Comments on the status of subspecies in the red-billed hornbill (*Tockus erythrorhynchus*) complex (Aves: Bucerotidae), with the description of a new taxon endemic to Tanzania

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The status of subspecies within the red-billed hornbill (*Tockus erythrorhynchus*) complex is discussed in the light of recent research that has described a new subspecies in West Africa with black circumorbital skin and a brown iris, and has shown that two other subspecies in Namibia behave as separate species . Another new subspecies, *T. e. ruahae,* also with black circumorbital skin but with a yellow iris, is described from central and southern Tanzania. This brings to at least five the taxa of red-billed hornbill that are clearly separable on the colour of the facial plumage, and colour of the circumorbital skin and iris. A sixth undescribed form from Kenya is confirmed by photographs. Based on this information and a preliminary molecular analysis of the mitochondrial DNA cytochrome *b* region, we recommend that each subspecies of red-billed hornbill should be recognized as a separate species until evidence to the contrary is provided.

Keywords: Bucerotidae, *Tockus erythrorhynchus, T. e. ruahae,* Subspecies, Tanzania, New Subspecies.

INTRODUCTION

The red-billed hornbill (*Tockus erythrorhynchus*) is the most studied hornbill in Africa (Kemp and Kemp, in press). It has been the subject of four post-graduate theses from across its entire range (Kemp, 1976; Wambuguh, 1987; Diop, 1993; Delport, 2001) that included all three subspecies then recognized in systematic revisions of the species (Sanft, 1960; Kemp and Crowe, 1985; Fry *et al.,* 1988; Kemp, 1995). These were the nominate *T. e. erythrorhynchus* (Temminck, 1823), across the savannas of western, northern and eastern sub-Saharan Africa, *T. e. rufirostris* (Sundevall, 1850), on the savannas of southern Africa, and *T. e. damarensis* (Shelley, 1888), on the more arid savannas of southwestern Africa (Fig. 1). The most widespread southern taxon, *T. e. rufirostris,* has sometimes been divided further into *T. e. ngamiensis* Roberts, 1932, in the western sector of its range and *T. e. degens* Clancey, 1964, in the eastern sector. However, these divisions appear to be based on geographical variations in size that grade from largest in the west (Roberts, 1935) to smallest in the east (Clancey, 1964), rather than on any geographically discrete set of characters. These two taxa have been excluded subsequently as valid subspecies (Sanft, 1960; Kemp and Crowe, 1985; Fry *et al.*, 1988; Kemp, 1995).

It was a surprise, therefore, when a pair of red-billed hornbills that belonged to an unrecognized form was observed alive by A.C.K. in the Jurong Bird Park, Singapore, in 1991. Their most unusual feature was that the bare circumorbital skin was black, whereas it had been recorded only as a pale colour (yellow or pink) in all previous descriptions of the species (Sanft, 1960; Kemp 1995). The label on the cage indicated that the pair came from South Africa, although enquiries to the Park staff indicated that their origin was uncertain (Kim May Nyunt, pers. comm.). A few years later, S. Stolberger (*in litt.,* 1994) also recognized that the red-billed hornbills in Ruaha National Park, Tanzania, differed from the general descriptions in having black circumorbital skin (Glen and Stolberger, 2001). Further investigation of dry museum specimens, on which the dark circumorbital skin can be distinguished, led to the recognition of not one but two new forms with black circumorbital skin (Kemp, 1995), both within what was previously considered as the range of the nominate subspecies. One group of specimens came from West Africa and has been described recently as *T. e. kempi* Tréca & Erard, 2000 (Fig. 1), and another from Tanzania which is described here.

In the meanwhile, the two southern subspecies, *T. e. rufirostris* and *T. e. damarenis,* had been the subject of a detailed behavioural, morphological and molecular study by W.D., especially along a hybrid zone that was known to exist through north-central Namibia (Sanft, 1960; Delport, 2001). The

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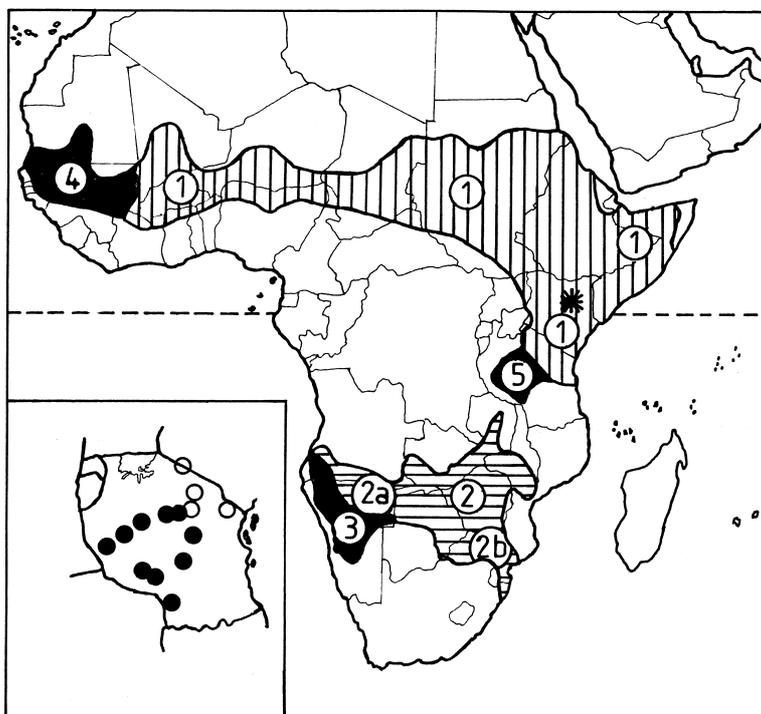[†]Present address: 8 Boekenhout Street, Navors, Pretoria, 0184 South Africa.

Fig. 1

Map of sub-Saharan Africa showing the distribution of each of the five discrete taxa of red-billed hornbill. **1**, North African red-billed hornbill *T. (erythrorhynchus) erythrorhynchus*; **2**, Southern African red-billed hornbill *T. (e.) rufirostris,* including **2a**, *T. e. ngamiensis* and **2b**, *T. e. degens*; **3**, Damaraland red-billed hornbill *T. (e.) damarensis*; **4**, West African red-billed hornbill *Tockus (e.) kempi*; and **5**, Tanzanian red-billed hornbill *T. (e.) ruahae.* The asterix indicates the location of the Samburu National Park, Kenya, where a sixth, undescribed taxon has been recorded photographically. The inset shows the outline of Tanzania with some individual distribution records marked for *T. (e.) ruahae* (solid circles) and *T. (e.) erythrorhynchus* (open circles).

results of this study indicated that the two subspecies behaved as good species and it was recommended that they should be recognized as such in future (Delport, 2001; Delport *et al.,* in press).

In this paper we aim to describe the new taxon of black-faced, red-billed hornbill from Tanzania and to recommend (supported by preliminary molecular results) that each subspecies of red-billed hornbill be recognized as a full species until further evidence to the contrary is presented.

RED-BILLED HORNBILL TAXONOMY

The three previously recognized subspecies of the red-billed hornbill have already been described in detail in various publications (Sanft, 1960; Fry *et al.*, 1988; Kemp and Crowe, 1985; Kemp, 1995; Delport, 2001). Recently, the nominate subspecies *T. e. erythrorhynchus,* within which the two newly recognized black-faced forms have been discovered, was also reviewed in detail (Tréca and Erard, 2000). This was necessary to accommodate the first of these new taxa, *T. e. kempi,* and to designate a new type specimen for *T. e. erythrorhynchus,*

sensu stricto, from within its newly restricted range (Tréca and Erard, 2000). *T. e. kempi* extends from Senegal eastwards to Mali, the nominate taxon, *sensu stricto,* from Mali eastwards to Somalia and south to northeastern Tanzania, while so far the new taxon described below has been recorded only from central and southern Tanzania (Fig. 1).

These three northern taxa are apparently separated from the southern *T. e. rufirostris,* by areas of tall miombo or *Brachystegia* woodland in northern Malawi and northeastern Zambia. *T. e. rufirostris* extends south from this woodland to northern South Africa and east to northern Namibia and southern Angola (Fig. 1). In northwestern Namibia, its distribution adjoins the restricted range of *T. e. damarensis,* with a narrow zone where they meet, coexist sympatrically and sometimes hybridize (Sanft, 1960; Delport 2001; Fig. 1).

The most obvious differences between adults of each of the subspecies are in the colours of the facial feathers (streaked with grey or pure white), iris (yellow or dark brown) and bare circumorbital skin (pale pink/yellow or black) (Table 1). The new taxon

Table 1
The basic colour and size differences between the described taxa of red-billed hornbill.

Taxon	Facial feathers	Eye colour	Skin colour	Male wing length mean (range, sample), mm
T. e. kempi, West Africa	White	Brown	Black	179 (171–185, $n = 40$)[a]
T. e. erythrorhynchus, North Africa	White	Brown	Pink	179 (172–189, $n = 16$)[a]
T. e. erythrorhynchus, East Africa	White	Brown	Pink	183 (170–192, $n = 35$)[a]
New Tanzanian taxon, *T. e. ruahae*	White	Yellow	Black	178 (170–185, $n = 7$)[b]
T. e. ngamiensis, Southwest Africa	Grey	Yellow	Pink	195 (194–195, $n = 2$)[c]
T. e. rufirostris, Southern Africa	Grey	Yellow	Pink	188 (177–202, $n = 32$)[d]
T. e. degens, Southeast Africa	Grey	Yellow	Pink	172 (166–179, $n = 10$)[e]
T. e. damarensis, Southwest Africa	White	Brown	Pink	195 (186–203, $n = 13$)[d]

Measurements taken from:
[a]Tréca and Erard (2000);
[b]Kemp (1995), this paper;
[c]Roberts (1935);
[d]Sanft (1960), Kemp (1995);
[e]Clancey (1964).

from Tanzania, described below, has a yellow iris combined with black circumorbital skin. Juvenile birds of all subspecies are excluded from the sample since they all have some grey feathers on the face and neck, a brown iris and pale pink circumorbital skin.

MATERIAL AND METHODS

Specimens and sightings

An adult male and female red-billed hornbill, but not members of a mated pair, were collected by Robert Glen just outside the southern boundary of the Ruaha National Park, Tanzania. These specimens are described here in detail. The male is designated as the type specimen and together they form the type series that is housed in the Transvaal Museum, Pretoria, South Africa. Other specimens, preserved as dried study skins in natural history museums, have been examined and measured wherever possible by A.C.K. (using the methods of Sanft, 1960; Tréca and Erard, 2000), or else examined by the resident curators for dark or light circumorbital skin and, where noted on the label, for iris colour and collecting locality. The series of red-billed hornbills in the following museums have been examined: Transvaal Museum (TM), Durban Natural Science Museum (DNSM), American Museum of Natural History (AMNH), British Museum (Natural History) (BMNH), Naturhistorische Museum Wien (NMW), National Museum of Kenya (NMK), Museum Alexander Koenig, Bonn (MAK), Zoologisches Museum der Humboldt-Universität zu Berlin (ZMB), Los Angeles County Museum (LACM) and the Royal Museum of Scotland, Edinburgh (RMS).

An appeal for sightings, photographs and sound or video recordings of red-billed hornbills from anywhere in Africa was also sent out for publication in various general bird-watching magazines in 1992 (e.g. Kemp, 1992, in *Scopus,* and also to *Malimbus, Birding World, Birdwatching* and *Dutch Birding*). All records received from readers of these magazines were then examined for any information that determined both taxonomic identification and geographical location.

Preliminary molecular analyses

The aim of the analyses was to determine if genetic differences between subspecies of red-billed hornbills were equivalent to those between recognized species of other birds. Fresh blood samples were obtained from *T. e. rufirostris* and *T. e. damarensis,* and from the closely related Monteiro's hornbill *T. monteiri* (Hartlaub, 1865), as an outgroup (Kemp, 1994; Delport, 2001). These samples were stored at 4°C in a blood storage buffer (0.1 M Tris-HCl, 0.04 M EDTA Na$_2$, 1.0 M NaCl, 0.5% SDS). A fresh tissue specimen of *T. e. kempi* was obtained from The Gambia by Clive Barlow and stored at –20°C. Finally, foot scrapings of the *T. e. ruahae* type specimen were obtained from the Transvaal Museum collection. Complete genomic DNA was extracted from each of these samples using either a standard phenol-chloroform method (for blood or tissue) or the Qiagen DNeasy kit, with modifications for foot scrapings as suggested by Mundy *et al.* (1997). Approximately 50 ng of extracted DNA were used as the template in a polymerase chain reaction (PCR), performed in a total volume of 50 μl in 200 μl microcentrifuge tubes. In addition to the DNA template, the reaction mix consisted of 2 mM MgCl$_2$, 5 μl 10× reaction buffer, 0.2 mM of each of four nucleotides, 1.5 U of Supertherm$^®$ DNA polymerase and 12.5 picamol of each of two primers. The primers L14841 (5′ CCA TCC AAC ATC TCA GCA TGA TGA AA 3′, Kocher *et al.*, 1989) and H15499 (5′ GGT TGT TTG AGC CTG ATT C 3′, Avise *et al.*, 1994) were used to amplify approx-

imately 650 bases at the 5′ end of the mitochondrial DNA (mtDNA) cytochrome *b* region. A Geneamp® PCR System 9700 (Applied Biosystems) was used to cycle the reaction mix through the following sequence of conditions: denaturing at 94°C for 2 minutes, 35 cycles of denaturing at 94°C for 30 seconds, primer annealing at 50 °C for 30 seconds, elongation at 72°C for 90 seconds, and finally an extended elongation period of 10 minutes at 72°C. The amplified PCR products were then purified with the High Pure™ PCR Product Purification kit (Boehringer Mannheim). Dye-terminator cycle sequencing (Big Dye DNA sequencing kit, Applied Biosystems) of the purified PCR products was performed according to the manufacturer's instructions, using the same PCR primers. Finally, sequences of both the heavy and light strands for each individual were determined with an ABI377 automated sequencer (Applied Biosystems).

Sequences were thereafter imported into Sequence Navigator (Applied Biosystems) and proofread. Consensus sequences of the 5′ region of the cytochrome *b* gene were aligned in ClustalX version 1.8 for Windows (Thompson *et al.*, 1997). Aligned sequences were imported into MEGA2 (Kumar *et al.*, 2000) where phylogenetic analyses were performed. First, the within- and between-sub-species sequence divergence was calculated using the Kimura two-parameter model of DNA sequence evolution. The within-subspecies sequence divergence was only calculated for two subspecies, *T. e. damarensis* and *T. e. rufirostris,* since more than one individual was sequenced only for these two subspecies. Second, a neighbour-joining phylogenetic tree was constructed, again with the Kimura two-parameter model of DNA sequence evolution. Statistical support of the phylogenetic hypothesis was determined using the bootstrap procedure with 1000 replicates.

RESULTS

Tockus erythrorhynchus ruahae subspec. nov.

DIAGNOSIS. Similar in plumage colour and size to nominate *T. e. erythrorhynchus, sensu stricto,* that occurs parapatrically to the north in northeastern Tanzania and Kenya, and also has white facial and breast plumage with light grey streaks only on the ear coverts. Clearly differentiated, when adult, by the black, bare circumorbital skin (not pale pink or yellow) and by the yellow iris (not brown). Allopatric from *T. e. rufirostris* that occurs to the south in Malawi and Zambia, which is also similar in size and has a yellow iris, but which has pink circumorbital skin and obvious grey streaks on the face, ear coverts, neck and upper breast.

DESCRIPTION. *Adult male*: plumage with dark grey forehead, crown and nape. White superciliary stripe and sides of face, including ear coverts, and all-white neck, breast, abdomen and thighs. Small area of black feathers around edge of gape. Back dark grey-brown with white stripe down centre, leading into all-dark grey-brown rump. Upperwing coverts black with large white terminal spots, especially over mainly white secondaries S5–6. Primaries and outer secondaries S2–4 black with white spot in centre, spots on secondaries with white extension down leading edge of each feather, but adjacent innermost primary P1 and outermost secondary S1 all black. Inner secondary S7 black with distal half white, remainder of inner secondaries S8–10 sooty brown. Central pairs of rectrices R1–2 all black, outer pairs with increasing white from distal one-third on R3 to almost all white on R5. Irregular black patch at inner edge of white on R4, reduced to small spot in centre of white on R5. Bill red, with base pale horn-coloured to white, leading into black centre half on sides of lower mandible. Bare skin around eye and at base of bill black, bare patches of skin on either side of throat pale pink, iris pale yellow, legs and feet black with grey soles. *Adult female*: plumage similar to adult male, but bill all-red, without black mark at base of lower mandible. *Juvenile*: plumage similar to adult, but white areas with slight grey tinge. Bill with smaller area of black at base of lower mandible than in adult male, apparently in both sexes. Circumorbital skin pale pink and iris dark brown.

DISTRIBUTION. At present known only from central and southern Tanzania (Fig. 1), with specimen records from the southern border of the Ruaha National Park (type series detailed below), Ussuangu steppes at the east end of Lake Rukwa (ZMB 9627), Wembere (ZMB 9623, ZMB 9666.47, ZMB 9666.50), Kakoma (ZMB 9630), Maronga near Mkali (ZMB 9632), Yanda on eastern shore of Lake Rukwa (ZMB 20.8616), Lake Rukwa (NMK 8487), Nyangwa River 10 km southeast of Tabora (NMK no number, Louisiana University Museum of Zoology collection number 5350/498), Ugombola (NMW 42483), Kidete near Dodoma (AMNH 202549, two specimens), Mawere (AMNH 428640, two specimens), Mwanansomano's 30 miles south of Tabora (AMNH 414130, AMNH 414132, AMNH 414133), north of Lake Niasa (=Malawi) (BMNH 1905.1.23.97) and Mpimbwe in Mpinda District (BMNH 1950.2.19), plus sightings from all over Ruaha National Park (D. Turner, *in litt.*; R. Glen, *in litt.*) and Katavi National Park (R. Glen, *in litt.*). The exact boundary with the nominate subspecies in northeastern Tanzania is not known at this stage, but specimen records of nominate birds are available for various localities in

Table 2

Within- and between-subspecies sequence diversity estimates calculated in MEGA2 (Kumar *et al.,* 2000) using the Kimura two-parameter model of sequence evolution. Within-subspecies estimates of sequence diversity estimates appear in bold face on the diagonal, whereas between-subspecies estimates appear on the lower half-matrix. Estimates of within-subspecies sequence diversity are shown only for *T. e. damarensis* and *T. e. rufirostris* since more than one individual was sequenced for only these two subspecies.

	1	2	3	4	5
1. *T. e. damarensis*	**0,001**				
2. *T. e. rufirostris*	0,013	**0,005**			
3. *T. e. ruahae*	0,038	0,040			
4. *T. e. kempi*	0,030	0,032	0,027		
5. *T. monteiri*	0,062	0,064	0,075	0,061	

Kenya while those from Tanzania include a photograph from Mkomasi Game Reserve (R. Glen, *in litt.*) and sightings from Meru National Park (R. Glen, *in litt.*), Tarangire National Park (P. Beaumont, pers. comm.) and Mpimbare (Dr Michael, *in litt.*)

ETYMOLOGY. Named for the Ruaha National Park and basin of the Ruaha River in central Tanzania, from where the taxon was first noted in the field by Susan Stolberger and from where the type series was collected (Glen and Stolberger, 2001).

MATERIAL EXAMINED. Specimens and photographs detailed under Distribution above.
Type material: *Holotype, adult male*: southern border, Ruaha National Park, Tanzania, 1700 m a.s.l., 1 November 1998, coll. Robert Glen, Transvaal Museum accession number TM 78009. Wing length 177 mm, tail length 198 mm, bill length 70 mm, tarsus length 44 mm, mass 128 g. *Paratype, adult female*: southern border, Ruaha National Park, Tanzania, 990 m a.s.l., 1 November 1998, coll. Robert Glen, TM 78008. Wing length 168 mm, tail length 184 mm, bill length 64 mm, tarsus length 43 mm, mass 125 g. The stomach contents of the holotype contained insect remains, including ants, and seeds and of the paratype insect remains, including a beetle larva and seeds.
Adult measurements (BMNH 1950.2.19, BMNH 1905.1.23.97, NMW 42483, TM 78008, TM 78009, ZMB 20.8616, ZMB 9623, ZMB 9627, ZMB 9630, ZMB 9632, ZMB 9666.47, ZMB 9666.50), mean (range) of lengths in mm: male ($n = 8$), wing 178 (170–185); tail 196 (185–212), bill 74 (65–81), tarsus 42 (38–46); female ($n = 4$), wing 166 (163–168), tail 186 (181–192), bill 70 (64–73), tarsus 40 (38–43).

Molecular results

The sequence divergence estimates indicate that variation of the cytochrome *b* gene within subspecies (0,1 and 0,5% for *T. e. damarensis* and *T. e. rufirostris,* respectively) is notably less than that between subspecies (Table 2). The comparisons between the subspecies *T. e. rufirostris* and *T. e. damarensis* are most similar, with a sequence divergence of 1,3%. The subspecies *T. e. rufirostris* and *T. e. ruahae* are least similar, with a sequence divergence of 4,0%. The sequence divergences of the various *T. erythrorhynchus* subspecies from the related outgroup species *T. monteiri* range from 6,1–7,5%. The phylogenetic analysis indicates that specimens from *T. e. rufirostris* and *T. e. damarensis* form separate monophyletic groups with good bootstrap support (Fig. 2), even though these two subspecies apparently are related more closely to one another than to any other subspecies. Although only one individual was sequenced for both *T. e. ruahae* and *T. e. kempi,* it is clear that these two subspecies are more closely related to one another than either is to *T. e. rufirostris* or *T. e. damarensis.* This separate northern grouping is again supported by a high bootstrap value. Unfortunately, no DNA could be extracted from the available specimens of nominate *T. e. erythrorhynchus, sensu stricto.*

DISCUSSION

Differences in visual and vocal signals, such as colours of signal areas, forms of displays or structures of calls, are expected to play an important role in mate recognition (Paterson, 1985; Ferguson, 1999). Accurate mate recognition has been proposed as an essential component for the stability and cohesion of genetic and phenotypic patterns within populations, while differences in mate recognition patterns between populations are also invoked in divergence and the process of speciation (Templeton, 1989, 1998; Ferguson, 1999). Furthermore, congruence between differences in signals, morphology and genetic distance are also important when making cladistic decisions on the systematic and taxonomic limits of species (Cracraft, 1989; Crowe, 1999).

Two new subspecies of red-billed hornbill, *T. e. kempi* and *T. e. ruahae,* have been recognized only recently, primarily on the basis of consistent differences in the colours of two important adult signal areas, the bare circumorbital skin and the iris.
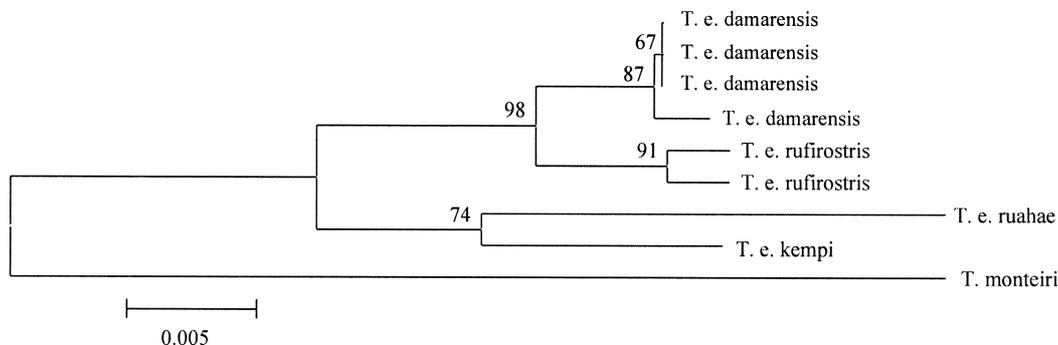
Fig. 2

Phylogenetic analysis of the sequence data for *c.* 650 bases of the mtDNA cytochrome *b* region of each red-billed hornbill taxon, using the programme MEGA2 (Kumar *et al.*, 2000) to construct a neighbour-joining phylogenetic tree with the Kimura two-parameter model of DNA sequence evolution. Numbers at nodes indicate bootstrap values expressed as percentage of 1000 simulations, whereas scale indicates sequence divergence as calculated using the Kimura two-parameter model of DNA sequence evolution.

For each of the five taxa of red-billed hornbill now recognized, apart from the obvious and consistent differences mentioned above, there are also some differences in size (Sanft 1960; Kemp, 1995; Tréca and Erard, 2000; Table 1), in the tones and extent of black and white areas in the plumage, especially on the rectrices and remiges, and in details of the main loud calls and territorial displays. These differences have not been examined in detail for an adequate sample of specimens from all taxa, especially not for the new taxon described above nor for an anomalous form from Kenya that is described below. We recommend further detailed study on these aspects for all subspecies.

Similar separation of taxa has also been proposed for the closely related yellow-billed hornbill species, *T. flavirostris* (Rüppell, 1835), and *T. leucomelas* (H. K. Lichtenstein, 1842), from eastern and southern Africa, respectively, that also involves black versus pink circumorbital skin, yellow iris colour and differences in calls, (Kemp and Crowe, 1985; Kemp 1995). *Tockus flavirostris* and its close relative *T. deckeni* (Cabanis), 1869, (Kemp, 1994) coincidentally both occur in east and northeast Africa, both having black circumorbital skin, while the iris is yellow in the former and brown in the latter.

We propose that consistent differences in the colour of signal areas between the geographically-discrete populations of the red-billed hornbill, currently named as subspecies, deserve their recognition as at least five different species (Fig. 1 and caption). Detailed work on two of the subspecies suggests that they deserve specific separation as the Damaraland red-billed hornbill, *T. damarensis,* and the southern African red-billed hornbill, *T. rufirostris* (Delport, 2001; Delport *et al.*, in press). This decision is supported even though they differ only in size, the colour of the facial plumage and iris,

and have the least molecular separation for the mtDNA cytochrome *b* gene for any pair of subspecies. Their separation is further supported by differences in calls and displays, despite the existence of a narrow zone of asymmetrical hybridization between the populations (Delport, 2001).

Subjective differences in calls and displays have also been reported for the three northern populations that are currently recognized as subspecies (Delport, 2001), while preliminary measures of genetic distance between all five subspecific populations are similar to values between recognized species in other avian taxa (Johns and Avise, 1998). We recommend that, since the northern subspecies are even more divergent than the two southern subspecies that have been studied in detail, they should all be considered as separate species by extrapolation.

Furthermore, apart from the evidence presented in this paper, we support the separation of the discrete populations as full species on pragmatic grounds, so that information about their biology is not conflated, confused and applied inappropriately to their future study and conservation. Overall, we propose that the subspecies of red-billed hornbill be considered as five separate species until evidence to the contrary is provided.

The range of *T. e. ruahae,* as currently known, is restricted to the basin between the mountains and lakes of the main Albertine Rift Valley in the east and the Eastern Arc Mountains in the west. A number of bird taxa have been described as endemic to the montane forests on either side (Rodgers and Humewood, 1982; Lovett and Wasser, 1993) but few are recognized from within the rain shadow to the west of the Eastern Arc Mountains and drier savanna that this produces. This description of a taxon endemic to the dry basin between the rift

mountains suggests that other distinctive taxa might also be expected from this region.

During the course of this investigation, four photographs were also submitted of nominate adult *T. e. erythrorhynchus, sensu stricto,* that were normal in every respect, with a white face and pale circumorbital skin, except that they had a yellow iris (three males and two females, H. de Groot, *in litt.*; G. Langsbury, *in litt.*; C. and A. Parnell, *in litt.*; L. Vinceguerra, *in litt.*). All photographs were taken in Samburu National Park, northeastern Kenya. Other sightings of red-billed hornbills with a yellow iris were reported for elsewhere in Kenya (Dr Michael, *in litt.*; D. Turner, *in litt.*), but more details are required. This suggests the possibility of a further, undescribed, sixth taxon of red-billed hornbill, apparently endemic to Kenya. Further study of this and other populations that comprise the widespread complex of the red-billed hornbill offer an excellent opportunity to understand patterns of speciation that might have occurred across the savannas of sub-Saharan Africa.

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REFERENCES

AVISE, J. C., NELSON, W. S. and SIBLEY, C. S., 1994. DNA sequence support for a close phylogenetic relationship between some storks and New World vultures. *Proceedings of the National Academy of Sciences USA* **91**: 5173–5177.

CLANCEY, P. A., 1964. Miscellaneous notes on African birds XXI. A new subspecies of red-billed hornbill *Tockus erythrorhynchus* (Temminck) from the south-eastern lowlands of Africa. *Durban Museum Novitates* **7**: 130–132.

CRACRAFT, J., 1989. Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. *In*: OTTE, D. and ENDLER, J. A., eds, *Speciation and its consequences,* pp. 28–59. Sinauer, Sunderland, Massachusetts.

CROWE, T. M., 1999. Species as multifaceted entities. *In*: ADAMS, J.J. and SLOTOW, R.H. eds, *Proceedings of the 22nd International Ornithology Congress, Durban,* pp. 1490–1405. BirdLife South Africa, Johannesburg.

DELPORT, W., 2001. The taxonomic status of the Damaraland redbilled hornbill (*Tockus erythrorhynchus damarensis*). A behavioural, morphological and molecular analysis. M.Sc. thesis, University of Pretoria, Pretoria.

DELPORT, W., FERGUSON, J. W. H., BLOOMER, P. and KEMP, A. C., *in press*. When should subspecies be elevated to species? A multidisciplinary approach to determining hornbill taxonomic status. *In*: POONSWAD, P., ed., *Proceedings of the 3rd International Hornbill Workshop, Phuket, Thailand, May 2001.* Hornbill Foundation Thailand, Bangkok.

DIOP, M. S., 1993. *Eco-ethologie du petit calao à bec rouge,* Tockus (Lophoceros) erythrorhynchus *(Temminck, 1823) en zone de savanne.* Thesis, Université Cheikh Anta Diop de Dakar, Dakar.

FERGUSON, J. W. H., 1999. The significance of mate selection and mate recognition in speciation. *In*: ADAMS, N. J. and SLOTOW, R. H., eds, *Proceedings of the 22nd International Ornithological Congress, Durban,* pp. 1496–1504. Birdlife South Africa, Johannesburg.

FRY, C. H., KEITH, S. and URBAN, E. K., 1988. *The birds of Africa,* Volume III. Academic Press, London.

GLEN, R. and STOLBERGER, S., 2001. Black-faced red-billed hornbills (*Tockus erythrorhynchus*) in Ruaha National Park, south-western Tanzania. *Scopus* **21**: 62–63.

JOHNS, G. C. and AVISE, J. C., 1998. A comparative summary of genetic distances in the vertebrates from the mitochondrial cytochrome *b* gene. *Molecular Biology and Evolution* **15**: 1481–1490.

KEMP, A. C., 1976. A study of the ecology, behaviour and systematics of *Tockus* hornbills (Aves: Bucerotidae). Transvaal Museum Memoir No. 20. Transvaal Museum, Pretoria

KEMP, A. C., 1992. Request: red-billed hornbills in Africa. *Scopus* **16**: 13.

KEMP, A. C., 1994. Abstract: Congruence of phylogenies for *Tockus* hornbills (Bucerotiformes) based on behaviour, ecology, morphology, DNA hybridisation and ectoparasites. *Journal für Ornitologie* **135**: 338.

KEMP, A. C., 1995. *Bird families of the world. The hornbills*: *Bucerotiformes.* Oxford University Press, Oxford.

KEMP, A. C. and CROWE, T. M., 1985. The systematics and zoogeography of Afrotropical hornbills (Aves: Bucerotidae). *In*: SCHUCHMANN, K., ed., *Proceedings of the International Symposium on African Vertebrates,* pp. 279–324. Zoologische Forschungsinstitut und Museum Alexander Koenig, Bonn.

KEMP, A. C. and KEMP, M. I., *in press.* An overview of hornbill studies in Africa. *In*: POONSWAD, P., ed., *Proceedings of the 3rd International Hornbill Workshop, Phuket, Thailand, May 2001.* Hornbill Foundation Thailand, Bangkok.

KOCHER, T. D., THOMAS, W. K., MEYER, A., EDWARDS, S. V., PÄÄBO, S., VILLABLANCA, F. X. and WILSON, A. C., 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proceedings of the National Academy of Sciences USA* **86**: 6196–6200.

KUMAR, S., TAMURA, K. and NEI, M., 2000. *MEGA*: *molecular evolutionary genetics analysis,* version 2.0.

Pennsylvania State University, University Park, Pennsyl-vania.

LOVETT, J. C. and WASSER, S. K., eds, 1993. *Biogeography and ecology of the rain forests of eastern Africa.* Cambridge University Press, Cambridge.

MUNDY, N. I., UNITT, P. and WOODRUFF, D. S., 1997. Skin from feet of museum specimens as a non-destructive source of DNA for avian genotyping. *Auk* **114**: 126–129.

PATERSON, H. E. H., 1985. The Recognition Concept of species. *In*: VRBA, E. S., ed., *Species and speciation,* pp. 21–30. Transvaal Museum Monograph No. 4. Transvaal Museum, Pretoria.

ROBERTS, A., 1932. Preliminary descriptions of sixty-six new forms of South African birds. *Annals of the Transvaal Museum* **15**: 21–34.

ROBERTS, A., 1935. Scientific results of the Vernay-Lang Kalahari expedition, March to September, 1930. *Annals of the Transvaal Museum* **16**: 237–245.

RODGERS, W. A. and HOMEWOOD, K. M., 1982. Species richness and endemism in the Usambara Mountain Forests, Tanzania. *Biological Journal of the Linnean Society* **18**: 197–242.

SANFT, K., 1960. Bucerotidae (Aves/Upupae). *Das Tierreich* **76**:1–176.

SHELLEY, G. E., 1888. On the hornbills of the Ethiopian Region. *Ibis* **(3)2**: 281–308.

SUNDEVALL, C. J., 1850. *Öfversicht Konglijk Vetenskap-Akademiens Förhandlingar, Stockholm* **7**: 108.

TEMMINCK, C. J., 1823. *Planches colorées.* II. Livraison 36. Espèce 19. J. C. Sepp, Amsterdam.

TEMPLETON, A. R., 1989. The meaning of species and speciation: a genetic perspective. *In*: OTTE, D. and ENDLER, J. A., eds, *Speciation and its consequences,* pp. 3–27. Sinauer, Sunderland, Massachusetts.

TEMPLETON, A. R., 1998. Species and speciation: geogra-phy, population structure, ecology, and gene trees. *In*: HOWARD, D. J. and BERLOCHER, S. H., eds, *Endless forms*: *species and speciation,* pp. 32–43. Oxford University Press, Oxford.

THOMPSON, J. D., GIBSON, T. J., PLEWNIAK, F., JEANMOUGIN, F. and HIGGINS, D. G., 1997. The ClustalX windows interface: flexible strategies for multi-ple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* **24**: 4876–4882.

TRÉCA, B. and ERARD, C., 2000. A new subspecies of the red-billed hornbill *Tockus erythrorhynchus* from West Africa. *Ostrich* **71** (3&4): 363–366.

WAMBUGUH, O. J. G., 1987. Report on the breeding biology of the red-billed hornbill (*Tockus erythrorhynchus*) in Tsavo National Park (East). *Occasional Research Paper of the Wildlife Conservation and Management Department,* Nairobi, Kenya.