. capricorni</i>
<i>Parus rufiventris stenotopicus</i>	<i>P. r. rufiventris</i> and <i>P. r. masukuensis</i>
<i>Parus niger ravidus</i>	<i>P. n. xanthostomus</i> (also <i>P. leucomelas insignis</i> )
<i>Salpornis spilonotus xylochromus</i>	<i>P. s. salvadorii</i>
<i>Monticola angolensis hylophila</i>	<i>M. a. angolensis</i>
<i>Thamnolaea cinnamomeiventris odica</i>	<i>T. c. subrufipennis</i>
<i>Hyliota australis australis</i>	<i>H. a. pallidipectus</i>
<i>Sylvietta whytii nemorivaga</i>	<i>S. ruficapilla chubbi</i> and <i>S. r. gephyra</i>
<i>Eremomela scotops scotops</i>	<i>E. s. extrema</i> and <i>E. s. pulchra</i>
<i>Camaroptera brevicaudata transitiva</i>	<i>C. b. intercalata</i>
<i>Calamonastes stierlingi irwini</i>	<i>C. s. stierlingi</i> and <i>C. s. irwini</i> *
<i>Cisticola aberrans nyika</i>	<i>C. a. nyika</i> *
<i>Batis molitor palliditergum</i>	<i>B. m. palliditergum</i> *
<i>Anthus nyassae frondicolus</i>	<i>A. n. nyassae</i> (? and <i>A. n. chersophilus</i> )
<i>Anthus caffer mzimbaensis</i>	<i>A. c. subsp. nov.</i>
<i>Nectarinia manoensis manoensis</i>	<i>N. m. pinto</i>
<i>Zosterops senegalensis anderssoni</i>	<i>Z. s. anderssoni</i> *
<i>Petronia supercilialis flavigula</i>	<i>P. s. rufitergum</i>

*afer* and Swainson's Francolin *F. swainsonii* (Clancey 1967), resulting no doubt from the recent disruption of previous habitat-partitioning structures among these gamebirds with the introduction of European agriculture in Zimbabwe. Natural hybridization, however, occurs between the Crested Francolins *Francolinus sephaena* and *F.(s.) rovuma* in the region of the lower Save River in Mozambique. The localized hybridization between the Brownheaded Parrot *Poicephalus cryptoxanthus* and Meyer's Parrot *P. meyeri* was determined and discussed by Clancey (1977), and that between the

Greenbacked Bleating Warbler *Camaroptera brachyura* and Greybacked Bleating Warbler *C. brevicaudata* in eastern Zimbabwe by Clancey (1970a). In a review of the subspecies of the Spottedbacked Weaver *Ploceus cucullatus* in southern Africa (Clancey 1970b, 1988) an extensive zone of hybridization between the blackcrowned forms *P. c. nigriceps* and *P. c. paroptus* and elements of the southern yellowcrowned phenotype—*P. c. dilutescens*—was identified over much of Zimbabwe, reaching the Indian Ocean coast immediately south of the Save River. Other cases are listed in Table 5.

**TABLE 3.** Species of the Zambezi/Limpopo interfluvium. Symbols: \* species whose ranges terminate on or immediately south of the Limpopo River in arid or semi-arid lowland, or else which are simply seasonal nonbreeding visitors to the south of the Limpopo River, their breeding grounds to the north of it (*Merops (nubicus) nubicoides*); + species whose ranges terminate on or north of the Save River on current evidence. The ranges of unmarked species terminate between the Save and Limpopo Rivers.

Non-passerines 23 species

<i>Falco fasciinucha</i> *	<i>Neafrapus boehmi</i> *
<i>Sarothrura boehmi</i> +	<i>Merops (nubicus) nubicoides</i> *+
<i>Vanellus albiceps</i> *	<i>Merops superciliosus</i> +
<i>Rhinoptilus cinctus</i> *	<i>Merops boehmi</i> +
<i>Glareola nuchalis</i> +	<i>Coracias spatulata</i> *
<i>Turtur afer</i> *	<i>Bycanistes brevis</i> *
<i>Agapornis lilianae</i>	<i>Stactolaema whytii</i> +
<i>Cercococcyx montanus</i> +	<i>Pogoniulus simplex</i>
<i>Macrodypteryx vexillarius</i> *	<i>Apus aequatorialis</i> +
<i>Indicator meliphilus</i> +	<i>Prodotiscus zambesiae</i>
<i>Schoutedenapus myoptilus</i> +	<i>Campethera scriptoricauda</i> +
<i>Telacanthura ussheri</i> *	

Passerines 57 species

<i>Pitta angolensis</i> *	<i>Batis soror</i> *
<i>Mirafraga africanaoides</i> *	<i>Erythrocerus livingstonei</i> *
<i>Hirundo senegalensis</i> *	<i>Trochocercus albonotatus</i> +
<i>Psalidoprocne orientalis</i> +	<i>Anthus nyassae</i> +
<i>Coracina pectoralis</i> *	<i>Laniarius aethiopicus</i> +
<i>Parus rufiventris</i> +	<i>Tchagra minuta</i> +
<i>Parus griseiventris</i>	<i>Prionops scopifrons</i>
<i>Salpornis spilonotus</i> *	<i>Lamprotornis mevesii</i> *
<i>Phyllastrephus debilis</i>	<i>Buphagus africanus</i> *
<i>Andropadus milanjensis</i> +	<i>Oriolus chlorocephalus</i> +
<i>Monticola angolensis</i> +	<i>Lamprotornis chloropterus</i> +
<i>Thamnolaea arnoti</i> *	<i>Nectarinia cuprea</i> +
<i>Cichladusa arquata</i> +	<i>Nectarinia shelleyi</i> +
<i>Alethe fuelleborni</i> +	<i>Nectarinia manoensis</i> +
<i>Swynnertonia swynnertonii</i> +	<i>Nectarinia venusta</i> *
<i>Sheppardia gunningi</i> +	<i>Anthreptes longuemarei</i>
<i>Pinarornis plumosus</i> +	<i>Ploceus olivaceiceps</i>
<i>Hylia flavigaster</i>	<i>Euplectes hordeaceus</i> +
<i>Hylia australis</i>	<i>Euplectes macrourus</i> +
<i>Acrocephalus cinnamomeus</i> *	<i>Pytilia afra</i> *
<i>Apalis chirindensis</i> +	<i>Cryptospiza reichenovii</i> +
<i>Apalis melanocephala</i>	<i>Pyrenestes minor</i> +
<i>Sylvietta whytii</i>	<i>Hypargos niveoguttatus</i> *
<i>Melocichla mentalis</i> +	<i>Estrilda quartinia</i> +
<i>Cisticola cantans</i> +	<i>Ortygospiza locustella</i> +
<i>Cisticola brachyptera</i>	<i>Vidua obtusa</i> *
<i>Heliolais erythroptera</i>	<i>Vidua codringtoni</i> +
<i>Oreophilais robertsi</i>	<i>Serinus mennelli</i>
<i>Bias musicus</i>	<i>Emberiza cabanisi</i> +

## 2. Limpopo—Umtamvuna Rivers

The arid middle and lower Limpopo Valley was an even more effective barrier than the Zambezi River during Pleistocene interglacials. As the northern Limpopo Valley delimits the southeastern periphery of the *Brachystegia*

savanna biome, all of the endemics of this particular woodland type likewise terminate their ranges with it, with only occasional stragglers to the south of the river in the eastern lowlands.

The zoogeographical significance of the Limpopo River valley is further underscored by the marked altitudinal and

**TABLE 4.** Secondary contacts between species and well-marked subspecies occurring over the Zambezi/Limpopo interfluvium. The list is not necessarily complete, but lists secondary contacts which have been discussed in the literature in recent years. Species marked \* are known to hybridize in the zone of secondary contact.

<i>Francolinus sephaena zuluensis</i>	<i>F. (s.) rovuma</i> *
<i>Poicephalus meyeri transvaalensis</i>	<i>P. cryptoxanthus</i> subsp. *
<i>Parus rufiventris stenotopicus</i>	<i>P. r. pallidiventris</i> * (possibly a single race ( <i>stenotopicus</i> ) with <i>pallidiventris</i> extralimital)
<i>Chlorocichla flaviventris flaviventris</i>	<i>P. f. ortiva</i> ?
<i>Cercomela familiaris hellmayri</i>	<i>C. f. modesta</i>
<i>Erythropygia leucophrys pectoralis</i>	<i>E. l. zambesiana</i> * and <i>E. l. simulator</i>
<i>Camaroptera brachyura constans</i>	<i>C. brevicaudata</i> subsp. *
<i>Laniarius ferrugineus</i> subsp.	<i>L. aethiopicus</i> subsp. *
<i>Tchagra australis tongensis</i>	<i>T. a. minor</i> and <i>T. a. littoralis</i> *
<i>Zosterops senegalensis anderssoni</i>	<i>Z. s. stierlingi</i> *
<i>Plocepasser mahali terricolor</i>	<i>P. m. pectoralis</i>
<i>Ploceus cucullatus dilutescens</i>	<i>P. c. nigriceps</i> and <i>P. c. paroptus</i> *
<i>Estrilda melanotis melanotis</i>	<i>E. quartinia stuartirwini</i>

**TABLE 5.** The more obvious instances of well marked subspecies with ranges terminating north of or on the arid Limpopo River valley, but laying no claim to a complete assessment, and a list of South African endemics with isolate populations between the Zambezi and Limpopo Rivers. These isolates are indicative of colonisation from south of the Limpopo River by elements of austral endemics. Numbers in parenthesis refer to the number of races of each species present to the south of the Limpopo River.

Subspecies	Representative immediately south of Limpopo River
<i>Francolinus afer swynnertoni</i>	<i>F. a. lehmanni</i>
<i>Coturnix coturnix erlangeri</i>	<i>C. c. coturnix</i>
<i>Sarothrura affinis antonii</i>	<i>S. a. affinis</i>
<i>Poicephalus robustus suahelicus</i>	<i>P. r. robustus</i>
<i>Tauraco livingstonii livingstonii</i>	<i>T. l. cabanisi</i> (in Mozambique) (by <i>T. corythaix phoebus</i> in Transvaal)
<i>Bubo capensis mackinderi</i>	<i>B. c. capensis</i>
<i>Rhinopomastus cyanomelas schalowi</i>	<i>R. c. intermedius</i>
<i>Alcedo semitorquata tephria</i>	<i>A. s. semitorquata</i>
<i>Ptyonoprogne fuligula fusciventris</i>	<i>P. f. pretoriae</i>
<i>Riparia cincta suahelica</i>	<i>R. c. cincta</i>
<i>Phyllastrephus flavostriatus dendrophilus</i> and <i>P. f. dryobates</i>	<i>P. f. flavostriatus</i>
<i>Andropadus importunus loquax</i>	<i>A. i. mentor</i>
<i>Chlorocichla flaviventris ortiva</i>	<i>C. f. flaviventris</i>
<i>Turdus olivaceus swynnertoni</i>	<i>T. o. transvaalensis</i>
<i>Phylloscopus ruficapillus alacris</i>	<i>P. r. ochraceiceps</i>
<i>Apalis thoracica rhodesiae</i>	<i>A. t. spelonkensis</i>
<i>Cisticola aberrans nyika</i>	<i>C. a. aberrans</i> ( <i>C. a. nyika</i> to Soutpansberg)
<i>Cisticola natalensis vigilax</i>	<i>C. n. natalensis</i> (by <i>C. n. vigilax</i> on Transvaal mountains).
<i>Onychognathus morio shelleyi</i>	<i>O. m. morio</i>
<i>Ploceus ocularis suahelicus</i>	<i>P. o. brevior</i>
<i>Euplectes ardens tropicus</i>	<i>E. a. ardens</i>
South African endemics	Zimbabwe representatives
<i>Sphenoaecus afer</i> (3)	<i>S. a. excisus</i>
<i>Batis capensis (sens. strict.)</i> (2)	<i>B. c. kennedyi</i> and <i>B. c. erythrophthalma</i>
<i>Macronyx capensis</i> (3)	<i>M. c. stabilior</i>
<i>Telophorus zeylonus</i> (3)	<i>T. z. restrictus</i>
<i>Promerops gurneyi</i> (1)	<i>P. g. ardens</i>

ecological environmental switches, which occur in the ranges of birds breeding in montane forest north of the Limpopo River but south of it occupying littoral forest communities. This occurs in the Goldenrumped Tinker Barbet *Pogoniulus bilineatus* (with both littoral and montane races north of the Limpopo River but only the former south of it), the Squaretailed Drongo *Dicrurus ludwigii* (south to northeastern Transvaal highland forests, but entirely coastal further south to the eastern Cape), and likewise in Yellowstreaked *Phyllastrephus flavostriatus*, and rather differently in the Yellowbellied *Chlorocichla flaviventris* and Sombre Bulbuls *Andropadus importunus*, and in the Natal Robin *Cossypha natalensis*. The reverse is found in the forest *Mesopicos griseocephalus* which extends north to the Soutpansberg, reappearing in the mid-Zambezi drainage. Other species involved are *Cossypha dichroa* (replaced north of the Limpopo River in highland forest by *Cossypha natalensis*), *Erythropygia signata* (replaced by the Bearded Robin *Erythropygia quadrivirgata* both to the east, and north in the Zambezi

drainage), and the Bluemantled Flycatcher *Trochocercus cyanomelas megalolophus* which extends parapatrically alongside a nominate-like form south to the Zululand coast, suggesting that a further species is involved.

Associated with the above is the finding that the coastal floodplain species south of the Limpopo River (e.g. the Natal Nightjar *Caprimulgus natalensis*, Pinkthroated Longclaw *Macronyx ameliae* and Palecrowned Cisticola *Cisticola brunnescens*) retreat to the continental plateau north of the river.

Details of the topography of the Transvaal south of the mid-Limpopo River between 22° and 28°S, and 25° and 32°E, with the altitude in the eastern lowveld about 150 m a.s.l., rising to as high as 2331 m to the north of Belfast in the eastern parts of the plateau, can be found in Tarboton *et al.* (1987). These latter authors recognize three major biomes in the Transvaal: steppe (plateau grassland), woodland savanna (divided into eastern lowveld and western bushveld), and Afromontane forest/grassland mosaic (escarpment). Rainfall

**TABLE 6.** Bird species with tropical African representation and a widely sundered population south and west of the Limpopo River.

Species	Comments on extralimital congeners
<i>Struthio camelus</i>	Northern limits of <i>S. c. australis</i> on the mid-Zambezi rather than the Limpopo. Further north in the Afrotropics replaced by <i>S. c. camelus</i> , <i>S. c. massaicus</i> and <i>S. c. molybdophanes</i>
<i>Podiceps cristatus</i>	Northeast African and southern isolates alike
<i>Podiceps nigricollis</i>	<i>P. n. gurneyi</i> in south, putative nominate <i>P. nigricollis</i> in East Africa
<i>Oxyura maccoa</i>	East African and southern isolates alike
<i>Gypaetus barbatus</i>	<i>G. b. meridionalis</i> in south and same race in eastern and northeastern Africa
<i>Buteo trizonatus</i>	With the allied <i>B. oreophilus</i> in East and northeastern Africa
<i>Polihierax semitorquatus</i>	Nominate <i>P. semitorquatus</i> in south, <i>P. s. castanonotus</i> in East and northeastern Africa
<i>Francolinus levaillantoides</i>	South African races possibly conspecific with forms in northeastern Africa
<i>Francolinus vaillantii</i>	Nominate race south of Limpopo, <i>F. v. crawshayi</i> , <i>F. v. benguellensis</i> and other forms to the north
<i>Ardeotis kori</i>	Nominate race in south, <i>A. k. struthiunculus</i> in East Africa
<i>Neotis denhami</i>	<i>N. d. stanleyi</i> , <i>N. d. jacksoni</i> and <i>N. d. denhami</i> in tropics
<i>Eupodotis senegalensis</i>	<i>E. s. barrowii</i> in south, <i>E. s. mackenziei</i> and nominate race in tropics and West Africa
<i>Vanellus melanopterus</i>	<i>V. m. minor</i> in south, nominate race in Ethiopia, <i>minor</i> also in East Africa
<i>Apus melba</i>	<i>A. m. africanus</i> south of Limpopo, also in western and eastern tropics
<i>Cryptolybia woodwardi</i>	A widely sundered allospecies of the Green Barbet superspecies with <i>C. w. woodwardi</i> in Zululand and <i>C. w. hylophona</i> in southeastern Tanzania
<i>Pogoniulus pusillus</i>	Nominate <i>pusillus</i> and <i>P. p. niethammeri</i> south of Limpopo, <i>P. p. affinis</i> and other taxa in East Africa
<i>Mesopicos griseocephalus</i>	Nominate race and <i>M. g. aureovirens</i> south of Limpopo, <i>M. g. persimilis</i> and <i>M. g. kilimensis</i> in eastern tropics
<i>Jynx ruficollis</i>	Nominate race and <i>J. r. striaticula</i> south of Limpopo, <i>striaticula</i> and other forms in equatorial belt
<i>Smutsornis africanus</i>	Four races in southern Africa, others in eastern and northeastern Africa
<i>Zoothera guttata</i>	Nominate race replaced from Zululand to Malawi by <i>Z. g. belcheri</i> , in Zaire by <i>Z. g. lippensi</i> , and other forms further north
<i>Anthus similis</i>	<i>A. s. nicholsoni</i> and four associated races, <i>A. s. dewittei</i> , <i>A. s. chyuluensis</i> and northern races in east-central and eastern Africa
<i>Anthus leucophrys</i>	<i>A. l. enunciator</i> and nominate race south of Limpopo, <i>A. l. prunus</i> and <i>A. l. bohndorffi</i> in Zambia and <i>A. l. tephridorsus</i> reaching northwestern Zimbabwe
<i>Anthus brachyurus</i>	Nominate race, putative nominate race also in north of Lake Malawi, other races to the west and north
<i>Hemimacronyx chloris</i>	<i>H. chloris</i> , replaced in Kenya by a close congener <i>H. sharpei</i>
<i>Euplectes progne</i>	<i>E. p. progne</i> , <i>E. p. delacouri</i> in Angola, <i>E. p. definita</i> in Zambia, <i>E. p. delamerei</i> in Kenya
<i>Ploceus capensis</i>	<i>P. c. rubricomus</i> and two other races replaced by <i>P. c. temporalis</i> in Angola, southern Zaire and adjacent northwestern Zambia
<i>Serinus scotops</i>	<i>S. s. transvaalensis</i> replaced by close analogue <i>S. citrinelloides</i> ( <i>S. c. hypostictus</i> and <i>S. c. frontalis</i> ) north of the Zambezi in east



varies from the west (with annual precipitation of up to 500 mm per year, and lying within the eastern limits of the South West Arid Zone) to the east (up to about 750 mm, rising further over the eastern escarpment regions and southeastern highveld to about 1000 mm of rain p.a. In the upper catchment of the Letaba and Olifants Rivers, rainfall may reach 1500 mm per year. The avifauna of the Transvaal is essentially South African over its elevated plateau which ends immediately south of the desiccated lowlands of the mid-Limpopo River. Many of the more significant birds are absent from Zimbabwe, yet some reappear further north in eastern Africa (Table 6).

No bird species is unique to the Transvaal and even the few larks (Alaudidae) and pipits (Motacillidae) endemic to the southeastern highland grasslands are shared with adjacent territories. Hybridization between full allopatric species is recorded only between *Poicephalus cryptoxanthus* and *P. meyeri*, but geographical variation in general size and levels of plumage colour saturation in accord with both Bergmann's and Gloger's Rules is shown by a wide range of species which extend from the dry west to the eastern lowveld (Clancey 1992).

Since the opening up of the Transvaal plateau to European industry, mining and agriculture from the middle of the 1800s large expanses of country have witnessed radical reduction in their virgin vegetation, with the result that the ranges of many bird species have been altered, some adversely and perhaps irreversibly, yet others having expanded their ranges and numbers into the new habitats. An analysis of the individual changes of status based on a study of the old literature and major bird collections compared with the results of the recent atlas survey of the regional avifauna awaits attention.

The avifauna of southern Moçambique was covered by Clancey (1970/71). Sul do Save lying to the south of the Save River is mainly a lowlying and largely unrelieved littoral plain, mostly below 200 m altitude. Over the western edge of the Maputo district the country rises fairly sharply in the Lebombo Mountains to over 600 m, and over the borders with the Kruger National Park the ground reaches elevations of between 200 and 500 m. The lowlying parts were at one stage seabed, with the result that the region south of the Limpopo River (and also far to the north) is sandy and the major rivers transecting it have wide alluvial floodplains. The interior of southern Moçambique is relatively dry with an annual rainfall of about 400 mm, increasing coastwise to reach about 800-1000 mm. In the Lebombos rainfall is also locally high to reach 1000 mm at Namaacha. This region is covered by different woodland facies (Wild and Fernandez 1967), the most extensive areas of virgin vegetation being occupied by *Terminalia* and *Colophospermum* savanna, which covers most of Gaza.

Around this to the east are extensive stands of other woodland aggregations (namely of *Boscia albitrunca* and *Acacia* spp.), while coastal dune formations are covered with scrub *Mimosa caffra*, and the mouths of rivers and the lower reaches of their floodplains support extensive stands of mangroves. Grassland is somewhat limited, but over the Lebombos *Themeda-Turbina* grassland occurs, extending north in the Maputo district to about 24°S on the Transvaal border. This area, eastern Swaziland and the littoral plain of Moçambique comprise an avifaunally highly complex region with some arid interior and Zimbabwean elements reaching the lowlands through the Limpopo Valley, where they are diverted southwards along the base of the eastern escarpment (and west of the Lebombos) to terminate their ranges on or just south of the Pongolo River. Some of the

species involved are the Longtailed Shrike *Urolestes melanoleucus*, Whitecrowned Shrike *Eurocephalus anguitemens*, Redbilled Helmetshrike *Prionops retzii*, Burchell's Starling *Lamprotornis australis*, Longtailed Starling *L. mevesii* and Redbilled Buffalo Weaver *Bubalornis niger*, with *mevesii* not extending much to the south of the mid-Limpopo River.

Of the species with extensive continental distributions ranging into the Southern African Subregion in the east, 19 species of the 156 subtracted from the avifauna in the Limpopo/Umtamvuna sector do not breed (or are not established as breeding) south of the Pongolo and the Moçambique/Natal frontier east of the Lebombo Mountains (Table 7). The rest drop out at points in Natal and Zululand and the adjacent Transkei, where the indigenous plant cover has been modified over the past century, largely through development of an extensive sugar industry on the Natal coast and eastern low country of Zululand, and coastal urbanization.

Suitable habitat for many of the more interesting tropical species is now limited and fragmented, with the result that local populations have declined in numbers and some have receded northwards in the face of relentless habitat loss. Species such as the Fasciated Snake Eagle *Circaetus fasciolatus*, Black Coucal *Centropus grillii*, Greyrumped Swallow *Pseudhirundo griseopyga*, *Macronyx ameliae* and others are no longer present as regular breeders south of the lower Tugela River. In Table 7, I have listed those species which range as far as the northern half of the lower Tugela basin and those which extend to the Umtamvuna River. From a zoogeographical rather than a conservation point of view, greater precision is no longer attainable in fixing the precolonial distributional limits of many species along the highly developed Natal coast.

The physical conditions and vegetation of Natal and Zululand and their bearing on the occurrence and distribution of birds are described by Clancey (1964). In Natal the land rises rapidly from the narrow littoral in a series of major steps or terraces to the high Drakensberg at altitudes in excess of 3000 m a.s.l. The Drakensberg is the source of several rivers, so that Natal is incised by many deep and often relatively arid valleys with rainfall often much lower than that of the adjacent plateau. The coastal strip is narrow south of the Tugela River, but north of it broadens to form become a wide littoral plain extension of the lowlands of Moçambique to the north. Within Zululand limits (i.e. Tugela River to Moçambique) the vegetation comprises coastal forest and thornveld and lowveld types (Acocks 1988). Natal and Zululand are part of the eastern summer-rainfall district, about three-quarters of the annual precipitation falling between October and March. The annual rainfall varies locally to a considerable degree from as low as 600 mm to as high as 1250 mm, and even 1750 mm on occasion at places such as Karkloof and Qudeni, both evergreen forest areas.

Over much of the area the primal vegetation cover is now much disturbed or lost. Generally speaking, it consists of extensive grassland with isolated patches of evergreen forest in the interior, xerophilous scrub woodland in the hot, lowlying valleys, and remnants of coastal pristine vegetation along the coast south of the Tugela River. Over the Zululand flats a mixed parklike savanna survives to the east of the Lebombo Mountains, while the lake and wetland mosaic present there furnishes a wide diversity of avian habitats.

Natal marks the southern limit of subtropical environmental conditions in the Southern African Subregion, as well as the ranges of a large number of wide-ranging Afrotropical species (Table 7). About 137 species drop out of the South African avifauna between the mid-Pongolo in the north and Umtamvuna River and adjacent Transkei in the southwest, in line with the temperate and subtropical climatic

**TABLE 7.** Species of the Limpopo/Umtamvuna interfluvium. Symbols for non-passerines and passerines: + species whose breeding range terminates north of the Natal and Zululand border, i.e., generally north of the Pongola River, \* species whose breeding range extends south of the Tugela River and terminates on or near the Umtamvuna River, \*? species whose range is now restricted to north of the Tugela River as a result of habitat loss, ++ species which have been recorded but are not established as breeding so far south. The breeding ranges of unmarked species terminate between the Pongola River and Moçambique border and the lower Tugela River.

Non-passerines 79 species

<i>Pelecanus rufescens</i>	<i>Falco dickinsoni</i> +	<i>Otus leucotis</i> *
<i>Ardea goliath</i> *	<i>Francolinus coqui</i> *	<i>Glaucidium perlatum</i>
<i>Casmerodius albus</i> *	<i>Francolinus sephaena</i>	<i>Caprimulgus natalensis</i> *
<i>Egretta ardesiaca</i> *	<i>Francolinus shelleyi</i> *	<i>Caprimulgus fossii</i> *
<i>Ixobrychus sturmii</i> *	<i>Francolinus natalensis</i> *	<i>Apus affinis</i>
<i>Ciconia episcopus</i> *	<i>Francolinus swainsonii</i>	<i>Cypsiurus parvus</i>
<i>Ephippiorhynchus senegalensis</i>	<i>Guttera edouardi</i> *	<i>Halcyon senegalensis</i>
<i>Anastomus lamelligerus</i>	<i>Bugeranus carunculatus</i> *	<i>Halcyon leucocephala</i> +
<i>Leptoptilos crumeniferus</i> +	<i>Crex egregia</i> *	<i>Halcyon chelicuti</i>
<i>Mycteria ibis</i>	<i>Sarothrura ayresi</i> *	<i>Merops bullockoides</i> *
<i>Dendrocygna bicolor</i> *	<i>Vanellus lugubris</i>	<i>Merops pusillus</i> *
<i>Sarkidiornis melanotos</i>	<i>Vanellus senegallus</i>	<i>Coracias caudata</i>
<i>Gypohierax angolensis</i>	<i>Vanellus crassirostris</i>	<i>Coracias naevia</i>
<i>Necrosyrtes monachus</i> +	<i>Rhinoptilus chalcopterus</i>	<i>Eurystomus glaucurus</i>
<i>Gyps africanus</i>	<i>Glareola pratincola</i> *	<i>Rhinopomastus cyanomelas</i> *
<i>Torgos tracheliotus</i>	<i>Rynchops flavirostris</i> +	<i>Tockus leucomelas</i>
<i>Trigonoceps occipitalis</i>	<i>Columba delegorguei</i> *	<i>Tockus nasutus</i>
<i>Macheirhamphus alcinus</i>	<i>Streptopelia decipiens</i> +	<i>Tockus erythrorhynchus</i>
<i>Aquila wahlbergi</i> *	<i>Turtur afer</i> +	<i>Stactolaema leucotis</i> *
<i>Hieraaetus ayresii</i> ++?	<i>Poicephalus cryptoxanthus</i>	<i>Cryptolybia woodwardi</i>
<i>Kaupifalco monogrammicus</i>	<i>Tauraco livingstonii</i>	<i>Pogoniulus chrysoconus</i>
<i>Circaetus fasciolatus</i>	<i>Gallirex porphyreolophus</i> *	<i>Pogoniulus bilineatus</i>
<i>Buteo augur</i> +	<i>Corythaixoides concolor</i>	<i>Trachyphonus vaillantii</i> *
<i>Accipiter ovampensis</i> +	<i>Clamator levaillantii</i> *	<i>Campethera bennettii</i>
<i>Accipiter badius</i>	<i>Pachyococcyx audeberti</i>	<i>Campethera abingoni</i> *
<i>Melierax metabates</i> +	<i>Ceuthmochares aereus</i> *	
<i>Falco cuvierii</i> ++?	<i>Centropus grillii</i>	

Passerines 77 species

<i>Smithornis capensis</i> *	<i>Cisticola ruflata</i> +	<i>Nectarinia neergaardi</i> +
<i>Mirafra rufocinnamomea</i>	<i>Cisticola chiniana</i> *	<i>Nectarinia talatala</i> *
<i>Mirafra sabota</i>	<i>Cisticola erythropus</i> *	<i>Nectarinia senegalensis</i> *
<i>Heteromirafra ruddi</i> *	<i>Cisticola galactotes</i> *	<i>Anthreptes reichenowi</i> +
<i>Eremopterix leucotis</i>	<i>Myioparus plumbeus</i>	<i>Zosterops senegalensis</i> +
<i>Hirundo atrocaerulea</i> *	<i>Melaenornis pallidus</i>	<i>Bubalornis niger</i>
<i>Hirundo smithii</i> *	<i>Platysteira peltata</i> *	<i>Ploceus intermedius</i>
<i>Hirundo semirufa</i>	<i>Batis fratrum</i>	<i>Ploceus xanthops</i> *
<i>Pseudhirundo griseopyga</i> *?	<i>Anthus caffer</i>	<i>Ploceus xanthopterus</i>
<i>Oriolus auratus</i> +	<i>Anthus brachyurus</i> *	<i>Anaplectes rubriceps</i>
<i>Anthoscopus caroli</i>	<i>Macronyx croceus</i>	<i>Anomalospiza imberbis</i> *
<i>Turdoides jardineii</i> *	<i>Macronyx ameliae</i> *?	<i>Euplectes albonotatus</i> *
<i>Chlorocichla flaviventris</i> *	<i>Urolestes melanoleucus</i>	<i>Pytilia melba</i> *
<i>Nicator gularis</i>	<i>Nilaus afer</i> *	<i>Hypargos margaritatus</i>
<i>Turdus libonyana</i> *	<i>Tchagra australis</i>	<i>Lagonosticta rhodopareia</i>
<i>Turdus litsitsirupa</i> *	<i>Telophorus quadricolor</i> *	<i>Uraeginthus angolensis</i> *
<i>Cossypha heuglini</i>	<i>Telophorus nigrifrons</i> +	<i>Estrilda perreini</i> *
<i>Cossypha humeralis</i> *	<i>Prionops plumatus</i> *	<i>Amadina fasciata</i> +
<i>Erythropygia quadrivirgata</i>	<i>Prionops retzii</i>	<i>Amadina erythrocephala</i> *
<i>Chloropeta natalensis</i> *	<i>Eurocephalus anguitimens</i> +	<i>Spermestes fringilloides</i> *
<i>Schoenicola brevirostris</i> *	<i>Cinnyricinclus leucogaster</i> *	<i>Vidua paradisaea</i> *
<i>Apalis ruddi</i>	<i>Lamprotornis australis</i>	<i>Vidua funerea</i> *
<i>Eremomela scotops</i>	<i>Lamprotornis chalybaeus</i> +	<i>Vidua purpurascens</i>
<i>Eremomela usticollis</i>	<i>Buphagus africanus</i> ++	<i>Vidua chalybeata</i> *
<i>Calamonastes stierlingi</i>	<i>Buphagus erythrorhynchus</i>	<i>Serinus citrinipectus</i>
<i>Cisticola brunnescens</i> *	<i>Nectarinia bifasciata</i> *	

convergence. Significantly, no bird species is peculiar to Natal and Zululand in line with findings on the middle and lower Limpopo and Pongolo Rivers, though five passerines, namely *Apalis ruddi*, *Batis fratrum*, *Nectarinia neergaardi*, *Hypargos margaritatus* and *Serinus citrinipectus* are shared with the southern littoral regions of Moçambique. Comparably some of the grassland endemics present over the southeastern interior highlands also have ranges impinging on Upper Natal.

Far southern and spatially remote isolates of uncommon to rare Afrotropical birds are located in both Natal and Zululand and adjacent Transkei, notable among these being Woodward's Barbet *Cryptolybia woodwardi*, which is represented by the small population of the nominate race in the Ngoye forest of Zululand. The second population of the species (*C. w. hylophona*) is likewise confined to a single forest on the Rondo Plateau, southwest of Lindi, in southeastern Tanzania (Clancey 1989b).

A somewhat comparable case is presented by that of the Transkei/Zululand populations of the Spotted Ground Thrush *Zoothera guttata*, a recent study of which reveals that birds which are extensively white and lightly spotted ventrally occur seasonally in the southern highlands of Malawi and the Ngoye Forest and other forest blocks of eastern Zululand, and should be treated as applicable to the same subspecies (*Z. g. belcheri*) (Clancey in press a). Uniquely, *Z. guttata* is not recorded from the intervening country, but breeds in some numbers in the coastal forests of the Transkei and adjacent southwestern Natal to the south, elements of which population spend the nonbreeding season along the Natal and Zululand coast as far north as the Lake St Lucia region. These represent the nominate race of *Z. guttata*. It remains to be ascertained if any migratory movement is involved in the occurrence of *Z. g. belcheri* in Zululand (Ngoye, Dlinza and Entumeni forests) and southern Malawi or if two more or less sedentary populations are involved (Clancey in press a).

Instances of secondary contact between species and well marked subspecies, including those exhibiting limited hybridization, are listed in Table 8. The absence of any species peculiar only to Natal and Zululand is in line with the premise that local bird species representation is largely the outcome of recent historical events, much of its recruitment emanating from eastern Africa and regions to the north.

### 3. Umtamvuna River—Sundays/Great Fish River

The Umtamvuna River forms part of the frontier between Natal and the Transkei, its lower reaches being a steep-sided gorge with rich valley bushveld. In this instance, aridity is not a supplementary range determinant, yet several species of birds terminate their ranges on or about the river (Table 7). In search of an alternative reason for this, I have postulated

the existence of a virtual bottleneck created by the close proximity of the Drakensberg massif to the Indian Ocean at this point and the concomitant loss of habitat diversity over the limited Transkeian plateau through overgrazing by stock and human settlement pressure.

The forested coast of Transkei is deeply incised by short streams and rivers, variably forested towards their mouths and backed in the interior by stands of valley bushveld and often mixed *Acacia* woodland. About 3,4% of the Transkei is forest compared to 0,9% for the Republic of South Africa (Quickelberge 1989). Inland of the forested coast, the land rises in a series of minor steps or escarpments to grassland plateau (Sourveld)—now little better than overgrazed prairie—with scattered mid-level evergreen forests and plantations of exotics up to the foothills of the Drakensberg, where high-altitude scarp forests occur, which, however, are in most instances of limited ornithological significance. Faunistically, the summit of the Drakensberg is of some importance, as the dominant vegetation (*Themeda-Festuca* Alpine Veld) supports a karroid alpine avifauna, the immediate affinities of which are to be found in the southwestern Cape and point to the chronologically staggered primary and secondary refugial roles of the central Drakensberg system. The rainfall of Transkei is about 750-1500 mm p.a., declining to about 500 mm in the karroid northwest of the territory (Quickelberge 1989).

To the immediate southwest of the Transkei, the thrust of the Karoo ecosystem to the coast between the lower Sundays and Great Fish Rivers forms a southwestern limit to the Umtamvuna/Fish River sector. Here aridity, exacerbated periodically by droughts, marks the termination of the ranges of many birds. Inland of this, the southeastern verge of the Karoo vegetation becomes increasingly altitudinally modified and more temperate with some characteristic species ranging in association with it as breeders to the Afro-alpine summits of the Drakensberg. This inland extension and altitudinal climb of the Karoo ecosystem to the east of the Great Fish River results in a further reduction of suitable habitat available to many wide-ranging tropical elements in the Transkei, which are increasingly forced into the apex of an ecological cul-de-sac, in association with which their ranges abruptly end. The Transkei is an area of convergence between the subtropical and temperate climatic zones in southeastern Africa, which prevents further southward expansion by many species. This furnishes a plausible explanation for the high Limpopo-Umtamvuna subtraction rate.

Apart from limited hybridization in *Cossypha dichroa* and *Cossypha natalensis* (Clancey 1982b), no interspecific interbreeding has been established in this sector, and no species is peculiar to it. In the northwest Karoo, the Greybacked Cisticola *Cisticola subruficapilla* and Wailing Cisticola *C. lais*

**TABLE 8.** Secondary contacts between species and well marked subspecies occurring in the Limpopo/Umtamvuna interfluvium. The list is not necessarily complete, but gives secondary contacts discussed in recent literature. Taxa marked \* known to hybridize in the zone of secondary contact.

<i>Accipiter tachiro tachiro</i>	<i>A. t. sparsimfasciatus</i> *
<i>Tauraco corythaix corythaix</i>	<i>T. livingstonii cabanisi</i>
<i>Campethera notata relicta</i>	<i>C. a. abingoni</i>
<i>Cossypha dichroa dichroa</i>	<i>C. natalensis egregior</i> *
<i>Terpsiphone viridis granti</i>	<i>T. v. plumbeiceps</i> *
<i>Nilaus afer solivagus</i>	<i>N. a. miombensis</i>
<i>Zosterops pallidus virens</i>	<i>Z. senegalensis tongensis</i> *
<i>Ploceus bicolor bicolor</i>	<i>P. b. lebomboensis</i> and <i>P. b. sclateri</i> *
<i>Hypargos niveoguttatus niveoguttatus</i>	<i>H. margaritatus</i>

are sympatric (mainly allopatric to the west), and the races of several polytypic species and of allospecies intergrade or replace one another along ecological lines, as in the case of the Karoo Prinia *Prinia maculosa exultans* and the Saffronbreasted Prinia *P. hypoxantha* (Clancey 1989a). The sharply differentiated phenotypes of the Cape White-eye *Zosterops pallidus atorii* (Karoo) and *Z.p. virens* (mesic woodland) complex intergrade broadly over the interior of the Transkei and especially along the base of the Drakensberg escarpment, where the populations are highly fluid (Clancey 1986a).

Some seasonal altitudinal displacement of species occurs, as in *Zoothera guttata* and the Orange Ground Thrush *Z. gurneyi*. *Z. guttata* breeds in coastal forest, the bulk thereafter moving northeast to the Natal and Zululand littoral, during which time the niche hiatus thus formed is temporarily filled by elements of *Z. gurneyi*, a breeder of interior temperate and mainly *Podocarpus* forest. Altitudinal movement of other forest birds occurs in the Cape Parrot *Poicephalus robustus*, Delegorgue's Pigeon *Columba delegorguei*, Bush Blackcap *Lioptilus nigricapillus* and others, the intermediate and high-forest breeders moving to lower levels after nesting. Elements of the Transkeian coastal race of *B. sylvaticus pondoensis*

are understood to move north in the southern dry season to the Natal coast (Clancey 1964), although this is doubted by Berruti *et al.* (1993).

In the Sundays-Great Fish River extension of karroid vegetation, intergradation between well marked subspecies occurs immediately east of the commencement of the southern-Cape coastal mountain ranges, as in certain cisticolas and, of some significance, in the local subspecies of *Turdus olivaceus*, where the nominate form interdigitates locally with the arid country *T.o. smithi*. This latter taxon is all but specifically discrete and confined to the steppe-like interior of southern Africa, being replaced to the south and east by forest-inhabiting races with more extensively orange underparts.

#### 4. From the lower Sundays River and southern Karoo to the Cape Peninsula

West of the lower Sundays River, several habitat types, significantly evergreen forest, are confined to a narrow coastal strip, compressed between the seaward slopes of the southern-Cape mountain ranges and the ocean, with no effective riverine barrier transecting the littoral between the Sundays River and

**TABLE 9.** Wide-ranging Afrotropical species with breeding ranges terminating between the Umtamvuna and Sundays/Great Fish Rivers.

Non-passerines 23 species	
<i>Butorides striatus</i>	<i>Clamator glandarius</i>
<i>Butorides rufiventris</i>	<i>Glaucidium capense</i>
<i>Gorsachius leuconotus</i>	<i>Scotopelia peli</i>
<i>Dendrocygna viduata</i>	<i>Ispidina picta</i>
<i>Nettapus auritus</i>	<i>Halcyon senegaloides</i>
<i>Turnix sylvatica</i>	<i>Bycanistes bucinator</i>
<i>Balearica regulorum</i>	<i>Bucorvus leadbeateri</i>
<i>Aenigmatolimnas marginalis</i>	<i>Lybius torquatus</i>
<i>Gallinula angulata</i>	<i>Pogoniulus pusillus</i>
<i>Microparra capensis</i>	<i>Prodotiscus regulus</i>
<i>Treron calva</i>	<i>Jynx ruficollis</i>
<i>Poicephalus robustus</i>	
Passerines 47 species	
<i>Mirafra africana</i>	<i>Telophorus sulfureopectus</i>
<i>Hirundo abyssinica</i>	<i>Malaconotus blanchoti</i>
<i>Dicrurus ludwigii</i>	<i>Lamprotornis corruscus</i>
<i>Parus niger</i>	<i>Nectarinia veroxii</i>
<i>Pycnonotus barbatus</i>	<i>Nectarinia olivacea</i>
<i>Phyllastrephus flavostriatus</i>	<i>Passer (griseus) diffusus</i>
<i>Zoothera guttata</i>	<i>Petronia superciliaris</i>
<i>Zoothera gurneyi</i>	<i>Amblyospiza albifrons</i>
<i>Thamnolaea cinnamomeiventris</i>	<i>Ploceus bicolor</i>
<i>Cossypha natalensis</i>	<i>Ploceus ocularis</i>
<i>Erythropygia leucophrys</i>	<i>Ploceus cucullatus</i>
<i>Erythropygia signata</i>	<i>Ploceus subaureus</i>
<i>Bradypterus barratti</i>	<i>Euplectes axillaris</i>
<i>Apalis flavida</i>	<i>Euplectes ardens</i>
<i>Cisticola ayresii</i>	<i>Euplectes progne</i>
<i>Cisticola natalensis</i>	<i>Mandingoa nitidula</i>
<i>Cisticola aberrans</i>	<i>Lagonosticta senegala</i>
<i>Prinia subflava</i>	<i>Lagonosticta rubricata</i>
<i>Muscicapa caerulescens</i>	<i>Sporaeginthus subflavus</i>
<i>Melaenornis pammelaina</i>	<i>Spermestes cucullatus</i>
<i>Batis molitor</i>	<i>Spermestes bicolor</i>
<i>Motacilla aguimp</i>	<i>Serinus mozambicus</i>
<i>Anthus lineiventris</i>	<i>Emberiza tahapisi</i>
<i>Tchagra senegala</i>	

the Cape Peninsula. Table 9 lists species whose ranges terminate between Umtamvuna and Sundays Rivers. Evergreen forest diminishes rapidly and becomes increasingly fragmented west of George, and many birds restricted to this habitat reach the austral limits of range and occur in greatly reduced numbers.

A precise figure of wide-ranging Afrotropical bird species with viable breeding populations reaching the southern and southwestern parts of the Cape (the very southern extremity of the African continent) is not readily arrived at, but is estimated to be between 190 and 200 species (Table 10). The passerine complement has been estimated to comprise 51 species, but in the case of non-passerines no comparable assessment in depth has been attempted, as data available in many instances are inconclusive. Using the data recently published by Hockey *et al.* (1989), 139 species are seen as presently involved. They list several more, particularly large, vulnerable species, which were recorded last century but have not been recorded since.

In the southwestern Cape, hybridization between full species is restricted to the Greyheaded Gull *Larus cirrocephalus* and Hartlaub's Gull *Larus hartlaubi*. At the subspecies level the Barthroated Apalis *Apalis thoracica* is represented by as many as three races, while there are additional cases of local polytypy among species such as *Turdus olivaceus*, *Cossypha caffra* and *Nectarinia chalybea*. These latter are represented by discrete additional populations conditioned to life in rain shadow and arid parts of the interior.

Evidence in a limited number of endemics without close relatives in other parts of the Afrotropics, namely Cape Sugarbird *Promerops caffer*, Cape Rockjumper *Chaetops frenatus* and Cape Siskin *Pseudochloroptila totta*, points to the southwestern region of the Cape as having constituted an avifaunal terminal point for a long time. The presence of close analogues over the Drakensberg in Gurney's Sugarbird *Promerops gurneyi*, Orangebreasted Rockjumper *Chaetops aurantius* and Drakensberg Siskin *Pseudochloroptila symonsi* confirms that this region has been split by the occasional spread of severe arid conditions into two faunal refugia, from which, in the case of the eastern refugium, there has been a measure of evolutionary differentiation and radiation in a northerly direction, as instanced by the presence of such austral endemics as the Bokmakierie *Telophorus zeylonus* and *Promerops gurneyi* in the frontier highlands of Zimbabwe and southern Mozambique.

Two other endemic passerines confined to the Winter Rainfall District of the southwestern Cape Province are closely related to spatially remote equatorial congeners, these being Victorin's Warbler *Bradypterus victorini* and the Protea Canary *Serinus leucopterus*. A third relict endemic, the Orangebreasted Sunbird *Nectarinia violacea*, was associated by Hall and Moreau (1970) with the widespread Olive Sunbird *N. olivacea*, but the supportive data presented cannot be sustained and the two sunbirds are certainly not closely allied. *N. violacea* appears to have no extant relatives. *N. olivacea* has been shown to be a species of a parapatric pair along with *N. obscura* of western and central Africa, differing in that the females carry male-like yellow pectoral tufts suggesting a difference in nuptial behaviour (Clancey in press b). The case of the two allospecies of olive sunbirds is particularly instructive biogeographically: one (*N. obscura*) is confined to forest over the eastern edge of the continental plateau of Zimbabwe, and the second (*N. olivacea*) is restricted to the coastal lowlands. The two are not in direct contact, yet further north in eastern Africa, *N. obscura* has leapfrogged over the coastal *N. olivacea changamwensis* and colonized the off-shore islands of Zanzibar and Pemba. The only established

instance of hybridization between the two sunbirds is known from Marble Hill, near Lusaka, Zambia, where it is an isolated population.

## 5. Lower Orange River

The valley of the lower Orange River west of Upington transects some particularly arid terrain with a rainfall of about 120 mm p.a. and below. The valley does not present an avifaunal barrier, as no full species have distributional ranges materially affected by it. Yet many species exhibit geographical variation in association with the southward thrust of particularly low rainfall conditions east of the uplands of northern Little Namaqualand; several Namibian taxa extend well south of the Orange River in this sector to reach the Bushman Flats and Great Bushmanland, and even further south to about Brandvlei and Vanwyksvlei. Variation within the limits imposed by rainfall is enhanced by the readiness by which certain terrestrial species' dorsal pigmentation and cryptic patterns simulate the texture and colour of the substrate, especially in certain larks of the *Certhilauda albescens/Pseudammomanes erythrochlamys* complex. On red sands and dunes south of the Orange River in Bushmanland, southeast to Vanwyksvlei, the Red Lark *P. (erythrochlamys) burra*, is locally present (Clancey 1990). Attention must also be drawn to the distinctive nominate race of the African Pied Wagtail *Motacilla aquimp*, the limited distribution of which is centred on the lower reaches of the Orange River. East of its range it is replaced by the widespread subspecies *M. a. vidua*.

Narrow range interdigitation in the lower Orange River region also occurs in the Southern Grey Tit *Parus afer* (coastwise to southwestern Great Namaqualand) and Ashy Tit *P. cinerascens* (on Orange River at Onseepkans and Pella Drift in the east), *Prinia maculosa psammophila* (coastal northwestern Cape to Aus in Great Namaqualand) with the nominate race of the Blackchested Prinia *P. flavicans* to the east, and in *Lanius collaris*, with the nominate race extending north of the lower Orange to southwestern Great Namaqualand, and the whitebrowed race *L. c. subcoronatus* south of the river in the immediate interior to the east. Several other cases are presented by further local larks, warblers and canaries and buntings (Table 11). While most species of the region are tolerant of relatively severe environmental conditions, many are nomadic.

## 6. Kunene and Okavango Rivers

Both the Kunene and Okavango Rivers on the northern regional limits have their sources in the moist highlands of Angola. Their lower reaches, especially in the case of the Kunene, transect desert. Their significance is that they do not present zoogeographical barriers, as do the Zambezi and Limpopo Rivers. They provide conversely corridors, enabling birds characteristic of the moist headwaters regions to extend well south to the northern periphery of the South West Arid Zone fauna (Table 12). The two rivers are not strictly avifaunally alike along their lower reaches, as only two full species, *Cichladusa ruficauda* and *Estrilda thomensis* enter the Subregion in riparian woodland on the Kunene, whereas on the Okavango more than 15 species do so. In the case of subspecies, the same imbalance is to be seen, with the following well marked subspecies listed for the Kunene: *Streptopelia s. semitorquata*, *Treron calva ansorgei*, *Halcyon senegalensis fuscopile*, *Merops superciliosus alternans*, *Turdoides m. melanops*, *Sylvietta rufescens ansorgei*, *Lamprotornis mevesii violaci*, *Lanius collaris capelli*,

*Malaconotus blanchoti citrinipectus*, *Estrilda astrild jagoensis* and *Estrilda melanotis bocagei*. In the case of the Okavango, more than 26 subspecies are on record. In Table 13 a comparison is made between the races of species or analogues occurring both along the Kunene and Okavango Rivers.

As both rivers have adjacent headwaters in the Huambo and other central highlands of Angola, the avifauna is probably largely homogeneous upstream, diverging lower down in line with the drier country transected by the Kunene. The average annual rainfall of the lower Kunene is 500 mm p.a., as against

750-1000 mm p.a. in the case of Okavango.

The valley of the mid-Okavango River where it forms the frontier between Angola and Namibia, constitutes an ecotone between the *Brachystegia* savannas of Angola and the dry *Acacia* woodland of the South West Arid Zone in Namibia. While there are no cases of interspecific hybridization for this ecotone, it is important to subspeciation, trends in geographical variation being towards greater bill size and wing-length and often greyer coloration.

An important zoogeographical feature of the lower

**TABLE 10.** Species with extensive Afrotropical breeding ranges which terminate to the south and southwest of the Karoo in the Cape Province.

Non-passerines 139 species			
<i>Podiceps cristatus</i>	<i>Milvus migrans parasiticus</i>	<i>Fulica cristata</i>	<i>Chrysococcyx cupreus</i>
<i>Podiceps nigricollis</i>	<i>Elanus caeruleus</i>	<i>Podica senegalensis</i>	<i>Chrysococcyx klaas</i>
<i>Tachybaptus ruficollis</i>	<i>Aquila verreauxii</i>	<i>Ardeotis kori</i>	<i>Chrysococcyx caprius</i>
<i>Pelecanus onocrotalus</i>	<i>Hieraaetus pennatus</i>	<i>Neotis denhami</i>	<i>Centropus burchellii</i>
<i>Phalacrocorax africanus</i>	<i>Lophaetus occipitalis</i>	<i>Actophilornis africanus</i>	<i>Tyto alba</i>
<i>Anhinga melanogaster</i>	<i>Polemaetus bellicosus</i>	<i>Charadrius tricollaris</i>	<i>Strix woodfordii</i>
<i>Ardea cinerea</i>	<i>Circaetus gallicus pectoralis</i>	<i>Rostratula benghalensis</i>	<i>Asio capensis</i>
<i>Ardea melanocephala</i>	<i>Haliaeetus vocifer</i>	<i>Charadrius marginatus</i>	<i>Bubo capensis</i>
<i>Ardea purpurea</i>	<i>Buteo trizonatus</i>	<i>Charadrius pallidus</i>	<i>Bubo africanus</i>
<i>Egretta garzetta</i>	<i>Buteo rufofuscus</i>	<i>Charadrius pecuarius</i>	<i>Bubo lacteus</i>
<i>Egretta intermedia</i>	<i>Accipiter rufiventris</i>	<i>Charadrius tricollaris</i>	<i>Caprimulgus pectoralis</i>
<i>Bubulcus ibis</i>	<i>Accipiter minullus</i>	<i>Vanellus coronatus</i>	<i>Caprimulgus rufigena</i>
<i>Ardeola ralloides</i>	<i>Accipiter melanoleucus</i>	<i>Vanellus armatus</i>	<i>Caprimulgus tristigma</i>
<i>Nycticorax nycticorax</i>	<i>Accipiter tachiro</i>	<i>Gallinago nigripennis</i>	<i>Apus caffer</i>
<i>Ixobrychus minutus</i>	<i>Micronisus gabar</i>	<i>Recurvirostra avosetta</i>	<i>Apus horus</i>
<i>Botaurus stellaris</i>	<i>Melierax canorus</i>	<i>Himantopus himantopus</i>	<i>Apus affinis</i>
<i>Scopus umbretta</i>	<i>Circus ranivorus</i>	<i>Burhinus capensis</i>	<i>Apus melba</i>
<i>Ciconia nigra</i>	<i>Polyboroides typus</i>	<i>Burhinus vermiculatus</i>	<i>Colius striatus</i>
<i>Bostrychia hagedash</i>	<i>Falco peregrinus</i>	<i>Smutsornis africanus</i>	<i>Urocolius indicus</i>
<i>Platalea alba</i>	<i>Falco biarmicus</i>	<i>Larus cirrocephalus</i>	<i>Apaloderma narina</i>
<i>Phoenicopterus ruber</i>	<i>Falco tinnunculus</i>	<i>Hydroprogne caspia</i>	<i>Ceryle rudis</i>
<i>Phoeniconaias minor</i>	<i>Falco rupicoloides</i>	<i>Sterna bergii</i>	<i>Megaceryle maxima</i>
<i>Dendrocygna viduata</i>	<i>Francolinus africanus</i>	<i>Sterna dougallii</i>	<i>Alcedo semitorquata</i>
<i>Alopochen aegyptiacus</i>	<i>Francolinus levaillantii</i>	<i>Chlidonias hybridus</i>	<i>Corythornis cristatus</i>
<i>Anas undulata</i>	<i>Coturnix coturnix</i>	<i>Columba guinea</i>	<i>Halcyon albiventris</i>
<i>Anas sparsa</i>	<i>Numida meleagris</i>	<i>Columba arquatrix</i>	<i>Merops apiaster</i>
<i>Anas capensis</i>	<i>Turnix hottentotta</i>	<i>Streptopelia semitorquata</i>	<i>Upupa epops</i>
<i>Anas hottentota</i>	<i>Rallus caerulescens</i>	<i>Streptopelia capicola</i>	<i>Phoeniculus purpureus</i>
<i>Anas erythrorhyncha</i>	<i>Amaurornis flavirostris</i>	<i>Streptopelia senegalensis</i>	<i>Tockus alboterminatus</i>
<i>Anas smithii</i>	<i>Porzana pusilla</i>	<i>Oena capensis</i>	<i>Tricholaema leucomelas</i>
<i>Netta erythrophthalma</i>	<i>Sarothrura rufa</i>	<i>Turtur tympanistria</i>	<i>Indicator indicator</i>
<i>Plectropterus gambensis</i>	<i>Sarothrura elegans</i>	<i>Aplopelia larvata</i>	<i>Indicator variegatus</i>
<i>Oxyura maccoa</i>	<i>Sarothrura affinis</i>	<i>Cuculus solitarius</i>	<i>Indicator minor</i>
<i>Thalassornis leuconotus</i>	<i>Porphyrio porphyrio</i>	<i>Cuculus clamosus</i>	<i>Dendropicos fuscescens</i>
<i>Sagittarius serpentarius</i>	<i>Gallinula chloropus</i>	<i>Clamator jacobinus</i>	<i>Mesopicos griseocephalus</i>
Passerines 51 species			
<i>Hirundo albigularis</i>	<i>Andropadus importunus</i>	<i>Cisticola tetrica</i>	<i>Nectarinia famosa</i>
<i>Hirundo dimidiata</i>	<i>Turdus olivaceus</i>	<i>Cisticola lais</i>	<i>Nectarinia amethystina</i>
<i>Riparia paludicola</i>	<i>Cercomela familiaris</i>	<i>Cisticola tinniens</i>	<i>Anthreptes collaris</i>
<i>Riparia cincta</i>	<i>Saxicola torquata</i>	<i>Cisticola fulvicapilla</i>	<i>Ploceus capensis</i>
<i>Psalidoprocne holomelas</i>	<i>Cossypha caffra</i>	<i>Muscicapa adusta</i>	<i>Ploceus velatus</i>
<i>Campephaga flava</i>	<i>Pogonocichla stellata</i>	<i>Batis capensis</i>	<i>Euplectes orix</i>
<i>Coracina caesia</i>	<i>Acrocephalus baeticatus</i>	<i>Trochocercus cyanomelas</i>	<i>Euplectes capensis</i>
<i>Dicrurus adsimilis</i>	<i>Acrocephalus gracilirostris</i>	<i>Terpsiphone viridis</i>	<i>Estrilda astrild</i>
<i>Oriolus larvatus</i>	<i>Bradypterus baboecala</i>	<i>Motacilla capensis</i>	<i>Serinus canicollis</i>
<i>Corvus capensis</i>	<i>Phylloscopus ruficapillus</i>	<i>Anthus leucophrys</i>	<i>Serinus sulphuratus</i>
<i>Corvus albus</i>	<i>Apalis thoracica</i>	<i>Lanius collaris</i>	<i>Serinus gularis</i>
<i>Corvus albicollis</i>	<i>Cameroptera brachyura</i>	<i>Dryoscopus cubla</i>	<i>Emberiza flaviventris</i>
<i>Phyllastrephus terrestris</i>	<i>Cisticola juncidis</i>	<i>Telophorus olivaceus</i>	

Okavango is the extensive delta system with tracts of papyrus swamp, which has been colonized by many species peculiar to this environment, but, strangely enough, not all, even among some which reach nearby Zambian wetlands. Even in the

case of the Shoebill *Balaeniceps rex*—a likely candidate—occurrence in the Okavango Delta still rests on equivocal grounds. The present composition of the avifauna of the mosaic of habitats in this part of the Afrotropics is seemingly a

**Table 11.** The arid lower Orange River basin as a broadly defined meeting point for subspecies and species.

North	South
<i>Melierax canorus argentior</i>	<i>M. c. canorus</i>
<i>Vanellus coronatus xerophilus</i>	<i>V. c. coronatus</i>
<i>Cursorius rufus theresae</i>	<i>C. r. rufus</i>
<i>Smutsornis africanus africanus</i>	<i>S. a. granti</i>
<i>Pterocles namaqua namaqua</i>	<i>P. n. furvus</i>
<i>Chersomanes albofasciata arenaria</i>	<i>C. a. bushmanensis</i> and <i>C. a. garrula</i>
<i>Calandrella cinerea witputzi</i>	<i>C. c. cinerea</i>
<i>Dicrurus adsimilis apivorus</i>	<i>D. a. adsimilis</i>
<i>Pycnonotus nigricans nigricans</i>	<i>P. capensis</i> and <i>P. n. nigricans</i> and <i>P. n. superior</i> to the east
<i>Oenanthe pileata neseri</i>	<i>O. p. pileata</i>
<i>Cercomela familiaris galtoni</i>	<i>C. f. familiaris</i> ( <i>familiaris</i> $\geq$ <i>galtoni</i> )
<i>Cercomela schlegelii namaquensis</i>	<i>C. s. pollux</i>
<i>Myrmecocichla formicivora minor</i>	<i>M. f. formicivora</i>
<i>Parisoma layardi aridicola</i>	<i>P. l. layardi</i>
<i>Eremomela gregaria gregaria</i>	<i>E. g. albigularis</i>
<i>Eurypytila subcinnamomea petrophila</i>	<i>E. s. subcinnamomea</i>
<i>Cisticola subruficapilla namaqua</i>	<i>C. s. karasensis</i>
<i>Phragmacia substriata confinis</i>	<i>P. s. substriata</i>
<i>Melaenornis infuscatus namaquensis</i>	<i>M. i. infuscatus</i>
<i>Batis pririt affinis</i>	<i>B. p. pririt</i>
<i>Anthus similis leucocraspedon</i>	<i>A. s. nicholsoni</i>
<i>Lanius collaris subcoronatus</i>	<i>L. c. collaris</i>
<i>Philetarius socius socius</i>	<i>P. s. eremnus</i> (polytopic)
<i>Serinus alario leucolaema</i>	<i>S. a. alario</i>
<i>Serinus flaviventris hesperus</i>	<i>S. f. aurescens</i>
<i>Serinus albogularis sordahlae</i>	<i>S. a. hewitti</i>
<i>Emberiza c. capensis</i> $\geq$ <i>bradfieldi</i>	<i>E. c. capensis</i>

**Table 12.** Non-passerine and passerine birds present in riverine vegetation along the mid- and lower Okavango River to Caprivi in northern Namibia and southern Angola, being a listing of species, races or vicariants.

Species	
<i>Circaetus cinerascens</i>	<i>Cisticola pipiens</i>
<i>Falco ardosiaceus</i>	<i>Macronyx fuelleborni</i>
<i>Musophaga rossae</i>	<i>Lanius souzae</i>
<i>Centropus cupreicaudus</i>	<i>Laniarius bicolor</i>
<i>Hirundo angolensis</i>	<i>Lamprotornis acuticaudus</i>
<i>Sylvietta ruficapilla</i>	<i>Lagonosticta nitidula</i>
<i>Cichladusa ruficauda</i>	<i>Vidua wilsoni</i>
<i>Acrocephalus rufescens</i>	<i>Turdoides hartlaubii</i>
Well marked subspecies	
<i>Vanellus senegallus solitaneus</i>	<i>Parus rufiventris diligens</i>
<i>Glareola pratincola riparia</i>	<i>Pycnonotus barbatus ngamii</i>
<i>Glareola nuchalis torrens</i>	<i>Turdoides melanops querulus</i>
<i>Streptopelia semitorquata maxima</i>	<i>Cossypha heuglini orphea</i>
<i>Treron calva damarensis</i> & <i>schalowi</i>	<i>Acrocephalus gracilirostris cunenensis</i>
<i>Halcyon albiventris hylophila</i>	<i>Motacilla capensis simplicissima</i>
<i>Tauraco livingstonii schalowi</i>	<i>Anthus leucophrys tephridorsus</i>
<i>Poicephalus meyeri damarensis</i>	<i>Anthus nyassae chersophilus</i>
<i>Lybius torquatus bocagei</i>	<i>Petronia superciliaris rufitergum</i>
<i>Prodotiscus zambesiae lathburyi</i>	<i>Ploceus ocularis tenuirostris</i> & <i>crocatu</i>
<i>Campethera bennettii capricorni</i>	<i>Euplectes axillaris bocagei</i>
<i>Mesopicus griseocephalus persimilis</i>	<i>Euplectes albonotatus asymmetrurus</i>
<i>Psalidoprocne orientalis reichenowi</i>	<i>Uraeginthus angolensis cyanopleurus</i>

comparatively recent development, as evidenced by the pipit *Anthus spp.* races occurring on its periphery (Clancey 1986b) and the weakly differentiated races of the *Acrocephalus* warblers in the papyrus.

Apart from the 16 species (see Table 12) extending marginally into the Southern African Subregion, the riparian woodland of the Okavango further permits the ranges of several moist-habitat races to extend further south than elsewhere. These transect an ecotone to abut on the South West Arid Zone. The subspecies given in Table 13 do not constitute a definitive list, but are some of those discussed in recent literature.

### Conclusions

A re-examination of the developmental role of major river valleys in the range patterns of birds in the Southern African Subregion shows that, contrary to earlier findings, they function as effective range barriers only where they separate or locally terminate major biomes. The valleys must be broad, lowlying, seasonally torrid and largely arid and sufficiently extensive.

Most endemic bird species in Southern Africa are confined to the South West Arid Zone, because of the long term stability of the arid climate and the indigenous biota. In sharp contrast, the larger avifaunal representation present over the moister eastern and southern regions has far fewer endemics, but at the same time has more spatially remote isolates of wide-ranging forest species centred on regions further north in Africa. I postulate that this derives from the immediate dynamic past of the eastern biota during the Pleistocene, when it was materially influenced by stressful east-west climatic oscillations on the eastern limits of the Lower Guinea Forest. As this rainforest expanded and contracted in response to the peaks and troughs of the northern glaciations it influenced recruitment of woodland or grassland birds from the northeast or from the south. During glacial troughs, the expansion of evergreen forest resulted in the spread of forest groups and species, the peripheral (parapatric) populations of which were in many cases the founders of present-day isolates.

I estimate that slightly more than 490 species with extensive extralimital continental ranges enter Southern Africa from the northeast, individual species reaching their southern limits

and steadily dropping out of the avifauna towards the south. The rate of subtraction is in part determined by the presence of an arid-valley barrier and the splitting or terminating of a biome, especially where these coincide. Of the four interfluves identified as of biogeographical significance in the eastern Subregional context, the largest subtraction rate (156 species) is from immediately south of the Limpopo River to the Umtamvuna River on the Natal/Transkei frontier. This high figure results from the coincidence and convergence of temperate and subtropical climatic zones in this region. Further south the subtraction rate declines, a further 69 species dropping out in association with the coastwise extension of karroid vegetation between the Sundays and Great Fish Rivers. This is the last of the major barriers to the eastern biota formed by the association of a biome and a major arid valley. About 190 further wide-ranging species, mainly entering the Subregion from the northeast, reach the southwestern Cape.

The valley of the lower Orange River has no bearing on the ranges of full species of birds inhabiting this particularly arid region, but is significant in respect of subspeciation, the patterns of variation lying in a west-to-east direction and in no way associated with the directional flow of the river. They mainly follow the isohyets. Up to this point, five river valleys are identified as of major zoogeographical significance in southern Africa: mid-Zambezi, middle and lower Limpopo, Umtamvuna and the Sundays and Great Fish, and to a small extent the lower Orange, and then only in so far as it affects subspecies.

### Acknowledgements

This contribution, while largely based on field and museum-centred research undertaken over a span of many years (1950-1993) by the Durban Natural Science Museum, particularly while I was its Director (1952-1982), also reflects considerable data input furnished by specimens and information made available by colleagues working elsewhere in South Africa and territories to our north, western Europe and North America. I must mention, apart from the contributions of many others, the assistance furnished by the loan of a vast number of specimens from south-central and southern Africa by M.P.S. Irwin, Ornithologist and one-time Regional Director of the National Museum of Zimbabwe, in Bulawayo. During

**Table 13.** Non-passerine and passerine bird species of the Kunene and Okavango Rivers within the Southern African Subregion, being a comparative list of subspecies or vicariants present in either valley. The list is not necessarily complete.

Species	Kunene	Okavango
<i>Pterocles bicinctus</i>	<i>P. b. bicinctus</i>	<i>P. b. chobiensis</i>
<i>Streptopelia semitorquata</i>	<i>S. s. semitorquata</i>	<i>S. s. maxima</i>
<i>Streptopelia capicola</i>	<i>S. c. damarensis</i>	<i>S. c. tropica</i>
<i>Treron calva</i>	<i>T. c. ansorgei</i>	<i>T. c. damarensis</i>
<i>Poicephalus rueppellii</i> and <i>P. meyeri</i>	<i>P. rueppellii</i>	<i>P. m. damarensis</i>
<i>Phoeniculus purpureus</i> and <i>P. (p.) damarensis</i>	<i>P. (p.) damarensis</i>	<i>P. p. angolensis</i>
<i>Indicator minor</i>	<i>I. m. damarensis</i>	<i>I. m. valens</i>
<i>Campethera abingoni</i>	<i>C. a. anderssoni</i>	<i>C. a. abingoni</i>
<i>Campethera bennettii</i>	<i>C. b. buyisi</i>	<i>C. b. capricorni</i>
<i>Chlorocichla flaviventris</i>	<i>C. f. occidentalis</i>	<i>C. f. zambesiae</i>
<i>Sylvietta rufescens</i>	<i>S. r. ansorgei</i>	<i>S. r. flecki</i>
<i>Batis pririt</i> and <i>B. molitor</i> :	<i>B. p. affinis</i>	<i>B. m. palliditergum</i>
<i>Lagonosticta rhodopareia</i>	<i>L. r. ansorgei</i>	<i>L. r. jamesoni</i>
<i>Lagonosticta senegala</i>	<i>L. s. pallidicrissa</i>	<i>L. s. rendalli</i>
<i>Estrilda astrild</i>	<i>E. a. jagoensis</i>	<i>E. a. ngamiensis</i>
<i>Uraeginthus angolensis</i>	<i>U. a. angolensis</i>	<i>U. a. cyanopleurus</i>



this period of scientific collaboration, staff of the National Museum and Durban Natural Science Museum joined forces to research the birdlife of Zimbabwe and Moçambique, and shared field experience, including noteworthy additions to the Southern African avifauna. The direct assistance of other workers includes that of J.G. Williams, former Ornithologist of the former Coryndon Memorial Museum, Nairobi, Kenya, the late Dr A.A. da Rosa Pinto (one-time Director of the Museu Dr Alvaro de Castro, Maputo, and later with the Instituto de Investigação Científica de Angola (Sá da Bandeira), Dr M. Courtenay-Latimer (former Director, East London Museum), the late Professor J.M. Winterbottom (first Director, Percy Fitzpatrick Institute of African Ornithology (Cape Town), and many others. In respect of overseas colleagues, I may mention the assistance of the late Dr A. Prigogine (Brussels), the late Dr H.E. Wolters (Bonn), and the late C.W. Benson (Cambridge, England), and Major M.A. Traylor Jnr (Chicago, U.S.A.). To all those named and many others I extend my profound gratitude. I also thank Professor T.M. Crowe and Richard Brooke of the FitzPatrick Institute, University of Cape Town, for reviewing the manuscript and drawing my attention to weaknesses in it, and the Editor for his prescience, assuring the validity of the final product.

#### REFERENCES

- ACOCKS, J.P.H. 1988. Veld types of South Africa, 3rd edition. Botanical Research Institute, Pretoria.
- BENSON, C.W., BROOKE, R.K., DOWSETT, R.J. and IRWIN, M.P.S. 1971. The Birds of Zambia. Collins, London.
- BENSON, C.W., IRWIN, M.P.S. and WHITE, C.M.N. 1962. The significance of valleys as avian zoogeographical barriers. *Annals of the Cape Provincial Museums* 2: 155-189.
- BERRUTI, A., TAYLOR, P.J. and VERNON, C.J. 1993. Morphometrics and distribution of the Knysna Warbler *Bradypterus sylvaticus* Sundevall and Barratt's Warbler *B. barratti* Sharpe. *Durban Museum Novitates* 18: 29-36.
- CAPPARELLA, A.P. 1991. Neotropical avian diversity and riverine barriers. *Acta XX Congressus Internationalis Ornithologici*: 307-316.
- CLANCEY, P.A. 1964. The Birds of Natal and Zululand. Oliver and Boyd Ltd, Edinburgh and London.
- CLANCEY, P.A. 1967. Gamebirds of Southern Africa. Purnell and Sons, Cape Town.
- CLANCEY, P.A. 1970a. Comments on some anomalous Bleating Bush Warblers from eastern Rhodesia. *Miscellaneous Taxonomic Notes on African Birds XXVII. Durban Museum Novitates* 8(17): 335-337.
- CLANCEY, P.A. 1970b. Variation in the weavers of the *Ploceus cucullatus sibilosus/nigriceps* complex. *Miscellaneous Taxonomic Notes on African Birds XXIX. Durban Museum Novitates* 8(20): 378-390.
- CLANCEY, P.A. 1970/71. A Handlist of the birds of Southern Moçambique. *Memórias do Instituto de Investigação Científica de Moçambique*, Lourenço Marques.
- CLANCEY, P.A. 1977. Variation in and the relationships of the Brown-headed Parrot of the Eastern African Lowlands. *Bonner zoologisches Beiträge* 28: 279-291.
- CLANCEY, P.A. 1980. On birds from the mid-Okavango Valley on the South West Africa/Angola border. *Durban Museum Novitates* 12(9): 87-127.
- CLANCEY, P.A. 1981. Further on the Southern African Sub-region races of *Cossypha caffra* (Linnaeus). *Miscellaneous Taxonomic Notes on African Birds LXI. Durban Museum Novitates* 13(4): 41-47.
- CLANCEY, P.A. 1982a. The Olive Thrush *Turdus olivaceus* Linnaeus in southern Africa. *Miscellaneous Taxonomic Notes on African Birds LXII. Durban Museum Novitates* 13(7): 65-70.
- CLANCEY, P.A. 1982b. On the robins *Cossypha dichroa* and *C. natalensis* (Aves: Turdidae) in southern Africa. *Bonner zoologisches Beiträge* 33: 293-302.
- CLANCEY, P.A. 1985. Species limits in the Long-billed Pipits of the southern Afrotropics. *Ostrich* 56: 157-169.
- CLANCEY, P.A. 1986a. Endemicity in the Southern African avifauna. *Durban Museum Novitates* 13(20): 245-284.
- CLANCEY, P.A. 1986b. Subspeciation in the Pipit *Anthus cinnamomeus* Rüppell of the Afrotropics. *Le Gerfaut* 76: 187-211.
- CLANCEY, P.A. 1988. On variant Afrotropical *Ploceus* weavers. *Ibis* 130: 567-568.
- CLANCEY, P.A. 1989a. Four additional species of southern African endemic birds. *Durban Museum Novitates* 14(7): 140-152.
- CLANCEY, P.A. 1989b. The taxonomy of the Green Barbets (Aves: Lybiidae) of the eastern Afrotropics. *Bonner zoologisches Beiträge* 40(1): 11-18.
- CLANCEY, P.A. 1990. Taxonomic and distributional findings on some birds from Namibia. *Cimbebasia* 11 (1989): 117-119.
- CLANCEY, P.A. 1992. Subspeciation, clines and contact zones in the southern Afrotropical avifauna. *Bulletin of the British Ornithologists' Club* 112A: 73-86.
- CLANCEY, P.A. in press a. The Ground Thrush *Zoothera guttata* (Vigors 1831) in the southern Afrotropics. *Le Gerfaut*.
- CLANCEY, P.A. in press b. The status of *Nectarinia olivacea* (Smith), 1840—a unitary species or two polytypic allospecies? *Le Gerfaut*.
- CLANCEY, P.A., BROOKE, R.K., IRWIN, M.P.S. and MARKUS, M.B. 1980. SAOS Checklist of Southern African Birds. Southern African Ornithological Society.
- CLANCEY, P.A., BROOKE, R.K., CROWE, T.M. and MENDEL-SOHN, J.M. 1987. S.A.O.S. Checklist of Southern African Birds. First Updating Report. Southern African Ornithological Society, Johannesburg.
- CLANCEY, P.A., BROOKE, R.K., CROWE, T.M. and MENDEL-SOHN, J.M. 1991. S.A.O.S. Checklist of Southern African Birds. Second Updating Report. Southern African Ornithological Society, Johannesburg.
- CLANCEY, P.A. and IRWIN, M.P.S. 1978. Species limits in the *Nectarinia afra* / *N. chalybea* complex of African doublecollared sunbirds. *Durban Museum Novitates* 11 (20): 332-351.
- CROWE, T.M. and CROWE A.A. 1982. Patterns of distribution, diversity and endemism in Afrotropical birds. *Journal of Zoology, London* 198: 417-422.
- FORD, J. 1987a. Minor isolates and minor geographical barriers in avian speciation in continental Australia. *Emu* 87: 90-102.
- FORD, J. 1987b. Hybrid zones in Australian birds. *Emu* 87: 158-178.
- HALL, B.P. and MOREAU, R.E. 1970. An Atlas of Speciation in African Passerine Birds. British Museum (Natural History), London.
- HOCKEY, P.A.R., UNDERHILL, L.G., NEATHERWAY, M. and RYAN, P.G. 1989. Atlas of the Birds of the Southwestern Cape. Cape Bird Club, Cape Town.
- IRWIN, M.P.S. 1981. The Birds of Zimbabwe. Quest Publishing Ltd, Salisbury (Harare), Zimbabwe.
- LOUETTE, M. 1992. Barriers, contact zones and subspeciation in central equatorial Africa. *Bulletin of the British Ornithologists' Club* 112A: 209-216.
- MOREAU, R.E. 1966. The bird faunas of Africa and its islands. Academic Press, London.
- QUICKELBERGE, C.D. 1989. The birds of the Transkei. Durban Natural Science Museum, Durban.
- SNOW, D.W. (ED.) 1978. An Atlas of Speciation in African Non-Passerine Birds. British Museum (Natural History), London.
- TARBOTON, W.R., KEMP, M.I. and KEMP, A.C. 1987. Birds of the Transvaal. Transvaal Museum, Pretoria.
- VAN WYK, A.E. 1990a. The sandstone regions of Natal and Pondoland: remarkable centres of endemism. In *Palaeoecology of Africa* 21: 243-257. Balkema, Rotterdam.
- VAN WYK, A.E. 1990b. A new species of *Leucadendron* (Proteaceae) from Pondoland, with a discussion of its biogeography. *South African Journal of Botany* 56: 458-466.
- WILD, H. and FERNANDEZ, H. 1967. *Flora Zambesiaca*. Salisbury (Harare), Zimbabwe.