# Recent proposed changes to the taxonomy of spurfowl and francolins: further commentary and concerns

Author: Hustler, Kit

Source: Bulletin of the British Ornithologists' Club, 144(3) : 191-210

Published By: British Ornithologists' Club

URL: https://doi.org/10.25226/bboc.v144i3.2024.a2

# Recent proposed changes to the taxonomy of spurfowl and francolins: further commentary and concerns

*by Kit Hustler*

*Received 27 March 2023; final revision 10 May 2024; published 2 September 2024*

*http://zoobank.org/urn:lsid:zoobank.org:pub1DB4518C-09C6-4996-AE32-F24F4A5C9E92*

Summary.—A recent taxonomic revision of African spurfowl and francolins (family Phasianidae) proposed to recognise 16 new species. The authors suggested that divergence in cytochrome-*b* (CYTB) of >1.5% is sufficient to recognise taxa as species. Their molecular material was obtained mainly from museum specimens. However, the study contained errors with some registration numbers and identifications as recorded on specimen labels, and assumptions were made concerning some taxa for which no museum specimens were examined. Given that CYTB sequences among three specimens of the same taxon from the same location and population were divergent by 8%, their framework for delineating species in this group must be considered highly questionable. Other CYTB divergence between taxa ranked as subspecies of the same taxon by the authors of the study were mostly >1.5%, further undermining their hypothesis, and some CYTB data appear to have been selectively excluded. Zero CYTB sequence divergence between geographically distant subspecies suggests interbreeding between them and undermines the assumption that there is none (or it is limited), which was one of the criteria they used to separate species. In addition, existing distributional data were misinterpreted or overlooked, and their own taxonomic decisions were omitted from their updated distribution maps thereby compounding errors already resulting from a misinterpretation of regional distributional data. Brief morphological descriptions were also provided, but not all taxa of some species were examined and sexual plumage dimorphism for others was ignored, producing some significant errors. Consequently, I conclude that these proposed new species should be rejected in the absence of further and more robust evidence.

Recently, spurfowls and francolins (Phasianidae) appear to have had a fairly settled taxonomy, with very few changes proposed between 2014 (del Hoyo *et al*. 2014) and 2022 (HBW & BirdLife International 2022). Most species in Africa were seemingly well understood, with many described subspecies relegated to synonymy. Large variations in plumage within some taxa that occur in reasonably discrete geographical areas was acknowledged in some of the recognised subspecies of Red-necked Spurfowl *Pternistis afer*, while in others, like Coqui Francolin *Peliperdix coqui* (sometimes placed in *Campocolinus*), individual and local variations in colour and mensural characters are so great as to make patterns of geographical variation difficult to identify (Mackworth-Praed 1922, Hall 1963).

Mandiwana-Neudani *et al*. (2019a,b) sought to update francolin and spurfowl taxonomy using a combination of morphological analysis (mostly of plumage characters), augmented with analyses of the calls of some taxa and genetic comparisons (1,143 base pair [bp] sequence of the mitochondrial cytochrome-*b* gene; CYTB). Their work, which derived from a doctoral thesis (Mandiwana-Neudani 2013), recommended that 16 new species be recognised (two spurfowl and 14 francolins), all in Africa.

ISSN-2513-9894 (Online)

Final determination of taxonomic status in Mandiwana-Neudani *et al*. (2019a,b) was based on CYTB divergence. They stated that '… morphologically, behaviourally and genetically distinct taxa were evaluated as putative species if there was little morphological evidence of inter-taxon interbreeding and molecular genetic divergence from their sister taxon in unweighted, uncorrected, overall molecular sequence divergence of mitochondrial CYTB (Swofford 2002) exceeded 1.5%' (Mandiwana-Neudani *et al*. 2019a: 149, 2019b: 196).

The papers by Mandiwana-Neudani *et al*. (2019a,b) have generated considerable controversy, with serious questions raised by Hunter *et al*. (2021) and Hustler (2021) concerning their methodology, analyses and distributional data. Responses by Mandiwana-Neudani *et al*. (2021) and Crowe *et al*. (2022) unfortunately did not fully address the concerns raised and have led, in turn, to more doubts and queries, partly because 'new' data omitted from Mandiwana-Neudani *et al*. (2019a,b) were included. This paper highlights issues in sample sizes, identification of specimens and relevant data not published in the original papers, mostly involving CYTB comparisons. Most problems are exemplified by reference to two species in Central and southern Africa with which I am most familiar: Coqui Francolin *Peliperdix coqui* and Red-necked Spurfowl *Pternistis afer*. Nonetheless, the issues raised are likely to apply across the entire study, as noted already by Hunter *et al*. (2021) and Hustler (2021). Except where stated, taxonomic treatment and nomenclature hereafter follows Mandiwana-Neudani *et al*. (2019a,b) for the purposes of clarity and does not imply endorsement.

Coqui Francolin (*sensu* McGowan 1994) is the most widespread African francolin species (Little 2016). The complexities of geographical variation in its plumage are probably related to an array of ecological factors (climate, habitat, geography, elevation), intersecting with population structure, gene flow and dispersal (Mackworth-Praed 1922, Hall 1963, Benson *et al*. 1971, Irwin 1981). The holotype was collected near Kurrichane (25°21′S, 26°11′E), South Africa (*cf*. Skead 1973); some of the history of its taxonomic treatment is shown in Table 1. Coqui Francolin was subject to the most extensive proposals for changes by Mandiwana-Neudani *et al*. (2019b), including five new species, among them *Peliperdix stuhlmanni*, a taxon otherwise long relegated to synonymy (e.g. Ogilvie-Grant 1893, Reichenow 1900–01, Peters 1934, Hall 1963), although Little (2005a) did list it as a valid subspecies.

The type locality of Red-necked Spurfowl (*sensu* McGowan 1994) is accepted as Benguela (*c*.12°34′S, 13°26′E), Angola. A partial history of its taxonomic treatment is shown in Table 2; the validity of several races continues to be considered doubtful by some authorities, whereas *Pternistis* (*a.*) *cranchii* (including *Pternistis a. leucoparaeus* and *Pternistis a. harterti*) has been separated as a species by several authors. Mandiwana-Neudani *et al*. (2019a) treated *cranchii* as a species and synonymised *leucoparaeus* within *afer*, together with the other taxa found east of the Rift Valley, namely *Pternistis a. melanogaster*, *Pternistis a. swynnertoni* and *Pternistis a. loangwae*. Mandiwana-Neudani *et al*. (2019a) employed *Pternistis a. humboldtii* for all taxa that occur east of the Rift Valley, based on nomenclatural priority. *Pternistis a. humboldtii* was certainly described before any of the other relevant taxa, but Mandiwana-Neudani *et al*. (2019a) presented no data to support synonymising the others.

White-throated Francolin *Peliperdix albogularis* (Hartlaub, 1854) is found in West and Central Africa, with the nominate in Senegal and Gambia, and *buckleyi* (Ogilvie-Grant, 1892) from eastern Ivory Coast to northern Cameroon. The other two subspecies, in Central Africa, *Peliperdix a. meinertzhageni* (White, 1944) (type locality, 13°32′S, 22°39′E), which occupies seasonally flooded grasslands in the upper Zambezi drainage, and *Peliperdix a. dewittei* (Chapin, 1937) (type locality, 07°59′53″S, 28°59′13″E) in high-elevation grassland on the west side of the African Rift Valley, were lumped by Crowe *et al*. (1986) with nominate

ISSN-2513-9894 (Online)

TABLE 1
Coqui Francolin *Peliperdix coqui* subspecies recognised by various authors over time. Crosses in bold font indicate those treated as full species by Mandiwana-Neudani *et al*. (2019b), wherein *vernayi*, *ruahdae* and *kasaicus* are considered subspecies of *coqui*.

| **Taxon** | **Peters (1934)** | **Urban et al. (1986)** | **McGowan (1994)** | **del Hoyo & Collar (2014)** | **Mandiwana-Neudani et al. (2019b)** | **HBW & BirdLife (2022)** | **Clements et al. (2022)** |
|---|---|---|---|---|---|---|---|
| ***coqui***<br>(A. Smith, 1836) | X | X | X | X | **X** | X | X |
| ***hubbardi***<br>(Ogilvie-Grant, 1895) | X | X | X | X | **X** | X | X |
| ***maharao***<br>(W. L. Sclater, 1927) | X | X | X | X | **X** | X | X |
| ***spinetorum***<br>(G. L. Bates, 1928) | X | X | X | X | **X** | X | X |
| ***vernayi***<br>(Roberts, 1932) | X | | | X | X | X | |
| ***ruahdae***<br>(van Someren, 1926) | X | | | | X | | |
| ***buckleyi***<br>(Ogilvie-Grant, 1895) | X | | | | | | |
| ***campbelli***<br>(Roberts, 1928) | X | | | | | | |
| ***angolensis***<br>(Rothschild, 1902) | X | | | X | | X | |
| ***schlegelii***<br>(Heuglin, 1863) | X | | | | | | |
| ***lynesi***<br>(W. L. Sclater, 1932) | X | | | | | | |
| ***kasaicus***<br>(C. M. N. White, 1945) | | | | | X | | |
| ***thikae***<br>(C. H. B. Grant & Mackworth-Praed, 1934) | | | | | **X** | | |
| ***stuhlmanni***<br>(Reichenow 1889) | | | | | **X** | | |

*Peliperdix albogularis*. This treatment was followed by Mandiwana-Neudani *et al*. (2019b) and is also discussed in this paper.

## Sample sizes

One problem identified by Hunter *et al*. (2021) and Hustler (2021) is the lack of information in Mandiwana-Neudani *et al*. (2019a,b) concerning sample sizes. While sample sizes per taxon for molecular analyses are often small because of the difficulty of obtaining adequate material and the cost of the analyses, the same should not be true for morphological work, since most francolin species are well represented in the museum collections visited by Mandiwana-Neudani *et al*. (2019a,b). In Mandiwana-Neudani *et al*. (2019a) the number of specimens examined was not stated, whereas Mandiwana-Neudani *et al*. (2019b) reported that 'up to 10' of each taxon were examined. This became 'more than 10 specimens' of each taxon in Mandiwana-Neudani *et al*. (2021), in response to Hunter *et al*. (2021). Knowing the number of specimens examined, and where they were collected, is an important facet of any taxonomic investigation because it indicates how representative the specimens are, particularly for a geographically widespread taxon like *Peliperdix coqui*. Unfortunately, the

ISSN-2513-9894 (Online)

TABLE 2

Red-necked Francolin *Pternistis afer* subspecies recognised by various authors over time. Crosses in bold font indicate those treated as full species by Mandiwana-Neudani *et al*. (2019a), wherein *castaneiventer* and *humboldtii* were considered subspecies of *afer*.

| **Taxon** | **Peters (1931)** | **Urban *et al.* (1986)** | **McGowan (1994)** | **del Hoyo & Collar (2014)** | **Mandiwana-Neudani *et al.* (2019a)** | **HBW & BirdLife (2022)** | **Clements *et al.* (2022)** |
|---|---|---|---|---|---|---|---|
| ***afer***<br>(Statius Müller, 1776) | X | X | X | X | **X** | X | X |
| ***cranchii***<br>(Leach, 1818) | X | X | X | X | **X** | X | X |
| ***castaneiventer***<br>Gunning & Roberts, 1911 | X | X | X | X | X | X | X |
| ***humboldtii***<br>(Peters, 1854) | X | | X | X | X | X | X |
| ***swynnertoni***<br>W. L. Sclater, 1921 | X | X | X | X | | X | X |
| ***melanogaster***<br>Neumann, 1898 | X | X | X | X | | X | |
| ***leucoparaeus***<br>(G. A. Fischer & Reichenow, 1884) | X | X | X | X | | X | |
| ***harterti***<br>Reichenow, 1909 | X | X | X | X | | | |
| ***nyanzae***<br>Conover, 1929 | X | | X | | | | |
| ***boehmi***<br>Reichenow, 1885 | X | | X | | | | |
| ***loangwae***<br>C. H. B. Grant & Mackworth-Praed, 1934 | | | | X | | X | |
| ***intercedens***<br>(Reichenow, 1909) | X | | X | | | | |
| ***itigi***<br>Bowen, 1930 | X | | X | | | | |
| ***punctulatus***<br>(J. E. Gray, 1830) | X | | X | | | | |
| ***benguellensis***<br>Bocage, 1893 | X | | X | | | | |

data cards on which much of this information was collated were discarded at the end of 2018 (Crowe *et al*. 2022: 283) and sample sizes per taxon ranged from one to 64, with a modal value of seven and all examined specimens were photographed (Crowe *et al*. 2022). One hundred and twelve specimens of *Peliperdix coqui* (12 subspecies but not *Peliperdix c. ruahdae*: Mandiwana-Neudani 2013: 177) and 46 specimens of *Pternistis afer* from 11 subspecies (including 11 specimens of *Pternistis a. humboldtii*) were examined (Crowe *et al*. 2022) but details of the numbers of other subspecies examined are now unavailable.

ISSN-2513-9894
(Online)

Crowe *et al*. (2022) stated that only two male and two female specimens of *Peliperdix c. stuhlmanni* were examined. Surely this not sufficient to upgrade its taxonomic rank, particularly as the holotype was not examined? No specimens of *Peliperdix albogularis dewittei* were examined (Mandiwana-Neudani 2013, Mandiwana-Neudani *et al*. 2019b, Crowe *et al*. 2022) and it seems that the prior treatment of Crowe *et al*. (1986) was followed, but this was not made explicit.

It is uncertain how many specimens of Red-necked Spurfowl subspecies from east of the African Rift Valley were examined (Mandiwana-Neudani *et al*. 2019a: appendix 1), as the limited information presented was contradicted by Crowe *et al*. (2022) and no further details were reported. The effect of these very small (or non-existent) samples on their taxonomic decisions are considered below.

## Type specimens, museum visits and assumptions

Questions about the accuracy of identification of specimens persist across a wide variety of taxa in Mandiwana-Neudani *et al*. (2019a,b). The inaccurate recording of specimen label details identified by Hustler (2021) suggests that many basic errors were made during their data collection phase and some specimens were identified by Mandiwana-Neudani *et al*. (2019a,b) as taxa different from the original specimen labels without any explanation or justification (Hustler (2021).

Some of the issues raised by Hustler (2021) around specimen registration numbers were not addressed by Crowe *et al*. (2022). For example, *Scleroptila crawshayi kikuyuensis*—AMNH 406156 and Genbank FR691606 from Kenya; the specimen number corresponds to a Lapland Bunting *Calcarius lapponicus* per the AMNH online catalogue. Crowe *et al*. (2022, supplementary data, p. 4) attempted to clarify the issue concerning *Pternistis cranchii cunenensis* raised in Hustler (2021) by identifying it as a *Pternistis cranchii/afer* '*cunenensis*' hybrid—TM 28584 and GenBank FR694160—from the Cunene River on the Namibia/Angola border. Crowe *et al*. (2022, supplementary data) stated that the specimen in question is genetically minimally divergent from *Pternistis a. cranchii sensu stricto* but provided no supporting data.

The CYTB sequences for *Pternistis cranchii* and *Pternistis a. afer* are both incomplete and the only apparently true *cranchii* specimen (GenBank FR694164) has continuous genetic data only from bp 1–449. Data for *Pternistis afer* (GenBank FR694158) has a gap in the 1,143 bp sequence between bp 477 and bp 753. The CYTB data on GenBank for the hybrid *Pternistis cranchii/afer* '*cunenensis*' (FR694160) is complete from bp 1–250, but then has a gap to bp 714. This means that there are comparable data only for the first 250 bp of all three specimens, and it is uncertain how the taxa supposedly contributing to this hybrid specimen could have been determined with any confidence based on such a restricted comparison, especially as admixture is difficult to evaluate accurately using (maternally inherited) mitochondrial sequences alone.

The revised interpretation by Crowe *et al*. (2022) that *Pternistis a. cunenensis* is a hybrid raises further concerns. It suggests that the analysis by Mandiwana-Neudani *et al*. (2019a) was incomplete and that the area along the Cunene River is also a hybrid zone, which contradicts their map for *Pternistis a. afer* and *Pternistis cranchii* (Mandiwana-Neudani *et al*. 2019a). The type locality of *Pternistis a. cunenensis* is Swartboois Drift (17º20′56″S, 13º52′04″E) on the Cunene River (Roberts 1932, Macdonald 1957) and it seems reasonable to treat this taxon as no more than a synonym at the southern end of the range of *Pternistis a. afer*, to which it is phenotypically similar (R. J. Dowsett *in litt*. 2023). Confusion over the identity of the *Pternistis cranchii/cunenensis* specimen used in the genetic analysis and its contradictory labelling on GenBank remains unresolved. Crowe *et al*. (2022) claimed some

ISSN-2513-9894 (Online)

of these errors can be rectified by simply changing the scientific names to the ones they proposed or because they are now considered to be hybrids, but without supporting data.

The legend to the supplementary data table in Crowe *et al*. (2022) provides a new source of confusion because it does not accurately differentiate between specimens at the American Museum of Natural History, New York, and some of the molecular data on GenBank; both of which are referenced AM. This confusion would have been eliminated if specimens at AMNH had been so labelled. Crowe *et al*. (2022) indicated that they were investigating some of the errors with relevant collection managers, but provided no timeline of when the outcome might be published. Photographs of the specimens examined, as outlined by Crowe *et al*. (2022: 283), could have been published to deal with some of these concerns but they were perhaps also discarded with the data cards in 2018.

For some taxa, changes to their status were recommended without examining the relevant holotype. For example, Mandiwana-Neudani *et al.* (2019b) did not examine the type of *Peliperdix c. stuhlmanni*. The Museum für Naturkunde, Berlin, kindly provided photographs of it on request (Fig. 1a). Significantly, the holotype shows no evidence of the reduced abdominal barring highlighted by Mandiwana-Neudani *et al*. (2019b) as the distinguishing character of *stuhlmanni* (Hustler & Marshall 2022; Fig. 1). Another specimen of *Peliperdix c. stuhlmanni* collected in Malawi (Fig. 1b) and held at the Bulawayo Natural History Museum, but seemingly overlooked during data collection by Mandiwana-Neudani *et al*. (2019b), also does not show a reduction in abdominal barring and is similar to *Peliperdix c. coqui* (Fig. 1c). That these important specimens were overlooked calls into question just how rigorous was their morphological investigation. The original description of *Peliperdix c. stuhlmanni* (Reichenow 1889), although brief, does not mention reduced abdominal barring

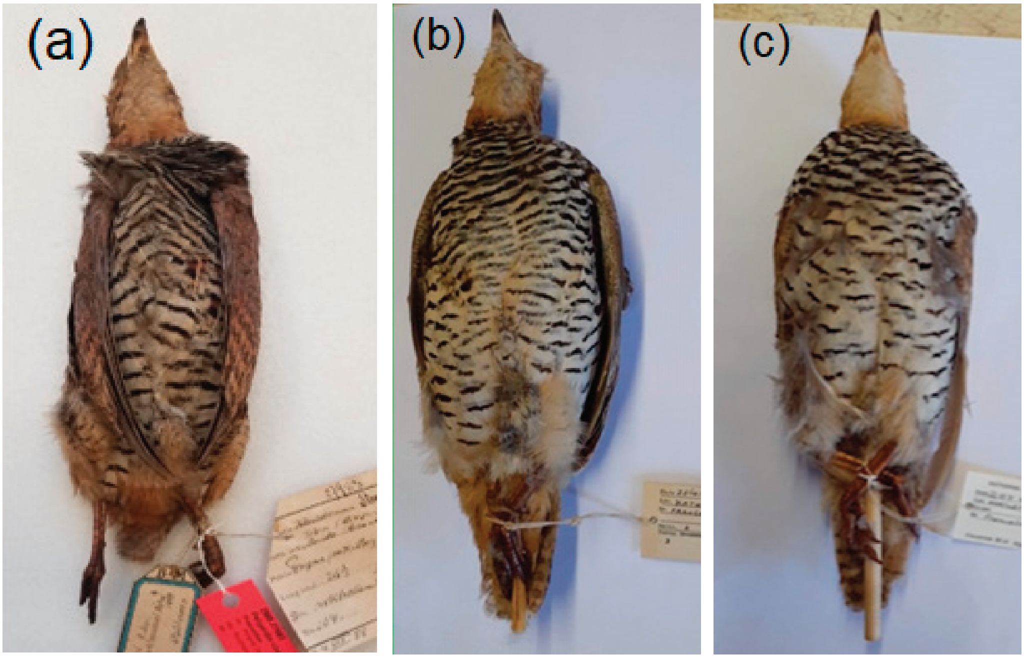

Figure 1. Specimens of male Coqui Francolins *Peliperdix coqui*; (a) the holotype of *P. c. stuhlmanni* collected in 1888 by F. Stuhlmann in north-east Tanzania (ZMB 27983) (courtesy of Museum für Naturkunde, Berlin); (b) a specimen from Malawi, collected by C. W. Benson in 1952, labelled as *stuhlmanni* with rufous undertail-coverts (NMZB 10221) and (c) a *coqui* specimen from Zimbabwe (b and c courtesy of Natural History Museum of Zimbabwe, Bulawayo), illustrating the variation in underparts barring, although not significantly reduced on the abdomen of the two *stuhlmanni* specimens; from Hustler & Marshall (2022).

(because there is none), but emphasises the unbarred rufous undertail-coverts, which were considered to be the distinguishing feature separating it from the otherwise similar *Peliperdix c. coqui* and which were apparently overlooked by Mandiwana-Neudani *et al*. (2019b). The molecular data for *Peliperdix stuhlmanni* were originally recorded on GenBank as *Peliperdix c. coqui* by Mandiwana-Neudani (14/09/2010, GenBank FR694152; but with no specimen or locality data) with a note that it was the subspecies *stuhlmanni*. Details of the specimen (TM 23158) were provided by Crowe *et al*. (2022), but this information was omitted by Mandiwana-Neudani *et al*. (2019b).

The holotype of *Peliperdix albogularis dewittei* is at the Royal Museum for Central Africa, Tervuren (Louette *et al*. 2010), contrary to the assertion by Crowe *et al*. (2022), meaning that the decision to lump this taxon with *Peliperdix albogularis* by Crowe *et al*. (1986) was also made without examining the holotype of *dewittei*. Two specimens of *Peliperdix a. dewittei* at the Natural History Museum, Tring, were apparently also overlooked during visits to that collection. A *Peliperdix a. meinertzhageni* specimen from Angola (NHMUK 1957.35.13) was used for the morphological and genetic analyses, but the data were allocated to *Peliperdix a. dewittei* by Mandiwana-Neudani *et al*. (2019b), presumably following Crowe *et al*. (1986). Mandiwana-Neudani (2013: 179–180) stated that the *Peliperdix a. meinertzhageni* collected in Angola is indisputably different morphologically from other subspecies of *Peliperdix albogularis*, and based on morphological, geographical and genetic evidence should be given species rank. This was ignored by Mandiwana-Neudani *et al*. (2019b) without explanation.

No data were presented concerning the relationship of *Peliperdix a. dewittei* to *Peliperdix a. meinertzhageni*, which were lumped by Mandiwana-Neudani *et al*. (2019b). *Peliperdix a. dewittei* is a localised submontane grassland taxon with relatively small feet, whereas *Peliperdix a. meinertzhageni* (Fig. 2) is a floodplain grassland taxon with large, heavy feet (M. P. S. Irwin pers. comm.) that may represent an adaptation to living in the seasonally flooded grasslands of the upper Zambezi drainage at much lower elevation. Given that the grassland habitats occupied by *dewittei* and *meinertzhageni* are ecologically different, the lack of attention to these two taxa by Mandiwana-Neudani *et al*. (2019b) is surprising.

Figure 2. Male specimens of *Peliperdix albogularis dewittei* (A, holotype) and *P. a. meinertzhageni* (B, topotype) to illustrate differences in plumage and foot size between them (A, courtesy of the Royal Museum for Central Africa, Tervuren; B, courtesy of the Natural History Museum of Zimbabwe, Bulawayo)

ISSN-2513-9894 (Online)

## Concerns over molecular data

For genetic samples of most taxa (Mandiwana-Neudani 2013, Mandiwana-Neudani *et al*. 2019a,b) CYTB sequences were derived from just one museum specimen per taxon. Large gaps in DNA sequences are frequent, as evidenced by the data on GenBank and are not unexpected when working with Sanger sequencing of museum material. It is unclear how Mandiwana-Neudani *et al*. (2019a,b) dealt with these gaps, as they are identical (in lacking DNA nucleotides), erroneously suggesting genetic similarity.

As no specimens of *Peliperdix a. dewittei* were examined by Mandiwana-Neudani (2013) or Mandiwana-Neudani *et al*. (2019b), the morpho-vocalisation scores presented for *dewittei* in Mandiwana-Neudani *et al*. (2019b) must refer to another taxon (*Peliperdix a. meinertzhageni*?) but this is not specified. The GenBank reference to this specimen (FR694148) and all statements relating to CYTB divergence data for *Peliperdix a. dewittei* refer to *Peliperdix a. meinertzhageni*.

Two specimens of *Pternistis afer castaneiventer* were sequenced by Mandiwana-Neudani (2013) but not identified by her as such; details were subsequently outlined in Crowe *et al*. (2022, supplementary data, p. 4). Data from one were used by Mandiwana-Neudani *et al*. (2019a) but allocated to *Pternistis a. afer*. The importance of these specimens to their taxonomic interpretations was overlooked by Mandiwana-Neudani *et al*. (2019a,b) and Crowe *et al*. (2022) but is considered further below.

## Coqui Francolin

Mandiwana-Neudani (2013) analysed genetic samples from three specimens of Coqui Francolin (*sensu lato*), all said to be from Luluabourg (now Kananga) in DRC. These were TM 23525, collected in 1939 and originally identified as *Peliperdix c. angolensis*, and NHMUK 1953.54.49 and NHMUK 1953.54.52, collected within a few months of each other in 1953 and identified by the collector as *Peliperdix c. kasaicus* (NHMUK online database).

Mandiwana-Neudani *et al*. (2019b: table 3, p. 198) assigned these specimens to three different subspecies, namely *angolensis* (TM32525), *kasaicus* (NHMUK 1953.54.49) (both per the original identifications) and *lynesi* (NHMUK 1953.54.52) (the latter changed from *kasaicus* without explanation). Only one of these taxa was classified as a subspecies of *Peliperdix coqui* by Mandiwana-Neudani *et al*. (2019b; see Table 1). The collection locality for the last two specimens was also changed, from the specific 'Luluabourg' to the vague 'DRC'. Their motivation is unknown but it obscures the fact that these specimens were probably all from the same population. CYTB sequence divergences between these taxa are highlighted in bold in Table 3 and were among some of the highest values recorded for *Peliperdix coqui* subspecies (Mandiwana-Neudani 2013); it is inexplicable that these were not reported by Mandiwana-Neudani *et al*. (2019b: table 7; pp. 202–203).

In total, between them Mandiwana-Neudani (2013), Mandiwana-Neudani *et al*. (2019b) and Crowe *et al.* (2022) recognised five *Peliperdix coqui* taxa (*angolensis*, *vernayi*, *lynesi*, *coqui*, *kasaicus*) from the three specimens collected at Luluabourg. It is very unlikely that two or more subspecies would co-occur at one locality and, irrespective of this confusion, the three specimens were, as already stated, probably from the same population (as confirmed by Crowe *et al*. 2022). CYTB divergence between the three specimens ranged from 0–8%, at considerable odds with the assertion that a 1.5% divergence is sufficient to separate species.

It is useful to examine the original data for Coqui Francolins in Mandiwana-Neudani (2013: table 5.6, p. 199), given the importance Mandiwana-Neudani *et al*. (2019b) attached to 1.5% CYTB divergence. These data (genetic distances as uncorrected *p*-distance values rounded to the nearest full percent) were copied from Mandiwana-Neudani (2013: table

ISSN-2513-9894 (Online)

5.6, p. 199) and have been rearranged here in Table 3, so that the three major groups, *sensu* Mandiwana-Neudani *et al*. (2019b) can be distinguished. It would have been preferable to have had access to the precise values, rather than those rounded to the nearest full percentage point used in Mandiwana-Neudani (2013). The first of these groups includes both *Peliperdix c. coqui* specimens and those taxa synonymised in the nominate (i.e. *Peliperdix c. angolensis*, *Peliperdix c. campbelli* and *Peliperdix c. lynesi*). Mean CYTB divergence within this group was 0.9 (range 0–2%), but *Peliperdix c. campbelli*, 2% divergent from the others, should be recognised as a species according to the criteria in Mandiwana-Neudani *et al*. (2019b).

The second group includes taxa retained as subspecies of *Peliperdix c. coqui* (i.e. *Peliperdix c. ruahdae*, *Peliperdix c. vernayi* and *Peliperdix c. kasaicus*) by Mandiwana-Neudani *et al*. (2019b). Hypothetically, all should have been treated as separate species as mean CYTB divergence from *Peliperdix c. coqui* was 4.8% (range 3–8%; see Table 3).

Within the third group, the newly elevated species (*Peliperdix hubbardi*, *Peliperdix maharao*, *Peliperdix spinetorum*, *Peliperdix stuhlmanni*), CYTB divergence averaged 6.2% (range 3–8%), compared to between them and *Peliperdix c. coqui* (6.1%; range 5–8%), and from the synonymised subspecies by 6.4% (range 5–8%). These values are mostly within the 0–8% range of the Luluabourg specimens, so there seems little justification for elevating them to full species.

TABLE 3

CYTB divergence values (uncorrected, rounded *p*-distance % values) for Coqui Francolin *Peliperdix coqui* taxa, extracted and rearranged from Mandiwana-Neudani (2013). The column headed MN lists the names as given in Mandiwana-Neudani (2013). The column headed MN+b are those that Mandiwana-Neudani *et al*. (2019b) synonymised with *coqui*, given as subspecies, or elevated to species (shown in bold font). * indicates the three Luluabourg specimens (CYTB values in bold font) not reported in MN+b (see text). Underlined CYTB values in italics are an order of magnitude greater than their equivalents shown in Table 4.

| MN | MN+b | ***thikae*** | ***stuhlmanni*** | ***spinetorum*** | ***maharao*** | ***hubbardi*** | *kasaicus** | *vernayi* | *ruahdae* | *lynesi** | *campbelli* | *angolensis** | *coqui* (Zambia) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Synonymised** | | | | | | | | | | | | | |
| *coqui* (South Africa) | *c. coqui* | 6 | 5 | 8 | 6 | 5 | *7* | *3* | *4* | 1 | 2 | 0 | 0 |
| *coqui* (Zambia) | *c. coqui* | 6 | 6 | 8 | 6 | 5 | 8 | 3 | 4 | 0 | 2 | 0 | |
| *angolensis** | *c. coqui** | 6 | 5 | 8 | 6 | 5 | **8** | 3 | 4 | **0** | 2 | | |
| *campbelli* | *c. coqui* | 6 | 7 | 8 | 8 | 6 | 6 | 3 | 4 | 2 | | | |
| *lynesi** | *c. coqui** | 6 | 6 | 8 | 6 | 5 | **8** | 3 | 4 | | | | |
| **Subspecies** | | | | | | | | | | | | | |
| *ruahdae* | *c. ruahdae* | 9 | 9 | 7 | 11 | 5 | *2* | 1 | | | | | |
| *vernayi* | *c. vernayi* | 8 | 7 | 6 | 10 | 4 | 0 | | | | | | |
| *kasaicus** | *c. kasaicus** | 7 | 5 | 10 | 9 | 9 | | | | | | | |
| **New species** | | | | | | | | | | | | | |
| *hubbardi* | ***hubbardi*** | 3 | 6 | 6 | 5 | | | | | | | | |
| *maharao* | ***maharao*** | 5 | 8 | 7 | | | | | | | | | |
| *spinetorum* | ***spinetorum*** | 7 | 8 | | | | | | | | | | |
| *stuhlmanni* | ***stuhlmanni*** | 7 | | | | | | | | | | | |

ISSN-2513-9894 (Online)

TABLE 4

CYTB values (uncorrected, *p*-distance % values) for Coqui Francolin *Peliperdix coqui* taxa extracted from Mandiwana-Neudani *et al*. (2019a: table 7). Names in bold font are new species proposed by Mandiwana-Neudani *et al*. (2019a) and the numerical values in bold differ from the corresponding entries in Table 3 by an order of magnitude (i.e. divided by ten).

| | ***thikae*** | ***stuhlmanni*** | ***spinetorum*** | ***maharao*** | ***hubbardi*** | *c. vernayi* | *c. kasaicus* | *c. ruahdae* |
|---|---|---|---|---|---|---|---|---|
| *c. coqui* | 5.5 | 5.5 | 8.0 | 5.9 | 4.5 | **0.3** | **0.7** | **0.4** |
| *c. ruahdae* | 8.8 | 9.2 | 6.9 | 10.9 | 5.1 | 0.8 | **0.2** | |
| *c. kasaicus* | 7.3 | 4.6 | 10.0 | 9.0 | 8.8 | 0.0 | | |
| *c. vernayi* | 7.6 | 7.4 | 6.1 | 9.8 | 4.2 | | | |
| ***hubbardi*** | 3.2 | 6.4 | 6.4 | 4.6 | | | | |
| ***maharao*** | 5.2 | 7.6 | 6.4 | | | | | |
| ***spinetorum*** | 7.2 | 6.4 | | | | | | |
| ***stuhlmanni*** | 7.0 | | | | | | | |

Even more troubling, however, are the divergence values between *Peliperdix c. coqui* and its three synonyms (*Peliperdix c. kasaicus*, *Peliperdix c. ruahdae* and *Peliperdix c. vernayi*) given in Mandiwana-Neudani *et al*. (2019b); see Table 4. The CYTB divergence values in Mandiwana-Neudani (2013: table 5.6, p. 199) were all >1.5%, and she proposed elevating *kasaicus* to species based on its 7–8% divergence from *Peliperdix coqui*. However, the same data in Mandiwana-Neudani *et al*. (2019b: table 7) are an order of magnitude lower (see Table 4 herein). This problem seems to apply only to those values for *Peliperdix coqui*, *Peliperdix c. kasaicus*, *Peliperdix c. ruahdae* and *Peliperdix c. vernayi* as those for *Peliperdix c. stuhlmanni* and other taxa were accurately transcribed. Divergence in CYTB of *Peliperdix c. kasaicus* from all other *Peliperdix coqui* taxa averaged 6.58% (range 0–10%) and is similar to that for *Peliperdix spinetorum* (mean 6.5%, range 6–10%). The latter is treated as a species (Mandiwana-Neudani 2013, Mandiwana-Neudani *et al*. 2019b) but *Peliperdix c. kasaicus* is not (Mandiwana-Neudani *et al*. 2019b), despite the opinion of Mandiwana-Neudani (2013). If they had not reduced these values, Mandiwana-Neudani *et al*. (2019b) would have been obliged to (a) elevate all subspecies of *coqui* to species, which is unlikely given the lack of divergence between some of them, suggesting widespread inter-breeding, or (b) abandon the 1.5% hypothesis and thus nullify their entire taxonomic revision.

Mandiwana-Neudani *et al*. (2019b) did not address two instances where no divergence in CYTB data was found between samples from disjunct populations. Firstly, between a nominate *Peliperdix c. coqui* specimen from 'South Africa' (no specific locality) and a *Peliperdix* [*c*.] *coqui* specimen from Mansa (11°10′S, 28°55′E) in northern Zambia (Table 3); details of the divergence of the Mansa specimen from other taxa are available in Mandiwana-Neudani (2013) but there is nothing about its bp sequence on GenBank, the specimen registration number or where it is held. The CYTB data were reported by Mandiwana-Neudani (2013) but inexplicably omitted from Mandiwana-Neudani *et al*. (2019b), then mentioned again in Crowe *et al*. (2022).

The second case involves a *Peliperdix c. vernayi* collected in Botswana (no precise locality) and a *Peliperdix c. kasaicus* collected at Luluabourg (Mandiwana-Neudani *et al*. 2019b: table 7; Table 3 herein). According to the map in Mandiwana-Neudani *et al*. (2019b;

ISSN-2513-9894 (Online)

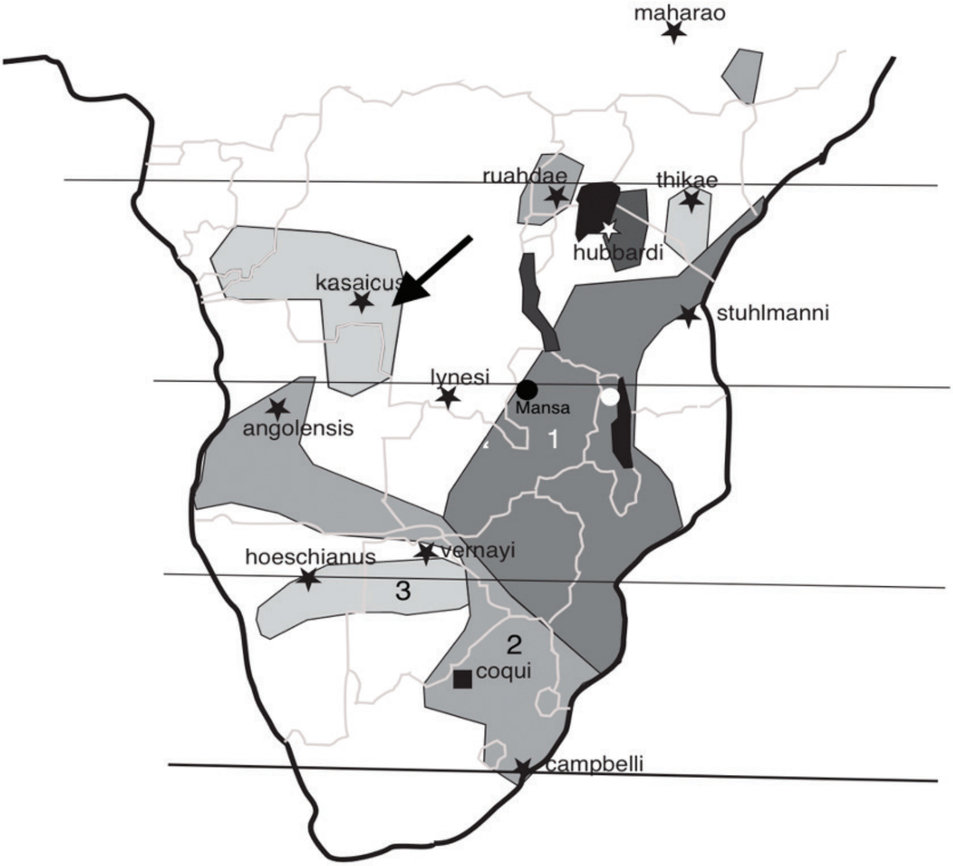

Figure 3. Distribution of Coqui Francolin *Peliperdix coqui* taxa (different shades of grey) in southern and Central Africa (re-drawn from Mandiwana-Neudani *et al*. 2019b); (1) *P. stuhlmanni*, (2) nominate *P. c. coqui*, (3) *P. c. vernayi*, *P. c. kasaicus* = shaded area adjacent to the arrow (which denotes the locality of Luluabourg). White circle = approximate collection localities of *P. stuhlmanni* specimens; black circle = collection locality of ignored *P. c. coqui* specimen from Mansa, northern Zambia. Stars = approximate type localities of subspecies; square = approximate type locality of nominate.

Fig. 3 herein) the southern limit of *Peliperdix c. kasaicus* is about 1,000 km from the northern limit of *Peliperdix c. vernayi*, with the nominate subspecies of *Peliperdix c. coqui* separating them. This suggests gene flow over a wide area between three supposedly different taxa and supports Benson *et al*.'s (1971) observation that the Phasianidae are 'particularly prone to interbreeding'. Indeed, hybridisation has been widely reported (e.g., Hall 1963, Benson *et al*. 1971, Irwin 1981, Little 2016). In contrast, Mandiwana-Neudani *et al*. (2019b) assume little interbreeding between these taxa despite their own data suggesting otherwise.

## White-throated Francolin

The statements relating to CYTB divergence of *Peliperdix a. dewittei* from *Peliperdix a. albogularis* are incorrect because the data derived from a specimen of *Peliperdix a. meinertzhageni* (Crowe *et al.* 2022, supplementary data, p. 2; GenBank database FR694148). Mandiwana-Neudani (2013: 179–180) stated that *Peliperdix a. dewittei* [i.e. *meinertzhageni*] is divergent genetically from the other subspecies in *Peliperdix albogularis*. This was confirmed by Mandiwana-Neudani *et al*. (2019b: table 7) who reported that divergence between *Peliperdix a. albogularis* and *Peliperdix a. dewittei* [*meinertzhageni*] was 5.3–5.5%. This is more than the 1.5% divergence threshold used by Mandiwana-Neudani *et al*. (2019b) and suggests that *meinertzhageni* is not a subspecies of *Peliperdix albogularis*. These data were overlooked by Mandiwana-Neudani *et al*. (2019b) without explanation.

## Red-necked Spurfowl

There is much uncertainty regarding the *Pternistis a. afer* specimens used by Mandiwana-Neudani *et al*. (2019a). Neither Mandiwana-Neudani (2013) or Mandiwana-Neudani *et al*. (2019a) presented adequate details about relationships among *Pternistis afer* subspecies. In response to Hustler (2021), Crowe *et al*. (2022, supplementary data, p. 4) confirmed that the data for *Pternistis a. afer* in Mandiwana-Neudani *et al*. (2019a) derived from South African *Pternistis a. castaneiventer*. This confirmed the suspicions of Hustler (2021), because the collection locality given in Mandiwana-Neudani *et al*. (2019a: table 3) was well outside the known distribution of *Pternistis a. afer*. Crowe *et al*. (2022, supplementary data, p. 4) stated that 'two Red-necked Spurfowl specimens from South Africa were sampled for genetic analysis, both from the eastern Transvaal (now Mpumalanga Province). One, NHMUK 1903.10.14.91, was identified only as from 'E. Transvaal'. The other was collected at Tudor Estates, Waterval Boven. Hall (1963) and Clancey (1967: 142) placed Red-necked Spurfowl from the eastern Transvaal in *lehmanni*—morphologically close to *castaneiventer*. Since both sequences were 2.7% divergent from Angolan *Pternistis* [*a.*] *afer*, the longer sequence from Waterval Boven was used in the taxonomic comparisons.'

The CYTB comparisons of various subspecies with *Pternistis a. afer* are therefore moot because the data collected were actually from *Pternistis a. castaneiventer*, which is not mentioned in the taxonomic analyses by Mandiwana-Neudani *et al*. (2019a).

Mandiwana-Neudani (2013: table 6.6, p. 259) reported CYTB divergence data for 12 different subspecies of *Pternistis afer* from across the continent with an *afer* specimen from Angola. Crowe *et al*. (2022) retrospectively reported the divergence between the Angola specimen and *Pternistis a. swynnertoni* as 3.5% and *Pternistis a. castaneiventer* as 3.6%. Mandiwana-Neudani *et al*. (2019a: table 7) presented divergence data for *Pternistis afer* and *Pternistis a. cranchii* which showed they differ by only 1.6%, but elevated *Pternistis cranchii* to a full species on this basis, whereas they ignored divergence data of >1.5% between *Pternistis a. afer* and other subspecies.

Details of the Angola specimen (Mandiwana-Neudani 2013: table 6.6, p. 259) were retrospectively provided by Crowe *et al*. (2022) which indicated that it was collected at Fort Quillengues (14°04′S, 14°05′E), Benguela province (AMNH 541525). This is within the *Pternistis cranchii*/*Pternistis afer* hybrid zone mapped by Mandiwana-Neudani *et al*. (2019a: fig. 7) and raises questions about the specimen's identification and/or delineation of the hybrid zone. The relationships of the known subspecies with nominate *Pternistis a. afer* are unresolved because it is uncertain which material was used in the comparison.

Mandiwana-Neudani *et al*. (2019a: table 3) did not sample molecularly or publish morphological data for *Pternistis a. melanogaster*, *Pternistis a. leucoparaeus*, *Pternistis a. loangwae* or *Pternistis a. humboldtii*, despite having access to specimens of at least some of these (Mandiwana-Neudani *et al*. 2019a: appendix 1). This created a 'data hole' in their analyses of these Central African taxa from east of the Rift Valley. They sort to circumvent this by reverting to nomenclatural priority by knowingly assigning the CYTB data from a topotypical *Pternistis a. swynnertoni* to *Pternistis a. humboldtii* (Crowe *et al*. 2022).

*Pternistis a. humboldtii* has long represented a taxonomic headache (e.g. White 1965), a situation not resolved by Mandiwana-Neudani *et al*. (2019a). It appears genuinely rare and

ISSN-2513-9894 (Online)

Hall (1963) suggested that it was a hybrid between *Pternistis a. melanogaster* and *Pternistis a. swynnertoni* found in the vicinity of Tete in Mozambique (*c*.16º09'S, 33º35'E) on the Zambezi River. The *Pternistis a. swynnertoni* CYTB sample allocated to *Pternistis a. humboldtii* by Mandiwana-Neudani *et al*. (2019a) was collected at the type locality of *Pternistis a. swynnertoni* (*c*.19º59'S, 33º12'E) in the eastern highlands of Zimbabwe. It is highly unlikely to be *Pternistis a. humboldtii*, as claimed by Mandiwana-Neudani *et al*. (2019a), because this is 500 km south of where *Pternistis a. melanogaster*, the other taxon suspected to be involved in the *Pternistis a. humboldtii* phenotype (Hall 1963), occurs.

Mandiwana-Neudani *et al*. (2019a) did not collect molecular material or present plumage scores from any of the 11 *Pternistis a. humboldtii* specimens they examined (Crowe *et al*. 2022). A plumage score and/or a molecular sample for this taxon would have been a notable contribution to the taxonomy of East African *Pternistis afer* taxa. Mandiwana-Neudani *et al*. (2019a) concluded that the taxon in East Africa is *Pternistis a. humboldtii* but this was based exclusively on nomenclatural priority. They ignored Hall (1963) and Clancey (1967: 143) who considered *humboldtii* to be a taxonomically unstable population and an 'unsatisfactory intermediate' between *swynnertoni* and *loangwae*, respectively. Allocation of genetic data from *Pternistis a. swynnertoni* to *Pternistis a. humboldtii* obscures the taxonomy of East African taxa, given the issues identified with this taxon (Hall 1963, White 1965, Clancey 1967).

It appears that Mandiwana-Neudani *et al*. (2019a) had identification issues with some of the other East African *Pternistis afer* taxa. CYTB data allocated to *Pternistis cranchii intercedens* (GenBank FR69416) were collected from a *Pternistis a. swynnertoni* specimen (AMNH 416180), originally identified as *Pternistis a. humboldtii* by the collector, as detailed by Hustler (2021: 326). *Pternistis a. humboldtii* and *Pternistis a. swynnertoni* are phenotypically quite different from *Pternistis c. intercedens* but Crowe *et al.* (2022) confirmed that the AMNH specimen phenotypically is *intercedens*. However, the statement in Crowe *et al.* (2022, supplementary data, p. 3) that the specimen was 'actually examined' does little to confirm their identification.

## Did the morpho-vocalisation approach adequately distinguish new species?

Mandiwana-Neudani *et al*. (2019a: 150, 2019b: 197) adopted what they called a morpho-vocalisation approach to define spurfowl and francolin species. This involved establishing a set of morphological and vocal characteristics, each of which was scored, presumably in an attempt to provide uniformity and objectivity in taxonomic descriptions. The vocal scores contributed little to this analysis (Mandiwana-Neudani *et al*. 2014) because they were based on just one recording per taxon and did not include all the subspecies under consideration, but this was not admitted by Mandiwana-Neudani *et al*. (2019a,b). The morphological approach listed 26 and 20 characters for spurfowl and francolins respectively, with up to seven character state scores for each.

This 'one-size-fits-all' approach did not always distinguish between the sexes, or adults and immatures, and was not always accurately applied. For example, Mandiwana-Neudani *et al*. (2019b) mentioned that Coqui Francolins are sexually dimorphic but did not specify to which sex the characters they scored applied. Thus, the scores allocated for the gorget (character no. 7), breast pattern (no. 8) and head pattern (no. 13) can apply only to females—had they been males, very different scores would have resulted—but this is not stated. Those allocated for breast pattern (no. 8), undertail pattern (no. 10), wing pattern (no. 11) and wing base colour (no. 12) were scored inconsistently. For example, the breast of *Peliperdix c. coqui* was scored 0 (unpatterned) whilst that of *Peliperdix c. stuhlmanni* was scored 1 (barred):

ISSN-2513-9894 (Online)

all male Coqui Francolins have barred breasts, which suggests some confusion between males and females, perhaps because of a lack of familiarity with this taxon and its sexually dimorphic plumages, and an inadequate and/or incomplete examination of specimens. It is unclear how scores were obtained for *Peliperdix a. dewittei*, as no specimens were examined. Recordings of *Peliperdix a. dewittei* and *Peliperdix a. meinertzhageni* vocalisations were not available at the time of publication by Mandiwana-Neudani *et al*. (2019a,b) and comparisons are, presumably, based on an unproven similarity with *Peliperdix a. albogularis*.

The sampling of *Pternistis afer* taxa in East and Central Africa is also confusing. Specimens of *Pternistis a. melanogaster*, *Pternistis a. leucoparaeus* and *Pternistis a. loangwae* were apparently examined by Mandiwana-Neudani *et al*. (2019a: appendix 1), but this is contradicted by Crowe *et al*. (2022) who stated that no *Pternistis a. loangwae* were examined and that examination of *Pternistis a. melanogaster* and *Pternistis a. leucoparaeus* specimens was based on photographs alone.

Mandiwana-Neudani *et al*. (2019a,b) also cited some literature inaccurately. For example, Crowe *et al*. (2022: 285) stated that they used the name *stuhlmanni* for their newly elevated 'Coqui Francolin' species because Benson had used it in his works on the birds of Zambia and Malawi (Benson *et al*. 1971, Benson & Benson 1977), when in fact this name was not mentioned in either. They also claimed that Peters (1934: 72) wrote that '… this terminal epithet was available for coqui-like francolins from Portuguese East Africa (Mozambique) and Nyasaland (Malawi)' whereas he stated, in a footnote, merely that '*stuhlmanni* is a synonym' [of *coqui*].

There is also a considerable body of relevant historical literature that apparently was not considered at all. For example, Mandiwana-Neudani *et al*. (2019b) appear to have overlooked information on plumage variability in Coqui Francolins published by Mackworth-Praed (1922), Hall (1963) and Irwin (1981), who stated that Central and south-eastern African populations of this species are so variable that patterns of geographical variation are difficult to determine. As a result, Mandiwana-Neudani *et al*. (2019b) identified three Coqui Francolin specimens variously as five different subspecies of *Peliperdix c. coqui* and erroneously used a reduction in belly barring as the unique character to identify *Peliperdix c. stuhlmanni*. Mackworth-Praed (1922) did not find Coqui Francolin specimens with redder and unbarred undertail-coverts (the unique diagnostic of *stuhlmanni*) from Central and East Africa, which alerted him to the possibility that *stuhlmanni* is a poorly defined taxon. The holotype of *stuhlmanni* was collected in the coastal lowlands of Tanzania (Pongue, Usegua; 06°18'S, 38°14'E; 365 m), east of the Rift Valley, whereas the specimens examined by Mandiwana-Neudani *et al*. (2019b) were from miombo woodland west of the Rift in Malawi (at 1,285 m), *c*.800 km south of the type locality.

## Inaccuracies in distribution maps

Crowe *et al*. (2022: 285) described types as 'highly valuable reference specimens necessary for historical comparative taxonomic analyses' and that type specimens and topotypes are irreplaceable. They are taxonomically valuable because they provide a source of reference to the original description and to where the taxon occurred, and are a baseline reference that can be checked any number of times should need arise. It is reasonable therefore to expect that distribution maps must contain the type locality unless significant habitat change has occurred subsequent to the taxon's discovery. Some of the distribution maps in Mandiwana-Neudani *et al*. (2019a,b) do not include the type localities of the taxa concerned.

Hunter *et al*. (2021) drew attention to inaccuracies in the distribution maps in Mandiwana-Neudani *et al*. (2019a,b) resulting from a failure to consult recent regional

ISSN-2513-9894
(Online)

atlases. They could have prevented many of these errors by referring to works such as those for Botswana (Penry 1994), Zambia (Benson *et al*. 1971, Dowsett *et al*. 2008), Zimbabwe (Irwin 1981), Malawi (Dowsett-Lemaire & Dowsett 2006) and central and southern Mozambique (Parker 1999, 2005).

An example can be seen in the distribution of the subspecies of *Peliperdix c. coqui* (Fig. 3). The discrete distribution for the subspecies mapped in Mandiwana-Neudani *et al*. (2019b) is inaccurate. It does not reflect known interbreeding of taxa, ignored the difficulties they had in identifying subspecies (five possible taxa from three specimens at Luluabourg) or the similarity of the CYTB data of some subspecies from well outside the distributions they reported on their map (e.g. *Peliperdix c. coqui* from South Africa and Zambia, *Peliperdix c. vernayi* from Botswana and DRC). Crowe *et al*. (2022) acknowledged that the Luluabourg specimens were all probably the same taxon, but made no further comment about the subspecies concerned or the impact this had on their distribution map.

Mandiwana-Neudani *et al*. (2019b) extended the range of *Peliperdix c. coqui* west into central Namibia and south into Lesotho and a large area of South Africa, despite the lack of evidence of its occurrence in these areas in Harrison *et al*. (1997) or the more recent SABAP 2 (https://sabap2.birdmap.africa/species/173). The extraordinary distribution shown by Mandiwana-Neudani *et al*. (2019b) for *Peliperdix c. coqui*, as widespread in northern and eastern South Africa, and extending narrowly along the Zimbabwe/Botswana border into western Zambia and Angola, was not explained or justified.

How such an extensive range for *Peliperdix stuhlmanni* across central and southern Africa could have been inferred from only two Malawian specimens, collected well north of the Zambezi River (Fig. 3), is unclear. The supposed contact zone between *stuhlmanni* and nominate *coqui* in Zimbabwe and southern Mozambique is, to my knowledge, unsupported by any specimen data, and seems to be entirely arbitrary.

Similarly, according to Benson *et al*. (1971) and Irwin (1981), the distribution of *Peliperdix c. vernayi* is closely linked to Kalahari Sands in western Zambia and north-west Zimbabwe, so it is unclear why Mandiwana-Neudani *et al*. (2019b) decided that *Peliperdix c. coqui* occurred there instead. Mandiwana-Neudani *et al*. (2019b) considered that the Luluabourg specimen of *Peliperdix c. angolensis* was a clinal variant of *Peliperdix c. vernayi*, despite the lack of Kalahari sand there, and the *Peliperdix c. lynesi* specimen to be *Peliperdix c. coqui*, but inexplicably neither decision is reflected on their distribution map, which reported *Peliperdix c. kasaicus* at this locality. Their map is inaccurate by *c*.1,500 km for *Peliperdix c. vernayi* and *Peliperdix coqui* as a result (see Fig. 3).

The distribution of *Peliperdix a. meinertzhageni* and *Peliperdix a. dewittei* is not contiguous as illustrated in Mandiwana-Neudani *et al*. (2019b). As mentioned above, these taxa are geographically isolated from each other, in floodplain grasslands of the upper Zambezi drainage on the Angola/Zambia border (*meinertzhageni*) and in high-elevation grasslands of the Albertine Rift in south-east DRC (*dewittei*), respectively. These are two quite distinct and geographically isolated habitats that do not extend across the geographical range shown by Mandiwana-Neudani *et al*. (2019b), thus the distribution shown therein is grossly inaccurate.

Re-evaluation of *Pternistis a. cunenensis* by Crowe *et al*. (2022) as a hybrid between *Pternistis a. afer* and *Pternistis cranchii*, creates a discrepancy with the distribution map in Mandiwana-Neudani *et al*. (2019a), where only *Pternistis a. afer* is shown in the relevant region. Nominate *Pternistis a. afer* occurs in the low-lying and quite arid coastal areas of south-west Angola, south to the Cunene River on the Namibian border. The locality and extent of the hybrid zone mapped by Mandiwana-Neudani *et al*. (2019a) is therefore inaccurate and should also include the Cunene River. The presence of *cranchii* here has not been confirmed, with no specimen records from this area (W. R. J. Dean *in litt*. 2020) or photographs, and this taxon seems to be restricted to higher ground inland.

Mandiwana-Neudani *et al*. (2019b) also ignored the current known distributions of Shelley's Francolin *Scleroptila s. shelleyi* and *S. whytei* based on specimens (Benson *et al*. 1971, Irwin 1981) and sightings (Dowsett-Lemaire & Dowsett 2006, Dowsett *et al*. 2008) and, as a result, their distribution map for both is incorrect. That of *S. shelleyi* (Mandiwana-Neudani *et al*. 2019b: fig. 7) is at variance with the known distribution in southern Africa (Irwin 1981, Harrison *et al*. 1997; https://sabap2.birdmap.africa/species/177). Mandiwana-Neudani *et al*. (2019b: fig. 7) incorrectly showed *S. shelleyi* only in the far north-east of Zimbabwe and did not include the type locality (*c*.18º05′44″S, 30º14′08″E), or much of Zimbabwe above *c*.1,200 m, where it still occurs.

The holotype of *whytei* is from the Nyika Plateau in Malawi. Its status in southern Tanzania is unclear, but the taxon appears to extend along the Zambia/Tanzania border into adjacent DRC, where there is a specimen from the western edge of the Albertine Rift (Schouteden 1971). There is no evidence that it extends beyond 14ºS in Zambia and it appears to be absent from the Luapula and Luangwa Valleys, whereas east of the Luangwa River it is replaced by *S. s. shelleyi* (Dowsett *et al*. 2008), which extends from there into western Malawi (Dowsett-Lemaire & Dowsett 2006). It does not occur up to or south of the Zambezi River (Benson *et al*. 1971, Irwin 1981, Harrison *et al*. 1997, Little 2005c, Dowsett *et al*. 2008, SABAP 2). Given this inaccuracy, the supposed presence of *whytei* as far south as Zimbabwe (Mandiwana-Neudani *et al*. 2019b: fig. 7) should be disregarded.

The distribution of other taxa is also incorrect. For example, Natal Spurfowl *Pternistis natalensis* is shown as extending into Angola and southern Malawi, although it has never been recorded in either country (Dowsett-Lemaire & Dowsett 2006, Mills & Melo 2013; https://sabap2.birdmap.africa/species/183). Also, Mandiwana-Neudani *et al*. (2019a) show it as absent in north-east and north-west Zimbabwe, despite Harrison *et al*. (1997) confirming the species' presence in both areas and where it is common (Howells 1985, Hustler 1986). Crested Francolin *Ortygornis sephaena rovuma*, a coastal lowland subspecies, is shown in the eastern highlands of Zimbabwe, which is inaccurate. Orange River Francolin *Scleroptila levaillantoides* extends to western Zimbabwe according to Mandiwana-Neudani *et al*. (2019b) but has yet to be recorded there (Irwin 1981, Harrison *et al*. 1997; https://sabap2.birdmap.africa/species/179) despite targeted searches (pers. obs.). Red-winged Francolin *Scleroptila levaillantii* is confined to tall, rank highland grassland (1,600–2,000 m) in south-east Africa (Mandiwana-Neudani *et al*. 2019b), but they contradict this by mapping it in the Limpopo River valley (Mandiwana-Neudani *et al*. 2019b: fig. 6; 240–750 m). The grassland habitat it prefers does not exist there, easily explaining the species' absence (Harrison *et al*. 1997, https://sabap2.birdmap.africa/species/178).

Mandiwana-Neudani *et al*. (2019a,b, 2021) stated that these maps represented 'approximate distributional ranges'. This is an understatement given the scale of the inaccuracies reported here, which include overlooking some of their own taxonomic decisions. On the other hand, the comment in Crowe *et al*. (2022) that the maps in Mandiwana-Neudani *et al*. (2019a,b) convey 'useful information for further taxonomic, phylogenetic and biogeographical research as well as for conservation planning, complemented by atlas information for fine-scale action' overstates their utility.

## Conclusion

The comment in Crowe *et al*. (2022: 289) that 'The concerns, criticisms and inconsistencies of Hustler and Hunter+ are largely a result of their varied continued support for Hall's (1963) long-outdated taxonomy, misunderstandings or overstatement' is incorrect. The concerns

ISSN-2513-9894
(Online)

raised were that the papers under discussion did not meet the standard expected of a modern taxonomic revision. Specimens in museums were the foundation of the data used by Mandiwana-Neudani *et al*. (2019a,b). Changes to the original identification of specimens may be expected as part of the re-examination process that occurs during taxonomic research, but the scale of confusion over specimen registration numbers and specimens used is not, and suggests a lack of attention to detail. It also undermines confidence in the re-identifications suggested. Mandiwana-Neudani *et al*. (2019a,b) appear to have little field experience in Central Africa and their work is poorer for the apparent lack of consultation of accounts by those who have studied the relevant taxa. All this creates uncertainty and questions the reliability of the data in GenBank.

Unjustified assumptions about some taxa for which specimens were not examined and/or relevant data not presented (e.g. plumage and morphology for *Peliperdix a. dewittei*, *Peliperdix a. meinertzhageni*, *Pternistis a. humboldtii*, *Pternistis a. loangwae*, *Pternistis a. melanogaster*, *Pternistis a. leucoparaeus*; vocalisations for *Peliperdix a. dewittei*, *Peliperdix a. meinertzhageni*, *Peliperdix stuhlmanni*, *Pternistis a. humboldtii*, *Scleroptila s. whytei*) have led to taxonomic opinions not based on verifiable data. In the case of *Peliperdix stuhlmanni*, the defining characteristic used by Mandiwana-Neudani *et al*. (2019b) is not apparent in the holotype, which they did not examine. Mandiwana-Neudani *et al*. (2019b) failed to note that a few years after its description it was synonymised by Ogilvie-Grant (1893) and by its author, Reichenow (1900–01). It is clearly a poorly defined taxon, and the revision by Mandiwana-Neudani *et al*. (2019b) has not changed this.

Responses to the commentaries of Hunter *et al*. (2021) and Hustler (2021) by Mandiwana-Neudani *et al*. (2021) and Crowe *et al*. (2022) have provided additional, albeit sometimes contradictory, CYTB data for several taxa initially reported in Mandiwana-Neudani (2013) but excluded from Mandiwana-Neudani *et al*. (2019a,b) without explanation. Significant transcription errors between the original data and final publications have influenced and, in some cases, confused taxonomic decisions.

The most controversial proposal is that CYTB sequence divergence greater than 1.5% is sufficient to elevate subspecies to species (Mandiwana-Neudani *et al*. 2019 a,b). The weakness of this hypothesis was revealed by their CYTB data from the Luluabourg specimens of *Peliperdix coqui* (Tables 3–4 herein), from specimens of *Pternistis a. castaneiventer* and variation between *Pternistis a. afer* and *Pternistis a. swynnertoni* and *Pternistis a castaneiventer* (Crowe *et al*. 2022), which were not mentioned in Mandiwana-Neudani (2019a). Acknowledgement by Crowe *et al*. (2022) that *Pternistis cranchii* and *Pternistis a. afer* varied by 1.6–3.5% (although these data were not reported by Mandiwana-Neudani *et al*. 2019a, and the sampled specimens were not listed), is further evidence that CYTB sequence divergence within some taxa can vary by more than 1.5%. Inconsistent application of their own rule, where some taxa divergent by >1.5% were considered species, but others were not, leaves open the possibility that decisions were influenced by opinions unsupported by the data.

The taxonomic results derived from the morpho-vocalisation and molecular data used by Mandiwana-Neudani *et al*. (2019a,b) seem redolent of the practice of 'nomenclatural harvesting' (Denzer & Kaiser 2023). In some cases, Mandiwana-Neudani *et al*. (2019a,b) did not fully consider prior taxonomic work and made significant assumptions without examining specimens to provide supporting evidence. Using *Peliperdix coqui*, one of the most widespread taxa on continental Africa, as an example, they provided few relevant novel data. Morphological and plumage data were confused by a lack of consideration of sexual dimorphism and the vocal comparisons between species were incomplete (missing calls from some taxa) and limited by sample size. Information on distribution did not take

ISSN-2513-9894 (Online)

into account data from several recent atlases. Mandiwana-Neudani *et al*. (2019b) failed to include some of their own taxonomic decisions in their distribution maps.

Treatments of other taxa are beset with problems of species identification, allocation of data pertaining to one taxon to another, inconsistent application of their criteria for determining species rank and inconsistencies between the original work (Mandiwana-Neudani 2013) and later publications (Mandiwana-Neudani *et al*. 2019a,b, Crowe *et al*. 2022). All compounded by an apparent lack of appreciation of intra-taxon variability in CYTB data, which at least sometimes easily exceeds the proposed threshold of 1.5% used to differentiate species.

Crowe *et al*. (2022) agreed that the recommendations in Mandiwana-Neudani *et al*. (2019a,b) were by no means exhaustively proven. They also stated (Crowe *et al*. 2022: 289) that 'Subject to examining a range of representative specimens and obtaining sequences for *humboldtii*, *melanogaster*, *loangwae* and *leucoparaeus*, if their morphology is uniform across their range and if the respective genetic distances from *afer*, *cranchii* and *castaneiventer* are found to be ≥3.0%, we argue that there are at least four species of Red-necked Spurfowl: *cranchii*, *afer*, *castaneiventer* and *humboldtii* sensu lato.' These statements recognised, perhaps inadvertently, some of the shortcomings of the earlier papers but gave an indication of how the study should have been conducted. Crowe *et al*. (2022: 289) in fact reported divergence between *Pternistis afer* (Angola) and *Pternistis a. swynnertoni* (= 3.5%) and *Pternistis a. castaneiventer* (= 3.6%) respectively, exceeding their threshold for species status but, inexplicably, these taxa and data were excluded from Mandiwana-Neudani *et al*. (2019a).

This is a further example of unexplained omissions from Mandiwana-Neudani *et al*. (2019a) and of new data being provided subsequently in response to concerns raised by Hunter *et al*. (2021) and Hustler (2021). It reinforces the plethora of inconsistencies that characterise the relevant publications and begs the question 'What else has been left out?'. It serves also to confirm that they do not meet the standard of a modern taxonomic review and provides further justification for disregarding the revisions proposed by Mandiwana-Neudani *et al*. (2019a,b).

## Acknowledgements

Discussions with Brian Marshall, Peter Frost and Nigel Hunter clarified some of the issues considered here. Critical comments by Lincoln Fishpool also improved the text, which further benefitted from the constructive criticism of Michael Mills, Bob Dowsett and an anonymous referee. The Royal Museum for Central Africa, Tervuren, Museum für Naturkunde, Berlin, and Natural History Museum of Zimbabwe, Bulawayo, generously provided photographs of specimens of *Peliperdix a. dewittei*, *Peliperdix c. stuhlmanni*, *Peliperdix coqui* and *Peliperdix a. meinertzhageni*.

References:

Benson, C. W. & Benson, F. M. 1977. *The birds of Malawi*. Montfort Press, Limbe.

Benson, C. W., Brooke, R. K., Dowsett, R. J. & Irwin, M. P. S. 1971. *The birds of Zambia*. Collins, London.

Chapin, J. P. 1932. The birds of the Belgian Congo. Part I. *Bull. Amer. Mus. Nat. Hist*. 65: 1–756.

Clancey, P. A. 1967. *Gamebirds of southern Africa*. Purnell, Cape Town.

Clements, J. F., Schulenberg, T. S., Iliff, M. J., Fredericks, T. A., Gerbracht, J. A., Lepage, D., Billerman, S. M., Sullivan, B. L. & Wood, C. L. 2022. The eBird/Clements checklist of birds of the world. https://www.birds.cornell.edu/clementschecklist/introduction/updateindex/october-2022.

Crowe, T. M., Keith, G. S. & Brown, L. H. 1986. Galliformes. Pp. 24–75 *in* Urban, E., Fry, C. H. & Keith, G. S. (eds.) *The birds of Africa*, vol. 2. Academic Press, London.

Crowe, T. M., Mandiwana-Neudani, T. G., Little, R. M. & Bowie, R. C. K. 2022. Why the taxonomy of francolins and spurfowls (Galliformes, Phasianidae) needs revision: responses to Hustler (2021) and Hunter et al. (2021a,b). *Ostrich* 93: 280–291.

Denzer, W. & Kaiser, H. 2023. Naming and gaming: the illicit taxonomic practice of 'nomenclatural harvesting' and how to avoid it. *J. Zool*. 320. 161–168.

Dowsett, R. J., Aspinwall, D. L. & Dowsett-Lemaire, F. 2008. *Birds of Zambia: an atlas and handbook*. Tauraco Press, Liège.

Dowsett-Lemaire, F. & Dowsett, R. J. 2006. *The birds of Malawi*. Tauraco Press, Liège.

ISSN-2513-9894
(Online)

Gill, F., Donsker, D. & Rasmussen, P. (eds.) 2023. IOC world bird list (v13.1). doi: 10.14344/IOC.ML.13.1.

HBW & BirdLife International. 2022. *Handbook of the birds of the world* and BirdLife International digital checklist of the birds of the world. Version 7. https://datazone.birdlife.org/species/taxonomy.

Hall, B. P. 1963. The francolins, a study in speciation. *Bull. Brit. Mus. (Nat. Hist.)* 10: 105–204.

Harrison, J. A., Allan, D. G., Underhill, L. G., Herremans, M., Tree, A. J., Parker, V. & Brown, C. J. 1997. *The atlas of southern African birds*, vol. 1. BirdLife South Africa, Johannesburg.

Howells, W. W. 1985. The birds of the Dande Communal Lands, middle Zambezi Valley, Zimbabwe. *Honeyguide* 31: 26–48.

del Hoyo, J. & Collar, N. J. 2014. *HBW and BirdLife International illustrated checklist of the birds of the world*, vol. 1. Lynx Edicions, Barcelona.

Hunter, N., Turner, D., Borrow, N., Finch, B., Kennedy, A. S., Stevenson, T., Baker, N. & Redman, N. 2021. Reflections concerning spurfowl and francolin species recommendations contained in Mandiwana-Neudani et al. (2019a and 2019b). *Ostrich* 92: 156–161.

Hustler, K. 1986. A revised checklist of the birds of Hwange National Park. *Honeyguide* 32: 68–87.

Hustler, K. 2021. Taxonomic revision of francolins – reflections from a central African perspective *Ostrich* 92: 324–328.

Hustler, K. & Marshall, B. 2022. Should Stuhlmann's Francolin be added to the Zimbabwean list? *Honeyguide* 68(2): 38–42.

Irwin, M. P. S. 1981. *The birds of Zimbabwe*. Quest, Harare.

Little, R. M. 2005a. Coqui Francolin. Pp. 62–63 *in* Hockey, P. A. R., Dean, W. R. J. & Ryan, P. G. (eds.) *Roberts—birds of southern Africa*. Seventh edn. Trustees of the John Voelcker Bird Book Fund, Cape Town.

Little, R. M. 2005b. Red-necked Spurfowl. Pp. 73–74 *in* Hockey, P. A. R., Dean, W. R. J. & Ryan, P. G. (eds.) *Roberts—birds of southern Africa*. Seventh edn. Trustees of the John Voelcker Bird Book Fund, Cape Town.

Little, R. M. 2005c. Shelley's Francolin. Pp. 66–67 *in* Hockey, P. A. R., Dean, W. R. J. & Ryan, P. G. (eds.) *Roberts—birds of southern Africa*. Seventh edn. Trustees of the John Voelcker Bird Book Fund, Cape Town.

Little, R. 2016. *Terrestrial gamebirds & snipes of Africa: guineafowls, francolins, spurfowls, quails, sandgrouse & snipes*. Jacana Media, Auckland Park.

Louette, M., Meirte, D., Louage, A. & Reygel, A. 2010. *Type specimens of birds in the Royal Museum for Central Africa, Tervuren*. Royal Museum for Central Africa, Tervuren.

Macdonald, J. D. 1957. *Contribution to the ornithology of western South Africa - results of the British Museum (Natural History) South West Africa Expedition, 1949-50*. Trustees of the Brit. Mus. (Nat. Hist.), London.

Mackworth-Praed, C. W. 1922. A short systematic review of the African francolins. *Ibis* (11)4: 105–136.

Mackworth-Praed, C. W. & Grant, C. H. B. 1952. *Birds of eastern and north eastern Africa*, vol. 1. Longmans, London.

Mackworth-Praed, C. W. & Grant, C. H. B. 1963. *Birds of the southern third of Africa*, vol. 1. Longmans, London.

Mandiwana-Neudani, T. G. 2013. Taxonomy, phylogeny and biogeography of francolins ('*Francolinus*' spp.) Aves: order Galliformes Family: Phasianidae. Ph.D. thesis. Univ. of Cape Town.

Mandiwana-Neudani, T. G., Bowie, R. C. K., Hausberger, M., Henry, L. & Crowe, T. M. 2014. Taxonomic and phylogenetic utility of variation in advertising calls of francolins and spurfowls (Galliformes: Phasianidae). *Afr. Zool*. 49: 54–82.

Mandiwana-Neudani, T. G., Little, R. M., Crowe, T. M. & Bowie, R. C. K. 2019a. Taxonomy, phylogeny and biogeography African spurfowls Galliformes, Phasianidae, Phasianinae, Coturnicini: *Pternistis* spp. *Ostrich* 90: 145–172.

Mandiwana-Neudani, T. G., Little, R. M., Crowe, T. M. & Bowie, R. C. K. 2019b. Taxonomy, phylogeny and biogeography of 'true' francolins: Galliformes, Phasianidae, Phasianinae, Gallini; *Francolinus*, *Ortygornis*, *Afrocolinus* gen. nov., *Peliperdix* and *Scleroptila* spp. *Ostrich* 90: 191–221.

Mandiwana-Neudani, T. G., Crowe, T. M., Little, R. M. & Bowie, R. C. K. 2021. The importance of adopting an integrative taxonomy framework in species delimitation: response to Hunter et al. (2021). *Ostrich* 92: 162–167.

McGowan, P. J. K. 1994. Family Phasianidae (pheasants and partridges). Pp. 434–479 *in* del Hoyo, J., Elliott, A. & Sargatal, J. (eds.) *Handbook of the birds of the world*, vol. 2. Lynx Edicions, Barcelona.

Mills, M. & Melo, M. 2013. *The checklist of the birds of Angola*. Associação Angolana para Aves e Natureza (Aves Angola) and Birds Angola, Luanda.

Ogilvie-Grant, W. R. 1893. *Catalogue of the birds in the British Museum*, vol. 22. Trustees of the Brit. Mus. (Nat. Hist.), London.

Parker, V. 1999. *The atlas of the birds of Sul do Save, southern Mozambique*. Endangered Wildlife Trust, Johannesburg.

Parker, V. 2005. *The atlas of the birds of central Mozambique*. Endangered Wildlife Trust, Johannesburg.

Penry, E. H. 1994. *The bird atlas of Botswana*. Univ. of Natal Press, Pietermaritzburg.

Peters, J. L. 1934. *Check-list of birds of the world*, vol. 2. Mus. Comp. Zool., Cambridge, MA.

Reichenow, A. 1889. Uber einevogelsammlung aus ostafrika. *J. Orn*. 37: 264–286.

Reichenow, A. 1900–01. *Die Vögel Afrikas*, Bd. 1(2). J. Neumann, Neudamm.

ISSN-2513-9894
(Online)

Roberts, A. 1932. Preliminary descriptions of sixty-six new forms of South African birds. *Ann. Trans. Mus*. 15: 21–34.
Schouteden, H. 1971. *La faune ornithologique de la Province du Katanga*. Doc. Zool. 17. Musée Royal de l'Afrique Centrale, Tervuren.
Skead, C. J. 1973. Zoo-historical gazetteer. *Ann. Cape Prov. Mus*. 10: 1–259.
Snow, D. W. 1978. *An atlas of speciation in African non-passerine birds*. Trustees of the Brit. Mus. (Nat. Hist.), London.
Swofford, D. L. 2002. *PAUP*: analysis using parsimony*, version 4. Sinauer Associates, Sunderland, MA.
White, C. M. N. 1965. *A revised checklist of African non-passerine birds*. Government Printer, Lusaka.

*Address*: 20 Dome Street, Georgetown, Invercargill, New Zealand, e-mail kitvix@orcon.net.nz

ISSN-2513-9894
(Online)