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ZONAL DISTRIBUTION IN AFROTROPICAL MONTANE

PIPITS (*ANTHUS*: MOTACILLIDAE)

by

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SUMMARY

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Taxonomic uncertainty has long surrounded the identity of certain African *Anthus* pipits, particularly those breeding on the summit grasslands of high mountains and in contiguous woodlands occurring peripherally at lower altitudes. Forms breeding on summit grasslands, notably Jackson's Pipit *Anthus latistriatus* and the Mountain Pipit *A. hoeschi*, are seen as closely allied relict (refugial) species derived from a major invasion by an ancestral form likewise responsible for the present Richard's Pipit *A. richardi* of the Palearctic and other allied taxa. On the other hand, the Wood Pipit *A. nyassae*, endemic to *Brachystegia* woodlands (Miombo), including areas adjacent to the montane grassland forms, is derived from an ancestor of the Longbilled Pipit *A. similis* (proto-*similis*), which adapted to a woodland existence during environmental changes in the Pleistocene and Pliocene. These three species now require general recognition in the arrangement of the African Anthinae. In the Afrotropics, intraspecific geographical variation in pipits is normally horizontal in distribution, apparent altitudinal replacement of races of polytypic species on high mountains actually involving separate species.

Keywords: Afrotropical pipits, *Anthus*, altitudinal zonation, taxonomy, diagnostic criteria.

INTRODUCTION

The taxonomy of certain Afrotropical pipits of the genus *Anthus* Bechstein has proved difficult to resolve, particularly the status of *A. latistriatus* Jackson 1899, *A. nyassae* Neumann 1906 and *A. hoeschi* Stresemann 1938. In her major revisionary study of *Anthus* species of the world, Hall (1961) alludes to the *A. nyassae* issue but avoids discussing either *A. latistriatus* or *A. hoeschi*. The taxonomy of these and closely related forms has been discussed in a series of papers by Clancey (1977, 1978, 1984, 1985, 1986 a,b,c,d, 1987). Clancey (1987) has shown that in their home range mountains, the allied allopatric forms show altitudinal separation of breeding grounds, and that sympatry usually occurs only when they are not breeding. The exception is the woodland-based *A. nyassae* subspp., which are not overtly subject to any appreciable post-breeding movement, and, moreover, do not associate with grassland forms with which they are only seasonal siblings. Where two or more morphologically and convergently similar *Anthus* forms occur on isolated mountains, the species seasonally inhabiting the stony summit grasslands will be of a species other than that of the form(s) occurring in altitudinally lower yet analogous habitat. The concept that the summit and sub-montane grassland (or savanna woodland) taxa are never conspecific has been criticized by Dowsett & Dowsett-Lemaire (1986), largely on the grounds that the conclusions reached in the museum were not followed up by an analysis of the vocalizations. The evidence supporting the recognition of *A. latistriatus*, *A. nyassae* and *A. hoeschi* as full species and the concept of altitudinal species replacement are discussed hereunder in both regional and continental contexts, while the diagnostic criteria of the various forms are detailed.

DISCUSSION

Altitudinal zonation of ranges of *Anthus* spp. on single mountains is known from south of the Equator and is most in evidence in or peripheral to the *Brachystegia* (Miombo) belt. Three species have been determined as constituting summit grassland taxa: *A. latistriatus* in three or four populations with the spatially remote *A. hoeschi* of the Drakensberg Mountains of south-eastern Africa seen as recently evolved from it (Figs. 1 & 2), and *A. similis* in one, perhaps two cases if the Marungu population of south-eastern Zaïre is included. The position in Cameroon is somewhat equivocal at this stage, in which region *A. latistriatus bannermani* Bates, 1930, is in – probably recent – contact with two far western races of *A. cinnamomeus* Rüppell, 1840 (*A. c. cameroonensis* Shelley, 1900, and *A. c. lynesii* Bannerman & Bates, 1927). Bannerman (1936) initially only recognised *A. l. bannermani* from the interior mountains of Sierra Leone, but later (Bannerman 1951) extended the range east to Cameroon. He believed the form to be a discrete species. In the region of the contact between *A. l.*

bannermani and *A. cinnamomeus* subssp. in Cameroon there is no record of altitudinal zonation of range. However, as *A. l. bannermani* is associated with rocky summit grassland in Sierra Leone, cleared mined areas on Mt. Nimba, Liberia (Colston & Curry-Lindahl 1986), and barren rocky hillside in Cameroon, the two species are evidently ecologically segregated. The reason why *latistriatus* and *hoeschi* were in limbo for so long is now clear, as both are in the main long distance migrants from restricted breeding grounds in remote highlands, which at the time of their description were unknown.

Clancey (1984) showed that the three races of *latistriatus* lie in a rough, extended and fragmented arc from the mountains of Sierra Leone and Guinea to Cameroon (*A. l. bannermani*), south-eastern Zaïre and adjacent

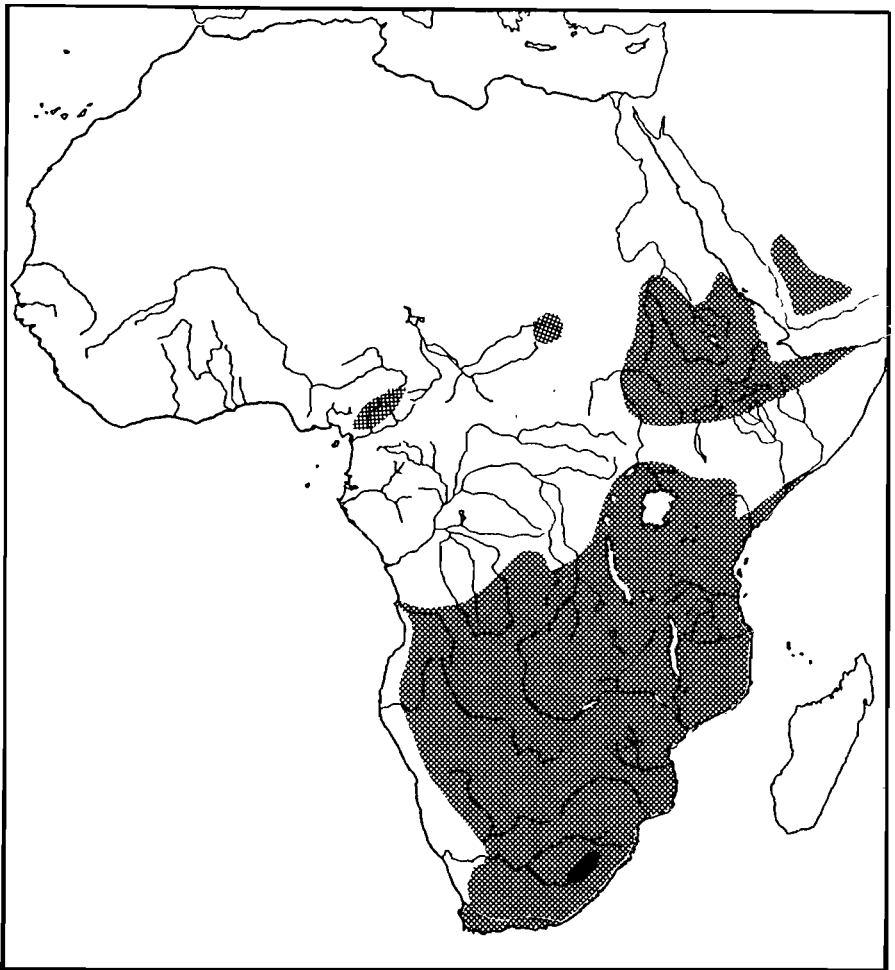


Figure 1. The distribution of *Anthus cinnamomeus* subssp. (shaded areas) and *A. hoeschi* (black area).

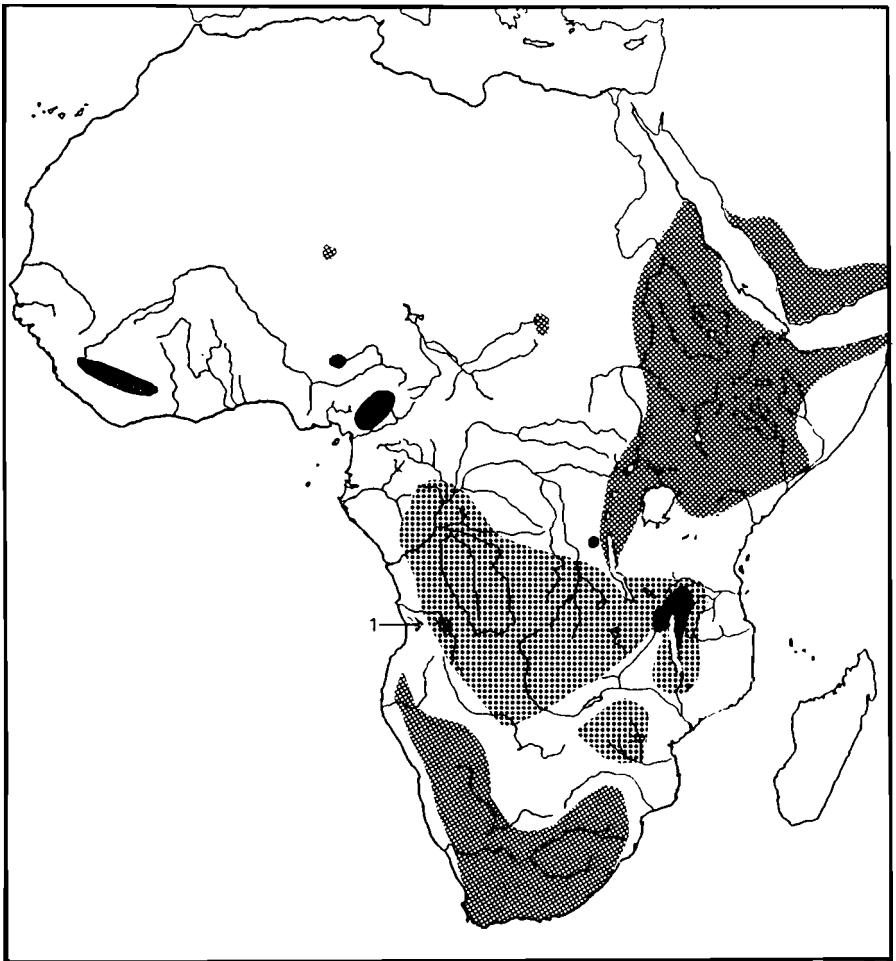




Figure 2. The distribution of three species of Afrotropical *Anthus* pipits.

A. latistriatus subspp.: small scattered black areas.

A. nyassae subspp.: 

A. similis subspp.: 

Distribution of *A. similis moco* is shown by arrowed 1.

western Tanzania (*A. l. latistriatus*), and the mountains to the northern end of Lake Malawi (*A. l. winterbottomi*) (Fig. 2), this chain of forms terminating in the disjunct *A. hoeschi* of the Drakensberg Range (Fig. 1). It is noteworthy that this group of forms is distributed immediately to the west of the northern Afrotropical *A. similis* subspp., and north and east of the forestal complex of *A. nyassae*, which, following Neumann's original

assignment of the form, had until recently been treated as part of the wide-ranging *A. similis* Jerdon. In the case of *nyassae*, the four subspecies are forms of the Miombo savannas of south-central Africa, differing markedly in their ecology from the steppe/montane oriented *A. similis*, *sens. strict.*, with which they had been associated until very recently. The ripple or wave-like pattern of these contemporary pipit ranges are the result of distant historical events, similar comparable north-eastern and south-western range patterns showing up in range maps of many polytypic species and superspecies of African birds.

In the Palaearctic, a somewhat parallel altitudinal zonation of breeding ranges is found in closely related allopatric *Anthus* species: the Rock Pipit *A. petrosus* (Montagu) of the rocky coasts of north-western France and the British Isles to the Faeroes and western Scandinavia, and its sibling, the Water Pipit *A. spinoletta* (Linnaeus) of the alpine zone of continental mountains from western mainland Europe, east to central Asia. East of this, and in the Nearctic, it is replaced by *A. rubescens* (Tunstall), which ranges as far east as western Greenland.

The Southern African Subregion: *Anthus hoeschi*.

South of the Limpopo River: The case which best demonstrates the stratified or zonal pattern of breeding distributions in Afrotropical montane pipits is that of the complex occurring in the Drakensberg Mountains of the south-east (Table 1, Fig. 1). This furnishes reliable guidelines in determining the relationships and status of confusingly similar *Anthus* species present in other Afromontane systems.

The establishment of the high level grassland breeding *Anthus* of the Drakensberg as the long mysterious *A. hoeschi* (Stresemann 1938, Mendelsohn 1984, Clancey 1984, Brooke 1984), described on three occasions on specimens from the breeding and wintering grounds and as a transient by three different ornithologists, has cleared the way for the resolution of the taxonomic status of several other equivocal pipit forms.

A. hoeschi is a long distance migrant, spending the nonbreeding season on the Zaïre/Zambezi River watershed in south-eastern Zaïre, eastern Angola and adjacent Zambia, migrating across the desertic interior of the Southern African Subregion in March and April, returning to its breeding highlands in late October and November (Clancey 1986a). It nests in the Drakensberg above about 1830 m a.s.l. (Fig.1), in the main replacing at these elevations allied pipits (*A. cinnamomeus* and *A. similis*), but with a measure of interdigitation with the former at the range interface in the north-eastern Cape (Naude's Nek Pass) (Table 1).

Below the breeding grounds of *A. hoeschi* and alongside *A. cinnamomeus* and *A. similis* in the Drakensberg occur two other pipit species, these being *A. crenatus* and *Hemimacronyx chloris*, which seem not to be in ecological competition with either. While the South African Rock Pipit (*crenatus*) inhabits terrain similar to that favoured by *A. similis*, *H. chloris* occurs

TABLE 1

The zonal breeding distribution and diagnostic criteria of three closely allied *Anthus* pipits in the Drakensberg Mountains of south-eastern Africa.

Zone	Altitude (metres) above sea level	Form
A. Summit (alpine & sub-alpine grassland)	1830–2865	<i>Anthus hoeschi</i>
B. Montane grassland	below 1829	<i>Anthus cinnamomeus rufuloides</i>
Mixed grass and broken ground	below 1829	<i>Anthus similis primarius</i>

Diagnostic criteria:

A. hoeschi. Male: wing-length 94-97,5 mm, tail-length 63-71 mm. Female: wing-length 88,5-92 mm, tail-length 61-66,5 mm. Crown broadly streaked brownish black. Breast spotting blackish. Light apical surface of outermost rectrix dull vinaceous-buff; penultimate rectrix generally plain. Base of bill flesh-coloured.

A. c. rufuloides. Smaller than *hoeschi*. Male: wing-length 88-94 mm. Female: wing-length 84,5-88 mm. Crown with finer streaking. Light surfaces to two outermost rectrices starkly white. Base of bill yellowish.

A. s. primarius. Wings and tail longer than in *hoeschi*. Male: wing-length 94-103 mm, tail-length 71-76 mm. Female: wing-length, 92-97 mm, tail-length 68-74 mm. Compared with two previous taxa, breast streaked dusky rather than spotted blackish. Light areas on two outermost rectrices dull vinaceous-buff, and penultimate rectrix never plain apically. Hind-claw shorter than in both the foregoing. Base of bill flesh-coloured.

narrowly in the same grassland as does *A. cinnamomeus*, but is more altitudinally restricted, breeding between 1400-2400 m a.s.l.

The Limpopo/Zambezi interfluvium: In this region the higher mountains are those along the Zimbabwe/Mozambique frontier from about 20°S, extending some 260 km, the highest point attained being Mt. Inyangani at 2592 m a.s.l. Unlike the Drakensberg to the south, these frontier highlands and the isolated feature of Mt. Gorongosa (in Mozambique to the east at 20°41'S, 34°09'E), do not support an endemic pipit, and those relevant to the present study occurring inhabit Miombo savanna (*A. nyassae frondicolus*), and grazed grassland and fallow tracts of cleared land (*A. cinnamomeus lichenya* and *A. vaalensis chobiensis*) – both latter taxa with extensive ranges. The presence of huge tracts of suitable terrain from the Chimanmani Mountains northwards to Mt. Inyangani notwithstanding, no representative of the steppe/montane oriented *A. similis* occurs in this sector. Indeed, the ecological niche normally favoured by *A. similis* is totally unexploited in this particular area.

Zonal structuring of ranges does not occur among medium-sized pipits in the Limpopo/Zambezi interfluvium. The plateau and highland breeding *A. cinnamomeus* population is the upland race *lichenya*, described from Mt. Mlanje in the southern highlands of Malawi, in which white on the pen-

ultimate rectrix is frequently vestigial or even lacking (Clancey 1977). This is also found in a second south-central African race – *A. c. itombwensis* of the Itombwe Range in south-eastern Zaïre, in contiguous races of *A. latistriatus*, and remotely in *A. hoeschi*, which isolate is seen as derived from the same stock as *latistriatus*. A significant correlate is that *A. hoeschi* spends much of the non-breeding season in regions of Africa where the loss of white in the penultimate rectrix is the norm in *A. cinnamomeus* and its generic affiliates.

Eastern Africa: *Anthus latistriatus*

Circumstances comparable to those found between the Limpopo and Zambezi Rivers are present in southern and central Malawi, giving way in the north and in adjacent territories to a more zonal pattern of montane pipit ranges. Here one finds the Miombo-associated *A. nyassae nyassae* replaced on the rocky grassland above the tree line of various mountain ranges by widely differing birds (Table 2). These are much darker,

TABLE 2

The zonal breeding disposition of three closely allied medium-sized *Anthus* pipits in the mountains round the north end of Lake Malawi. The only other pipit occurring in grassland alongside *A. l. winterbottomi* appears to be the diminutive *A. brachyurus*? *subsp.*

Zone	Altitude	Form
A. Summit grassland	ca above 1830–2440 m a.s.l.	1. <i>Anthus latistriatus</i> , subsp. <i>winterbottomi</i>
B. Montane savanna woodland (Miombo)	ca 1830 m a.s.l. and below	2. <i>Anthus nyassae</i> , subsp. <i>nyassae</i>
C. Sub-montane grassland and cultivation	ca 1830 m a.s.l. and below	3. <i>Anthus cinnamomeus</i> , subsp. <i>lichenya</i> .

Diagnostic criteria:

A. l. winterbottomi. Male: wing-length 88-93 mm, tail-length 65-68 mm. Feathers of back with vinaceous brownish black centres, edged paler. Hind-neck not paler than rest of dorsum. Ventrally vinaceous-buff, heavily streaked on breast and sides with blackish brown. In tail, penultimate rectrix plain or with vestigial light apical surface. Hind-claw 10 mm. Base of lower mandible probably flesh-coloured.

A. n. nyassae. Male: wing-length 88-97 mm, tail-length 65-68 mm. Dorsal surface paler and browner, less blackish, than *A. l. winterbottomi* the feathers edged ochraceous or rust-colour; hind-neck lighter and greyer than rest of upper surface, and in wing “wrist” not greyish. Ventral streaking less extended caudad, and more restricted to upper breast. In tail, penultimate rectrix with prominent whitish wedges to both vanes. Base of bill yellowish?

A. c. lichenya. Male: wing-length 90-95 mm. Female: wing-length 83-89 mm. Lacks the light hind-neck bar of *nyassae*. Differs further in having the outermost rectrix with outer vane and tip of inner pure white, and with white variably extended to the penultimate tail-feather. Hind-claw in male and female 10-16 mm. Base of lower mandible yellow.

less ochraceous-rufous, over the upper-parts and wings, the broad shaft-streaking vinaceous brownish black, and the hind-neck not paler than the rest of the dorsum. In the wings, the lesser-coverts are greyer, and the fringes to the rest of the coverts and the remiges redder. Such birds are also more heavily streaked over the breast and sides, and the outer tail pattern is as described for *A. latistriatus* (Clancey 1984, 1985). The size is also somewhat smaller. Populations exhibiting these characters are known from the summit grasslands of the Mafinga and Makutu Mountains, north-eastern Zambia, the Nyika Plateau, Zambia/Malawi, Tanzania in mountains north of Lake Malawi (in the Poroto Mountains, at Njombe, and in the Matengo Highlands (11°S, 35°E), and on the Njesi Plateau to the north of Unango in Niassa, Mozambique (Fig. 2). Post-breeding movement has been determined as occurring in these elements. They have been collected at lower elevations in savanna after breeding (in Tanzania, and, perhaps, Caconda, in Huila, Angola (Dowsett & Dowsett-Lemaire 1980). After years of uncertainty as to the correct taxonomic attribution of these dark birds, Clancey (1985) separated this population from *A. nyassae* and characterized them as *A. latistriatus winterbottomi*. The type-locality, the Mafinga Mountains, is on the Zambia/Malawi frontier. The only other pipit occurring in grassland alongside *A. l. winterbottomi* appears to be the diminutive *A. brachyurus*. In the Malawi highlands to the south of *winterbottomi* the savannas are occupied by *A. nyassae* and the grasslands and cultivation by *A. cinnamomeus*, as in Zimbabwe and adjacent Mozambique (Figs. 1 & 2).

The three known specimens of nominate *A. latistriatus* are listed in Clancey (1984), these being from the Kavirondo Gulf, south-western Kenya (the type), a second from Lugaga, in Ankole, Uganda at 0°48'S, 31°04'E, and the third from Luiko in the Itombwe Mountains of eastern Zaïre. While the Kenyan and Ugandan specimens are clearly from distant breeding grounds, the Itombwe skin, which was collected in the same general area as a large series of *A. c. itombwensis* (Prigogine 1981), was assuredly on or near its breeding ground when shot. As nominate *A. latistriatus* and *A. c. itombwensis* are remarkably and deceptively alike, and are seen on the limited evidence as being sympatric in the breeding season, it is postulated that their ranges are altitudinally stratified (Table 3), paralleling the situation in the mountains at the northern end of Lake Malawi and in the Drakensberg.

As the length of the hind-claw of *latistriatus* is much shorter than in *A. c. itombwensis* (7-8 mm, versus 10-16 mm), it assuredly inhabits a coarser, less densely grassed and perhaps stony, substrate and is in all probability the summit grassland breeding species. In this event, *itombwensis* – a race of *cinnamomeus* – would occupy habitat suitable to it at lower elevations in the same mountains. However, much further collecting and field work will be needed in order to test the validity of this hypothesis.

Britton *et al.* (1980) draw attention to a comparable situation on Mt. Mahari to the east of Lake Tanganyika at 6°12'S, 29°50'E. Unfortunately,

no specimens from this mountain have been available for critical study, and the pipit occurring at high altitudes on the mountain appears to have been ascribed to *A. cinnamomeus* simply on the basis of visual determination. This is described as being "markedly darker than birds along the nearby shores of Lake Tanganyika." In my recent revision of *A. cinnamomeus* (Clancey 1986b), the western Tanzanian – the eastern shore of Lake Tanganyika – elements are referred to *A. c. lichenya*, in which case the summit grassland breeders are in all probability part of *A. latistriatus*.

Study of the variation in *A. cinnamomeus* confirms that important morphological parameters vary horizontally and mosaically in sympathy with precipitation levels and, to an extent, the nature of the substrate and the evolutionary history of the species in Africa (as in the taxa *A. c. spurium* and *A. c. grotei*). Variation is not clinal as claimed by White (1957). On individual mountains only a single subspecies is present as a breeder and in instances where the contrary is believed to occur two discrete species have been found to be involved. In the case of the Itombwe and adjacent ranges of south-eastern Zaïre, the postulated altitudinal zonation of pipit species is given in Table 3. It is suggested that altitudinal zonation will occur on Mt. Mahari, although different taxa will probably occur.

TABLE 3

Hypothetical zonal distribution of closely allied *Anthus* species occurring on the Itombwe and other south-eastern Zaïrean highlands.

On Mt. Mahari, Western Tanzania, the same altitudinal range structure will probably occur, but the individual taxa will naturally differ.

Summit grassland	<i>Anthus latistriatus</i> subsp. <i>latistriatus</i>
Sub-montane grasslands	<i>Anthus cinnamomeus</i> subsp. <i>itombwensis</i> . also probably present: <i>A. similis dewittei</i> and, in Miombo, <i>A. nyassae nyassae</i>
Diagnostic criteria as given Table 2.	

Eastern and north-eastern Africa north of about 4°S

To the north of the western and south-western highlands of Tanzania and of south-eastern Zaïre, summit (alpine) grassland *Anthus* forms are absent from the higher mountains, such as Ruwenzori, Mt. Elgon, the Central Kenyan Highlands (including Mt. Kenya), Mt. Kilimanjaro, the Usambara and Paré Mountains, and eastern Tanzanian mountain ranges such as of Nguru, Uluguru and Ukaguru. This is noteworthy, bearing in mind the opportunistic behaviour of certain *Anthus* species in their ready colonization of recently cleared land.

A. cinnamomeus and *A. similis* are sympatric in eastern Africa, but favour different habitats, yet there is no evidence of strict altitudinal range zonation. Furthermore, it is significant that no localized montane form of either species has evolved. Fundamental to an understanding of this situ-

ation is that by and large the alpine grassland is normally too high (in excess of 3 000 m a.s.l.) and its composition perhaps unsuitable. The presence of an apron of montane evergreen forest below the ecotone may also be a determining factor, because in the case of marked range zonation from further south in Africa discussed above, evergreen forest, if present, is fragmented and largely – often totally – replaced by savanna woodland or stunted scrub, both of which niches may be arrogated by *Anthus* forms (e.g. *A. nyassae* and to an extent *A. similis*).

The Ethiopian highlands appear comparable despite the depauperate state of the region resulting from long-term denudation of the environment and land misuse. As a result of this, any possible biotic isolating mechanisms may have long since been eradicated. In Ethiopia, *A. cinnamomeus* and *A. similis* races occur in close association to high altitudes without any overt zonal disposition of their ranges, both also occurring alongside *A. leucophrys omoensis* and *A. vaalensis zaphiroi*.

Western equatorial Africa: *Anthus similis moco*

Isolated in the savanna woodlands of Angola is *A. (similis) moco*, described by Traylor (1962) on a limited series collected by Gerd Heinrich on the grassland summit of Mt. Moco, in Huambo. Traylor appreciated that *moco* was a different species to the forestal *A. n. schoutedeni* present in Miombo woodlands on the mountain below the summit and in the surrounding lowlands, yet was hesitant in associating it with *similis*. This procedural uncertainty arose from the view then widely held that the atypical woodland *similis*-like pipits of the Miombo savannas were part of the essentially steppe/montane oriented *A. similis*, rather than a separate, and at that stage unrecognised, species. With the recognition of *schoutedeni* as a race of a species *A. nyassae*, the status of *moco* as part of *A. similis* is seen to have been correctly assessed from the outset. This is confirmed by the longer tail-length, as given in Table 4.

TABLE 4

Zoned altitudinal distribution of medium-sized *Anthus* species occurring on Mt. Moco, Huambo, Angola. Perhaps also on other peaks in the highlands of Huambo.

Zone	Altitude	Form
A. Summit grassland	above ca 2000 m a.s.l.	1. <i>Anthus similis</i> , subsp. <i>moco</i>
B. Montane savanna woodland (Miombo) Grassed clearings	below ca 2000 m a.s.l. –	2. <i>Anthus nyassae</i> , subsp. <i>schoutedeni</i> Uncertain. If present probably <i>Anthus cinnamomeus</i> , subsp. <i>bocagii</i> .

The species criteria are as given for *similis* in Table 1 and for *nyassae* in Table 2. In males of *moco* tails are >72, females >70, the bills <19; in *schoutedeni* tails in males <70, females <68 and bills <16.5 mm.

As *moco* differs sharply from the xeric South West African (Namibian) races of *similis* (*A. s. palliditinctus* and *A. s. leucocraspedon*), its racial affinities are seen as being with *A. s. dewittei* of the Marungu Highlands of south-eastern Zaïre, north to Rwanda, Burundi and the Kigezi/Ankole region of Uganda. Unfortunately, it has not been possible to examine the limited material of *A. s. moco*, so that a comparison between it and *A. s. dewittei* remains to be effected. *A. s. dewittei* is not a localized summit grassland form confined to the Marungu Highlands (Clancey 1986c) as previously suggested (Clancey 1985). Nevertheless, the Marungu population is virtually surrounded by elements of the eastern nominate race of *A. nyassae* resident in the Miombo at lower elevations.

West Africa: *Anthus latistriatus bannermani*

The taxon *bannermani* was named from Sierra Leone by Bates (1930) as a race of *A. richardi* Vieillot. Bannerman (1936) in turn viewed it as a full species, but in recent times it has been considered to be an element of the steppe/montane *A. similis* assemblage, with which it shares comparable ecological attributes and certain morphological characters. That the ascription of the form to *similis* is incorrect was noted by Clancey (1985, 1986d), and it was transferred to *latistriatus* by Clancey (1986d).

The far western Afrotropical subspecies of *A. similis* - the xeric *A. s. asbenaicus* Rothschild of Aïr in Niger is longer-winged and longer-tailed than *bannermani*: wing-lengths 96 mm and 93 mm and tail-lengths 75 mm and 71 mm respectively, and is paler above and less heavily streaked on the underside. In its dimensions, outer tail-pattern features, dark dorsal colouration and coarse ventral streaking, *bannermani* compares best with the two races of Jackson's Pipit *A. latistriatus*. The only notable difference between the West African form and the nominate subspecies is the shorter and rounder wing: male wing lengths 93 mm and 95 mm respectively and female wing-lengths 84 mm and 89 mm. The tail-lengths overlap. In its morphometrics, *A. l. bannermani* matches closely with *A. l. winterbottomi* Clancey of the mountains at the northern end of Lake Malawi, but is again smaller than the isolated *A. hoeschi* of the south-eastern Drakensberg Mountains. In this latter, long wing-length may simply be a manifestation of its post-breeding vagility, whereas *bannermani* is apparently largely sedentary.

A. l. bannermani extends disruptedly from interior mountains in the states of Guinea, Sierra Leone, Liberia and the Ivory Coast, east to eastern Nigeria and Cameroon (Mt. Cameroon and the Bamenda Highlands) (Fig. 2). At the eastern extremity of its range it is in contact with *A. cinnamomeus cameroonensis* and *A. c. lynesii*. Both *A. c. cameroonensis* and *A. c. lynesii* are longer winged than *bannermani*, which also has a rounder wing-tip: male wing-lengths 92,5-96 mm and 95-100,5 mm respectively; female wing-lengths 89-94 mm and 90-95 mm respectively. Bannerman (1936) restricted *bannermani* to Sierra Leone, but extended it later to include

Cameroon (Bannerman 1951). Specimens of *bannermani* examined during the course of this research were taken in Sierra Leone, Liberia, eastern Nigeria (Jos Plateau) and Cameroon. The two pipits meet in the Bamenda region, and from the sparse data available there is limited evidence of an altitudinal arrangement of their ranges at the contact interface. Bannerman (1951) records *bannermani* as frequenting rocks on the heights of the Birwa Plateau, Sierra Leone, and of constructing its nest under a boulder on a steep barren hillside in Cameroon. Such terrain is unacceptable to breeding *A. cinnamomeus*. These ecological factors suggest that in Cameroon the species are allopatric, with *bannermani* resorting to higher rocky, and, apparently, more barren ground, in so doing adumbrating the altitudinal zonation of breeding ranges found further south. The role of the species concerned here is therefore reversed.

CONCLUSIONS

The pipits discussed above stem from two separate lineages responsible for two or more expansionary thrusts into Africa from Eurasia, the contemporary representatives in the Palaearctic being *A. richardi* and *A. similis* (Table 5) (Clancey 1985). It is noteworthy that in the five or so instances where it has been established that a medium-sized *Anthus* species is restricted as a breeder to the summit grasslands of mountains, three of the differentiates are subspecies of a single polytypic species represented nowhere else (*A. latistriatus*), and a fourth is clearly derived from the same

TABLE 5

A schematic evolutionary arrangement of Afrotropical montane *Anthus* pipits.*

A. Eurasian progenitor of the <i>richardi</i> lineage (proto- <i>richardi</i>)	
First colonization:	<i>A. hoeschi</i> ♂ <i>A. latistriatus</i> <i>A. l. winterbottomi</i> <i>A. l. latistriatus</i> <i>A. l. bannermani</i>
Second colonization:	<i>A. cinnamomeus</i> <i>A. c. rufuloides</i> <i>A. c. lichenya</i> <i>A. c. itombwensis</i> <i>A. c. cameroonensis</i> <i>A. c. lynesi</i>
B. Eurasian progenitor of the <i>similis</i> lineage (proto- <i>similis</i>)	
First colonization:	<i>A. nyassae</i> <i>A. n. nyassae</i> <i>A. n. schoutedeni</i>
Second colonization:	<i>A. similis</i> <i>A. s. primarius</i> (<i>A. s. dewittei</i>) <i>A. s. moco</i>

* As interpreted in the present communication.

immediate evolutionary horizon (*A. hoeschi*). The fifth (*A. s. moco*) is a subspecies of a widespread pipit inhabiting steppe/montane country. It is suggested that the first four forms are relicts of an old lineage, whereas the subspecies of *similis* of Mt. Moco, in Angola, and *A. s. dewittei* of Marungu, south-eastern Zaïre, result from recent extension of range by the modern *A. similis*. This is substantiated by the determination that *dewittei* is not a Marungu isolate.

A. latistriatus subsp. derive from an initial expansion into Africa by a distant progenitor of the contemporary Eurasian *A. richardi*. More recent invasions by similar stock from the same region in turn resulted in the evolution and spread of the Afrotropical representative of the *A. richardi* complex: *A. cinnamomeus*, which has a predilection for plain-like conditions. *A. latistriatus* and *A. hoeschi* favour an environment often also utilized by *A. similis* subsp. but in the single case where representatives of these species occur virtually sympatrically – on the south-eastern African Drakensberg – *A. hoeschi* favours higher country than *A. s. primarius* (Table 1). The fact that the environments inhabited by breeding *latistriatus* subsp., *hoeschi* and *similis* subsp. are in many respects alike is seen as one of the reasons for their convergent similarities. While related to the modern *A. cinnamomeus*, the relict isolates of *A. latistriatus* and *A. hoeschi* are not in competition with it, inhabiting as they do coarse rocky grassland terrain in high mountains. The altitudinal disposition of breeding ranges determined as occurring in association with these pipits is seen as one of the isolating mechanisms by which specific uniqueness is maintained and competition averted.

Clancey (1985) postulated that *A. nyassae* is derived from a primary expansion into Africa by a Eurasian ancestor of the contemporary *A. similis*, the descendants of which occupied the savanna-type woodland which spread with the onset of a more pluvial climatic regime. This hypothesis presupposes that in the face of this climatic change, the birds of *richardi* lineage retreated to montane grassland refugia.

As some students may be inclined to query Eurasia as the centre from which the ancestors of the pipits discussed above initially spread into Africa, before diverging and in turn radiating within the confines of the continent, relevant evidence is hereunder presented.

The lineages from which the purely Afrotropical *Anthus* species – *A. cinnamomeus*, *A. latistriatus*, *A. hoeschi* and *A. nyassae* – considered here stem are also those of two wide-ranging modern species present in both the Palaearctic and Oriental Regions, the necessary linkage provided by the wave or ripple-like north-east/south-west pattern of ranges to be seen on distribution maps. These patterns demonstrate lucidly that colonizations by both plexuses have been from regions to the north-east of the African continent and that the African avifauna has been the recipient in all instances.

A. cinnamomeus, with which is linked in evolutionary terms *A. latistriatus* and *A. hoeschi* (both descendants of a primal colonization of the same an-

cestral stock), is only allospecifically discrete from *A. richardi* of the Palearctic and Oriental Regions. At present, *cinnamomeus* extends no further east than the south-western part of the Arabian Peninsula (*A. c. annae* and *A. c. eximius*) and is spatially remote from *A. richardi* subsp. (including *A. (r.) rufulus*), the break of long standing and occasioned by the presence of now unsuitable and arid terrain. Significantly, this type of situation does not occur in *A. similis*, the first incursion into Africa of which it is suggested produced the woodland *A. nyassae*. The birds of the second incursion, more adapted to xeric conditions, differ only at the subspecies level from Asiatic forms, which extend in a chain of races as far east as Burma. The spread of arid steppe-like environments in Africa since the Pleistocene has clearly favoured colonization by *A. similis*, the secondary spread of which has largely avoided the savanna regions (Miombo) tenanted by the descendants of its earlier incursion into Africa (*A. nyassae*) and the grassed summits of certain hygic mountains occupied by *A. latistriatus* subsp.

To summarize, recent research on pipits of the genus *Anthus* terminating in the admission of three additional species to the Afrotropical avifauna, has also established that two of these are closely allied. Both are localized relicts of an expansion into Africa by elements of ancient Eurasian *A. richardi* stock. These interesting forms: *A. latistriatus* and the Mountain Pipit *A. hoeschi* – nest on rocky summit (alpine) grasslands of mountains, and in one, three subspecies are recognisable. The second (*hoeschi*) is a spatially distant southern monotypic isolate with a long-distance post-breeding migration, which, significantly, takes it back to the general area from which it is believed it initially radiated. In exploiting the atypical alpine grassland niche (for birds of *A. richardi* stock) the pipits concerned contribute to a system of altitudinally zoned breeding ranges which ensures survival of close congeners in the face of potential competition. This last could conceivably be posed by, among others, *A. cinnamomeus*, an expansionary and adaptive analogue evolved from more recent *A. richardi* stock.

The third newly recognised species is *A. nyassae*, which is an endemic of the Miombo savannas of Africa, and is resident in such associations on many mountains on which alpine or summit grassland elements of other species are present. Four subspecies of *nyassae* are admitted. This species is postulated as being descended from a primal invasion of Africa by an ancestor of the contemporary *A. similis*, and, being based on woodland, is not in direct competition with races of the latter, which may replace it in open grassland on the summits of certain mountains. *A. nyassae* is seen as having adjusted to living in a woodland environment in the face of distant climatic and vegetational changes.

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