



Martin Woodcock

A new genus and species of perdicine bird (Phasianidae, Perdicipini) from Tanzania; a relict form with Indo-Malayan affinities

LARS DINESEN, THOMAS LEHMBERG, JENS OTTO SVENDSEN,
LOUIS A. HANSEN & JON FJELDSÅ

Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark

A very distinctive perdicine bird was discovered in July 1991 during fieldwork in montane evergreen forests in parts of the Udzungwa Mountains in Tanzania which were so far ornithologically unexplored. The bird is described here as a new genus and species with affinities to the hill-partridges *Arborophila* of the Indo-Malayan region. The relict occurrence in Africa of taxa with affinities to Oriental biota is discussed.

During fieldwork in montane evergreen forests in the Udzungwa Mountains, east of Iringa town, Tanzania, a new and very distinctive perdicine bird was discovered in July 1991. The fieldwork was done by the first four authors as part of a long-term biogeographic study of East African montane forests coordinated by the last author. All authors took part in the phylogenetic analysis. The study area was two isolated forest tracts in so far unexplored parts of the large highland area between Iringa and the wet southeastern scarp of the Udzungwa Mountains (Fig. 1). The western part of the forest tract surrounding Mount Luhombero, in the Ndundulu Mountains, was studied from 30 June to 10 September 1991 and from 5 November 1991 to 10 January 1992. The forest of the Nyumbanitu Mountains was investigated from 12 March to 10 April 1992. Extensive mist-netting programmes were carried out and detailed observations made on the community structure and ecology of birds of montane evergreen forests at altitudes between 1350 and 2400 m.

The study areas are about 50 km west of Mwanihana Forest, which is on the eastern scarp of the Udzungwa Mountains, where a new species of sunbird was discovered in 1981 (Jensen 1983). That species is still known only from the Udzungwa Mountains, an area with several other endemic species and relict populations of birds found in a few other East African montane forests (Jensen & Brøgger-Jensen 1992, Dinesen *et al.* 1993). On 3 July 1991, a flock was observed of four or five peculiar francolin-shaped birds which did not correspond to any known species. This species was later found to be locally common; altogether 246 birds were seen on 85 occasions in the Ndundulu Mountains and Nyumbanitu Mountains.

The birds were not captured in mist-nets, but three specimens were collected with the help of local people who used snares. After studies of the literature and museum collections, and a comprehensive character analysis, we conclude that the specimens represent a new species and genus of perdicine bird. We propose the generic name

Xenoperdix, gen. nov.

TYPE SPECIES

Xenoperdix udzungwensis Dinesen, Hansen, Lehmborg, Svendsen & Fjeldså.

DIAGNOSIS

A small-sized (220–239 g) perdicine bird with a moderately short tail with 14 rectrices, rounded wings, a red, rather small bill with moderately hooked upper mandible like that of the smaller francolins and partridges and yellow legs without spurs. Diagnostic features are olive-brown upperparts with rufous bars margined with black. Inner vanes of the humerals are chestnut with broad black bars. A black forehead interrupts the anterior supercilium. Underparts below the throat are grey with large round black spots centrally on most feathers. Characters shared with certain species of *Arborophila* comprise rufous sides of head; rufous throat demarcated from grey breast and sides by a thin black-and-white necklace; the grey colour of breast and sides grades into white on lower belly, olive-grey on flanks and under tail-coverts, these latter parts with black marks centrally and white to rufous tips on most feathers; and wing-linings with a contrasting pattern of blackish and white. However, *Xenoperdix* does not share the vestigial tail of *Arborophila* and instead shows similar chestnut outer tail-feathers with broad black subterminal bar as certain *Francolinus* species.

Xenoperdix udzungwensis, sp. nov.,
Udzungwa Forest Partridge

TYPE SPECIMEN

The Zoological Museum of Copenhagen cat. no. 91.301, adult male, collected on 28 November 1991 in the Ndundulu Mountains (36°29'E, 7°47'S) at the peak with the local name Mufu at about 1700 m eastsoutheast of the village Udekwa, Mahenge District, Iringa Region, Tanzania.

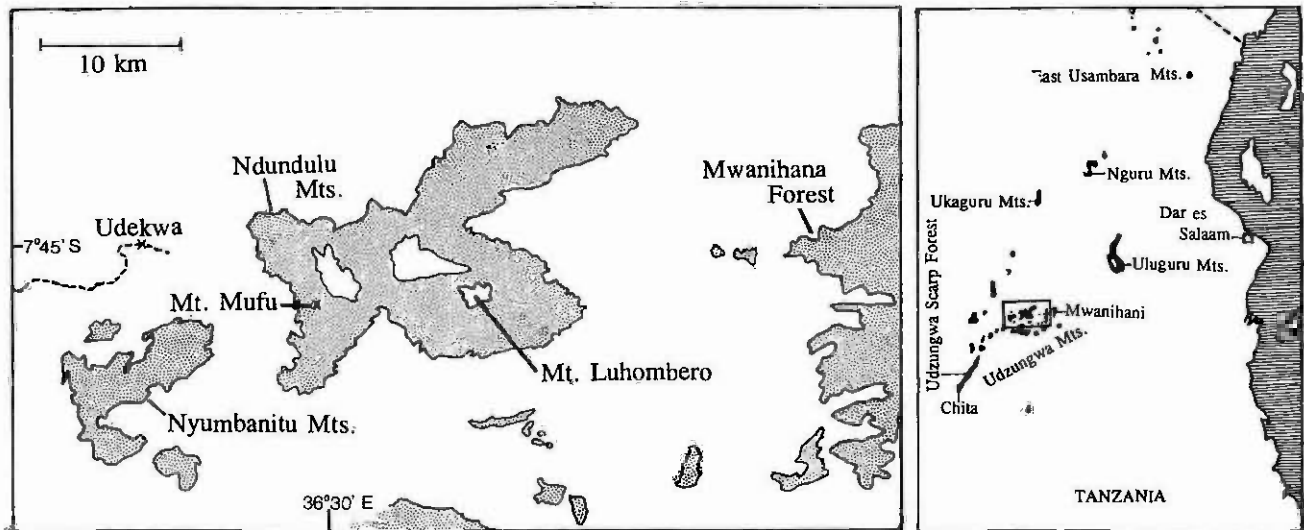


Figure 1. Map showing the position of the Ndundulu Mountains and Nyumbanitu Mountains, the presently known range of *Xenoperdix udzungwensis*. The shaded area denotes the distribution of montane forests. To the right, the extension of montane forests in Tanzania: the rectangle shows the position of the left map.

ETYMOLOGY

The genus name *Xenoperdix* comes from Greek *xenos*, strange or foreign, and Greek *perdix*, meaning partridge, and alludes to the peculiar combination of characters, making it a stranger among African partridge-like birds. The epithet refers to the Udzungwa Mountain Range, where the species was discovered.

DESCRIPTION OF TYPE SPECIMEN

In the description below, all colours written with capital letters refer to colour standards set by Ridgway (1912). Primaries (P) as well as secondaries (S) are numbered from the carpal joint, and rectrices (R) are numbered from the centre of the tail. The colour patterns of the head and various typical feathers of the upperparts and flanks are illustrated in Figure 2.

Upperparts

Forehead black, on the transition towards the crown with Cinnamon-Buff feather tips which expand as broad buff shafts on some feathers. Crown and nape with scaly pattern, feathers Dark Olive diffusely margined with darker lines and Medial Bronze subterminally. Feathers of hindneck, mantle, back, rump and upper tail-coverts Buff Olive, each feather with 2–4-mm-wide subterminal bar and central chevron-shaped mark coloured Orange Rufous to Cinnamon-Rufous or Cinnamon-Buff, these rufous marks more or less distinctly outlined with thin black bars. Broad black feather tips are found only on the hindneck and some feathers on the mantle, as olive terminal fringes of the feathers become gradually broader towards the rump, the black bars gradually weaker,

usually as fine vermiculations, although some feathers on the rump show a prominent expansion of black inside the rufous bar.

Outermost rectrices (R4–R7) distinctively Auburn, all feathers with a broad blackish subterminal bar and a narrower whitish terminal bar; R7 has six blackish bars, R4–R6 have progressively fewer markings, with only the base of R6 barred. R2 and R3 are intermediate towards the central feathers, which are barred Clay Color washed with dull Buff Olive, irregularly barred and vermiculated with black; broad subterminal bar blackish, narrow (worn) tip dull Buff Olive.

Scapulars distinctly bicoloured giving a streaked effect. Inner-vanes, at least on the distal part, barred Mahogany Red and black with a tendency to a solid black spot on some feathers; outer-vanes fading almost to pale grey, with rufous; and dusky barring weakly indicated but the outer edge Mahogany Red; shafts of some feathers whitish. However, a few anterior scapulars are "reversed" with the outer-vane mahogany and black.

Wings

Wings rounded; emargination on P4–P8, slightly less on P2–P3 and P9; longest primaries are P4–P6; P1 slightly longer than P10. The primaries are Mummy Brown, outer-vanes with faint Capucine Orange marginal notches. The ten secondaries brownish black with four or five vermiculated bars coloured Ochraceous-Buff to Ochraceous-Orange, most conspicuously on the outer-vane. Basal part of tertials greyish brown with blackish vermiculations and with six bars mainly coloured Ochraceous-Buff to Ochraceous-Orange; distal part with inner-vanes Mahogany Red and black (like scapulars); outer-vanes "faded" and greyish like scapulars, margins Mahogany Red. Lesser coverts brownish black with an

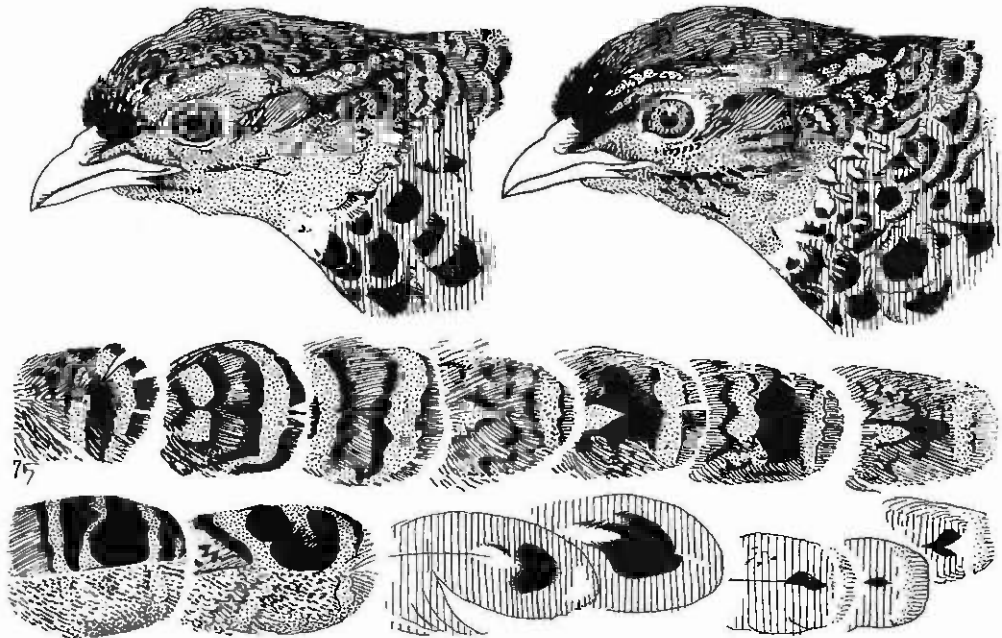


Figure 2. Portraits of the holotype and the paratype of *Xenoperdix udzungwensis*, showing variation in the amount of black spotting on the orange "face" and patterns of some typical feathers: upper row (left to right), dorsal feathers from nape to rump; lower row (left to right), two tertials, two feathers of the underside and three under tail-coverts. Stippling, orange-brown to chestnut colour; vertical shading, grey colour; dense shading, olive-brown colour.

Ochraceous-Buff band. Median and greater coverts like tertials and scapulars, with terminal parts of the largely hidden inner-vanes Mahogany Red and black, outer-vanes Buffy Olive and Ochraceous-Orange.

Underwing Mouse Grey on remiges, greater primary and greater and median secondary coverts similar but with broad white margins, which form a white band contrasting the lesser coverts, which are Mummy Brown with faint Ochraceous-Buff spots.

Face and underparts

Lore, cheek and supercilium Amber Brown, the latter almost interrupted by black from the forehead in front of eye, broad behind eye and tapering towards nape. The stiff, bristlelike ear-coverts and neck-side are Morocco Red streaked with blackish. Indistinct moustachial stripe blackish. Chin and central throat Amber Brown, pale centrally. The feathers of the lower margin of the gular area are white, forming a "necklace" with black distal spot and a thin grey margin on most feathers. Breast and sides Light Neutral Grey, most feathers of the sides with a white zone subterminally and some with a small white spot in the middle. From lower breast to belly, the feather margins become increasingly white. On the entire breast, sides and belly (except the pure white downy feathers on the central lower belly), each feather has a diagnostic oval black spot of variable size, up to 8 mm in diameter.

Feathers of flanks and thighs olivaceous grey with an

Ochraceous-Buff or Ochraceous-Orange and/or whitish bar subterminally and inside that a black spot of somewhat variable shape. Under tail-coverts mainly greyish or Buffy Olive with Ochraceous-Orange and white terminal bars and an occasional blackish streak.

Bare parts

Bill Scarlet-Red merging to orange at tip. Legs yellow, lacking spurs, sculation reticulate except for transverse scutes in front of tarsus and on upperside of toes. Iris Chestnut-Brown. Eye rim and the surrounding skin with rudimentary feathering, orange inclining towards Ochraceous-Orange.

Measurements of type

Body-weight 239 g; flattened and straightened wing-length (Svensson 1984, method w[3]) 149.0 mm; tail-length (T(R) method) 73.0 mm; culmen (skull method) 23.7 mm; tarsus (bent method) 39.0 mm; total length 29 cm (measured on the skin).

DESCRIPTION OF PARATYPE

ZMUC cat. no. 91.302, adult female, collected on 26 December 1991 at type locality.

There is a great similarity between the sexes, but the paratype differs in the following subtle ways. Crown less scaly and darker. Upperparts with a slightly stronger orange hue,

mantle feathers with more pronounced blackish bars. Scapulars more contrasting because extension of Mahogany Red and especially of black is greater. The colour of the ear-coverts continues slightly towards the cheeks, which have a number of small blackish spots, most of them arranged in rows, which are continuous with the moustachial stripe. The blackish oval spots on the underside are bigger and extend further down towards the belly. Several under tail-coverts have a black streak along the shaft. Primaries slightly darker, more uniform with virtually no indication of marginal notches; secondaries with warmer coloured bars and tips, wing-linings darker, almost blackish, which makes the white pattern stand out more clearly. The blackish on the upper wing-coverts has a greater extension.

Measurements of paratype

Weight 220 g (2 days after death); wing 148.5 mm; tail 76.0 mm; culmen 23.7 mm; tarsus 38.0 mm; total length about 29 cm.

ADDITIONAL MALE

An additional adult male was collected on 7 April 1992 in the Nyumbanitu Mountains (36°23'E, 7°49'S) at about 1700 m. In moult. Resembles the type, but crown less scaly, lower back with very little black, usually only as faint dusky lines demarcating the rufous bars. Secondaries with whitish trailing edge. This specimen will be deposited in the skin collection of the University of Dar es Salaam, Tanzania.

Weight 222 g; wing 137.5 mm; tail 68.0 mm; culmen 23.7 mm; tarsus 35.5 mm; total length about 29 cm.

GEOGRAPHICAL RANGE

Known only from the Ndundulu Mountains (the type locality) and nearby Nyumbanitu Mountains, both sites located in the Udzungwa Mountains, Tanzania. The species has not been recorded in the well-studied Mwanihana or the Udzungwa Scarp Forests (Fig. 1) (Stuart *et al.* 1987, Jensen & Brøgger-Jensen 1992, Moyer & Lovett in press) in the Udzungwa Mountains and may therefore be absent from the wet southeastern edge of the highland.

In the Ndundulu Mountains, the altitudinal range of the species was 1350–1900 m. The altitudinal range of this forest is 1350–2400 m. The whole forest ranges longitudinally from 36°27'E to 36°42'E and latitudinally from 7°39'S to 7°51'S and covers 240 km². It is separated from the Mwanihana Forest by 15–20 km of grassland.

In the Nyumbanitu Mountains, the species was found only between 1500 and 1700 m, but this forest was not as well investigated as the former one. The altitudinal range of the investigated part of the forest is 1350–2300 m. It ranges longitudinally from 36°19'E to 36°26'E and latitudinally from 7°47'S to 7°54'S and covers 55 km². The forest on the Nyum-

banitu Mountains is separated from the forest on the Ndundulu Mountains by at least 5 km of grassland.

The species is easy to detect and we found it to be locally common in the Ndundulu Mountains and expect it to be so in the Nyumbanitu Mountains as well. The two forest localities are situated west of the newly established Udzungwa Mountains National Park. Both forests are situated within the West Kilombero Scarp Forest Reserve. Although small cultivated fields (*shambas*) occur right up to the northern edge of the Nyumbanitu Mountains, the human impact on the area is slight. No people live near the forests, but a few may use snares and collect some minor forest products. Contact has been made with World Wildlife Fund for Nature, WWF, in Dar es Salaam, with respect to an extension of the National Park.

HABITAT

The Udzungwa Partridge *Xenoperdix udzungwensis* was seen exclusively within habitat classified by Pócs (1976) as montane and submontane evergreen forest. The vegetation of the West Kilombero forest reserve has been described by Hall (unpubl. thesis) and Moyer (1992). All observations are from different parts of the forest interior, from ridges as well as steep slopes and more flat parts, especially where an open understorey occurs. Few of the African perdicine birds, currently in the genus *Francolinus*, are restricted to montane evergreen forest. Two forest species, Latham's Forest and Nahan's Francolins *F. lathamii* and *F. nahani*, inhabit lowland rainforest up to 1400 m (Urban *et al.* 1986). Scaly Francolin *F. squamatus* was found to live sympatrically with *X. udzungwensis* along the lower forest edge (1350–1400 m), but *F. squamatus* was confined to the surrounding grassland and the forest edge.

BEHAVIOUR

The birds usually were seen walking slowly on the forest floor, mainly in small, close flocks. Contact calls were heard often, especially when the birds were anxious. The calls are a series of subdued, high-pitched peeping notes. A whistling song was heard also.

The birds fed by scratching through dead leaves in the same way as chickens, moving leaves with their bills to uncover food and also snapping at small herb leaves (for insects?). At dusk they were often seen feeding on and along paths.

The birds were not shy and would forage as close as 3 m to a person sitting on the forest floor. If approached, they normally escaped by running through the understorey and did not fly even when pursued. If disturbed suddenly, the birds flew but dropped into cover after flying less than 10 m.

During the night they roosted in trees. On one occasion a bird was seen on a branch 8 m above the ground, and on

another occasion two birds were seen 4–5 m above the ground sleeping shoulder to shoulder.

The flock size in the Ndundulu Mountains ranged from single individuals to flocks of eight birds (see Table 1). The average flock size was significantly larger between July and September (3.4 ± 0.3 [mean \pm s.e.], $n = 40$) compared with November to January (2.8 ± 0.4 , $n = 28$) (Kolmogorov-Smirnov two-sample test, $P < 0.05$), though flocks of seven and eight birds were seen in the last period as well. The explanation could be that the birds breed in the last period and therefore segregate in pairs. On 29 November 1991, one adult was seen with at least three chicks in dense cover at 1800 m. In the beginning of December 1991, two adults with chicks were seen in dense understorey at 1550 m. These breeding observations are from the onset of the rainy season and indicate a breeding season like that of most of the other bird species of the forest.

Xenoperdix udzungwensis eats invertebrates as well as plant seeds. The stomach contents of the male caught on 7 April 1992 contained finely disintegrated chitin among which about ten small beetles (Coleoptera), one ant (Formicidae) and one fly (Diptera) were recognized; three larvae (including one Ceratopogonidae, Diptera) and two woodlice (Isopoda) as well as grit were also present. Plant material included six seeds, the largest 9 mm long.

SYSTEMATIC AFFINITIES

The galliform fauna of Africa is dominated by the members of the large genus *Francolinus* (*sensu* Hall [1963], hereafter called francolins), comprising 36 African and five Asiatic species. *Xenoperdix* has a partridge-like shape and posture, a moderately short tail with 14 rectrices, rounded wings with P4–P6 longest, P1 longer than P10, and the bill hooked in a similar way as in a partridge. Being relatively conservative in perdicine birds, the structural morphology does not provide a clear basis for associating *Xenoperdix* with specific other lineages of known perdicine birds. *Xenoperdix* differs strongly from typical francolins in plumage colours and patterns and in the combination of characters, but so do the two small forest-adapted *Francolinus lathamii* and *F. nahani*. Our first thoughts were, therefore, that *Xenoperdix* represented another forest-adapted form with an isolated systematic position amongst francolins.

Thorough studies of the perdicine specimens of the Field Museum of Chicago, the Natural History Museum (Tring) and the Zoological Museum of Copenhagen have now revealed strong similarities with hill-partridges, *Arborophila*, of Asia, and convinced us that *Xenoperdix* falls outside the radiation of francolins. The genus *Arborophila* comprises 16 species inhabiting thick evergreen forest and thickets in Indo-Malaysia, southern China and the Greater Sunda Islands, with one species extending westward in the foothills of Himalaya.

In the following discussion we will compare the new spe-

Table 1. Flock-sizes of *Xenoperdix udzungwensis*. Chicks and flocks that were only heard are excluded. Repetitions are excluded in cases when the same birds were seen at the same time by more than one observer. Altogether 10 observations were excluded for the Ndundulu Mountains, two for the Nyumbanitu Mountains

	Flock-size							
	1	2	3	4	5	6	7	8
Ndundulu Mountains								
30 July to 10 September	7	8	5	10	4	5	1	0
Ndundulu Mountains								
5 November to 10 January	7	14	1	1	0	2	1	2
Nyumbanitu Mountains								
12 March to 10 April	2	1	0	0	0	1	1	0

cies primarily with francolins and Indo-Malayan perdicines and thereafter present a phylogenetic discussion.

A comparison with francolins

The francolins are strongly differentiated, many species being endemic to a small area or disjunctly distributed (review in Johnsgard [1988]).

Based on morphological and ecological characters, Hall (1963) considered the francolins to be monophyletic, with the species falling into eight groups. However, the two small African "forest francolins", *F. lathamii* and *F. nahani*, and the Asiatic Swamp and Grey Francolins *F. gularis* and *F. pondicerianus* could not be assigned to any of the groups. Milstein and Wolff (1984) divided the francolins into two major clades comprising quail-like and partridge-like francolins. Quail-like francolins are generally small, ground-roosting birds with the dorsal plumage streaked and barred as in quails; they have high-pitched, tonal calls. Partridge-like francolins are generally larger, tree-roosting birds with dark dorsal plumage vermiculated with white or buff but some of them rather uniform grey-brown; they give low-pitched, raucous calls. *Xenoperdix udzungwensis* would immediately seem to be a "quail-like francolin". Although its red bill and plumage are aberrant, it agrees with the red-tailed group of quail-like francolins (Coqui Francolin *F. coqui*, White-throated Francolin *F. albogularis* and Schlegel's Francolin *F. schlegelii*) in size, soft voice, yellow legs and rufous tails. The chestnut outer tail-feathers of *X. udzungwensis* are shared by *F. gularis* and *F. pondicerianus*, the latter species even sharing the white trailing edge and broad black sub-terminal bar. The Amber Brown bib and extensively barred back represent a strong overall similarity with *F. gularis*. However, the back pattern of *F. gularis* (and *F. pondicerianus*) is quail-like in arrangement, except that the white feather shafts are vestigial and, therefore, unlikely to be homologous with the type of barring shown by *X. udzungwensis* (Fig. 2). *Xenoperdix udzungwensis* differs from quail-like francolins by

agreed with that of Crowe *et al.* (1992) on most points but differed on some. However, a closer examination of the information value of individual characters suggested that the deepest nodes, at least, still rest on uncertain assumptions. We therefore doubt that the rather slight structural variation and confusing variation in plumage pattern provide reliable information about the deepest nodes of the tree.

For this reason, we will not publish a tree but will limit ourselves to commenting on certain parts of the branching sequence. The Asiatic lineages, *Galloperdix*, *Bambusicola* and *Arborophila*, appear to form deep branches which are distinct from the francolins, although very few characters support any specific sequence of these branches. *Xenoperdix* seems to have its closest relatives in the group of *Arborophila* (the supporting characters have been specified above). We feel convinced that this is a correct placement of *Xenoperdix*.

We support the view of Crowe & Crowe (1985) and Crowe *et al.* (1992) that quail-francolins form a paraphyletic assemblage, with the spotted and red-tailed groups representing deep branches and the partridge-francolins representing another radiation, which includes the Asiatic montane groups (*Alectoris*, etc.). However, *F. nahani* seems to be more closely related to *Galloperdix* (and the African *Ptilopachus*) and *F. lathamii* to the Asiatic lineages. This is more or less also supported by Crowe *et al.* (1992), as they suggest that *F. nahani* is not a francolin but may be a relictual form most closely related to an Indo-Malaysian taxon. Supporting characters are mainly structure and shape of bill and tail (see above). *Francolinus nahani* also has been shown to differ from francolins in its skeletal anatomy (Crowe *et al.* 1992). We fail to support the specific association of *F. gularis* and *F. pondicerianus* with francolins of the "spotted group" (*F. francolinus*, *F. pictus* and *F. pintadeanus*) (Crowe *et al.* 1992), as the former two seem to form a separate deep branch amongst the quail-francolins according to our analysis.

Biogeographic considerations

Crowe & Crowe (1985) explained the disjunct distribution of francolins in Asia and Africa by inferring dispersal across oceanic gaps by early quail-like forms, assuming sedentary habits to have evolved later (see Grant & Little [1992] for a critical review). The relationship between *Xenoperdix* and *Arborophila* and the probable Asiatic affinities of *F. lathamii* and *F. nahani* suggest that there may also have been early vicariance events among forest-dwelling forms.

In order to provide a background for interpreting the biogeographic history, we summarize here the vegetation scenarios given by Crowell & Frakes (1970) and Axelrod & Raven (1978). The drifting of the Indian subcontinent away from eastern Africa happened too long ago to have "transported" perdicine birds from Africa to Asia. A more significant event was probably that the Tethys Sea, which had separated Africa and Asia for hundreds of millions of years, was closed in the Miocene by the union of Africa-Arabia with Iran. This event materially altered the latitudinal sys-

tem of atmospheric circulation, and at the same time rifting and local uplift blocked the ingress of moist air across Africa. The widespread tropical forests were fragmented and replaced by woodland and seasonal deciduous forests. Savanna woodland dominated eastern and northern Africa in the early Miocene, with montane rainforest in Ethiopia and on the Hoggar, Air and Tibetsi and with subtropical rainforest in the Mediterranean area. The widespread change to sclerophyll woodland, savanna and shorn scrub was manifest in the late Miocene. However, opportunities for interchange of forest biota between tropical Africa and the Orient may well have existed in the mid-Miocene, before desertification and rifting of the Red Sea isolated the two regions.

It is evident from biogeographic patterns that opportunities for dispersal and isolation of forest birds must have alternated. Pleistocene cycles are often invoked to explain the differentiation of forest birds in the tropics (Crowe & Crowe 1982, Mayr & O'Hara 1986). Prigogine (1988) suggested two main periods of dispersal of montane forest birds. This may be too simplistic, since there were several large and small climatic cycles during the last 6 million years. Continent-wide attempts to correlate DNA distance measures (Sibley & Ahlquist 1990) and geographical patterns (Fjeldså 1993, in press) suggest that African forest birds differentiated gradually over a long time span, while Pleistocene diversification took place mainly in savannas and at the periphery of major rainforest tracts. This view is consistent with recent interpretations for arthropods and plants. Several African forest birds (White-crested Tiger Heron *Tigriornis leucolophus*, Congo Peacock *Afropavo congensis*, Nkulengu Rail *Himantornis haematopus*, Grey-throated Rail *Canirallus oculus*, Congo Bay Owl *Phodilus prigoginei*, African Green Broadbill *Pseudocalyptomena graueri*, trogons *Apaloderma*, African Piculet *Sasia africana*, African River Martin *Pseudochelidon eurystomina*, babblers *Alcippe* and *Trichastoma*, tailorbirds *Orthotomus*) show affinities to birds of the Oriental Region or even the Indo-Malayan Archipelago (Olson 1973). They can be assumed to be western relicts of groups which inhabited the Miocene forest and woodland formations across Africa and southern Asia. Our study adds *X. udzungwensis* to this list and suggests that *F. nahani* (and maybe *F. lathamii*) and *P. petrosus* may be other examples (although the latter species and its sister taxon *Galloperdix* may inhabit thorn scrub).

Similar affinities to Asia can be found in the montane forest plants of eastern Tanzania. For example, the large tree *Balthasaria schliebenii* is closely related to the Asiatic genus *Adinandra*, and the upper montane forest tree *Ternstroemia poly-petala* is one of two African species in a genus of 80 or so Asian and Neotropical species (Lovett, 1993). The monotypic Eastern Africa endemic tree genus *Neohemsleya* with its closest relative *Sarcosperma* in India-Malesia is another plant species showing this pattern (Pennington 1991). The *Neohemsleya* type locality is on the western Usambara Mountains at Shagayu in montane forests which are botanically similar to the Udzungwa Mountain forests, at least at the scarp of Mwanihana (J. Lovett, pers. comm.).

Sibley & Ahlquist (1985) suggested that Cape and Natal

roosting in trees and from all francolins except Black and Painted Francolin *F. francolinus* and *F. pictus* and the aberrant *F. nahani* in lacking spurs. The rear of the tarsus of *X. udzungwensis* has a fine reticulate scalation, while that of francolins is scutellate, even in forms lacking spurs. Furthermore, it differs from all francolins by having grey underparts with a peculiar pattern of round spots.

The two "forest francolins", *F. lathamii* and *F. nahani*, resemble *X. udzungwensis* in size but are very different in other respects, especially their very dark plumage with obscurely vermiculated upperparts and tails and black underparts with white spots (placed centrally on each feather in *F. lathamii* but along the lateral feather edges in *F. nahani*), their rather slender bills with cere and rudimentary feathering below the nostrils, and slightly vaulted tails.

A comparison with Indo-Malayan perdicines

Arborophila species show highly variable combinations of colours and patterns on the face, throat and breast, but the majority of species share several patterns and combinations with *X. udzungwensis* and differ from other perdicines in these respects. Many species have an orange face, a long and narrow supercilium with some scaly marks, a somewhat contrasting black-and-white ornament on the transition between throat and breast, and a grey main colour of breast and sides (compare Fig. 2). The under tail-coverts of most hill-partridges are olive-grey with white to ochraceous-buff bars and a black patch, no matter what the colour of the rest of the bird (compare Fig. 2). Most species have an olive-grey main colour of the upperparts and a black barring on the mantle very similar to that of the second back-feather of *X. udzungwensis* (Fig. 2, from the left in the upper row of feathers). Few *Arborophila* species have orange or buff sub-terminal bars on the back-feathers and never as sharply outlined as in *X. udzungwensis*. Black barring is reduced or completely lost in certain species; however, black marks centrally on the feathers of the lower back, as shown to the right in Figure 2, are always retained.

Xenoperdix udzungwensis and *Arborophila* species share a unique pattern of the under wing-coverts, which are dark grey-brown or blackish with a contrasting white stripe formed by the outer webs of the middle coverts. They also share tree-roosting habits and a series of whistling calls.

The highest number of similarities in plumage characters with *X. udzungwensis* are found in the Scaly-breasted Hill-Partridge *A. charltoni*, a polytypic Indo-Malayan species, and in the greybreast group (*A. torqueola*, *A. rufipectus*, *A. mandelli*, *A. gingica*, *A. rufogularis*, *A. atrogularis*, *A. crudigularis*, *A. ardens*, *A. orientalis*), whose range extends from the Himalayan foothills to southern China. Most other species, notably those from the Greater Sunda Islands, are more or less aberrant.

Xenoperdix udzungwensis and *Arborophila* have a very similar reticulate scalation along the rear of the tarsus, and spurs are absent.

The most conspicuous difference is the tail, as *X. udzung-*

wensis has a partridge-like tail and *Arborophila* has a very short tail almost hidden by the upper tail-coverts, although not vaulted as in quails. The red outer tail of *X. udzungwensis* was a conspicuous signal when flushed; the outer tail-feathers of *Arborophila* are blackish and unpatterned, and probably the tail has lost its signal function here. However, among other Asiatic perdicines, *Bambusicola* has outer tail-feathers with a similar chestnut hue to that of *X. udzungwensis*. *Bambusicola* also resembles *X. udzungwensis* in having round blackish spots on the feathers of the underparts, which is not seen in *Arborophila*.

Phylogenetic discussion

Various authors have attempted to solve the systematic position within the perdicine birds, but there is still great uncertainty. This is stressed by McGowan (1992). Phylogenetic analyses by Crowe & Crowe (1985), using 26 morphological, vocal and behavioural characters, and Crowe *et al.* (1992), using 34 morpho-behavioural characters supplemented with RFLP analysis of mtDNA and characters from the relatively conserved skeletal anatomy, led to the conclusion that the francolins do not represent a natural unit and should be split into four genera with several subgenera.

In our first attempt to place *X. udzungwensis* in phylogenetic context, we used characters already defined by Crowe & Crowe (1985) and Crowe *et al.* (1992) and the same computer programmes (the *Hennig86* and the *mhennig*bb** tree searching commands and the PAUP program [ver. 3.0; Swofford 1991]). The shortest tree found differed in several respects from that published by Crowe *et al.* (1992), but their character set did not give strong support to any particular tree. With the enormous variation in mottled and striped feather patterns, the classification of character states will necessarily be subjective. Particular problems apply to assumptions about homology of similar-looking patterns in different main groups. Much of the variation could well be explained by the presence of some basic elements and various genes modifying their expression, which makes any classification of a character into a few phenotypes controversial. Finally, there may be doubts about the right choice of outgroup (*Synoicus* according to the phylogeny by Sibley & Ahlquist [1990]) or the use of hypothetical outgroups (a generalized quail; Crowe & Crowe 1985, Crowe *et al.* 1992).

Many of the characters defined by Crowe *et al.* (1992) were difficult to apply to *X. udzungwensis*, which in the shortest phylogenetic tree came out together with Stone Partridge *Ptilopachus petrosus* and near *F. nahani* and an *Arborophila*. This could be because the programme simply "dumped" it together with other species that deviate from the francolin norm.

A new set of morphological characters, altogether 118 character states, for all perdicine species except some aberrant Asiatic taxa, was defined. Using the PAUP programme, we made several heuristic searches with different typesets (weights and assumptions about the polarization of characters). A fairly consistent result was obtained, which

Francolins *F. capensis* and *F. natalensis* diverged 9 million years ago, but the recalculated data presented by Sibley & Ahlquist (1990) suggest a more recent divergence. The radiation of partridge-like francolins probably was in the Pliocene and Pleistocene, but the early radiation of perdicines must have been in the early Miocene (see DNA data of Crowe *et al.* [1992]).

One very interesting aspect of biogeographic patterns of East African forest birds is some cases of strong congruence between old and young species. Although most old species (Ostrich *Struthio camelus*, Secretary-bird *Sagittarius serpentarius*, etc.) are widespread, a few have very restricted distributions, and these species tend to occur together with endemic species which are members of young radiations. Two distinctive (old) species appear to be endemic to the Udzungwa Mountains, namely *X. udzungwensis* and Rufous-winged Sunbird *Nectarinia rufipennis*, while others have populations also in the East Usambara Mountains and in more remote localities, suggesting a relict pattern (Dappled Mountain-Robin *Arcanator orostruthus*, Swynnerton's Robin *Swynnertonia swynnertoni*, Amani Sunbird *Anthreptes pallidigaster* [see Dinesen *et al.* 1993]). At the same time, the Udzungwa Mountains appear to have played a role in the recent diversification of other groups, such as akalats (*Sheppardia*) and sunbirds (*Nectarinia*), with sister-group relationships to the Uluguru or Usambara Mountains or in the Albertine Rift area.

The East Usambara, Uluguru and Udzungwa Mountains are strongly influenced by monsoons from the Indian Ocean. Studies of marine sediments from the Indian Ocean reveal that the surface temperature here was only 1–2°C lower during the ice-age and did not decline at all off the Tanzanian coast (Prell *et al.* 1980). This coastal zone may therefore have been permanently warm and humid, and the above-mentioned mountains may have had humid forest permanently. With marked ecological gradients within each mountain block, the individual species will have found permanently suitable conditions over millions of years within few kilometers. Evidently, these mountains played a role in temporary isolation of populations of groups with a strong recent radiation and, at the same time, served as "elephant graveyards" for some old lineages.

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