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Source: Journal of East African Natural History, 87(1) : 37-58

Published By: Nature Kenya/East African Natural History Society

URL: https://doi.org/10.2982/0012-8317(1998)87[37:FIOTEA]2.0.CO;2

Journal of East African Natural History **87**: 37–58 (1998)

FAUNAL IMPORTANCE OF THE EASTERN ARC MOUNTAINS OF KENYA AND TANZANIA

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ABSTRACT

Published and unpublished data are used to assess the faunal (animal) values of the Eastern Arc Mountains in terms of the numbers of endemic species, and number of species shared with the adjacent lowland Coastal Forests and with the Tanganyika-Nyasa Mountain Forest Group. Emphasis is placed on vertebrates, although some data for invertebrate groups are also provided.

At least 74 vertebrate species are strictly endemic to the Eastern Arc Mountains, split as follows: birds 10 species, mammals 11 species, reptiles 23 species and amphibians 30 species. A further 40 species are near-endemics, but range slightly more widely than the strict definition of the Arc. Eastern Arc Mountain blocks that possess endemic vertebrates are the Taita Hills (two species), the East and West Usambaras (12 species), the Ngurus (one species), the Ulugurus (13 species) and eastern Udzungwas (13 species).

A minimum estimate of 265 invertebrate species confined to single Eastern Arc Mountain blocks was obtained, although insufficient collection and taxonomic work means that this figure is certainly an underestimate. Detailed work in the Uluguru Mountains provided an estimation of 169 invertebrate species endemic to that mountain alone.

Almost all endemic species are closed-forest specialists, although there are Eastern Arc endemic birds and butterflies confined to montane grasslands and heathlands. The most important locations for the conservation of biodiversity are the east-facing scarps directly influenced by the Indian Ocean in the largest highlands. The North and South Pare Mountains, Rubehos and Ukagurus seem genuinely poorer in endemics than other areas. The Eastern Arc Mountains possess species with both an ancient history and those of more recent evolution. Ancient affinities of the fauna are with West Africa, Madagascar and even SE Asia. An extremely long history of forest cover and environmental stability are the likely causes of these remarkable affinities.

INTRODUCTION

Lovett & Wasser (1993) summarised available data on Eastern Arc Mountains and

demonstrated that as a whole the Arc possesses an important fauna with high numbers of endemic and threatened species. Additional conservation priority-setting assessments have ranked the Eastern Arc as the second or third most important area in Africa for the conservation of restricted-range bird species (ICBP, 1992; Dinesen *et al.*, 1993), and as the most important area of the world for the conservation of elephant shrews (Nicoll & Rathbun, 1990). A more recent global analysis of plant and animal endemism ranks the Eastern Arc/Coastal Forests area as the second-most important 'endemism hotspot' on mainland Africa (Myers *et al.*, in press). It is thus clear that we are discussing an area of great importance for the conservation of African animals.

The derivation of the Eastern Arc fauna is both long and complex. This biogeographical complexity is well illustrated by the fact that, in addition to species found throughout Africa and those confined to eastern Africa, there are also genera and species linking the Eastern Arc with the Guineo-Congolian forest block further to the west (Fjeldså & Lovett, 1997), the forested areas of Madagascar (Emberton *et al.*, 1997), and southeast Asia (Dinesen *et al.*, 1994). The presence of this wide variety of relationships, comprising relics as well as members of recently diversified groups, makes this area extremely interesting for studies of evolution and biogeography (*e.g.* Axelrod & Raven, 1978; Fjeldså & Lovett, 1997; Roy, 1997; Roy *et al.*, 1997; Roy *et al.*, in press).

This paper presents a review of endemism in the vertebrate fauna of the Eastern Arc, illustrating total numbers of endemics and near-endemics, their distribution patterns, and the conservation priority rankings of the Eastern Arc forests compared with each other and with areas elsewhere in Africa. Discussion on how to interpret the results focuses on the potential importance of a long history of forest cover in the mountains and on the degree to which the endemic species of the Eastern Arc are ancient relics that evolved millions of years ago and now only survive in the Eastern Arc, or the products of recent evolution within the Eastern Arc Mountains themselves.

STUDY AREA

The Eastern Arc comprises the ancient crystalline mountains that run from the Taita Hills in Kenya to the Makambako Gap just to the south-west of the Udzungwa Mountains, Tanzania (figure 1; table 1), and that are under the direct climatic influence of the Indian Ocean (Lovett, 1990). These mountains originally supported forest and some grassland and heathland vegetation, although considerable areas have now been converted to agriculture and plantations. There is a chain of somewhat similar montane forest areas extending from southern Tanzania to Malawi, Mozambique and Zimbabwe. However, these more southern forests are not under the Indian Ocean climatic regime, and are subject to more variable convectional rainfall patterns. Together, the Eastern Arc and these other montane forest areas comprise the Tanganyika-Nyasa Mountain Forest Group (Moreau, 1966).

The Eastern Arc Mountains range up to 2,635 m in altitude (Kimhandu Peak in the Ulugurus). From 2,635 m to *c.* 2,400 m the habitats are elfin woodlands/forests, montane grasslands and bogs. Forest habitat extends downwards from *c.* 2,400 m (except where the lower slopes have been cleared). The forest formations have been divided into upper montane (1,800–2,635 m), montane (1,250–1,800 m) and sub-montane (800–1,250 m) forest (*e.g.* Pócs, 1976a, b).

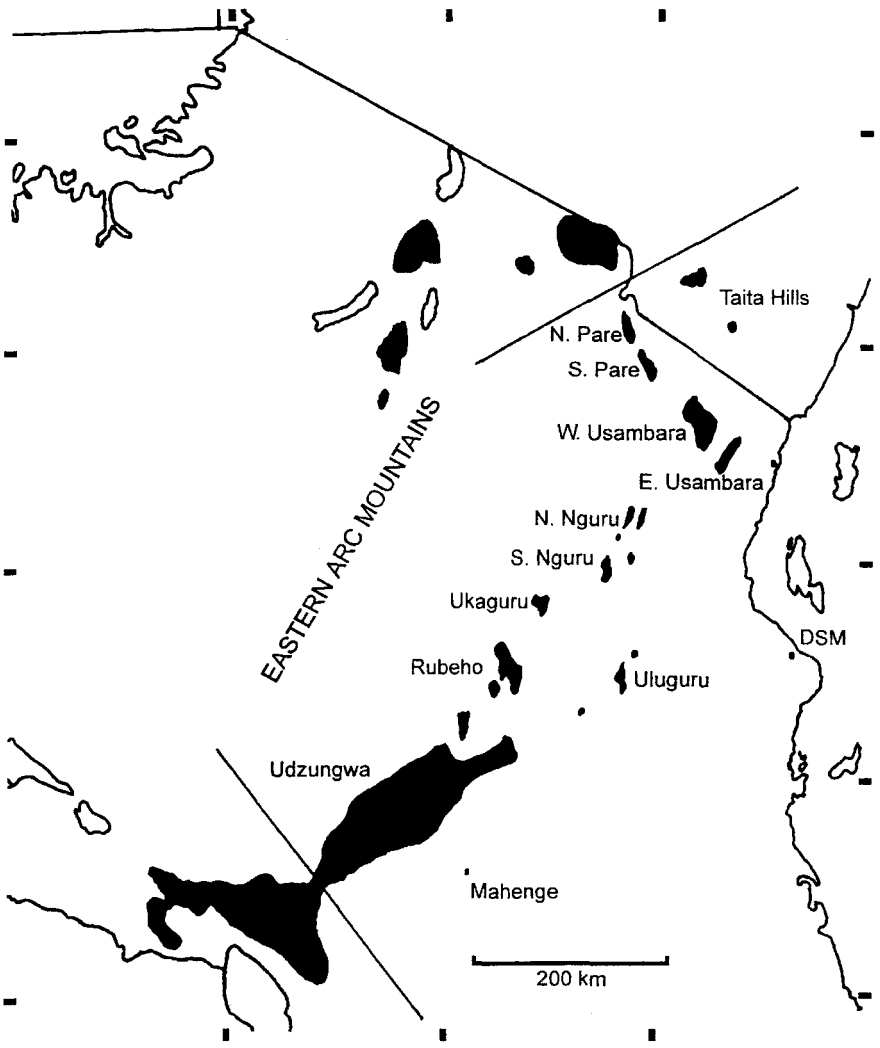

Figure 1. The Eastern Arc Mountains in Kenya and Tanzania (from Lovett, this volume), related to the Tanganyika-Nyasa Mountain Forest Group. Highland areas above 800 m, and not remaining forest areas, are indicated.

At lower altitudes (regarded by Pócs, 1976a, b as below 800 m) the forest grades in species composition and physiognomy into that of the lowland Coastal Forests, found along the eastern seaboard of Africa from Somalia in the north to Mozambique in the south (Burgess & Clarke, in press). Due to the gradation in forest types, and the sharing of some otherwise narrowly endemic species we have also compiled the Eastern Arc/Coastal Forest endemics (appendix 2). Species found only in forests at the foothills of the Eastern Arc Mountains are presented in parentheses as we regard these as Coastal Forest endemics (following Burgess & Clarke, in press). This approach differs from that of some others (*e.g.* Lovett, 1993), where the 'lowland rain forests' in the foothills of the mountains are considered a part of the Eastern Arc. In reality, there is a continuum between the two forest types and the position of boundaries between them is arbitrary.

Table 1. Location, area, and altitudinal range of forested habitats in the Eastern Arc Mountains

Sites	Coordinates (degree and minutes)	Forest area (km²)	Distance to coast (km)	Altitudinal range of forest (m)
Taita Hills [1, 13]	0325S 3820E	3	165	1500–2140
North Pare [2, 3]	0335–0346S 3733–3740E	25	220	1300–2113
South Pare [2]	0404–0434S 3745–3801E	211.1	150	820–2463
West Usambara [4, 5]	0420–0507S 3806–3841E	220	100	1200–2200
East Usambara [3, 4, 5, 9]	0445–0520S 3826–3848E	450	50	130–1506
Nguu [10]	0527–0538S 3736–3732E	140.42	150	1000–1550
Nguru [2]	0527–0613S 3726–3737E	328.35	150	400–2000
Ukaguru [2, 11]	0619–0635S 3653–3703E	155.38	220	1500–2250
Rubeho [7]	0648–0722S 3634–3658E	654	300	520–2050
Uluguru [2, 8]	0651–0712S 3736–3745E	291	180	300–2400
Malundwe Hill [12]	0724S 3718E	4.5	270	1200–1275
Mahenge [2]	0837–0838S 3642–3644E	5	300	460–1040
Udzungwa [2, 6]	0722–0843S 3507–3658E	1017	300	300–2580

Sources
1: Waiyaki, unpublished; 2: Lovett & Pócs (1993); 3: Cordeiro & Kiure (1995); 4: Iversen (1991); 5: Evans (1997); 6: Moyer (1992); 7: Fjeldså *et al.* (1997); 8: Svendsen & Hansen (1995); 9: Johansson and Sandy (1996); 10: Seddon *et al.* (1995); 11: Evans & Andersen (1992); 12: Lovett & Norton (1989); 13: Tetlow (1987); 14: Lovett *et al.* (in press).

METHODS

Standard taxonomic lists were used to define the species considered in this paper (see appendix 1 & 2 for references). This means that data for some species defined using other taxonomic sources are not presented (for example some bird species in Brooks *et al.*, this volume and Cordeiro, this volume). Within this taxonomic framework, the distributions of animal species in the Eastern Arc were defined in terms of those endemic (appendix 1) or near-endemic (appendix 2) to this area.

Chapters in Lovett & Wasser (1993) provided the basic species-distribution data, but these were updated using recent publications (*e.g.* Burgess & Clarke, in press; Fjeldså & Rabøl, 1995; Fjeldså *et al.*, 1997b), and by using data held in the Biodiversity Database of the Department of Zoology and Marine Biology at the University of Dar es Salaam in Tanzania, and Afrotropical species distributional databases at the Danish Center for Tropical Biodiversity in Denmark. The former has collected point records of the flora and fauna of Tanzania from the literature, museum collections and specialists. The latter has compiled confirmed and interpolated distributional data from a large number of sources (publications,

museum data, and unpublished information from taxonomic experts). This distributional data covers all species of Afrotropical birds, mammals, snakes and amphibians on the basis of presence/absence in 1 x 1 degree squares. Data on invertebrate groups come from chapters in Lovett & Wasser (1993) (Hoffman, 1993: millipedes; de Jong & Congdon, 1993: butterflies; Scharff, 1992, 1993: linyphiid spiders) and Johanson & Willassen (1997: caddis flies). More detailed data for the Uluguru Mountains are compiled from Scharff *et al.* (1981) and references therein. For near-endemics Coastal Forest species ranging into the lower altitudes of the Eastern Arc were also considered (Hoffman, in press; Kielland & Cordeiro, in press).

Priority analyses, where the relative importance of the Eastern Arc was compared with other parts of Africa, were undertaken in Denmark using 1 x 1 degree and 15' x 15' species distributional databases and the computer program WORLDMAP IV (Williams, 1995). Distributional data held in this program can be analysed in various ways to illustrate patterns of species richness, range-restrictedness (a measure of endemism), and priority areas for species conservation. Priority areas are selected by their complement of species, in such a way that these areas cover the entire assemblage of species in the Afrotropical Region. We used the Greedy Area algorithm to select 'minimum sets' of areas based on the complement of species they contain. For further explanations of 'complementarity' see Burgess *et al.* (this volume), papers in Forey *et al.* (1994) and Williams *et al.* (1996; in press). For this paper we further ranked areas selected in the minimum set according to their range size rarity scores as a further measure of conservation priority.

RESULTS

The Eastern Arc endemic fauna

Vertebrates

Seventy-four species of vertebrates are endemic to the Eastern Arc Mountains (appendix 1; table 2). The degree of forest dependence varies between the groups. In the birds all strict endemics are found in forest, and seven (70 %) are confined to dense primary forest. For the mammals and amphibians, 100 % of the endemics are confined to dense forest.

A further 18 species of vertebrates are endemic to the Eastern Arc Mountains and to the lowland Coastal Forests (appendix 2). Moreover, an additional 19 species also range from the Eastern Arc southwards to other parts of the Tanganyika-Nyasa Mountain Forest Group (appendix 2). All of these are forest-confined species, or are apparently reliant on forest for their long-term survival in an area.

Invertebrates

For invertebrates, a total of 265 species are considered to be endemic to single mountain blocks (table 3). The most endemic-rich mountains are the East and West Usambaras, the Udzungwas and especially the Ulugurus. However, the known total number of endemics, and their currently understood distribution in the Eastern Arc, is strongly influenced by collecting effort. Many mountains have never been investigated, and thus any endemics they might contain have not been discovered. Moreover, large numbers of species that have been collected remain undescribed (N. Scharff and L. Sørensen, pers. comm.), hence considerable basic taxonomy needs to be completed before a definitive picture of invertebrate endemism in the Eastern Arc can be presented.

In the less mobile invertebrate groups, endemics are generally confined to a single Eastern Arc Mountain. For example, Scharff (1992, 1993) shows that single site endemism for linyphiid spiders is over 80 %. Moreover, for carabid beetles the Uluguru Mountains

Table 2. Distribution of endemic vertebrates in the Eastern Arc Mountains (data sources in the text and appendix 1)

	Birds			Mammals			Reptiles			Amphibians		
	Strict	EArc	Near	Strict	EArc	Near	Strict	EArc	Near	Strict	EArc	Near
Taita Hills	0	0	0	0	0	0	1	0	0	1	1	0
South Pare	0	1	0	0	0	2	0	0	2	0	1	0
West Usambara	1	0	0	1	0	1	0	0	0	1	0	0
East Usambara	0	3	6	2	2	7	4	7	9	5	12	5
Nguru	0	2	2	0	1	3	1	4	0	0	7	2
Ukaguru	0	2	3	0	0	1	0	2	0	0	0	0
Rubeho	0	2	0	0	0	0	0	0	0	0	0	0
Uluguru	2	4	4	2	2	5	3	10	7	6	11	5
Mahenge	0	0	0	0	0	0	0	0	0	0	0	1
Udzungwa	2	4	8	4	1	5	3	4	5	4	9	8

Table 3. Known distribution of single mountain endemic invertebrates in the Eastern Arc Mountains of Tanzania

Biological Group	Pare	W. U	E.U	Nguru	Ukag-uru	Ulug-uru	Rubeho	Udzun-gwa
Arachnida (Araneae - spiders)								
Linyphiidae	-	6 (both)		-	-	12	-	25
Diplopoda (millipedes)								
Spirostreptidae	-	1	2	-	-	2	-	1
Harpagophoridae-	1	2	-	-	1	-	-	
Odontopygidae	-	-	-	-	-	1	-	-
Paradoxosomatidae	-	-	-	-	-	1	-	-
Gomphodesmidae	-	1	1	-	-	1	1	-
Oxydesmidae	-	6	2	2	-	7	3	11
Opiliones (harvestmen)	-	-	-	-	-	15	-	-
Trichoptera (caddisflies)								
Heliopsyche	-	3	1	-	-	2	-	0
Coleoptera (beetles)								
Carabidae	-	-	-	-	-	47	-	-
Tenebrionidae	-	-	-	-		17	-	-
Pselaphidae	-	-	-	-	-	41	-	-
Dermaptera (earwigs)	-	-	-	-	-	12	-	-
Leidoptera (butterflies)								
Montane grassland	-	0	0	0	0	1	0	2
Montane forest	-	15 (both)		0	0	10	1	8
TOTALS	1	13	3	2	1	169	5	47
		40 (both)						

Data sources: spiders from Jocgué & Scharff (1986), Scharff (1992; 1993); millipedes from Hoffman (1993); caddisflies from Johanson & Willassen (1997); butterflies from de Jong & Congdon (1993) updated by Kielland & Cordeiro (in press); Uluguru endemic Coleoptera, Opiliones and Dermatoptera from Scharff *et al.* (1981) derived from Basilewsky (1962; 1976) and Berger & Leleup (1975).

have 95% endemism (Basilewsky, 1962, 1976), and for harvestmen this site has 88 % endemism (Scharff *et al.*, 1981). This situation is similar in the millipedes (Hoffman, 1993) and presumably in other groups of forest invertebrates. The scale of the local endemism is finer than for vertebrates, and forest patches on the same mountain block, separated by only a few kilometres, can possess several endemic invertebrate species.

Broad-scale faunal priorities in the Eastern Arc

Priority 1 x 1 degree grids within the Afrotropical Region, in terms of their complement of species and endemism scores (figure 2; table 4), always feature some (generally the same) Eastern Arc grids regardless of the taxonomic group being studied. This 'ranked minimum set' approach identifies five 1 x 1 degree grids which are essential for the conservation of endemic vertebrates in the Tanzanian part of the Eastern Arc. From North to South these are 4.5°S 38.5°E (East and West Usambaras), 6.5°S 37.5°E (northern Ulugurus), 7.5°S 37.5°E (southern Ulugurus), 6.5°S 36.5°E (Mwanihana; Ndundulu and Nyumbanitu Mountains in the Udzungwa Range) and 8.5°S 35.5°E (Chita/Udzungwa scarp area in the Udzungwa Range). It are these areas that have the highest conservation priority in the Eastern Arc. If the taxonomy presented in Brooks *et al.* (this volume) is adopted then the Taita Hills would be identified as a sixth essential area, based on its three 'endemic' bird taxa.

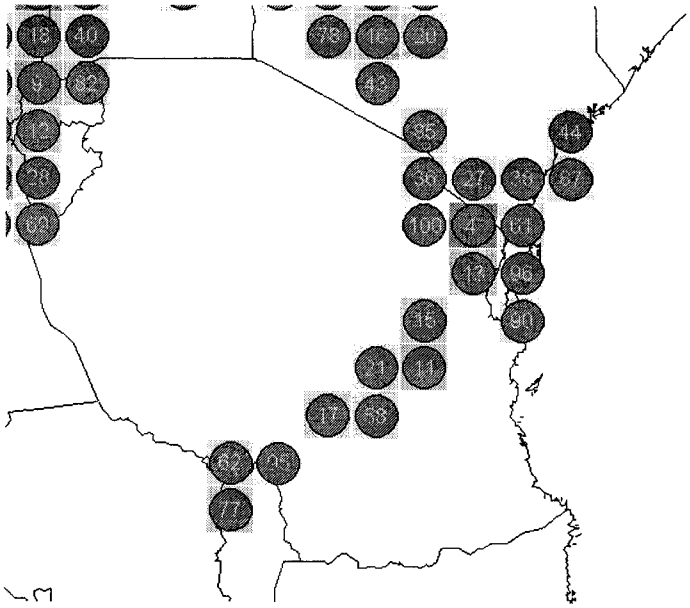

Figure 2. Ranked grids (top 100 1 x 1 degree squares) in terms of range size rarity scores for all vertebrates. Lowest scores represent the highest priorities, e.g. East Usambaras. Only the eastern African portion of an analysis that covers all of the Afrotropical Region is shown.

Finer-scale faunal priorities

A finer scale analysis uses the number of endemic vertebrate species uniquely confined to a single Eastern Arc mountain block, the number of 'Eastern Arc' endemics found in different blocks, and the numbers of the unique and 'Eastern Arc' endemics in relation to the remaining area of forest cover (table 2; figure 3). The Usambaras, Ulugurus and Udzungwas rank of greater importance than the other mountains for all groups considered.

In another analysis, species richness and species-endemism scores for birds from 15' x 15' WORLDMAP grids along the Eastern Arc range are plotted (figure 4). Bird species richness scores vary somewhat along the Eastern Arc, but are generally similar in the main forested blocks, and lower in the northernmost part of the Arc and in the Southern Highlands (see also Fjeldså & Rabøl, 1995). There is much greater variation in the bird endemism scores, with the main peaks of endemism found in the Usambaras, Ulugurus and Udzungwas (figure 4). The two areas with the highest bird endemism scores in the Eastern Arc are the Ndundulu and Nyumbanitu Mountain plus Mwanihana/Sanje area of the Udzungwas, and the eastern face of the East Usambaras up to and around Amani. Other areas with above-average bird endemism scores are in the Udzungwa Scarp Forest Reserve, in all the Uluguru Mountains grids and the West Usambaras. Areas of the Eastern Arc with the lowest bird endemism scores are the northern forests on the Pare and Taita Hills, the Rubeho Mountains, the Nguus and the Mufindi area of the Udzungwas. However, in this analysis the three Taita endemic birds of Brooks *et al.* (this volume) and the one Pare endemic bird of Cordeiro (this volume) were not recognised, which lowers the resulting scores. The Ukagurus and the south Ngurus are close to the average for bird endemism scores along the Arc.

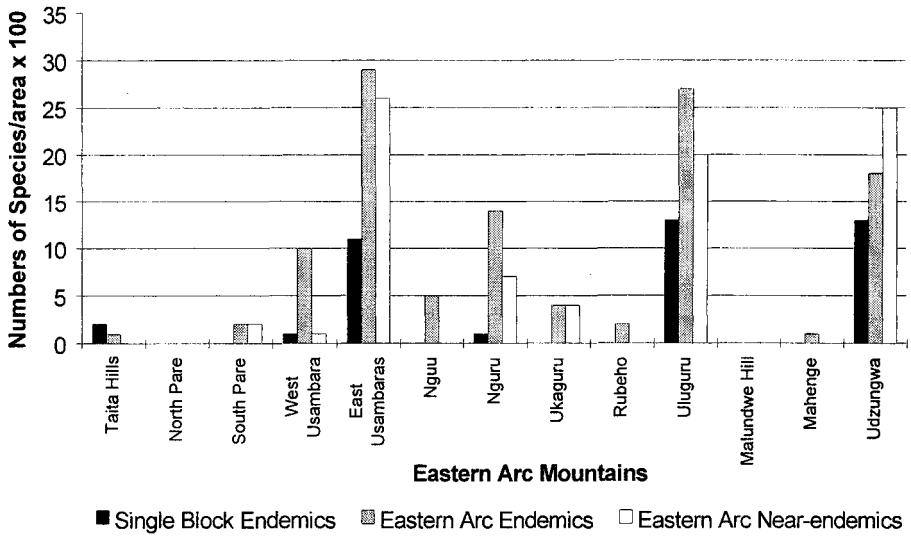

Figure 3. Numbers of endemic vertebrate species in relation to the remaining forest area.

Habitat distributions and vulnerability to disturbance

Data compiled for birds, mammals and amphibians indicate that most Eastern Arc endemic species are confined to dense forest habitats. For the mammals and amphibians 100 % of the endemic species are dense forest specialists, which are unable to tolerate much forest disturbance. Where there is disturbance many of the amphibians are replaced by more widespread forest edge or 'farmbush' species (Schiøtz, 1976). The same seems to be true of many endemic forest birds (Fjeldså, 1999).

Altitudinal distributions

Data on the altitudinal distribution of the Eastern Arc endemic fauna are sparse. Only for the birds is there a reasonable degree of information on the altitudinal ranges of the different species (appendix 1). The Eastern Arc endemic birds seem not to undertake seasonal altitudinal movements, although the more widespread forest birds in these mountains often do (Burgess & Mlingwa, in press). Most (60 % at least) of the endemic birds are not known below 1,200 m altitude, and few (examples are *Nectarinia loveridge* and *Sheppardia loweii*) are found at more than 2,000 m altitude (note however the little study above this altitude). Eastern Arc endemic birds are thus concentrated in the montane forest habitats, and most do not move to other altitudes very often, if ever (Burgess & Mlingwa, in press; Fjeldså, 1999).

DISCUSSION

Why are there so many endemics in the Eastern Arc?

Accumulation of ancient species

Many studies have suggested that the forest cover on the Eastern Arc mountains is very ancient (*e.g.* papers in Lovett & Wasser, 1993; Fjeldså & Lovett, 1997 and this volume).

Table 4. Top-10 grids (1 x 1 degree squares) in the Afrotropical Region ranked in terms of their endemism scores from within the minimum set identified using the Greedy Area (*) complementarity algorithm. Eastern Arc grids are printed in ***bold.*** *DRC=Democratic Republic of Congo.*

	All Vertebrates[a]		Birds[b]		Mammals[c]		Snakes[d]		Amphibians[e]	
Rank	Coords	Country	Coords	Country	Coords	Country	Coords	Country	Coords	Country
1	4.5N 9.5E	Cameroon	3.5S 28.5E	DRC	0.5N 12.5E	Gabon	4.5S 15.5E	DRC	5.5N 10.5E	Cameroon
2	**4.5S 38.5E**	**Tanzania**	4.5N 9.5E	Cameroon	4.5N 9.5E	Cameroon	**4.5S 38.5E**	**Tanzania**	7.5N 8.5W	Guinea
3	7.5N 8.5W	Gui/l.C/Lib	**7.5S 36.5E**	**Tanzania**	1.5S 28.5E	DRC	5.5S 18.5E	DRC	**4.5S 38.5E**	**Tanzania**
4	3.5S 28.5E	DRC	11.5S 14.5E	Angola	6.5N 39.5E	Ethiopia	0.5S 30.5E	DRC/Ug	4.5N 9.5E	Cameroon
5	0.5N 29.5E	DRC	9.5N 39.5E	Ethiopia	2.5N 27.5E	DRC	2.5N 45.5E	Somalia	4.5S 28.5E	DRC
6	5.5N 10.5E	Cameroon	**4.5S 38.5E**	**Tanzania**	0.5S 36.5E	Kenya	0.5S 25.5E	DRC	0.5N 29.5E	DRC
7	0.5S 36.5E	Kenya	0.5S 36.5E	Kenya	7.5N 8.5W	Guinea	2.5S 40.5E	Kenya	**7.5S 37.5E**	**Tanzania**
8	**7.5S 37.5E**	**Tanzania**	0.5N 30.5E	DRC./Ug	**4.5S 38.5E**	**Tanzania**	26.5S 32.5E	S. Af/Moz	33.5S 18.5E	S. Africa
9	6.5N 39.5E	Ethiopia	2.5N 45.5E	Somalia	0.5S 37.5E	Kenya	8.5S 36.5E	DRC	15.5S 35.5E	Malawi
10	33.5S 18.5E	S. Africa	7.5N 8.5W	Gui/l.C/Lib	4.5W 5.5N	Ivory Coast	9.5N 45.5E	Somalia	6.5N 39.5E	Ethiopia

(*) The Greedy Area selection algorithm uses complementarity of all species distributions to select the minimum number of areas that will represent all the species. Here the ranking of this 'Greedy Area Minimum Set' is made using the range size rarity scores of the squares selected. Rare Size Rarity scores are calculated for each of the databases as the sum of rarity scores for all species (the average number of grid-cells occupied by all species divided by the number occupied by the species in question.

a = 253 areas (1 x 1 degree grids) required to represent all the 3922 vertebrate species in Sub-Saharan Africa at least once. Other Earc squares in top 20: 8.5S 35.5E as 11.
b = 84 areas required to represent all the 1911 species of birds in Sub-Saharan Africa at least once (all species are well mapped). Other Earc squares in top 20: 6.5S 37.5E as 20.
c = 113 areas required to represent all the 942 species of mammals in Sub-Saharan Africa at least once (881 species are mapped in the database used, with mainly rodents missing).
d = 80 areas required to represent all the 454 species of snakes in Sub-Saharan Africa at least once (375 species are mapped in the database used). Other Earc squares in top 20: 8.5S 35.5E as 12; 7.5S 37.5E as 16; 3.5S 38.5E as 18.
e = 121 areas required to represent all the 622 species of amphibians in Sub-Saharan Africa at least once (612 species are mapped in the database used).

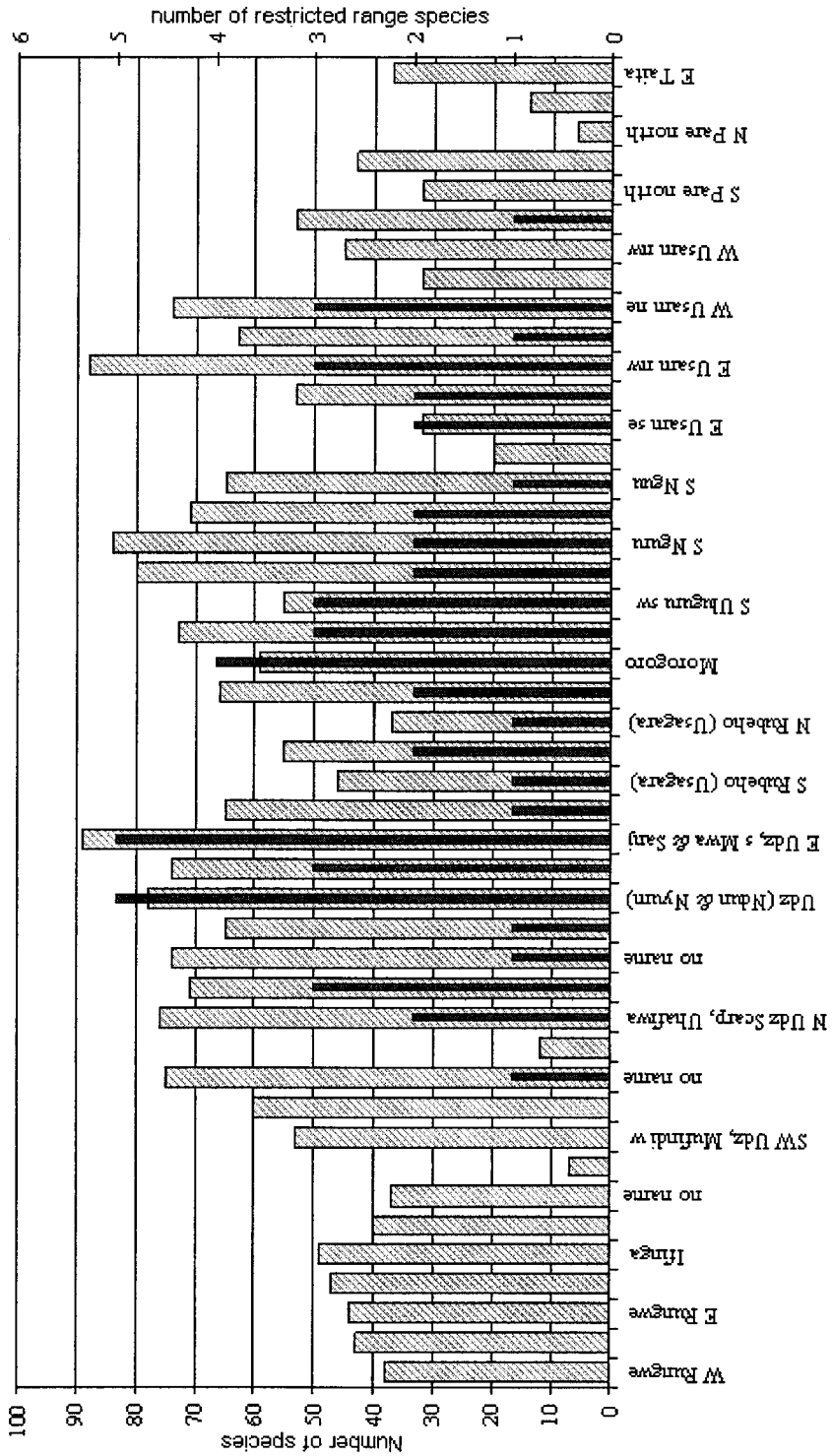

Figure 4. Species richness (shaded block) and species endemism (black line) scores in 15' x 15' grids along the Eastern Arc mountains. Data are derived from a forest birds database for eastern Africa and are analysed using WORLDMAP software (Williams, 1995). Species richness on left axis=numbers of species in each grid unit. Endemism score on right axis=summed inverse range size scores for all species found within each grid unit. The line is the average endemism score.

The direct evidence for this is lacking, but there is a considerable amount of circumstantial evidence to indicate that the forests are very old. This information is as follows:

There are genetically ancient bird species in the Eastern Arc Mountains. Analyses of DNA data for Afrotropical birds (Fjeldså, 1994; Fjeldså & Lovett, 1997) indicate that these ancient species may be from lineages stretching back to the Miocene (*c.* 30 million years ago). Some of these species have their strongest affinities with those now found in forested areas in south-eastern Asia. The best example of this is the partridge *Xenoperdix udzungwensis*, which is related to Indo-Malayan hill partridges (Dinesen *et al.*, 1994).

Direct (DNA) evidence for the relative ages of the endemic species of mammals, reptiles and amphibians in the Eastern Arc are not available so far, but there are some other lines of evidence which indicate an ancient lineage for many of them. For the mammals, the elephant shrew group is often considered primitive (Kingdon & Howell, 1993) and this group is most diverse in the eastern African forests, including those of the Eastern Arc. Traditional taxonomists also regard the pouched rats (*e.g. Beamys hindei* in these forests) as primitive and these are also found most commonly in the forests of eastern Africa. Hochkirch (this volume) presents some preliminary information, which also indicates an ancient history for the grasshoppers of the Eastern Arc. There are ancient faunal connections to Madagascar (molluscs: Emberton *et al.*, 1997), although these seem not as pronounced as in the bryophytes (Pócs, this volume).

For the more widespread forest bird species, Eastern Arc populations are often outliers of the main population in the Guineo-Congolian forest. Although this may indicate recent colonisation, it may also suggest an ancient shared fauna, now extinct, with the maximum age of the fauna being from the time when the eastern and western African forests were separated (perhaps 17 million years ago—reviewed in Axelrod & Raven, 1978). DNA analyses of some of the isolated eastern subspecies of birds shows that they are sufficiently divergent to be regarded as separate species (Roy, 1997; Roy *et al.*, in press).

Numbers of endemic species are higher on the Eastern Arc forested blocks, than on the geologically recent volcanoes in the area. For example, instead of the 80 % plus rates of spider endemism in the Eastern Arc blocks, the volcanoes have under 35 % endemism (*e.g.* Mt Elgon 25 %; Mt Kenya 33 %) (Scharff, 1992). This indicates that species have been evolving and accumulating in the Eastern Arc forests for a long time. Under this scenario the fact that the geologically younger volcanic forests (such as Kilimanjaro) have fewer endemic species would be explained due to the shorter time available for the evolution of new single-site endemics. This situation is paralleled in the reptiles (Howell, 1993), vascular plants (Lovett, this volume) and the bryophytes (Pócs, this volume).

Evolution of new species

The high number of endemic species in the Eastern Arc could also be caused by evolution over the past few million years. In the birds DNA data, albeit still fragmentary (Roy, 1997; Roy *et al.*, 1997 and Roy *et al.*, in press), indicate that there are recently evolved species in the Eastern Arc Mountains in addition to the genetically more ancient species. The presence of both ancient and newly-evolved species in the same area indicates that these mountains are both centres of current evolution as well as centres of species relictualisation. This is at variance to the nearby lowland Coastal Forests, where recent speciation is less evident and most endemic species seem to be ancient (Burgess *et al.*, 1998).

Collection biases

Confident interpretation of the available data is hindered by the uneven survey effort in the different Eastern Arc Mountains. Those mountain areas ranked as most important here are

also those which have received the highest study effort, especially the Usambaras and Ulugurus. Apart for the birds, some other forests have had only provisional investigations of their fauna, and thus additional new species may be present (see *e.g.* Rodgers & Homewood, 1982).

However, for the birds recent investigations of the avifauna of the Rubehos (Fjeldså *et al.*, 1997a), the Nguus (Seddon *et al.*, 1995) and the Ukagurus (Evans & Andersen, 1992, 1993) have not resulted in many new findings, whereas investigations of the lowland East Usambaras (the best known Eastern Arc block) (Evans, 1997) and the Udzungwas (Dinesen *et al.*, 1993, 1994) discovered much of ornithological interest, including a new bird genus in the last locality. A recent herpetological study has discovered two new species in the lowland East Usambaras and three new species in the Udzungwas (Broadley & Howell, in press; Poynton, in press; Westergaard, Howell & Schiøtz, pers. comm.). If this pattern is repeated in other animal groups, then the priorities we have identified here will not change, but further fieldwork in the poorly known areas is required to test the assumption.

The potential role of climate

The current African climate is dominated by rain originating from either the Atlantic climatic system or the Indian Ocean monsoon, but with considerable orographic modification. Within the period covered by rainfall records, the African climate has shown marked annual fluctuations in both wet and dry areas, with the climate in some places having a much greater inter-annual variability than others (Nicholson, 1994). Wider fluctuations are thought to have occurred in the past, especially in the convectional rainfall areas near the great lakes (*e.g.* Owen *et al.*, 1990). The Eastern Arc Mountains stand out by being under the direct climatic influence of the Indian Ocean monsoon (Lovett *et al.*, 1988; Lovett, 1993). Marine drill-core data suggest that the coastal waters of Tanzania were little influenced by Pleistocene climatic changes (Prell *et al.*, 1980), maintaining warm and seasonally humid conditions in the coastal regions. Recent studies of 10 years meteorological satellite climate data (Fjeldså *et al.*, 1997b) indicate that there are small areas in the Eastern Arc that possess exceptionally stable climatic regimes, and that there is an apparent correlation between these areas and those where the highest concentrations of endemic species are found.

Further studies that would assist conservation prioritisation

In the Eastern Arc Mountains there are still many areas requiring additional basic fieldwork to determine what is present. Study effort is quite uneven between the main forest blocks of the Arc, and between the forests within a single block. This makes the recognition of patterns and priorities in the distribution of biodiversity quite problematic. The East Usambaras are the best-studied area, and the West Usambaras and north Ulugurus have also been investigated for most vertebrate groups. In comparison, the Udzungwas, Ukagurus, Ngurus, Nguus and especially the Rubehos are poorly known. The highest remaining priorities for further study are the Nguru-Nguu ranges, the Rubehos, the south Ulugurus and higher altitudes in the Udzungwas. The first area seems particularly in need of additional survey work as it is already known to be of moderate importance and further study would confirm whether or not it should be considered alongside the three most important mountains.

ACKNOWLEDGEMENTS

Neil Burgess thanks the Danish Center for Tropical Biodiversity for providing support to the development of the biodiversity databases used in this paper. These databases contain much

unpublished information, which has kindly been provided by a number of collaborating scientists. Those with the greatest involvement, or who have provided the greatest amount of unpublished data are: birds—BirdLife International (especially Mike Crosby and Colin Bibby), Helen de Klerk and Tim Crowe (Percy FitzPatrick Institute); mammals—Dieter Kock and Jakob Fahr (bats), Rainer Hutterer and Paula Jenkins (shrews), the late William Ansell (large mammals); Jens Rasmussen (snakes), Van Wallach (*Typhlops, Leptotyphlops, Rhinotyphlops*); amphibians—Arne Schiøtz (treefrogs), John Poynton (bufonids), Alan Channing (Southern African amphibians). The field collection efforts of students from DCTB are also acknowledged as this provides the new data to be used in a compilation such as this. Paul Williams of the Natural History Museum in London provided and altered WORLDMAP IV to our requirements.

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APPENDIX 1: ENDEMIC VERTEBRATE SPECIES IN THE EASTERN ARC MOUNTAINS

Habitat codes: FF = strict forest endemic; F = forest endemic which are ranges outside of forest on some occasions, but is probably dependent on forest for breeding; G/H = grassland or heathland species; W = montane wetland species.

BIRDS (updated from Stuart *et al.*, 1993). Taxonomy follows Sibley & Monroe (1990, 1993), where Taita (Brooks *et al.*, this volume) and Pare (Cordeiro, this volume) endemic bird species are not recognised.

Anthreptes rubritorques Sclater & Moreau, 1935, F, 250-1600m, Udzungwa, E. Usambara, Uluguru, Nguru

Bathmocercus winifredae (Moreau, 1938), FF, 1500-1850m, Ukaguru, Uluguru, Udzungwa, Rubeho

Bubo vosseleri Reichenow, 1907, F, 300-1000 m+, E. Usambara, Uluguru, Udzungwa, S. Pare (last three unpublished sound records)

Malaconotus alius Friedmann, 1927, FF, 1320-1710 m, Uluguru

Nectarinia loveridgei (Hartert, 1922), FF, 1200-2580 m, Uluguru

Nectarinia moreaui (Sclater, 1933), F, 1500-1850 m, Nguru, Ukaguru, Rubeho, Uvidunda

Nectarinia rufipennis Jensen, 1983, FF, 600-1710 m, Udzungwa

Ploceus nicolli Sclater, 1931, FF, Usambara, Uluguru, Udzungwa

Sheppardia montana (Reichenow, 1907), FF, 1500-1850 m, W. Usambara

Xenoperdix udzungwensis Dinesen *et al.*, 1994, FF, 1350-1900 m, Udzungwa

MAMMALS (updated from Kingdon & Howell, 1993). Taxonomy follows Wilson & Reeder (1993), with *Galagoides* updated.

Cercocebus 'sangei', FF, Udzungwa
Crocidura tansaniana Hutterer, 1986, FF, Usambara
Crocidura telfordi Hutterer, 1986, FF, Uluguru
Crocidura usambarae Dippenaar, 1980, FF, West Usambara only
Galagoides cfr *orinus* (Montane) P. Honess, 1996, FF, Usambara, Uluguru, Nguru, Udzungwa
Galagoides udzungwensis P. Honess, 1996, FF, Udzungwa
Myosorex geata (Allen & Loveridge, 1927), FF, Uluguru (if *M. zinki* is included then Kilimanjaro, Mt Meru, Southern Highland)
Paraxerus vexillarius (Kershaw, 1923), FF, Usambara (if *P. byatti* is included then Kilimanjaro, Uluguru, Udzungwa and Southern Highland)
Philocolobus 'gordonorum', FF, Udzungwa
Sylvisorex howelli Jenkins, 1984, FF, Usambara and Uluguru

REPTILES (updated from Howell, 1993). Taxonomy mainly follows Broadley & Howell (1991), with updates, and Taita Hills species.

Agama montana Barbour & Loveridge 1928, Usambara, Nguru, Uluguru
Amblyodipsas teitana Broadley, 1971, Taita Hills
Atheris ceratophorus Werner, 1895, Usambara, Uluguru, Udzungwa
Bradypodion oxyrhinum Klaver & Böhme, 1988, Uluguru, Udzungwa
Bradypodion spinosum Matschie, 1892, Usambara
Chamaeleo deremensis Matschie, 1892, Usambara, Nguru
Chamaeleo laterispinis Loveridge, 1953, Udzungwa
Chamaeleo werneri Tornier, 1899, Uluguru, Udzungwa
Dipsadoboa werneri Boulenger, 1897, Usambara (one record from Tanga; Broadley & Howell, in press)
Elapsoidea nigra Günther, 1888, Usambara, Uluguru
Geodipsas procterae Loveridge, 1922, Uluguru, Udzungwa
Geodipsas vauerocegae Tornier, 1902, Usambara, Uluguru
Leptosiaphos rhomboidalis Broadley, 1989, Udzungwa
Lycophidion uzungwense Loveridge, 1932, Udzungwa
Lygodactylus gravis Pasteur, 1964, Usambara
Proscelotes eggeli Tornier, 1902, Usambara
Prosymna ornatissima Barbour & Loveridge, 1928, Uluguru
Rhampholeon uluguruensis Tilbury & Emmrich, 1996, Uluguru
Rhampholeon sp. nov., Tilbury & Emmrich, in press, Nguru
Scelotes uluguruensis Barbour & Loveridge, 1928, Uluguru, Nguru
Typhlops gierrai Mocquard, 1897, Usambara, Uluguru, Nguru, Ukaguru
Typhlops uluguruensis Barbour & Loveridge, 1928, Uluguru
Urocotyledon wolterstorffi Tornier, 1900, Usambara, Uluguru

AMPHIBIANS (updated from Schiøtz, 1981; Howell, 1993). Taxonomy from Frost (1985) and Duellman (1993), with updates.

Afrixalus uluguruensis Barbour & Loveridge, 1928, FF, Usambara, Uluguru, Nguru, Udzungwa (possible same species from Mkwaja Coastal Forests, Poynton, in press)
Arthroleptides martiensseni Nieden, 1910, FF, Usambara, Uluguru, Nguru, Udzungwa (300 m in E. Usambara; Poynton, in press)
Arthroleptis tanneri Grandison, 1983, FF, Usambara
Arthroleptis xenodactylus Boulenger, 1909, F, Usambara, Nguru, Uluguru?
Bufo brauni Nieden, 1910, FF, Usambara, Uluguru, Udzungwa (at 300 m in E. Usambara)

Callulina kreffti Nieden, 1910, FF, Usambara, Nguru, Uluguru, Udzungwa, Taita
Hoplophryne rogersi Barbour & Loveridge, 1928, FF, Usambara
Hoplophryne uluguruensis Loveridge, 1925, FF, Uluguru and Usambara
Hyperolius tanneri Schiøtz, 1982, FF, Usambara
Hyperolius tornieri Ahl, 1931, FF?, Uluguru
Hyperolius sp. nov., Schiøtz & Westergaard, in press, FF, Udzungwa
Leptopelis barbouri Ahl, 1929, FF, Usambara, Udzungwa (at 300 m in E. Usambara).
Leptopelis parkeri Barbour & Loveridge, 1928, FF, Usambara, Uluguru, Udzungwa (at 300 m in the E. Usambara; Poynton, in press)
Leptopelis uluguruensis Barbour & Loveridge, 1928, FF, Usambara, Uluguru, Nguru, Udzungwa (at 300 m in the E. Usambara)
Nectophrynoides cryptus Perret, 1971, FF, Uluguru
Nectophrynoides minutus Perret, 1972, FF, Uluguru
Nectophrynoides tornieri Roux, 1906, FF, Usambara, Uluguru, Nguru, Udzungwa
Nectophrynoides wendyae Clarke, 1988, 1989, FF, Udzungwa
Nectophrynoides sp. nov. A, FF, Udzungwa
Nectophrynoides sp. nov. B, FF, W. Usambara
Parahoplophryne usambarica Barbour & Loveridge, 1928, FF?, Usambara
Phrynobatrachus kreffti Boulenger, 1909, F, Usambara
Phrynobatrachus uzungwensis Grandison & Howell, 1983, FF, Udzungwa, Uluguru
Phlyctimantis keithae Schiøtz, 1974, F, G/H, Udzungwa
Probreviceps uluguruensis Loveridge, 1925, FF, Uluguru
Scolecomorphus uluguruensis Barbour & Loveridge, 1928, FF, Uluguru
Scolecomorphus vittatus Boulenger, 1895, FF, Usambara, Uluguru, Pare?
Boulengerula boulengeri Tornier, 1896, FF, Usambara, Nguru
Boulengerula taitana Loveridge, 1935, ?, Taita Hills
Boulengerula uluguruensis Barbour & Loveridge, 1928, FF, Uluguru

APPENDIX 2: NEAR-ENDEMIC VERTEBRATE SPECIES IN THE EASTERN ARC MOUNTAINS

Habitat codes: FF = strict forest endemic; F = forest endemic which are ranges outside of forest on some occasions, but is probably dependent on forest for breeding; G/H = grassland or heathland species; W = montane wetland species. Species in parentheses means that it is only known from lowland forests at the base of the Eastern Arc Mountains, Kimboza or lowland East Usambaras. These species might also be regarded as a lowland Coastal Forest endemic (*sensu* Burgess & Clarke, in press).

BIRDS

Anthreptes pallidigaster Reichenow, 1905, F, 200-1550 m, Usambara and Udzungwas (Arabuko-Sokoke Coastal Forest)
Arcanator orostruthus (Vincent, 1933), F, Usambara, Udzungwas and Mt. Namuli Mozambique
Modulatrix stictigula Reichenow, 1906, F, Usambara, Nguru, Ukaguru, Uluguru, Udzungwa (E & W), and Rungwe
Orthotomus moreaui (Sclater, 1931), F, Usambara and Njesi Plateau, Mozambique,
Orthotomus metopias (Reichenow, 1907), FF, 1200-2570 m, Usambara, Nguru, Ukaguru, Uluguru, Udzungwa (E & W), Matengo Highlands and Njesi Plateau (last in Mozambique)
Serinus whytii Shelley, 1897, F?, Udzungwa, and Zambia and Mozambique
Sheppardia lowei (Grant & Mackworth-Praed, 1941), F, Livingstone Mts, Udzungwas
Sheppardia sharpei (Shelley, 1903), F, Usambara, Ukaguru, Uluguru, Udzungwa (Mufindi), and Rungwe

Swynnertonia swynnertoni (Shelley, 1906), F, Usambara, Udzungwa, Mozambique/Zimbabwe

MAMMALS

Acomys ignitus Dolman, 1910, ?, Eastern Arc and some Kenyan sites, possible near-endemic

Crocidura desperata Hutterer *et al.*, 1991, FF, Udzungwa, Rungwe

Crocidura xantippe Osgood, 1910, FF?, Usambara, Nyiru & Voi (southern Kenya) and S. Lake Turkana? Coastal Forests: Burgess *et al.*, in press

Kerivoula africana Dobson, 1878, FF, Lowland E. Arc and Coastal Forests: Burgess *et al.*, in press

Myonycteris relicta Bergmans, 1980, FF, Lowland E. Arc and Coastal Forests: Burgess *et al.*, in press

Rhynchocyon petersi Bocage, 1880, F, S. Pare, Usambara, Uluguru?, Nguru?, Coastal Forests in Burgess *et al.*, in press

Rhinolophus sp. nov., FF, Usambara (Coastal Forests: Burgess *et al.*, in press)

Beamys hindei Thomas, 1909, F, Coastal and Eastern Arc forests

REPTILES

Adenorhinos barbouri Loveridge, 1930, Udzungwa and Rungwe area

Aparallactus werneri Boulenger, 1895, Pare, Usambara, Uluguru (Coastal Forests: Broadley & Howell, in press)

Bradypodion tenue Matschie, 1892, Usambara (Coastal Forests: Broadley & Howell, in press)

Chamaeleo tempeli Tornier, 1899, Udzungwa and Southern Highlands

Cnemaspis barbouri Perret, 1986, Usambara, Ukaguru?, Uluguru, Tongwe and Ruvu Coastal Forests

Cnemaspis uzungwae Perret, 1986, Udzungwa and Kiwengoma Coastal Forest (Broadley & Howell, in press)

Crotaphopeltis tornieri Werner, 1908, Usambara, Uluguru, Udzungwa, S. Highlands, N. Malawi (Mt Misiku)

Lygodactylus conradti Matschie, 1892, Usambara, Uluguru (Coastal Forests: Broadley & Howell, in press)

Lygodactylus kimhowellii Pasteur, 1994, FF, Usambara, and Tanga Coastal Forest; Broadley & Howell, in press

(Lygodactylus williamsi) Loveridge, 1952, FF, Kimboza only (Eastern Arc or Coastal Forest type)

Lygodactylus uluguruensis Pasteur, 1964, Uluguru and Tongwe Coastal Forest (Broadley & Howell, in press)

Prosymna semifasciata Broadley, 1996, FF, Usambara (from lowland forest up to *c.* 600 m; Coastal/Eastern Arc endemic)

Rhampholeon brevicaudatus Matschie, 1892, Usambara, Uluguru, Udzungwa (Coastal Forests: Broadley & Howell, in press)

Rhampholeon temporalis Matschie, 1892, Usambara, Shimba Hills

AMPHIBIANS

Arthroleptis affinis Ahl, 1939, FF, Usambara, Udzungwa (Pugu and Rondo Coastal Forests; Poynton, in press)

Arthroleptis reichei Nieden, 1910, FF, Uluguru, Udzungwa, Rungwe and Malawi montane areas

Bufo uzungwensis Loveridge, 1932, FF, Udzungwas, Rungwe

Hyperolius spinigularis Stevens, 1971, F & G/H, Usambara, Udzungwa, Mulanje

Leptopelis vermiculatus Boulenger, 1909, FF, Usambara, Nguru?, Udzungwas, Rungwe

Mertensophryne micranotis Loveridge, 1952, FF, Usambara, Uluguru (Coastal Forests - Poynton, in press)
Probreviceps macrodactylus Nieden, 1926, FF, Usambara, Uluguru, Udzungwa, Rungwe
Nectophrynoides viviparus Tornier, 1905, FF, Uluguru, Udzungwa, Rungwe
Spelaeophryne methneri Ahl, 1924, FF, Uluguru, Udzungwa, Mahenge, Matengo Highlands (Rondo Coastal Forest, Poynton, in press)
Scolecomorphus kirkii Boulenger, 1883, FF?, Nguru, Southern Highland, S. Malawi