

Short title: Taxonomy, phylogeny and biogeography of African spurfowls

Taxonomy, phylogeny and biogeography of African spurfowls (Galliformes, Phasianidae, Coturnicinae, *Pternistis* spp.)

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Abstract

During much of the 20th Century, partridge/quail-like, Afro-Asian phasianine birds referred to commonly as African spurfowls, francolins and/or partridges had a tortuous taxonomic history. Because of striking autapomorphic differences in plumage, vocalizations and ecology in some of these taxa, as many as nine genera and nearly 200 clinal and/or idiosyncratic subspecies, embedded within a polyphyletic *Perdicinae*, were recognized. In 1963, two clades, 28 ‘francolin’ and ‘spurfowl’ species (*fisante* in Afrikaans) and 13 Afro-Asiatic ‘francolins’ and ‘partridges’ (*patryse* in Afrikaans), were combined into a single genus (*Francolinus*) – the largest within the Galliformes – comprising about 100 subspecies. Furthermore, *fisante* and *patryse* were partitioned into several unnamed “Groups” and four “Unplaced” species. Here, we use morphological, behavioural and DNA evidence to produce: a

comprehensive revision of the taxonomy and phylogeny of the *fisante* clade; a stable classification system for its component taxa; and hypotheses vis-à-vis eco-biogeographical processes that promoted their speciation and cladogenesis. We shift *Francolinus* spp. sensu stricto (members of the Spotted Group) and the Unplaced ‘*Francolinus*’ *gularis* from the *fisante* clade to the *patryse* [discussed in Mandiwana-Neudani et al., in review]. An Unplaced *fisante*, ‘*F.*’ *nahani*, is linked with *Ptilopachus petrosus* (another African endemic ‘partridge’) within the Odontophoridae (New World ‘Quails’). We recognize 25 species of *fisante* (hereafter spurfowls), including seven with subspecies. They comprise 34 terminal taxa placed within a single genus, *Pternistis*, sister to *Ammoperdix* and *Perdicula* spp., *Coturnix* ‘quails’ and *Alectoris* ‘partridges’, within the now monophyletic Coturnicinae. Only one of four putative Groups of spurfowls, the Bare-throated Group, is monophyletic. The other three Groups (Montane, Scaly and Vermiculated) are para- or polyphyletic. Several species pairs of spurfowls, most notably *P. afer* and *cranchii*, hybridize in para/sympatry. One Bare-throated spurfowl, *P. rufopictus*, may be the product of stabilized hybridization between *P. afer* and/or *cranchii* and *P. leucoscepus*.

Introduction

During much of the 20th Century, there was little consensus relating to the taxonomy and phylogeny of Afro-Asian quail and partridge-like galliforms within the Phasianidae, variously commonly known as francolins, spurfowls and/or partridges. As many as nine genera [1] and nearly 200 clinal and/or idiosyncratic subspecies [2], embedded within a polyphyletic *Perdicinae* [3] were recognized. In 1963, Mrs B.P. ‘Pat’ Hall comprehensively revised the taxonomy of many of these taxa [2]. She argued convincingly that they should be combined within a single ‘mega-genus’, *Francolinus*, comprising 41 species - the largest genus in the order Galliformes and the twelfth largest in Aves [4]. Thirty-six of these species are endemic to Africa, five to Asia. Hall also synonymized many subspecies, reducing the nearly 200 to just over 100 [2].

However, literally immediately after this ‘lumping/ synonymizing’ exercise, Hall divided “francolins” into two, unnamed, putatively monophyletic major clades, comprised of eight (also unnamed and putatively monophyletic) “Groups” and four “Unplaced” species [2]. The major clades

of francolins correspond to what Afrikaans-speakers commonly refer to as *fisante* ('pheasants') and *patryse* ('partridges') [5, 6]. We deal with the *patryse* elsewhere [Mandiwana-Neudani et al., in review]. Hall's *fisante* (hereafter spurfowls) included an Asiatic Spotted Group (incorporating the nominate species *F. francolinus* and congeners), four other Groups (Vermiculated, Montane, Scaly and Bare-throated) and two Unplaced species (*nahani* and *gularis*) [2]. Morphologically, these taxa generally have: plain or plain-vermiculated back-plumage; brown/black/red tarsi with long – sometimes multiple – spurs; emit raucous, grating vocalizations; and roost/perch in large bushes or trees [6]. Members of one Group of spurfowls (the Bare-throated), differ from the others in having bare, brightly coloured skin around the eye and/or on the throat [2].

Within the spurfowls, Hall [2] recognized 28 species, which are generally sexually monomorphic, with males (and females of some taxa) of most species having at least a single (often two), long tarsal spurs. The species differ markedly in plumage, ecology, behaviour and distributional patterns [7, 8, 9].

Table 1. African spurfowl clade, groups, species, subspecies (with synonymized taxa in parentheses) and 'unplaced' species recognized by Hall followed by alternative generic epithets [2]. Common and scientific names are according to the IOC list [1].

Species Group	Common name	Scientific names (synonymized subspecies in parentheses) abandoned generic epithets below
Spotted	Black Francolin	<i>Francolinus francolinus</i> (Linnaeus, 1766) <i>francolinus</i> (<i>caucasicus</i> , <i>sarudyni</i> , <i>billypaynei</i>), <i>arabistanicus</i> , <i>henrici</i> (<i>festinus</i> , <i>bogdanovi</i>), <i>asiae</i> (<i>parkeri</i>), <i>melanotus</i>
	Painted Francolin	<i>F. pictus</i> (Jardine & Selby, 1828) <i>pictus</i> , <i>pallidus</i> , <i>watsoni</i>

	Chinese Francolin	<i>F. pintadeanus</i> (Scopoli, 1786) <i>pintadeanus</i> (<i>wellsi</i> , <i>boineti</i>), <i>phayrei</i>
Bare-throated	Red-necked Francolin	<i>Pternistis afer</i> (Müller, 1776) <i>cranchii</i> (<i>punctulate</i> , <i>nyanzae</i> , <i>manueli</i> , <i>comabtela</i> , <i>mackenziei</i>), <i>intercedens</i> (<i>bohmi</i> , <i>tornowi</i>), <i>harterti</i> <i>afer</i> (<i>palliditectus</i> , <i>cunenensis</i> , <i>benguellensis</i> , <i>angolensis</i>), <i>castaneiventer</i> (<i>krebsi</i>), <i>notatus</i> , <i>leucoparaeus</i> , <i>swynnertoni</i> , <i>humboldtii</i> , <i>melanogaster</i> (<i>itigi</i> , <i>aylwinae</i>), <i>loangwae</i> , <i>lehmanni</i>
	Swainson's Francolin	<i>P. swainsoni</i> (Smith, 1836) <i>swainsonii</i> , <i>lundazi</i> (<i>chobiensis</i>), <i>gilli</i> , <i>damarensis</i>
	Yellow-necked Francolin	<i>P. leucoscepus</i> (Gray, 1867) <i>leucoscepus</i> , <i>infuscatus</i> (<i>holtemulleri</i> , <i>muhammedbenabdullah</i> , <i>keniensis</i> , <i>kilimensis</i> , <i>tokora</i> , <i>oldowai</i>)
	Grey-breasted Francolin	<i>P. rufopictus</i> Reichenow, 1887
Montane	Erckel's Francolin	<i>P. erckelii</i> (Rüppell, 1835)

erckelii, pentoni

Djibouti Francolin *P. ochropectus* (Dorst & Jouanin, 1952)

Chestnut-naped Francolin *P. castaneicollis* Salvadori, 1888
castaneicollis, atrifrons, ogoensis, kaffanus
(patrizii)

Jackson's Francolin *P. jacksoni* O. Grant, 1891
jacksoni (gurae), pollenorum

Handsome Francolin *P. nobilis* Reichenow, 1908
nobilis, chapini

Mount Cameroon Francolin *P. camerunensis* Alexander, 1909

Swierstra's Francolin *P. swierstrai* (Roberts, 1929)
swierstrai (cruzi)

Scaly Ahanta Francolin *P. achantensis* Temminck, 1854
ahantensis, hopkinsoni

Scaly Francolin *P. squamatus* Cassin, 1857
squamatus (whitei), schuetti (tetraoninus,
zappeyi, dowashanus), maranensis
(kapitensis keneinsis chyuluensis),
usambarae, udzungwensis, doni

Grey-striped Francolin	<i>P. griseostriatus</i> O. Grant, 1890
Vermiculated Double-spurred Francolin	<i>P. bicalcaratus</i> (Linnaeus, 1766) <i>bicalcaratus (molundensis), ayesha, adamauae, thornei, ogilviegranti</i>
Heuglin's Francolin	<i>P. icterorhynchus</i> Heuglin, 1863 <i>icterorhynchus (griseus), dybowskii (emini, ugandensis)</i>
Clapperton's Francolin	<i>P. clappertoni</i> (Children & Vigors, 1826) <i>clappertoni (voteggi, gofanus, tchadensis), gedgii (cavei), heuglini, sharpii (testis), konigseggii, nigrosquamatus</i>
Hildebrandt's Francolin	<i>P. hildebrandti</i> Cabanis, 1878 <i>hildebrandti (helleri), johnstoni (grotei, lindi), altumi</i>
Natal Francolin	<i>P. natalensis</i> Smith, 1833 <i>natalensis (thamnobium), neavei</i>
Hartlaub's Francolin	<i>P. hartlaubi</i> Bocage, 1869 <i>crypticus, bradfieldi (ovambensis) Chapinortyx</i>
Harwood's Francolin	<i>P. harwoodi</i> Blundell & Lovat, 1899

Red-billed Francolin

P. adspersus Waterhouse, 1838

adspersus (*kalahari*)

Cape Francolin

P. capensis (Gmelin, 1789)

Chaetops

Unplaced

Species

Swamp Francolin

Ortygornis gularis (Temminck, 1815)

Nahan's Francolin

Ptilopachus nahani (Dubois, 1905)

Acentrortyx

70

71

72 Hall's [2] revision was adopted in many subsequent taxonomic and regional treatments of
73 Galliformes [7, 8, 10, 11]. Nevertheless, other treatments assigned generic status to some of her
74 spurfowl groups and subsets thereof. For example, with regard to African spurfwowls, Roberts [12, 13]
75 restricted *Pternistis* to Hall's Bare-throated Group, and assigned three of her Vermiculated species
76 (*capensis*, *natalensis* and *adspersus*) and a fourth (*hartlaubi*) to separate genera, *Chaetops* and
77 *Chapinortyx* respectively. In sharp contrast, Wolters [14] lumped members of her Vermiculated,
78 Montane, Scaly and Bare-throated Groups into a much enlarged *Pternistis*.

79 Post-Hall' analyses of francolin/spurfowl syringeal morphology [15], chick plumage [2, 9, 16],
80 vocalizations [17, 18] and DNA [19, 20] decisively reject a sister relationship between Hall's two
81 clades of 'francolins' [*sensu* 2]. A consensus from the above studies is to recommend phylogenetically
82 placing somewhat modified versions of the Hall francolin and spurfowl taxa within two evolutionarily
83 distantly related phasianine lineages, aligned with the now monophyletic Gallinae and Coturnicinae
84 [20].

For example, the Asiatic Spotted Group (*Francolinus* spp. sensu stricto) and the Swamp Francolin '*F. gularis*' should be removed from the spurfowls and placed within the francolin/*patryse* clade [20], with Spotted/*Francolinus* spp. placed as basal within this clade, and *gularis* with Hall's unplaced '*F. pondicerianus*' with some of Hall's Striated taxa (e.g. *sephaena*) [20]. The enlarged 'true' francolin assemblage is, in turn, sister to *Gallus* and *Bambusicola* spp. within the Gallinae [20]. Nahan's 'Francolin' [21] should also be removed from the spurfowl clade and placed outside francolins sensu Hall as sister to another phylogenetically enigmatic African 'partridge', *Ptilopachus petrosus* [22]. These now congeneric *Ptilopachus* spp. (Ptilopachinae) are sister to New World 'quails' (Odontophorinae) [23]. African spurfowls (Hall's spurfowls minus *Francolinus* spp. sensu stricto, '*F. nahani*' and *gularis*) are sister to *Ammoperdix* and *Perdica* spp., *Coturnix* 'quails' and *Alectoris* 'partridges', within the now monophyletic Coturnicinae [20].

In the present study, we deal with the remaining African spurfowls: Hall's Montane, Scaly, Vermiculated and Bare-throated Groups [2]. We use more modern species [24] and subspecies [25] concepts and phylogenetic methods to reassess Hall's and others' taxonomic, phylogenetic and biogeographical findings.

Materials and methods

Taxon sampling

Taxa and specimens studied herein (Appendix 1) include all putative African spurfowl species, the vast majority of putative subspecies and all specimens examined by Hall [2] at The Natural History Museum (Tring, UK), supplemented by a broader array of material from other major natural history museums mentioned in the Acknowledgements. Where possible, at least 10 specimens for each putative taxon were examined.

Taxonomy

Taxonomy involves the discovery, description, naming and classification of taxa at all levels of the evolutionary hierarchy. Generally, however, it focuses on the fundamental (terminal) components of

111 biodiversity, which are traditionally species and subspecies [24, 25]. Great emphasis has previously
112 been placed on the relative merits of different ‘species concepts’ with less emphasis on the linked
113 processes through which species are determined [26].

114 Empirically, we view species as reciprocally monophyletic groups of specimens that are
115 qualitatively similar in terms of suites of diagnostic, consilient characters (from e.g. morphology,
116 vocalizations and DNA markers); and geographically ‘meaningfully’ distributed (e.g. in relation to
117 past/present vegetation types and/or topography, and well-established biogeographical
118 provinces/regions [27]).

119 Our goal is to identify evolutionarily independent lineages buffered from the homogenizing effects
120 of tokogeny [28]. This is important for spurfowls since hybridization between putative species taxa is
121 thought to be common [29].

122 Subspecies are groups of populations delineated by geographically steep, congruent clinal variation
123 in multiple characters where their distributional ranges meet. The zones of parapatry (distributional
124 overlap) are characterized by morphologically intermediate individuals or individuals with ‘shuffled’,
125 undiagnosable sets of characters that appear to reflect hybridization between the largely allopatric
126 populations. Thus, our goal for subspecies is for them to reflect a common phylogeographic genealogy
127 characterized by consilient, potentially adaptive, anatomical, behavioural and ecological differences
128 maintained by constrained interbreeding between taxa. Subspecies in one clade may have
129 geographically similar distributions to those in other clades comprised of much more well-marked
130 evolutionarily significant units [30] and full species. Ultimately, one has to draw the taxonomic line
131 somewhere, with the goal of finding meaningful evolutionary entities. When in doubt, we recognize
132 terminal taxa as subspecies.

133 A good example of the application of the multifaceted consilient approach is the southern African
134 Black Korhaan (*Eupodotis afra/afraoides*). This taxon was treated as a subspecies pair by avian
135 taxonomists until it was demonstrated that the two taxa were diagnosable as ‘good’ species through a
136 series of consilient evolution of morphological, molecular, vocal, life history and habitat characters;

despite evidence of a narrow hybrid zone [31]. Indeed, hybridization, particularly in birds, can still occur even long after speciation [32, 33].

In sharp contrast, 27 putative species/subspecies of Helmeted Guineafowl in the genus *Numida* were combined into a single polytypic species (*meleagris*) with nine subspecies [34]. Subspecies were recognized by high, but imperfect, character consilience, and were connected by narrow to broad zones of ‘hybridization’ between parapatric entities between which there are no discernible differences in courtship behaviour, vocalizations and ecology throughout the entire range of this polytypic species.

Reflecting elements of both the above studies, the sunbird *Cinnyris whytei* of the Malawi highlands was split from the Angolan *C. ludovicensis* [35] due to clear morphological, genetic and distributional differences. But, it was also necessary to describe a newly discovered population of *C. whytei* from Tanzania as a subspecies of *C. whytei* (*C. w. skye*), due to the presence of only minor morphological differences and multi-locus coalescent analyses not being able to exclude the possibility of recurrent gene flow between *whytei* and *skye*. Both examples illustrate the multifaceted consilience approach we adopt, and more generally reflect the view that species are separately evolving metapopulation lineages [26].

In practice within this study, the decision to rank a taxon as a species was made using a consilience framework where entities were:

1. morpho-behaviourally diagnosable (as defined above) and \geq to 2% difference in unweighted, uncorrected, overall, molecular sequence divergence of mitochondrial DNA [19];
2. reciprocally monophyletic using morpho-behavioural and molecular characters [24]; and
3. were primarily restricted to a commonly accepted biogeographical region or subsection thereof [27].

Morpho-behavioural characters

The basic body plan of study skins was divided into discrete sections (Fig 1) and scored for variation in colour and patterning: 33 organismal characters reflecting assessment of plumage/integument colour/pattern, measurements of study skins, and vocal characters (Table 2).

164 Measurements (bill length from cere, wing/tail/tarsus/spur length) were taken using a Vernier Calliper
165 or a wing rule.

166

167 **Fig 1. Spurfowl body parts scored when generating plumage characters.** C = crown, HN = hind
168 neck, LN = lower neck, B= back, UPTC = upper tail coverts, T = throat, G = throat patch, BR = breast,
169 BE = belly, UNTC = under tail coverts, SOH = side of the head, W = wing.

170

171 **Table 2. Thirty-three morpho-behavioural characters with scoring criteria used for the**
172 **phylogenetic analyses of spurfowls.**

	Characters	Character scores
1.	Crown margins	unmargined = 0; grey = 1; buff = 2; grey brown = 3
2	Nares	black = 1; chestnut = 2; grey brown = 3; buff or white = 4; white = 5
3	Hind neck patterning	unpatterned = 0; mottled = 1; streaked = 2
4	Hind neck base colour	grey brown = 1; grey black = 2; grey chestnut = 3; rufous brown = 4; black = 5
5	Hind neck margins	unmargined = 0; grey = 1; buff = 2; grey brown = 3
6	Lower neck patterning	streaked = 1; mottled = 2; barred = 3
7-10.	Back plumage	plain = 0; streaked = 1 (7); mottled = 1 (8); vermiculated = 1 (9); barred = 1 (10)
11-13.	Upper tail coverts	plain = 0; barred = 1 (11); vermiculated = 1 (12); streaked = 1 (13)
14.	Throat	feathered = 1; yellow skin = 2; orange skin = 3; red skin = 4
15-18.	Under tail coverts	plain = 0; barred = 1 (15); streaked = 1 (16); vermiculated = 1 (17); mottled = 1 (18)
19.	Bare skin around eye	none = 0; red = 1; yellow = 2
20.	Leg colour	yellow = 1; red = 2; orange red = 3; orange = 4; olive green = 5; orange yellow = 6; black = 7

21.	Number of spurs	one = 1; two = 2
22.	Wing length (mm)	< 160 = 1; 160–180 = 2; 181–200 = 3; > 200 = 4
	males	
23.	Culmen length / Wing length (mm)	< 0.16 = 1; 0.17–0.2 = 2; > 0.2 = 3
24.	Tail length / Wing length (mm)	< 0.54 = 1; > 0.54 = 2
25.	Sexual dimorphism (plumage)	absent = 0; present = 1
26.	Sexual dimorphism (wing length)	♀ > 0.9 of ♂ = 0; ♀ < 0.9 of ♂ = 1
27.	Vocalisation strophe duration (secs)	< 0.3 = 1; 0.3–0.6 = 2; > 0.6 = 3
28.	Number of elements	one = 1; two = 2; > 2 = 3
29.	Inter element interval	absent or indistinct = 1; distinct = 2
30.	Cackle trill	absent = 0; present = 1
31-32.	Strophe character	tonal = 0 (31); trill = 1 (32)
33.	‘Ko-waaark’ advertisement call	absent = 0; present = 1

Molecular characters and samples

For within-group molecular analyses of spurfowls, 51 putative terminal taxa were studied (Table 3) with respect to four mitochondrial markers: Cytochrome *b* (CYTB - 1143 base pairs), Control region (CR - 820 bp), NADH dehydrogenase subunit 2 (ND2 - 1041 bp) and 12S rRNA (12S - 706 bp); three nuclear DNA markers: Ovomuroid G (OVO-G - 449 bp), Glyceraldehyde-3-phosphodehydrogenase (GAPDH – 361 bp) and Trans Globulin Growth Factor Beta2 intron-5 (TGFB - 596 bp) (Appendix 1).

181 **Table 3. Sample information for spurfowl taxa recognized by Hall [2] for which DNA sequences**
 182 **were generated.** Acronyms; AMNH = American Museum of Natural History, FHHM = French
 183 Natural History Museum, TM = Transvaal Museum - Ditsong National Museum of Natural History,
 184 BM = British Museum - Natural History Museum at Tring, SAM = Iziko Museums of Cape Town
 185 (Natural History), FIAO = FitzPatrick Institute of African Ornithology, TMC = Timothy M. Crowe,
 186 University of Cape Town, South Africa, GB = GenBank, Br. muscle = Breast muscle. Generic
 187 terminology follows that generated in this study.

Taxa	Sample number	Origin	Date collected	Sample type
Bare-throated Group				
<i>F. afer</i>	PFIAO 108	Tudor East, Watervalboven	2004	Liver
<i>F. a. benguellensis</i>	AMNH 267682	Mombola		Toe pad
<i>F. a. harterti</i>	AMNH 541485	Russisi River		Toe pad
<i>F. a. nudicollis</i>	BM 1903.10.14.91	E. Transvaal	1903	Toe pad
<i>F. a. böhmi</i>	BM 1932.5.10.214	S. Tanganyika	1932	Toe pad
<i>F. a. cunenensis</i>	TM 28584	Cunene River	1957	Toe pad
<i>F. humboldtii</i>	TM 20341	Selindu, Mabsettler	1935	Toe pad
<i>swynnertoni</i>				
<i>F. cranchii cranchii</i>	BM 1953.54.56	Mwinilunga, N. Rhodesia	1953	Toe pad
<i>F. c. itigi</i>	AMNH 202502	Poona Singida		Toe pad
<i>F. c. intercedens</i>	AMNH 416180	Tukuyu		Toe pad
<i>F. c. nyanzae</i>	AMNH211906	Buhumbiro		Toe pad
<i>F. swainsonii</i>	TMC 40	Marico River	2004	Liver
<i>F. s. lundazi</i>	SAM 2055756a	Deka	1969	Toe pad
<i>F. s. chobiensis</i>	SAM 2003501	Victoria falls	1904	Toe pad

<i>F. rufopictus</i>	AMNH 202503	Gagayo, Muranza		Toe pad
<i>F. leucoscepus</i>	PFIAO 109	Kenya-	2004	Heart
<i>F. l. infuscatus</i>	AMNH 419169	Tana River, Kenya		Toe pad
<i>F. l. muhamed-benabdullah</i>	AMNH 541581			Toe pad
Montane Group				
<i>F. erckelii</i>	AMNH 541471	Badaltino, Shoa		Toe pad
<i>F. erckelii</i>	AMNH DOT11039	Ethiopia		Liver
<i>F. ochropectus</i>	FNHM 1971-1072	Djbouti		Toe pad
<i>F. castaneicollis</i>	GB			Toe pad
<i>F. c. bottegi</i>	AMNH541435	Rafissa, Abyssinia		Toe pad
<i>F. c. ogoensis</i>	AMNH541426	Lower Sheikh		Toe pad
<i>F. jacksoni</i>	AMNH261929	East slope, Mt. Kenya		Toe pad
<i>F. nobilis</i>	AMNH1759	West Ruwenzori		Toe pad
<i>F. camerunensis</i>	TMC 42	Mount Cameroon		Liver
<i>F. swierstrai</i>	AMNH 419126	Angola		Toe pad
<i>F. swierstrai</i>	TMC 67	Angola, 14.49S 13.23E	2010	Blood
Scaly Group				
<i>F. ahantensis</i>	AMNH 541409	Nr York Pass, Sierra Leone		Toe pad
<i>F. squamatus</i>	PFIAO 117			Tot. DNA
<i>F. s. maranensis</i>	AMNH 541407	Kilimanjaro district		Toe pad
<i>F. s. schuetti</i>	AMNH 763912	Tshibati, D. R. Congo		Toe pad
<i>F. griseostriatus</i>	AMNH 541411	Ndalla Tanda		Toe pad
Vermiculated Group				
<i>F. bicalcaratus</i>	TM 14682	Gold Coast, Hinterland	1901	Toe pad
<i>F. b. ayesha</i>	AMNH 541250	Forest of Mamora		Toe pad

<i>F. b. thornei</i>	AMNH 541280	Kavene, Sierra Leone		Toe pad
<i>F. b. adamauae</i>	AMNH 704359	Cameroon		Toe pad
<i>F. clappertoni</i>	AMNH 541305	Takoukout, Cameroon		Toe pad
<i>F. clappertoni</i>	TMC 68	Cameroon	2005	Br. Muscle
<i>F. c. sharpie</i>	AMNH 541324	Adarte		Toe pad
<i>F. c. nigrosquamatus</i>	AMNH 541341	S. Ethiopia		Toe pad
<i>F. icterorhynchus</i>	AMNH 156922	Fanadji		Toe pad
<i>F. hildebrandti</i>	GB			Blood
<i>F. h. altumi</i>	AMNH 551345	Gilgil River		Toe pad
<i>F. h. fischeri</i>	AMNH 261945	N. Tanganyika Territory		Toe pad
<i>F. h. johnstoni</i>	AMNH 347277	Mafinga Mt., N. Rhodesia		Toe pad
<i>F. h. helleri</i>	AMNH 207771	Neng		Toe pad
<i>F. natalensis</i>	TMC 120	Marico River, South Africa	2004	Liver
<i>F. hartlaubi</i>	TMC 121	Namibia	2006	Br. Muscle
<i>F. h. crypticus</i>	AMNH 703654	Erungu Plateau		Toe pad
<i>F. capensis</i>	PFIAO 229	Kakamas, South Africa		Heart
<i>F. adspersus</i>	PFIAO 206A			Liver
<i>F. harwoodi</i>	BM 1927.11.5.18		1927	Toe pad

188

189 Primers used in sequencing are listed in Tables 4 and 5. The 1143 bp long CYTB was sequenced for
190 all taxa included in this study while data for the other markers may be missing for some taxa. Contrary
191 to earlier work [19, 36] which focused on few species, all putative species and most subspecies
192 attributed to African spurfowls were included (Appendix 1). Some 72% of specimens sequenced in
193 this study derived from DNA extractions of toe-pad scrapes off museum skins. As a result, only CYTB
194 was sequenced for both fresh and historical tissues and the other six markers were sequenced for

195 species for which there were fresh tissues. Due to the fragmented nature of the historical sourced
196 DNA, the CYTB gene for the toe-pads was sequenced in multiple fragments (six for each sample)
197 using spurfowl-specific primers (Table 5).

198

199 **Table 4. DNA markers sequenced and primers used for PCR-amplification and sequencing of**
200 **preserved tissues.**

Primer name	Primer sequence (5' to 3')	References
Cytochrome <i>b</i>		
L14578	cat gga atc atc cta gcc cta ga	J.G. Groth (personal commun.)
MH15364	act cta cta ggg ttg ggc c	P. Beresford (personal commun.)
ML15347	atc aca aac cta ttc tc	P. Beresford (personal commun.)
H15915	aac gca gtc atc tcc ggt tta caa gac	Edwards & Wilson [37]
Control region		
PHDL	agg act acg gct tga aaa gc	Fumihito et al. [38]
PH-H521	tta tgt gct tga ccg agg aac cag	E.A. Scott (personal commun.)
PH-L400	att tat tga tgc tcc acc tca cg	E.A. Scott (personal commun.)
PHDH	cat ctt ggc atc ttc agt gcc	Fumihito et al. [38]
12S rRNA		
L1267	aaa gca tgg cac tga ag(atc) tg	Moum et al. [39]
H2294	gtg cac ctt ccg gta cac ttac c	O. Haddrath (S. Pereira personal commun.)
NADH dehydrogenase subunit 2 (ND2)		
L5216	gcc cat acc ccr aaa atg	Sorenson et al. [40]
H6313	ctc tta ttt aag gct ttg aag gc	Sorenson et al. [40]
Ovomucoid G		
OVO-G Forward	caa gac ata cgg caa caa rtg	Armstrong et al. [41]
OVO-G Reverse	ggc tta aag tga gag tcc crt t	Armstrong et al. [41]

GAPDH intron-11

GapdL890 acc tt t aat gcg ggt gct ggc att gc Friesen et al. [42]

GapdH950 cat caa gtc cac aac acg gtt gct gta Friesen et al. [42]

Tran Globulin Growth Factor Beta2 intron-5

TGFb2-5F ttg tta ccc tcc tac aga ctt gag tc Primmer et al. [43]

TGFb2-6R gac gca ggc agc aat tat cc Primmer et al. [43]

201

202

203 **Table 5. DNA markers sequenced and primers used for PCR-amplification and sequencing of**
204 **museum toe pads.**

Primer name	Primer sequence (5' to 3')	References
Cytochrome <i>b</i>		
Spurfowl-specific primers		
L14851 (General)	cct act tag gat cat tgg ccc t	Kornegay et al. [44]
Pt-H195	ttt cgr cat gtg tgg gta cgg ag	R. Moyle & T. Mandiwana-Neudani
Pt-H194	cat gtr tgg gct acg gag g	R. Bowie
MH15145	aag aat gag gcg cca ttg gc	P. Beresford
Pt-L143	gcc tca tta ccc aaa tcc tca c	R. Moyle & T. Mandiwana-Neudani
Pt-H361	gtg gct att agt gtg agg ag	R. Moyle & T. Mandiwana-Neudani
Pt-L330	tat act atg gct cct acc tgt ac	R. Bowie
Pt-H645	ggg tgg aat ggg att ttg tca gag	R. Moyle & T. Mandiwana-Neudani
Pt-L633	ggc tca aac aac cca cta ggc	R. Moyle & T. Mandiwana-Neudani
Pt-H901	agg aag ggg att agg agt agg at	R. Moyle & T. Mandiwana-Neudani

L2-2312	cat tcc acg aat cag gct c	R. Bowie
H15696	aat agg aag tat cat tcg ggt ttg atg	Edwards et al. [45]
Pt-L851alt	cct att tgc cta cgc cat cct ac	R. Bowie
Pt-H1050	gat gct gtt tgg ccg atg	R. Bowie
Pt-L961	cga acc ata aca ttc cca c	R. Moyle & T. Mandiwana-Neudani
Pt-L961alt	ctc atc cta ctc cta atc ccc	R. Bowie
HB20 (General)	tgg gtt cac aag acc aat gtt	J. Feinstein (personal commun.)

Phylogenetic methods

Taxa were placed phylogenetically, following the principle of character consilience to reflect progressively more inclusive reciprocally monophyletic groupings [46]. Qualitative morpho-behavioural characters (morphology, behaviour, life history) were analyzed in combination with DNA sequence characters, in a ‘total evidence’ phylogenetic analysis. This approach was chosen because combined data sets may show clade support and resolution that is ‘hidden’ by separate analysis of character partitions. For instance, when data are concatenated, different types of characters that evolve at somewhat different rates may ‘click in’ at different levels of phylogeny [i.e. deep, shallow and intermediate nodes; 47, 48].

Parsimony was employed as the optimality criterion for the combined DNA and morpho-behavioural character analyses [49]. Indeed, the meta-analysis of more than 500 articles using model- and parsimony-based methods found strongly supported topological incongruence in only two of the studies examined [50].

All the data matrices were rooted on *Perdicula asiatica* and *Ammoperdix heyi* following [4]. For inter-taxon genetic distances, uncorrected pairwise distances were calculated in PAUP ver. 4.0b10 and were transformed into percentages.

Distributional range maps

Another challenging and indispensable aspect in the analyses outlined below was to produce maps showing the distributional ranges of the various spurfowl taxa ultimately recognized. In Step 1 in developing the range (as opposed to point locality) maps for each taxon that emerged, the ‘Atlas of Speciation in African Non-passerine Birds’ [51] was used since it still presents the best distribution ranges of species produced from the point localities of the specimens collected. This was supplemented in Step 2 - consulting the ‘Atlas of Southern African Birds’ [52] which was helpful in filling distribution gaps for southern African species. Step 3 involved using Hall’s inferred distributions [2] to complete the ranges of species and subspecies recognized.

Results

Morpho-behavioural characters

Character information for morpho-behavioural characters are presented in Table 6.

Table 6. Morpho-behavioural character scores matrix used for the phylogenetic analysis of spurfowls.

	Character reference numbers (see Table 4).																																			
											1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3
Taxon	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3			
<i>Pternistis</i>																																				
<i>hartlaubi</i>	0	1	1	1	0	1	1	1	0	0	1	1	0	1	1	0	0	0	0	1	2	1	3	2	1	0	3	3	2	0	1	1	0			
<i>P.</i>																																				
<i>camerunensis</i>	0	1	1	2	0	2	0	1	1	0	1	1	0	1	1	0	0	0	1	2	2	2	1	1	1	0	2	2	2	0	1	0	0			
<i>P. nobilis</i>	0	1	1	2	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	2	2	3	1	1	0	0	2	2	2	0	1	1	1			
<i>P. erckelii</i>	0	2	1	3	0	1	0	0	1	0	0	0	0	1	0	1	1	0	0	2	2	4	1	2	0	1	3	3	2	1	0	1	0			
<i>P. swierstrai</i>	0	1	0	5	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	2	2	3	2	2	1	0	3	3	2	1	0	1	0			
<i>P.</i>																																				
<i>castaneicollis</i>	0	1	0	3	0	1	1	0	1	0	0	0	0	1	0	1	0	0	1	2	2	4	1	2	0	1	3	3	2	1	0	1	0			
<i>P. atrifrons</i>	0	1	2	1	2	1	1	0	1	0	0	0	0	1	0	1	0	0	1	2	2	4	1	2	0	1	3	3	2	1	0	1	0			

P.

<i>ochropectus</i>	0	2	1	3	0	1	0	0	1	0	0	0	0	1	0	1	1	0	0	2	2	4	1	2	0	1	2	2	2	0	1	0	0
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<i>P. jacksoni</i>	0	1	0	3	0	1	1	0	1	0	0	0	0	1	0	1	0	0	0	2	2	4	1	2	0	0	?	?	?	?	?	?	0
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<i>P. squamatus</i>	0	3	0	1	0	2	0	1	1	0	1	1	0	1	0	0	0	1	0	3	2	2	1	2	0	0	3	3	2	0	1	1	0
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<i>P. s. schuetti</i>	0	3	1	1	0	2	0	1	1	0	1	1	0	1	0	1	0	0	0	3	2	2	1	2	0	0	3	3	2	0	1	1	0
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<i>P. achantensis</i>	0	4	0	1	0	1	1	0	1	0	0	1	0	1	0	1	1	0	0	4	2	2	1	2	0	0	2	2	2	0	1	1	0
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P.

<i>griseostriatus</i>	0	3	0	1	0	1	1	0	1	1	1	0	0	1	0	0	0	0	0	3	1	1	1	2	0	0	3	1	1	0	0	1	0
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P.

bicalcaratus

<i>bicalcaratus</i>	0	1	1	4	0	1	1	0	1	0	1	1	0	1	0	1	0	0	0	5	2	2	2	1	0	0	1	2	1	0	0	1	0
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<i>P. b. ayesha</i>	0	1	1	4	0	1	1	0	1	0	1	1	0	1	0	1	0	0	0	5	2	2	2	1	0	0	1	2	1	0	0	1	0
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P. b.

<i>adamauae</i>	0	1	1	2	0	2	1	0	1	0	1	1	0	1	0	1	0	0	0	5	2	2	2	1	0	0	1	2	1	0	0	1	0
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<i>P.</i>	0	1	1	2	0	1	0	0	1	1	1	1	0	1	1	0	0	0	2	6	2	2	2	1	0	0	1	2	1	0	0	1	0
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icterorhynchus

s

P.

<i>clappertoni</i>	0	1	1	4	0	1	1	0	0	0	1	1	0	1	0	1	0	0	1	2	2	2	2	1	0	0	2	2	1	0	0	1	0
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<i>P. c. sharpii</i>	0	1	0	1	0	1	1	0	0	0	1	1	0	1	0	1	0	0	1	2	2	2	2	1	0	0	2	2	1	0	0	1	0
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<i>P. harwoodi</i>	0	1	1	4	0	1	1	0	0	0	1	1	0	1	0	1	0	0	1	2	2	2	2	2	?	1	2	2	1	0	0	1	0
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P. h.

<i>hildebrandti</i>	1	1	2	2	1	1	0	0	1	1	1	1	0	1	1	0	1	0	0	2	2	2	1	2	1	0	1	3	2	0	0	1	0
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<i>P. h. fischeri</i>	1	1	2	2	1	1	0	0	1	1	1	1	0	1	1	0	1	0	0	2	2	2	1	2	1	0	1	3	2	0	0	1	0
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<i>P. natalensis</i>	0	3	0	1	0	1	0	0	1	1	1	1	0	1	1	0	0	0	0	2	1	2	1	2	0	0	2	3	2	0	1	1	0
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<i>P. adspersus</i>	0	1	0	2	0	3	0	0	0	1	1	0	0	1	1	0	0	0	2	2	1	2	1	2	0	0	3	3	2	1	1	1	0
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<i>P. capensis</i>	2	3	2	1	2	1	1	0	0	0	1	0	0	1	0	1	0	0	0	2	2	4	1	2	0	0	3	3	2	0	1	0	0
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P.

<i>leucoscepus</i>	3	4	2	1	3	1	1	0	1	0	1	1	0	2	0	0	1	0	1	7	2	3	2	1	0	0	3	2	2	0	0	1	1
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<i>P. l.</i>	0	1	2	1	0	1	0	0	1	0	1	1	0	2	0	0	1	0	1	7	2	3	2	1	0	0	3	2	2	0	0	1	1
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infuscatus

P. rufopictus 0 3 0 1 0 1 1 0 1 0 0 1 1 3 0 1 0 0 1 7 2 4 2 1 0 0 2 2 2 0 0 1 1

P. afer afer 3 5 2 1 0 1 1 0 0 0 0 0 0 4 0 1 0 0 1 2 2 3 2 1 0 0 2 2 2 0 1 1 1

P. a. cranchii 0 1 0 1 0 1 1 0 1 0 0 1 0 4 0 1 1 0 1 2 2 3 2 1 0 0 2 2 2 0 1 1 1

P. a.

humboldtii 3 4 2 1 3 1 1 0 0 0 0 0 0 4 0 0 0 0 1 2 2 3 2 1 0 0 2 2 2 0 1 1 1

P. swainsonii 3 3 2 1 3 1 1 0 1 0 0 1 1 4 1 0 1 0 1 7 1 3 2 1 0 0 3 2 2 0 1 1 1

238 **Phylogenetics**

239 The ‘total evidence’ parsimony analysis based on 5149 characters (33 organismal and 5116 DNA
240 bases) and 33 terminal taxa produced two equally parsimonious trees of length 2124, the strict
241 consensus of which is presented as (Fig 2). Since only one of Hall’s spurfowl species groups [2], the
242 phylogenetically terminal Bare-throated Group, emerged as monophyletic and the others are para- or
243 polyphyletic, we recognize only one monophyletic genus for the African spurfowls: *Pternistis*.

244
245 **Fig 2. Strict consensus parsimony tree for spurfowls constructed from two most parsimonious**
246 **trees.** Numbers mapped above nodes are jackknife support values. MS = Montane spurfowls, SCS =
247 Scaly spurfowls, SVS = Southern Vermiculated spurfowls, NVS = Northern Vermiculated spurfowls
248 and BTS = Bare-throated spurfowls.

250 **Cladogenesis**

251 *Pternistis hartlaubi*, one of Hall’s Vermiculated taxa [2], is the basal African spurfowl. Hartlaub’s
252 Spurfowl occupies dense, mixed grass-shrub cover on boulder-strewn slopes and rocky outcrops in
253 hilly and mountainous regions within a granite and sandstone substrate surrounded by semi-desert
254 open savanna [53]. It is confined to central and northern Namibia, particularly on the Namibian
255 escarpment and extreme southwestern Angola [54].

256 The upper mandible of *P. hartlaubi* is horn coloured and the lower yellowish. The male has a dark
257 grey-brownish crown, a pronounced white eyestripe, offset by a black line below and chestnut ear
258 coverts. The back is grey, faintly streaked and barred with brown. The belly is pale grey, heavily
259 streaked with brown. The black and white under-tail coverts are conspicuous in flight and in courtship

display. The adult female has an orange-brown eyestripe, and a grey-brown head, cheeks, chin and belly. The back is grey-brown with strong vermiculations [53].

Hartlaub's Spurfowl is markedly distinct from other African spurfowls [2, 53]. Indeed, it differs from 'francolins' *sensu lato* in general, in that it: (1) has markedly sexually dimorphic plumage [2]; (2) has a disproportionately long bill used for digging underground corms and tubers [53]; (3) is the smallest spurfowl and is markedly sexually size-dimorphic (males 245-290 g., females 210-240 g. – 54]; (4) has yellow (normally black or red/orange-red in spurfowl) tarsi with virtually no tarsal spurs – actually only tiny bumps [2]; (5) is socially monogamous throughout the year [53]; (6) has vocalizations markedly different from (but still link with) the rest of the spurfowls [17, 18]; (7) demarcates and defends its territory year-round, using a combination of uniquely antiphonal duet calling (initiated by the hen) and displays, rather than overt aggression [53]; and (8) seems not to require standing/flowing water for drinking [53].

With regard to putative subspecies, populations from southern Angola (nominate '*hartlaubi*') are somewhat smaller than those from Namibia. Those from the Kaokoveld and Erongo ('*crypticus*') are paler than those from the Waterburg and Otavi ('*bradfieldi*') in the east. We regard these differences as clinal variation. The two specimens (from Erongo and the Waterburg) were 0.4% CYTB divergent. We recognize no subspecies for this taxon.

Hartlaub's Spurfowl's closest CYTB taxon is *P. squamatus* at 7.8% sequence divergence.

Hall's [2] Montane spurfowls follow on phylogenetically from *hartlaubi*, but are paraphyletic (Fig. 2). They are forest-dwelling taxa, forming two, monophyletic clades: *camerunensis* + *nobilis* and *erckelii* + *ochropectus* + *castaneicollis*, linked by *swierstrai*. Then comes *jacksoni* as a link to the also paraphyletic, lowland/secondary forest-dwelling Scaly spurfowls.

Thereafter come the also paraphyletic woodland, savanna, scrub and bush dwelling Vermiculated (divided into northern and southern assemblages) and the monophyletic Bare-throated taxa.

The Montane spurfowls

There are seven Montane spurfowl species, one with two subspecies: *swierstrai*, *camerunensis*, *nobilis*, *erckelii*, *ochropectus*, *castaneicollis* (*castaneicollis*, *atrifrons*) and *jacksoni*.

They are distributed across the mountains of north-eastern Africa from Eritrea to Mt. Kenya, extending west through the Albertine Rift, to Mt. Cameroon and south to the highlands of Angola [2] (Fig 3). Montane spurfowls are confined to forested habitat, which provides roosts and cover, although some taxa (e.g. *P. erckelii*) will venture out into wooded scrub, heath and grassland with shrubs [54].

Fig 3. Geographical distributions of Hartlaub's Spurfowl, Montane spurfowls and the 'Arid Corridor'. Arrows draw attention to phylogenetically sequential cladogenesis.

The Montane spurfowls are the morphologically least homogeneous of Hall's spurfowls [2]. There is no diagnostic 'Group' morphological character other than that the males have the crown, lower back, primaries and tail plain brown or red-brown. Females of the relatively small, moderately sexually dimorphic species (*P. camerunensis*, *P. swierstrai*) have vermiculated primaries, lower back and tail.

Variation in some characters follows geographically clinal trends, with the birds of the extreme northeast being: the largest and most heavily spurred with dark bills, yellowish tarsi, no bare skin round the eyes, with the sexes alike [2]. The two isolated, sexually dimorphic western species (*camerunensis* and *swierstrai*) are the least heavily spurred and the smallest species. Thus, they most closely resemble the basal, and also sexually dimorphic, *P. hartlaubi*. The central African species,

305 *nobilis*, ‘connecting’ these three species to those in the northeast is of intermediate body mass [54].

306 Generally, Montane spurfowls differ from one another primarily in their belly plumage, particularly on
307 mid- and lower belly.

308 The closest non-montane CYTB taxon to them is *P. squamatus* at 5.3% sequence divergence.

309

310 *Pternistis swierstrai* is an uncommon, endemic of Angola, confined to undergrowth within patches
311 and edges of relict evergreen forest in the highlands of western Angola, Mountains Moco and Soque,
312 the Bailundu highlands and Mombolo Plateau along the escarpment, with isolates on the Chela
313 escarpment, Tundavala (Huila District) and Cariango (Cuanza Sul District) (Fig 3) [54]. It ventures
314 into grass- and bracken-covered slopes and gullies [54].

315 Swierstra’s Spurfowl is a small spurfowl (both sexes 375–565 g [54]), and has an orange-red bill, a
316 yellow ear-patch, yellow eye-ring on males (blue in females), red tarsi with one spur, only in males. It
317 is weakly sexually dimorphic in plumage. Both sexes have a conspicuous white eyestripe and throat,
318 brown back plumage (irregularly blotched in the female). The male’s black breast contrasts with the
319 white throat, whereas the lower belly feathers have broad buff central streaks with blackish margins.
320 The belly plumage of the female is white, barred/blotched with dark brown [2].

321 Its closest CYTB taxon is *P. squamatus* at 5.3% sequence divergence.

322

323 *Pternistis camerunensis* is sister to *nobilis*. It is endemic to, and locally distributed within dense
324 undergrowth and edges of forests on the south-eastern slopes of Mt. Cameroon, between 850 and 2100
325 m above sea level (Fig 3) [54]. The Mt Cameroon Spurfowl is a small (male ~593 g., female ~509 g.),
326 sexually dimorphic spurfowl, and has an orange-red bill, red eye-ring, and orange-red tarsi with 1-2
327 spurs, only in males. The male has a dark brown crown and nape. Its throat is grey-buff with the belly

328 feathers chestnut with grey edges. Its upper tail coverts and primaries are grey brown, and wing
 329 coverts and the lower neck are deep maroon, with light grey scalloping on the lower neck. Its back is
 330 rich dark brown (excluding the lower neck). The belly and lower neck are plain grey with some black
 331 feather centres and shaft streaks. The chest and belly plumage of the female is mottled and
 332 vermiculated with black, dark brown and buff with some off-white U- to V-patterning on the belly and
 333 lower neck .

334 The closest CYTB taxon to *P. camerunensis* is its sister-taxon, *P. nobilis*, at 7.4% sequence
 335 divergence.

336

337 *Pternistis nobilis* [54] is endemic to the highland Ruwenzori and Kivu forests in the Albertine Rift
 338 and mountains in far western DR Congo, south-western Uganda and borders of Rwanda and Burundi,
 339 and is locally common in dense undergrowth, forest edge and moist bamboo thickets (Fig 3). The
 340 Noble Spurfowl [54] is medium-sized and sexually monomorphic (males averaging 877 g., females
 341 635 g.). It has a red bill, eye-ring and tarsi with 1-2 spurs (upper shorter), only in the male. It has a
 342 grey-brown head, primaries and rump, and a buff throat. It is dark maroon overall, particularly on the
 343 wings and back, with light grey scalloping on the lower neck. The rest of the belly feathers are
 344 chestnut with narrow grey or whitish edges or scallops [2].

345 With regard to subspecies of *P. nobilis*, we regard ‘*chapini*’, from the Ruwenzori Mountains as an
 346 idiosyncratic variant since it differs only by having somewhat narrower greyish edges to the belly
 347 feathers [2].

348 The closest CYTB taxon to *P. nobilis* is its sister-taxon, *P. camerunensis*, at 7.4% sequence
 349 divergence.

350

351

352 *Pternistis erckelii*, the most northerly distributed Montane spurfowl, is sister to *P. ochropectus*. It is
 353 distributed in giant heath, forest scrub remnants and edges above 2000 m, extending, relatively
 354 continuously up to 3000 m, from the vicinity of Addas Ababa in the massif of central and northern
 355 Ethiopia southwards to southern Eritrea (Fig 3). Unlike other Montane spurfowls, it will venture out of
 356 forest into adjacent heath and grassland. Erckel's Spurfowl is the largest African spurfowl (males
 357 1050-1590 g., one female 1136 g. [54]). It has a black bill and yellowish tarsi with two spurs (upper
 358 longer), only in the male. It is sexually monomorphic, and has a black forehead and eyestripe, chestnut
 359 crown, grey ear coverts and white throat. Its lower neck is grey like the upper belly, but with greyish
 360 brown margins and a thin central buff streak, whereas the upper belly feathers have central greyish
 361 black streaks. Lower belly feathers have a broad buff central streak constricted in the middle and
 362 expanded distally into a tear-drop, margined with rufous [2]. The "somewhat greyer" [2] putative
 363 subspecies, 'pentoni', an isolated population from the Red Sea Hills at Erkowit, is not recognized.

364 The sister and CYTB closest species to *P. erckelii* is *P. ochropectus* at 2.6% sequence divergence.

365

366 *Pternistis ochropectus* is a large spurfowl (one male 809 g., one female 605 g. [54]) endemic to the
 367 evergreen juniper forest mostly above 1200 m. on the Plateau du Day of Djibouti (Fig 3). The Djibouti
 368 Spurfowl [54] has a black bill with the lower mandible yellowish and yellow tarsi with two spurs
 369 (upper longer), only in the male. The lower belly feathers of *P. ochropectus*, *P. erckelii* and *P.*
 370 *castaneicollis* are similar, but *P. erckelii* and *P. castaneicollis* are more heavily marked with brown on
 371 the back and breast. The belly feathers of *ochropectus* have a broad buff central streak constricted in
 372 the middle and expanded distally into a tear-drop, margined by a greyish black U-shaped streak [2].

373 The CYTB closest and sister-species to *P. ochropectus* is *P. erckelii* at 2.6% sequence divergence.

374

375 *Pternistis castaneicollis* is a large spurfowl (males 915-1200 g, females 550-650 g. [54]), and is
 376 restricted to montane heath moorlands, juniper forests and forest edge/scrub above 2800 m. It extends
 377 broadly in montane ‘islands’ along the mountain ranges of central and south Ethiopia on both sides of
 378 the Rift Valley to Somalia in the extreme northwest, and to the Kenyan border in the extreme south
 379 (Fig 3) [54]. The Chestnut-naped Spurfowl is morphologically geographically variable, but most
 380 similar to *P. erckelii* [54]. It has a red bill, yellow ear-patch, yellowish eye-ring in males (blue in the
 381 female) and orange-red legs with two equally long spurs, only in the male. It is sexually monomorphic
 382 in plumage, but females are smaller. It has less black on the face than *erckelii* and *ochropectus*. Its
 383 belly feathers having a broad buff central streak, constricted in the middle and expanded distally into a
 384 tear-drop, margined with rufous. Its eastern Ethiopian populations have an extensive double-U-
 385 patterning on the back with wing coverts and breast clearly defined in black and white, with some
 386 ochre and chestnut, grading to mainly white on the belly [2].

387 The closest CYTB taxon is *P. erckelii* at 4.2% sequence divergence.

388 The subspecies *atrifrons* (for which we had no DNA sequence data) is confined to the Mega
 389 Mountains of southern Ethiopia (Fig. 3). It was recently elevated to full species [55] and is 1.2-1.3%
 390 CYTB divergent from *P. c. castaneicollis*. It differs from other populations of *castaneicollis* by having
 391 the throat and belly cream instead of white and reduced or absent chestnut colouration and U-
 392 patterning on the neck and flanks. Despite these genetic and morphological differences, *atrifrons* has
 393 similar vocalizations, habits and habitat to other forms of *P. castaneicollis* [2, 54]. Hence, in terms of
 394 our stated criteria, its elevation to full species is not supported. The putative subspecies from Somalia,
 395 ‘*ogoensis*’, is clinally more grey [2], and those from isolated populations west of Lake Zwai,

396 ‘*kaffanus*’ are clinally less well-defined and U-patterned [2]. Moreover, their CYTB divergence from
 397 nominate *castaneicollis* is 0.2-0.7%. Hence, these taxa are synonymized within *castaneicollis*.

398

399 *Pternistis jacksoni* occurs between 2200 and 3700 m [54], primarily in forests, forest edges,
 400 moorlands, bamboo patches and within the Aberdares and Mt. Kenya, Mau Escarpment and
 401 Cherangani Mountains in *Podocarpus*, *Juniperus* and other Afro-alpine forests of western and central
 402 Kenya, extending marginally into Uganda (Fig 3). Jackson’s Spurfowl is large (~1130–1160 g, with
 403 females slightly smaller [54]). It has a red bill, yellow-orange ear-patch and eye-ring and tarsi with 1-2
 404 spurs (upper shorter), only in the male. Its throat is buff and the lower neck greyish with the proximal
 405 part of the lower neck similarly patterned to the rest of the belly. Lower neck feathers are chestnut-
 406 coloured edged with buff to white, but the degree of chestnut and buff and white varies among
 407 individuals [2]. The subspecies ‘*pollenorum*’ from Mt. Kenya is not recognized because it is only
 408 somewhat darker [2] than other forms of *P. jacksoni*.

409 The closest CYTB taxon is *P. griseostriatus* at 5.0% sequence divergence.

410

411 **The Scaly spurfowls**

412 The paraphyletic Scaly spurfowls comprise three allopatric species (*P. squamatus*, *P. achantensis*
 413 and *P. griseostriatus*). The fourth species, *P. schuetti*, is parapatric with *P. squamatus* [Fig.4] [2].
 414 Scaly spurfowls have the plainest plumage [2], with the least patterning and no strong colour. They are
 415 characterized by having ‘scaly’ underparts, and inhabit vestigial patches of montane and lowland
 416 forest, secondary and riverine forests, forest edges and clearing/cultivation therein of West Africa
 417 eastwards to the Sudan and north-eastern Tanzania, and Central Africa and the Benguela district of
 418 north-western southern Africa (Fig 4) [54].

Fig 4. Geographical distributions of Scaly spurfowls.

Compared with other spurfowls, these taxa are poorly diagnosed in terms of plumage pattern and colouration [54]. All taxa have unpatterned faces, whitish throats and brown upperparts, some with faint vermiculations. The underparts are brown or creamy-buff with very narrow darker edges, providing the characteristic ‘scaly’ appearance. There is no marked plumage dimorphism, with the exception that females tend to be more vermiculated than males [2].

Pternistis squamatus is sister to *P. schuetti*, and occurs in forested areas in south-eastern Nigeria, extending east into the DR Congo and up to 3000 m (on Mt Elgon) in Uganda/Kenya (Fig 4) [54]. It has a red bill, orange-red tarsi with 1-2 spurs (lower longer) in males only [54]. There is no size dimorphism (males 372-565 g., females 377-515 g.) and plumage, with U-patterned vermiculated upperparts, less so in males. It is the least distinctly patterned scaly taxon. The brown upperparts are indistinctly vermiculated faint grey with each feather with a blackish centre tinged maroon, and the upper back has faint buff U-patterning. The scaly underparts are brown with ill-defined dark shaft streaking [2].

The closest CYTB taxon is its sister-species, *P. schuetti*, at 3.4% sequence divergence.

Pternistis schuetti occurs in eastern DRC extending east to Uganda, Ethiopia, Kenya, Tanzania and Malawi [54] (Fig 4). It resembles *squamatus*, but is less vermiculated overall, and the scaly pattern on the lower neck is less clearly defined, each feather has a deep red-brown centre [2]. Populations west of the Rift Valley in Kenya south towards Kilimanjaro, Monduli and Mt. Meru in northeastern

442 Tanzania [2], become clinally increasingly darker and greyer (more readily seen in males), and tend to
 443 have less white on the belly. Poorly sampled, isolated populations to the south ‘*usumbarae*’,
 444 ‘*uzungwensis*’ and ‘*doni*’ are clinal or idiosyncratic variants of *schuetti*, but may warrant subspecific
 445 status should they exhibit significant genetic divergence.

446 The closest CYTB taxon to *schuetti* is *griseostriatus* at 2.7% sequence divergence.

447 *Pternistis s. maranensis* (1.2% divergent from nominate *schuetti*) occurs further east on Mt
 448 Kilimanjaro (up to 2000 m), Monduli, Mt Meru and in the Chyulu Hills (Fig 4). It is much darker and
 449 less patterned than *schuetti* [2]. There are scattered populations of Scaly spurfowls that show variation
 450 in plumage. About 240 km southeast of Kilimanjaro, birds (‘*usambarae*’) from the Usambara
 451 Mountains [2] have the areas around their eyes and cheeks freckled with black and white instead of
 452 uniform brown. Another isolated population from forests on the Vipya Plateau between 900 and 2800
 453 m (‘*doni*’) in Malawi has upper and underparts that are more red-brown with some white streaking on
 454 the underparts [2]. These, for now, are included within nominate *schuetti*.

455
 456 *Pternistis achantensis* [54] occurs within gallery and secondary, coastal lowland West African
 457 forests in three disjunct populations west of the Niger River: southern Senegambia and northern
 458 Guinea-Bissau; southern Guinea, Sierra Leone and western Liberia; and north-eastern Ivory Coast and
 459 Ghana through the central Togo and central Benin to south-western Nigeria (Fig 4).

460 The Ahanta Spurfowl is a medium-sized spurfowl (males +-608 g., females +- 487 g.) and has an
 461 orange bill with a black base and yellow-orange tarsi with 1-2 spurs (lower longer), only in the male
 462 [54]. It is the most patterned Scaly spurfowl, with breast and flank feathers having paler edges and
 463 darker centres. The feathers on its upperparts are vermiculated (distinct on the lower neck, indistinct
 464 on the back) with blackish centres and a reddish-brown shaft-streaking, those on the lower neck have

some white U-patterning. The underparts are dark-brown chestnut with white and darker brown U-patterning [2]. The isolated western populations (*'hopkinsoni'* for which we had no CYTB information) are paler overall [2] than those in the east and probably do not warrant taxonomic status.

The closest CYTB taxon to *ahantensis* is *P. squamatus* at 4.2% sequence divergence.

Pternistis griseostriatus is a small spurfowl (males 265-430 g., females 213-350 g. [54]) endemic to vestigial patches of forest in the Angolan western escarpment (Fig 4). The Grey-striped Spurfowl has a black bill with a red base (lower mandible orange-red) and its tarsi are orange-red with a single spur in the male. It is sexually monomorphic, and its lower neck feathers and wing coverts are chestnut and broadly edged and vermiculated with grey, similar to the pattern in *squamatus* and *ahantensis*, but paler. However, the underparts are plain, and the upper belly and flank feathers are chestnut and edged with greyish or creamy buff [2].

The closest CYTB taxon is *P. schuetti* at 2.7% sequence divergence.

The Vermiculated spurfowls

Hall's Vermiculated taxa [2] are the most widely distributed spurfowls within Africa. They occur more or less continuously from Senegal to Eritrea southwards to Namibia and South Africa (Figs 5 and 6). There is even an isolated population (*ayesha*) of *bicalcaratus* in Morocco, making it one of the few sub-Saharan bird species with natural populations north and south of the Sahara [56]. Northern taxa frequent grasslands and cultivation within woodlands and acacia savanna and steppe. South of the equator, Vermiculated taxa frequent thick bush on hillsides and riparian watercourses. All taxa have brown or grey-brown heads, backs, wings and tails, with lighter vermiculations and/or V- and U-shaped patterning. Most taxa have a white eye-stripe.

488

489 **Fig 5. Geographical distributions of Vermiculated spurfowls (SOUTH).**490 **Fig 6. Geographical distributions of Vermiculated spurfowls (NORTH).**

491

492 There are eight species and seven subspecies: *P. hildebrandti* (*hildebrandti* and *fischeri*), *P.*
 493 *natalensis*, *P. adspersus*; *P. capensis*, *P. icterorhynchus*, *P. bicalcaratus* (*bicalcaratus*, *adamauae*,
 494 *ayesha*), *P. clappertoni* (*clappertoni*, *sharpii*), and *P. harwoodi*.

495 Within the southern taxa, *P. hildebrandti*, occurs from sea level to about 2500 m. in east and south-
 496 central Africa, east and south from Lake Victoria through Kenya, most of Tanzania, northern
 497 Mozambique, north-eastern Zambia and Malawi (Fig 5) [54]. The species is sparsely distributed on
 498 rocky ground associated with dense thicket along rivers and on hillsides, acacia savanna, Miombo
 499 woodland and forest edge.

500 Hildebrandt's Spurfowl is a medium-sized spurfowl (two males 600 and 645 g., two females 430
 501 and 480 g. [54]) and comprises two subspecies (*hildebrandti* and *fischeri*) with the former being
 502 sexually dimorphic. It has a reddish mandible and brown culmen with a yellow base, a yellow ear-
 503 patch and eye-ring, red tarsi with 1-2 spurs on both sexes. The dorsal plumage of males resembles that
 504 of *P. icterorhynchus*. It is greyish brown with vermiculations, and the hind and lower neck are streaked
 505 black with white margins, and the belly plumage has marked black blotching. Females have similar
 506 back plumage to males, but (especially in *P. h. fischeri*) differ markedly in having orange-brown
 507 underparts [2].

508 *Pternistis h. fischeri* [2] (1.0% sequence divergent from *hildebrandti*) from southern Malawi,
 509 Mozambique and south-western Tanzania differs from *hildebrandti* in that females have an
 510 unpatterned nape, hind neck and upper belly, in sharp contrast to an orange-brown abdomen. Birds

511 from Kenya, ‘*altumi*’ [2], do not warrant taxonomic recognition because their plumage is intermediate
 512 between nominate *hildebrandti* and *fischeri*.

513 The sister-taxon to *P. hildebrandti* is *P. h. fischeri* with a CYTB (for *fischeri*) sequence divergence
 514 of 0.8%. Other forms of *hildebrandti* are >2% divergent from *natalensis*, its sister-species. In the
 515 Luangwa valley, the presence of specimens with intermediate plumage suggests that *P. hildebrandti*
 516 may interbreed (or have interbred) with *P. natalensis* [2].

517

518 *Pternistis natalensis* is a medium-sized spurfowl (males 415-723 g. females 370-482 g. [54])
 519 distributed across south-eastern Africa, from Zambia, Zimbabwe, inland Mozambique, eastern
 520 Botswana, Swaziland and north-eastern South Africa (Fig 5). It occurs in thick riverine bush, but will
 521 venture into dry lowveld savanna and adjacent grasslands [9]. The Natal Spurfowl [54] has an orange
 522 bill with a dull greenish base, and the orange tarsi have a single spur, only in the male. It is normally
 523 sexually monomorphic, but some populations ‘*neavei*’ from southern Zambia and western
 524 Mozambique are slightly dimorphic. The hindneck is mottled black and white, the back is highly
 525 vermiculated in greyish-brown and black, with white and buff markings. The belly is buff with the
 526 upper belly to mid-belly being heavily patterned in black and buff U-patterning is concentrated on the
 527 breast with the extreme lower abdomen having no or few marks [2].

528 The closest CYTB taxon is *P. hildebrandti fischeri* at 0.8% sequence divergence. Next closest is *P.*
 529 *h. hildebrandti* at 3.1% divergence.

530

531 *Pternistis adspersus* is a smallish spurfowl (males 340-635 g., females 340-549 g. [9, 54]) and
 532 occurs in dense bush, mixed woodland and low scrub thickets interspersed with open ground, mostly
 533 on Kalahari sands along watercourses in Namibia, Botswana, southern Angola and south-western

534 Zambia (Fig 5). The Red-billed Spurfowl is a monotypic species with an orange-red bill and tarsi,
 535 yellow ear-patch and eye-ring. Males have a single spur. The upperparts are finely vermiculated, and
 536 the underparts are narrowly distinctly barred with black and white, variably on the lower neck [2].

537 The closest CYTB taxon is *P. capensis* at 3.8% sequence divergence.

538

539 The monotypic *Pternistis capensis* is the largest Vermiculated spurfowl (males 870-1000 g.,
 540 females 640-900 g.). It is endemic to thick cover and rocky river valleys in the Fynbos Biome of south-
 541 western South Africa, with isolated populations extending deep into the Karoo biome and lower
 542 stretches of the Orange River (Fig 5) [9]. The Cape Spurfowl [9] has a brown upper mandible (lower
 543 red), and orange red tarsi with one spur (females) and sometimes two (males). It has distinctive
 544 uniform brown and white double V- or U-shaped patterning on the back, breast and belly, while the
 545 throat has irregular black flecking. The breast and belly feathers have broad white shaft streaks [2].

546 The closest CYTB taxon is *P. adspersus* at 3.8% sequence divergence.

547

548 Moving to the northern vermiculated taxa, *P. icterorhynchus* is a medium-sized spurfowl (males
 549 504-588 g. females 20-462 g. [54]) and occurs in grasslands, open woodlands and adjacent agricultural
 550 lands in the Central African Republic, northern DR Congo, extending east to South Sudan and Uganda
 551 (Fig 6). Heuglin's Spurfowl has a yellow-orange black bill, small yellow eye-patch, yellow-orange
 552 tarsi with 1-2 (upper longer), in males only. It is monotypic and sexually monomorphic species (Fig 6),
 553 with a chestnut crown, brown back diagnosed by having less V-shaped patterning on the lower neck
 554 and more vermiculations on the back than other vermiculated taxa. Its underparts are buff heavily
 555 marked with dark brownish-back V-shaped markings [2].

556 The closest CYTB taxon is *P. bicalcaratus* at 3.3% sequence divergence.

557

558 *Pternistis bicalcaratus* comprises three sexually monomorphic subspecies (Fig 6). All the taxa are
 559 similarly patterned above and below, differing in the degree of colouration and vermiculation, and the
 560 size of the arrow-shaped buff marks in the centre of the belly feathers [2]. They occur [54] in dry
 561 grasslands, open savanna, palm groves and cultivated areas of West Africa from Senegal east to
 562 northern Cameroon and southern Chad (Fig 6).

563 The nominate form of the Double-spurred Spurfowl [54], *bicalcaratus* is a medium-sized (males +-
 564 507 g., females +-381 g.) spurfowl, and has a greenish-black bill and 1-2 greenish tarsi (upper longer),
 565 much shorter in females. It has no bare facial skin. It has a pale rufous crown, and a white eyestripe. It
 566 has rufous-chestnut on the lower neck and the remaining upperparts are vermiculated with V-shaped
 567 patterning. It has buff underparts, distinctly and heavily streaked with black and chestnut small arrow-
 568 shaped buff marks on most belly feathers [2]. The more heavily patterned *ayesha* (from Morocco, not
 569 mapped) is similar (1.0% CYTB divergent) to *bicalcaratus*, but is faintly vermiculated and slightly
 570 more rufous on the lower neck, with small arrow-shaped buff marks on the belly feathers [2]. The
 571 darkest form is *adamauae* (1.7% CYTB divergent) with very little rufous on the lower neck, and the
 572 underparts are more buff with extremely reduced chestnut and larger arrow-shaped buff marks long the
 573 centres of the belly feathers [2].

574 The closest CYTB species is its sister-species, *P. icterorhynchus*, at 2.7% sequence divergence.

575

576 *Pternistis clappertoni* [54] comprises two widespread subspecies extending up to 2300 m in semi-
 577 arid grassland and bushy savanna and adjacent cultivations across north-central Africa from far eastern
 578 Mali, central Niger, far north-eastern Nigeria, Chad, southern Sudan, South Sudan, northeastern
 579 Uganda and western Ethiopia (Fig 6). It also occurs in the Nile and Blue Nile River valleys [2].

580 Clapperton's Spurfowl is a medium-sized spurfowl (males 450-604 g. females 300-530 g. [54]). It
 581 has a black bill with a red base and red tarsi with 1-2 spurs in males only. The bare skin around the eye
 582 distinguish it from *P. bicalcaratus*, *P. icterorhynchus* and *P. castaneicollis*. The brown upperparts of
 583 the nominate form, *clappertoni*, have U-shaped patterning (very similar to those of *P. icterorhynchus*),
 584 but are more orange brown and vary geographically in the degree of vermiculation and U-patterning. It
 585 has a fairly extensive white throat and the neck is buff below with black to brownish marks. *P. c.*
 586 *sharpii* (1.4% CYTB divergent from *clappertoni*) has marks on the belly which are streakier than those
 587 in *clappertoni* in having a more buffy white background below with the upper belly being similarly U-
 588 patterned extending onto the back [2]. A single specimen collected at "Ngeem" at Lake Chad (possibly
 589 Nguigmi), the type of *Francolinus' tschadensis* is possibly a hybrid between *clappertoni* and
 590 *icterorhynchus* [2].

591 The closest CYTB taxon to *clappertoni* is its sister-species, *P. harwoodi*, at 1.4% sequence
 592 divergence. The next closest taxon is *P. bicalcaratus*, jumping to 3.1% divergence.

593
 594 *Pternistis harwoodi* is a medium-sized (one male 545 g., one female 446 g. [54]), poorly known
 595 species occurring in *Typha* reedbeds, scrub, thicket and adjacent cultivations along the gorges of the
 596 Jemmu valley, the Blue Nile and its tributaries of East Africa, and the highlands of central Ethiopia
 597 (Fig 6).

598 Harwood's Spurfowl [2] has a red bill with a black tip, bare red eye-ring and tarsi with 1-2 spurs, in
 599 males only. It most closely resembles *P. natalensis*, which lacks the bare red facial skin, but has more
 600 defined U-patterning on the nape, with similar U-patterning on the underparts. The upperparts of the
 601 male that we examined is grey speckled and finely barred with blackish and buff above. The lack of a
 602 white eyestripe sets it apart from other Vermiculated spurfowls. The hind and lower neck, sides of

603 face, and throat are speckled with black and white. It has irregular double-V shaped patterning on its
 604 underparts which tends to be scattered on the lower extreme of the buff belly.

605 The closest CYTB taxon is *P. clappertoni* ‘*sharpii*’ at 0.7% sequence divergence. The next closest
 606 taxon is *P. natalensis* at 4.8%.

607

608 **The Bare-throated spurfowls**

609 We recognize five species and five subspecies: *leucoscepus* (*leucoscepus*, *infuscatus*), *cranchii*, *afer*
 610 (*afer*, *castaneiventer*, *humboldtii*), *swainsonii*, and *rufopictus*.

611 The Bare-throated spurfowls [2, 54] are largely allo/parapatric and ecologically segregated meta-
 612 populations, extending from Ethiopia and Eritrea in northeast Africa, westwards through Kenya,
 613 Tanzania, Sudan and Uganda to the Congo and Gabon, and south through Angola, northern Namibia,
 614 Botswana, Zimbabwe, and Mozambique to South Africa (Figs 7 and 8). Species inhabit mesic lowland
 615 grasslands and open woodland savanna/bush often adjacent to water.

616

617 **Fig 7. Geographical distributions of Bare-throated spurfowls (part).**

618 **Fig 8. Geographical distributions of Bare-throated spurfowls (concl.).**

619

620 Bare-throated spurfowls are sexually monomorphic in plumage (although females of some species
 621 are slightly vermiculated), with a body mass ranging from 340–950 g [2, 54]. They are distinguished
 622 from other spurfowls by having bare skin on the throat and a patch around the eye and plain dark
 623 upperparts without pale vermiculations. Their tarsi are black, red, orange or brown with spurs well-
 624 developed in males only. They have a long robust lower spur and, in some taxa (*P. leucoscepus* and *P.*
 625 *rufopictus*), often a shorter blunt upper spur, less prevalent in *P. afer* and rare in *P. swainsonii* [2].

626

627 *Pternistis leucoscepus* is a medium-sized, markedly dimorphic spurfowl (males 615-896 g., females
 628 400-615 g. [54]). This species is the most morphologically and ecologically differentiated species and
 629 comprises two subspecies: *leucoscepus* and *infuscatus* (Fig 3). It occurs in arid-acacia savanna and
 630 sub-desert scrub in eastern Africa (most of Kenya, north-eastern Uganda, south-eastern South Sudan
 631 and northern Tanzania), extending north and east through Ethiopia and Somalia nearly to the tip of the
 632 'Horn' of Africa (Fig 7) [2, 54].

633 Both subspecies of the Yellow-necked Spurfowl [2, 54] have black bills with a red base, bare red
 634 skin around the eye, bare yellow throat skin, and black tarsi with 1-2 spurs on the males. The upper
 635 back plumage is dark brown with white shaft streaks and the underparts are streaked with white and
 636 chestnut with narrow white edges and a triangular white patch at the tip, tapering up the shaft. The
 637 primaries have a conspicuous white patch, which is visible during flight. The northern subspecies
 638 *infuscatus* at 0.9% sequence divergence from *P. l. leucoscepus*, differs in having more chestnut than
 639 white on the underparts in contrast with the dominant white over chestnut present in *leucoscepus*.

640 The closest CYTB taxon to *P. leucoscepus* is *P. cranchii* at 3.5% sequence divergence.

641

642 Hall's [5] 'Red-necked' Spurfowl [2, 54] is the most widespread and morphologically variable
 643 'species' of Bare-throated spurfowl. It has a complex geographical distribution and occurs in relatively
 644 mesic evergreen forest edges, and woodland in central Africa and Kenya, extending southwards
 645 through, Zambia, Malawi, Tanzania, south-western Angola, north-western Namibia, eastern
 646 Zimbabwe, Mozambique into eastern South Africa (Fig 8) [9].

647 All taxa ascribed to this spurfowl were lumped into one species [2], *afer*, with two polytypic
 648 subspecies, *afer* and *cranchii* [h]. We elevate *cranchii* to full species status (Fig. 8). Both species are

649 medium-sized (males 480-1000 g., females 370-690 g.) and have a red bill, throat skin and tarsi with
 650 1-2 spurs in males only [9].

651

652 *Pternistis cranchii* [2, 9] includes populations from southern Congo, northern Angola, northern
 653 Zambia, western Tanzania, Uganda and Lake Victoria shores (Fig 8). It is characterized by having no
 654 white on the head or black on the abdomen. The underparts are heavily and finely vermiculated with
 655 grey with heavy chestnut brown streaking on the abdomen. Its lower belly feathers have buff central
 656 streaks vermiculated with blackish grey and margined with broad chestnut (degree of chestnut colour
 657 varies geographically) and a black and grey facial pattern. Populations from the Ruzizi valley, north of
 658 Lake Tanganyika, (*'harterti'*) are much darker overall, and the streaking on the abdomen is maroon,
 659 rather than chestnut [2].

660 Within Hall's [2] '*cranchii*' forms (*cranchii*, '*nyanzae*', '*harterti*'), the CYTB divergences are c.
 661 1%, and the lowest CYTB divergence between a form of *cranchii sensu lato* to one within *afer* (from
 662 Angola) is 1.6% sequence divergence. Thereafter, the pairwise divergence values for forms of *cranchii*
 663 versus *afer* well exceed 2%. All 'hybrid' forms studied (*'intercedens'*, '*bohmi*', '*itigi*', '*cunenensis*'
 664 and '*benguellensis*') are 0.7-0.8 % divergent from 'pure' *cranchii* and >2% divergent from *afer* taxa.

665

666 In marked contrast to *cranchii*, populations of *P. afer sensu stricto* [2, 9, 54] have unvermiculated
 667 underparts, and are strongly patterned black and white on the face and underparts, which have broadly
 668 streaked greyish black central streaks with buff margins (particularly in the nominate subspecies *afer*)
 669 or have thin greyish black central streaks separating the long buff parallel streaks margined with black
 670 or sometimes maroon (in south-eastern South African specimens).

671 In the nominate *P. a. afer*, confined to south-western Angola (Fig 8), the face is white, and the
 672 underparts are streaked broadly with black and white, with black centres and white margins. Elsewhere
 673 in Angola, specimens from the Upper Okavango basin generally resemble *cranchii* with some
 674 intermediate plumage forms ‘hybrids’ – ‘*cunenensis*’ genetically closest (0.5% divergent) to *cranchii*.

675 The closest CYTB species to Angolan *P. a. afer* is *P. c. cranchii* at 1.6% sequence divergence. It is
 676 2.7% divergent from South African *P. afer*.

677 In south-eastern Africa, *P. a. castaneiventer*, occurs in South Africa from KwaZulu-Natal south and
 678 west into the Eastern Cape Province (Fig. 8). It has a wholly black face with the upper breast and
 679 abdomen streaked with black and white, edged maroon in birds from KwaZulu-Natal. Birds from
 680 eastern Zimbabwe and southern Mozambique have a white face and ‘necklace’ above the breast.

681 *P. a. castaneiventer* is 2.7% divergent from South African *P. afer*.

682 The closest non-*afer* CYTB species-level taxon is the *P. c. ‘cunenensis’* at 2.7% sequence
 683 divergence.

684 *Pternistis a. humboldtii* ranges within eastern Africa, from southern Kenya and Tanzania south to
 685 Mozambique (Fig. 8). It is 1.3% divergent from *P. a. castaneiventer* and 2.6% from *P. cranchii*, has a
 686 black face with a white jaw-beard and black belly patch. Feathers on the upper belly are mainly grey
 687 with black shaft streaks which contrast with the abdomen to form a black patch, and the flanks which
 688 are streaked black and white. Birds from coastal Kenya, have a white face and black and white
 689 eyestripe. Birds from northern Tanzania southwards to Malawi and southeastern Zambia have a wholly
 690 black face [2].

691 A range of additional idiosyncratic subspecies of intermediate phenotype relative to the *cranchii*
 692 and *afer* have been described where these three forms are para/sympatric, but they lack the
 693 morphological cohesion necessary for recognition. These occur mainly in two hybrid zones between

694 *cranchii* and *afer*. One stretches from Kondoa Dodoma in central Tanzania through central Malawi
 695 into the Luangwa Valley (Fig. 8). Hybrids have well-defined streaks on the abdomen and varying
 696 amounts of chestnut and black-and-white depending on relative proximity to the respective parental
 697 forms, but show little within-locality morphological variation [2]. The second hybrid zone in northern
 698 and central Angola is characterized by morphologically relatively unstructured populations [2].

699

700 *Pternistis rufopictus* is a monotypic medium-large spurfowl (males 779-964 g., females 400-666 g.
 701 [2, 54]) distributed in dry savannas, thickets and plains from the south-eastern shores of Lake Victoria
 702 to the Wembere River in north-western Tanzania (Fig 7). It is narrowly sympatric with *P. leucoscepus*
 703 where their distribution overlaps in the southern parts of its range [2].

704 It has a red bill, orange-pink throat skin, bare red skin around the eye, and brown tarsi with 1-2
 705 spurs on males only. The eye-stripe and sides of the face are black and white. It also has a white chin
 706 stripe on either side of the bare throat. Its upper back plumage is grey-brown with dark vermiculations
 707 and dark shaft streaks, grading posteriorly to black, white and chestnut streaking. The wing coverts and
 708 feathers on the back are edged with rufous chestnut. The upper belly is grey with black shaft streaks
 709 and the lower belly is streaked black and white. The lower belly feathers have narrow central black
 710 streaks separated from rufous chestnut margins by broad buff to white streaks. *P. rufopictus* is similar
 711 to the *cranchii*-type taxa in western Tanzania, except for the white chin stripes on either side of the
 712 throat (as in *humboldtii*), and no vermiculations [2].

713 Its closest CYTB taxon is *P. afer cranchii* at 1.7% sequence divergence. Its next closest CYTB
 714 taxon is *P. leucoscepus* at 4.0%.

715

716 *Pternistis swainsonii*, is a monotypic, medium-sized spurfowl (males 400-875 g., females 340-750
 717 g. [9]) distributed across south-western Africa from northern Namibia, eastern Botswana, Zimbabwe,
 718 southern and eastern Zambia, southwards to north-eastern South Africa (Fig 7). It frequents
 719 acacia/mopane savanna and tall grassland, almost anywhere where there is suitable cover. It is
 720 especially partial to cultivated lands. Its range and numbers have increased in recent decades in the
 721 south-eastern parts of its distribution due to agriculture-related alteration of the environment.

722 Swainson's Spurfowl [9] has a black upper mandible (lower dull orange), bare red throat skin and
 723 black tarsi, normally with a single spur in the male. Its upperparts are grey brown with faint dark shaft-
 724 streaking. The underparts are similar but with a grey wash on the breast and chestnut streaking lower
 725 down. Specimens from southern Zimbabwe and northern South Africa have blackish mottling on the
 726 abdomen. The feathers have a narrow central greyish black streak separated from greyish chestnut
 727 margins by broad buff grey vermiculated streaks [2].

728 The closest CYTB taxon to *P. swainsonii* is *P. cranchii* at 3.6% sequence divergence.

729

730 Discussion

731 Origin of African spurfowls and 'groups'

732 The African spurfowls represent a remarkable biogeographical, morphological, behavioural and
 733 ecological radiation within the entire African continent. The existence of a subspecies of *Pternistis*
 734 *bicalcaratus* in Morocco, exceptional amongst Afrotropical birds [56], demonstrates relatively recent
 735 biogeographic connectivity between North and sub-Saharan Africa.

736 African spurfowls are sister to *Ammoperdix heyi* [native range from Egypt and Israel east to
 737 southern Arabia] and *Perdicula asiatica* [native range India, Nepal, Bangladesh, Pakistan and Sri

Lanka] [20], which are both arid-zone taxa [8]. The phylogenetically most basal African spurfowl, *hartlaubi*, is also a highly peculiar, desertic bird [9, 53]. Therefore, African spurfowls may have been derived from an arid-adapted taxon that dispersed from the Middle East or Asia into Africa (30-40 mybp, 20] during a continent-wide arid era. Hall [2] also suggested an Asiatic origin. Within Africa, dispersal to the south may have been facilitated by an ‘Arid Corridor’ that has multiply connected the northeast arid Horn of Africa to arid Namibia and the Karoo in the southwest [57, 58, 59, 60].

Montane and scaly spurfowls

The Montane and Scaly spurfowls follow on from *hartlaubi* paraphyletically (Fig 2). They are probably results of invasions of, and diversification within, forested biotopes where they predominated thereafter during subsequent wetter eras. Initially, when forests subsequently contracted geographically during renewed dry eras, proto-Montane spurfowls became isolated in relictual, island-like patches of montane forest. This scenario is supported by two of the relatively basal, most isolated, western Montane taxa (*camerunensis* and *swierstrai*) being geographically most proximal to the hill/mountain-dwelling *hartlaubi*, and relatively small, sexually dimorphic, and poorly spurred.

The Noble Spurfowl, *P. nobilis*, this Montane taxon is geographically intermediate between western and north-eastern African Montane taxa and is sister to *camerunensis* and phylogenetically ‘links’ all of these western taxa to those in the northeast. It is also of intermediate body mass between the two species assemblages [54].

The divergence of Scaly spurfowls from Montane taxa is probably more a consequence of ecologically opportunistic speciation during multiple expansions and contractions of lowland forests separated by intervening savanna/steppe, hence the relatively close genetic propinquity between montane *jacksoni* and scaly *griseostriatus*, and montane *swierstrai* and scaly *squamatus*.

761 Although the core ranges of *ahantensis* and *squamatus* closely coincide with the current distribution
 762 of present-day lowland forest, the existence of peripheral, island-like isolates suggests a much broader
 763 continuous distribution in more widespread forest during wetter eras. Indeed, the primordial ‘scaly’
 764 spurfowl may have been a single species distributed continuously from West Africa eastwards to the
 765 East African coast and south to Angola, with an initial vicariance event producing *griseostriatus*. The
 766 second major forest vicariance event and physical barrier of the Niger River may have split *ahantensis*
 767 from *squamatus*.

768 Furthermore, vicariant ‘subspeciation’ within proto-*squamatus*, may have promoted the divergence
 769 of *schuetti* in paleo-forest isolates in the east (Fig 4) during drier eras, as it seems to have done within
 770 Latham’s Forest Francolin, *Afrocolinus lathamii* [Mandiwana-Neudani et al., in review] and Plumed
 771 Guineafowl, *Guttera plumifera* [61].

772 Finally, Hall [2] noted that *squamatus* extends its range to higher altitudes on mountains
 773 uninhabited by montane spurfowls, suggesting that competition might also limit its range.

774

775 **Vermiculated and Bare-throated Spurfowls**

776 Moving into relatively open arid-steppe, savanna, woodland and bush biotopes, the vicariant speciation
 777 of Vermiculated and Bare-throated taxa was within pockets of these biotopes promoted by physical
 778 barriers (lakes, rivers and valleys), other geomorphological events and expansion and contraction of
 779 forest [62, 63].

780 For example, the southern Vermiculated *P. hildebrandti* and *natalensis* have similar habitats and are
 781 separated by the valleys of the Shire and Luangwa Rivers [2]. Within the northern Vermiculated taxa,
 782 Lake Chad probably played a similar role in speciation between proto-*bicalcaratus* and proto-
 783 *icterorhynchus* + *clappertoni* [62]. These latter two spurfowls perhaps diverged in broad stretches of

784 arid (*clappertoni*) and mesic (*icterorhynchus*) savanna/grassland. Riverine forest along the Nile and in
 785 Kenya/Uganda could also have separated proto-*icterorhynchus* in the north from proto-*hildebrandti* in
 786 the south [2].

787 The initial divergence of Vermiculated taxa probably occurred in central/southern Africa with the
 788 proto-southern taxa radiating within the region into xeric western (*adpersus* + *capensis*) and mesic
 789 eastern (*hildebrandti* + *natalensis*) clades. Northern taxa may be a result of invasion from the south via
 790 the ‘Arid Corridor’.

791 In sharp contrast, the northward dispersal of *bicalcaratus* from West Africa into Morocco was via a
 792 relatively recent corridor of savanna biotope that subsequently reverted to the western Sahara.

793 With regard to Bare-throated taxa, proto-*leucoscepus* originated in arid biotopes in the north and
 794 subsequently dispersed southwards, once again via the ‘Arid corridor’, with proto-
 795 *cranchii/afer/swainsonii* biogeographically insinuating themselves within southern Vermiculated taxa.

796 Ecological speciation due to competition may also have contributed to speciation in Vermiculated
 797 taxa. Those north of the equator are birds of grasslands and cultivations in woodlands, savannas and
 798 steppe. But, south of the equator, these habitats are occupied by Bare-throated taxa, and southern
 799 Vermiculated taxa are relegated to thickets on rocky hillsides and along rivers.

800

801 **Relevance of the ‘Realm’ of Tokogeny**

802 There is also evidence that tokogenetic processes may have played significant roles in the evolution of
 803 *Pternistis* species and subspecies. Interbreeding is most apparent in the Vermiculated and Bare-
 804 throated taxa which may continue to ‘hybridize’ in captivity or where they come into contact in nature.
 805 For example, where *P. cranchii* and *afer* hybridize along the ‘Arid corridor’ and especially in eastern
 806 Zambia west of the Luangwa River, south to 13°30’ and also in the Eastern Province plateau in

807 Lundazi, hybrid forms show remarkably high within-locality morphological homogeneity, forming
 808 microgeographic ‘races’. But, where *cranchii* and *afer* hybridize in southern Angola and northern
 809 Namibia, there is no such morphological homogeneity. Indeed, Roberts [64] described a ‘new species’
 810 of spurfowl, *P. cooperi*, from near Harare, Zimbabwe (Fig. 7), which turned out to be a hybrid
 811 between *cranchii* and *swainsonii*, probably due to range expansion by *swainsonii* into *cranchii* habitat
 812 which was transformed by agriculture.

813 McCarthy [29] also reports a range of spurfowl hybrids, mainly within and between Vermiculated
 814 and Bare-throated taxa: *afer* X *leucoscepus*; *afer* X *swainsonii*; *bicalcaratus* X *erckelii*; *castaneicollis*
 815 X *erckelii*; *hildebrandti* X *natalensis*; *leucoscepus* X *rufopictus*; *natalensis* X *swainsonii*; *adpersus* X
 816 *natalensis*, and *adpersus* X *swainsonii* recorded by Little [65, 66].

817 Perhaps the most interesting taxon in this regard is *P. rufopictus*, which Hall [2] speculated might
 818 have resulted from stabilized hybridization. This is because it is ‘diagnosed’ by a combination of
 819 characters of the other Bare-throated taxa (e.g. orange, rather than red or yellow facial skin) and
 820 ‘hybrid’ (vermiculated, chestnut, white and black) plumage. Genetically, it is +-4% divergent from
 821 *leucoscepus*, +-1.8% from *cranchii* and hybrids, and 2.4-3.2% from *afer*. Phylogenetically, it ‘links’
 822 *swainsonii* + *cranchii* with *afer*. Vocally, it sounds very similar to *P. leucoscepus* except that its call is
 823 much ‘faster’. The strophes of *P. leucoscepus* and *P. rufopictus* are both high-pitched, with an element
 824 of screeching and more protracted trilling [17]. Nevertheless, its specific status seems appropriate
 825 since it seems to exist partially sympatric with *leucoscepus* and *afer* without unfettered hybridization.
 826 Its putative hybrid origins remain to be tested using genomic data.

827

828

829

Acknowledgements

We acknowledge ‘Pat’ Hall’s contributions as a pioneering systematist/biogeographer and as a generous mentor. We thank the curators and collection managers at the American Museum of Natural History (New York), the Natural History Museum (Tring), Humboldt-Museum (Berlin), the National Museum of Natural History - Smithsonian Institution (Washington, D.C.), the Ditsong National Museum of Natural History (Ditsong Museums of South Africa), the Iziko Museum of Natural History, the Natural History Museum of Zimbabwe (Bulawayo), the Field Museum of Natural History (Chicago), Carnegie Museum of Natural History (Pittsburgh), Academy of Natural Sciences of Philadelphia, Natural History Museum of Los Angeles County, Museum of Comparative Zoology (Harvard University), and the Royal Museum for Central Africa (Tervuren) for access to specimens under their care. We thank Robert Moyle for help with designing primers and Julie Feinstein for helping with the sequencing of toe pads sub-sampled from museum skins. This project was funded by the South African Department of Science and Technology (DST) and the National Research Foundation (NRF) through their South African Biosystematics Initiative and Centre of Excellence Programmes, and the African Gamebird Research, Education and Development Trust. Amy Bruce kindly assisted with constructing the figures.

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1009 **Appendix 1. Spurfowl taxa examined and, where relevant, Genbank accession numbers for taxa**
 1010 **sequenced for different molecular markers.**

Taxon	GenBank accession numbers			
	CYTB	12S	Control region	ND2
<i>Pternistis hartlaubi</i>	FR691618	FR691555	FR716656	FR691572
<i>P. h. crypticus</i>	FR691619			
<i>P. adspersus</i>	FR691623	DQ832113	FR691381	DQ768276
<i>P. a. kalahari</i>				
<i>P. afer</i> Angola	FR694158			FR691579
<i>P. a. benguellensis</i>	FR694159			
<i>P. a. itigi</i>				
<i>P. a. bohmi</i>	FR694162			
<i>P. cranchii cranchii</i>	FR694164			
<i>P. afer cunenensis</i>	FR694160			
<i>P. a. harterti</i>	FR694161			
<i>P. a. intercedens</i>	FR694165			
<i>P. a. itigi</i>	FR694166			
<i>P. a. nudicollis</i>	FR694163			
<i>P. a. nyanzae</i>	FR694167			
<i>P. a.</i> South Africa	AM236908	DQ832111	DQ834533	DQ768280
<i>P. a. swynnertoni</i>	FR694168			
<i>P. a. humboldti</i>				
<i>P. a. melanogaster</i>	FR691624	FR691551	FR691370	FR691578

P.a. castaneiventer

P.a. krebsi

P.a. notatus

P. bicalcaratus bicalcaratus

P. b. adamauae FR691626

P. b. ayesha FR691625

P. b. thornei FR691627

P. b. ogilviegranti

P. camerunensis FR691591 FR691552 FR691382 FR691577

P. capensis AM236909 DQ832112 DQ834534 DQ768282

P. castaneicollis AM236903

P. c. bottega FR691629

P. c. ogoensis FR691628

P. c. gofanus

P.c. kaffanus

P. clappertoni FR691602 FR716655 FR691383 FR691576

P. c. nigrosquamatus FR691604

P. c. sharpii FR691603

P. erckelii FR691589 FR691553 FR691575

P. griseostriatus AM236905 FR691554 FR691384 DQ768284

P. harwoodi FR691600

P. hildebrandti FR691595 FR691385

<i>P. h. altumi</i>	FR691597			
<i>P. h. fischeri</i>	FR691598			
<i>P. h. helleri</i>	FR691599			
<i>P. h. johnstoni</i>	FR691596			
<i>P. icterorhynchus</i>	FR691601			
<i>P. i. griseus</i>				
<i>P.i. emini</i>				
<i>P. i. ugandensis</i>				
<i>P. i. dybowskii</i>				
<i>P. jacksoni</i>	FR691594			
<i>P. leucoscepus</i>	AM236906	FR691556	FR691387	DQ768283
<i>P. l. infuscatus</i>	FR691587			
<i>P. l. muhamed-ben-abdullah</i>	FR691586			
<i>P. l. holtemulleri</i>				
<i>P. natalensis</i>	AM236911	FR691557	DQ834536	DQ768285
<i>P. n. thamnobium</i>				
<i>P. nobilis</i>	FR691592			
<i>P. ochropectus</i>	FR691590			
<i>P. rufopictus</i>	FR691588			
<i>P. squamatus</i>	AM236904	DQ832109	FR691388	DQ768286
<i>P. s. maranensis</i>	FR691630			
<i>P. s. schuettii</i>	FR691631			
<i>P. s. tetraoninus</i>	AM236907	DQ832110	DQ834532	DQ768287

P. s. zappeyi

P. swainsonii

P. s. chobiensis FR694170

P. s. lundazi FR694169

P. swierstrai FR691593

P. cl. cavei

P. cl. gedgii

1011

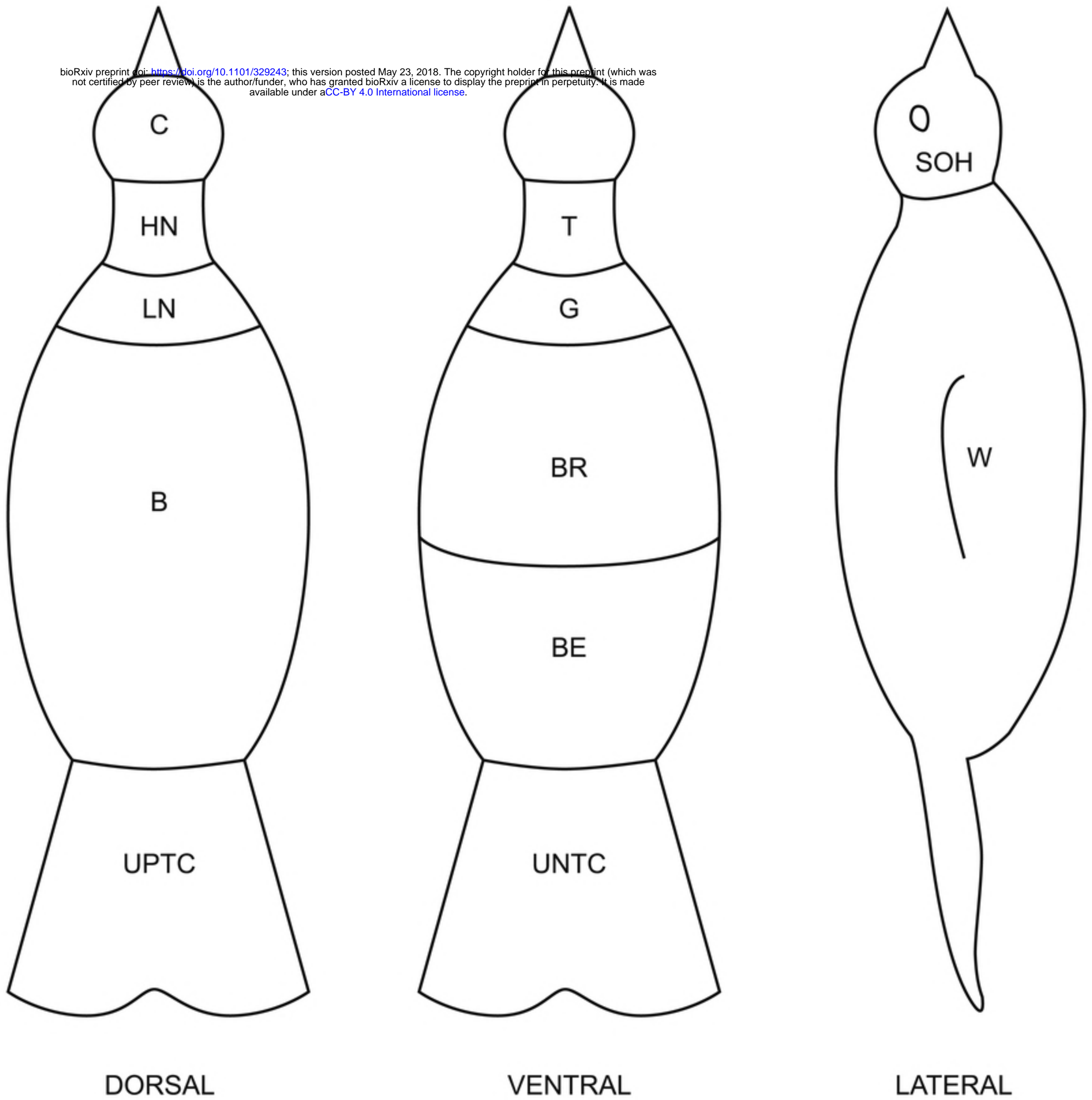
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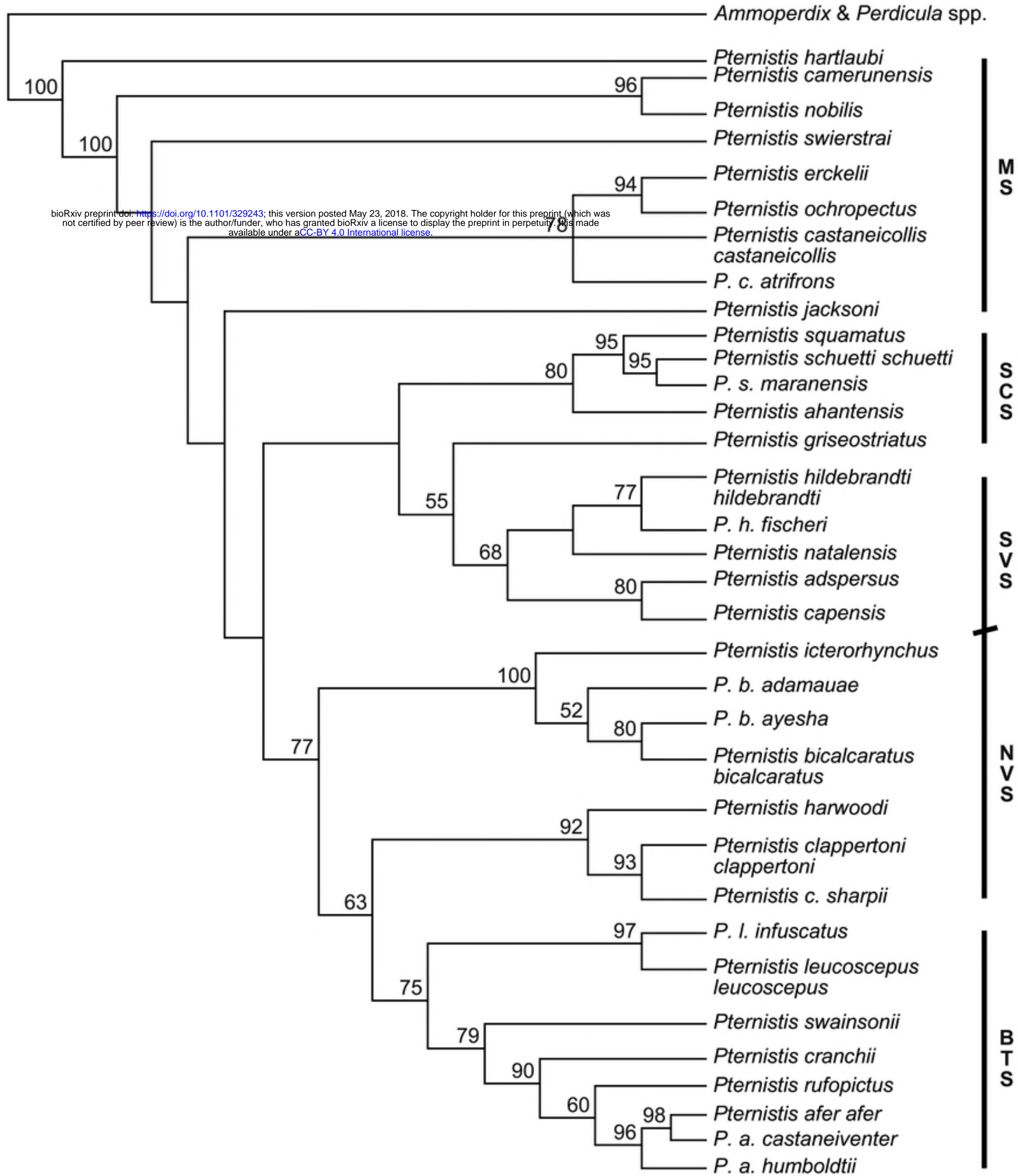
1013 **Appendix 2. Revised classification and common names for spurfowls based on multiple lines of**
 1014 **evidence presented in this study.** Family: Phasianidae; sub-family: Coturnicinae

Genus, species, subspecies	Common names
<i>Genus: Pternistis</i>	
<i>P. hartlaubi</i>	Hartlaub's Spurfowl
<i>P. camerunensis</i>	Mount Cameroon Spurfowl
<i>P. nobilis</i>	Handsome Spurfowl
<i>P. swierstrai</i>	Swierstra's Spurfowl
<i>P. erckelii</i>	Djibouti Spurfowl
<i>P. ochropectus</i>	Djibouti Spurfowl
<i>P. castaneicollis castaneicollis</i>	Chestnut-naped Spurfowl
<i>P. c. atrifrons</i>	Black-fronted Spurfowl
<i>P. jacksoni</i>	Jackson's Spurfowl
<i>P. squamatus</i>	Scaly Spurfowl
<i>P. schuetti schuettii</i>	Schuett's Spurfowl
<i>P. s. maranensis</i>	
<i>P. ahantensis</i>	Ahanta Spurfowl
<i>P. griseostriatus</i>	Grey-striped Spurfowl
<i>P. hildebrandti hildebrandti</i>	Hildebrandt's Spurfowl
<i>P. h. fischeri</i>	
<i>P. natalensis</i>	Natal Spurfowl
<i>P. adspersus</i>	Red-billed Spurfowl
<i>P. capensis</i>	Cape Spurfowl

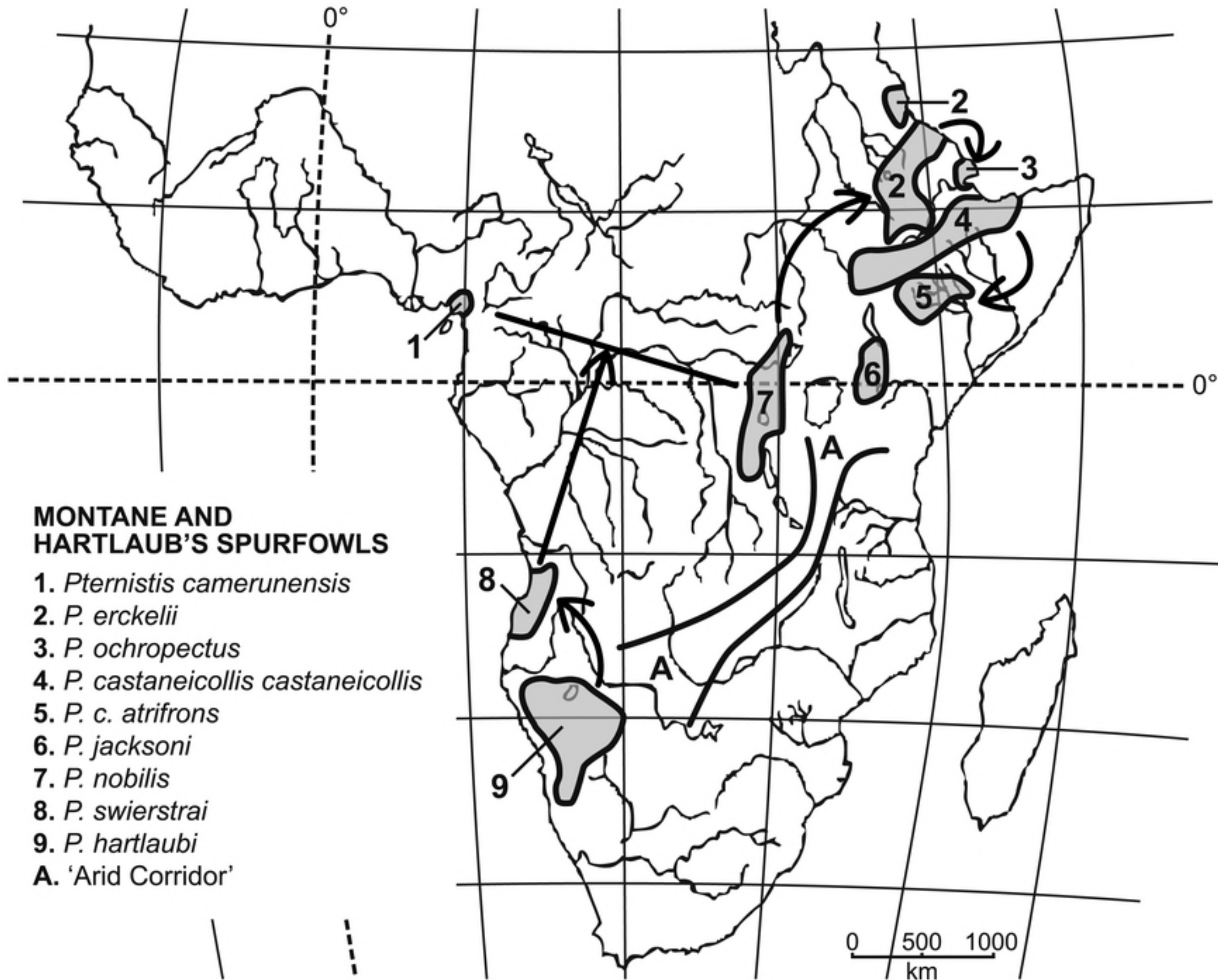
<i>P. icterorhynchus</i>	Heuglin's Spurfowl
<i>P. bicalcaratus bicalcaratus</i>	Double-spurred Spurfowl
<i>P. b. ayesha</i>	Moroccan Spurfowl
<i>P. b. adamauae</i>	
<i>P. harwoodi</i>	Harwood's Spurfowl
<i>P. clappertoni clappertoni</i>	Clapperton's Spurfowl
<i>P. c. sharpii</i>	
<i>P. leucoscepus leucoscepus</i>	Yellow-necked Spurfowl
<i>P. l. infuscatus</i>	
<i>P. swainsonii</i>	Swainson's Spurfowl
<i>P. cranchii</i> *	Cranch's Spurfowl
<i>P. rufopictus</i>	Grey-breasted Spurfowl
<i>P. afer afer</i>	Red-necked Spurfowl
<i>P. a. castaneiventer</i>	
<i>P. a. humboldtii</i>	

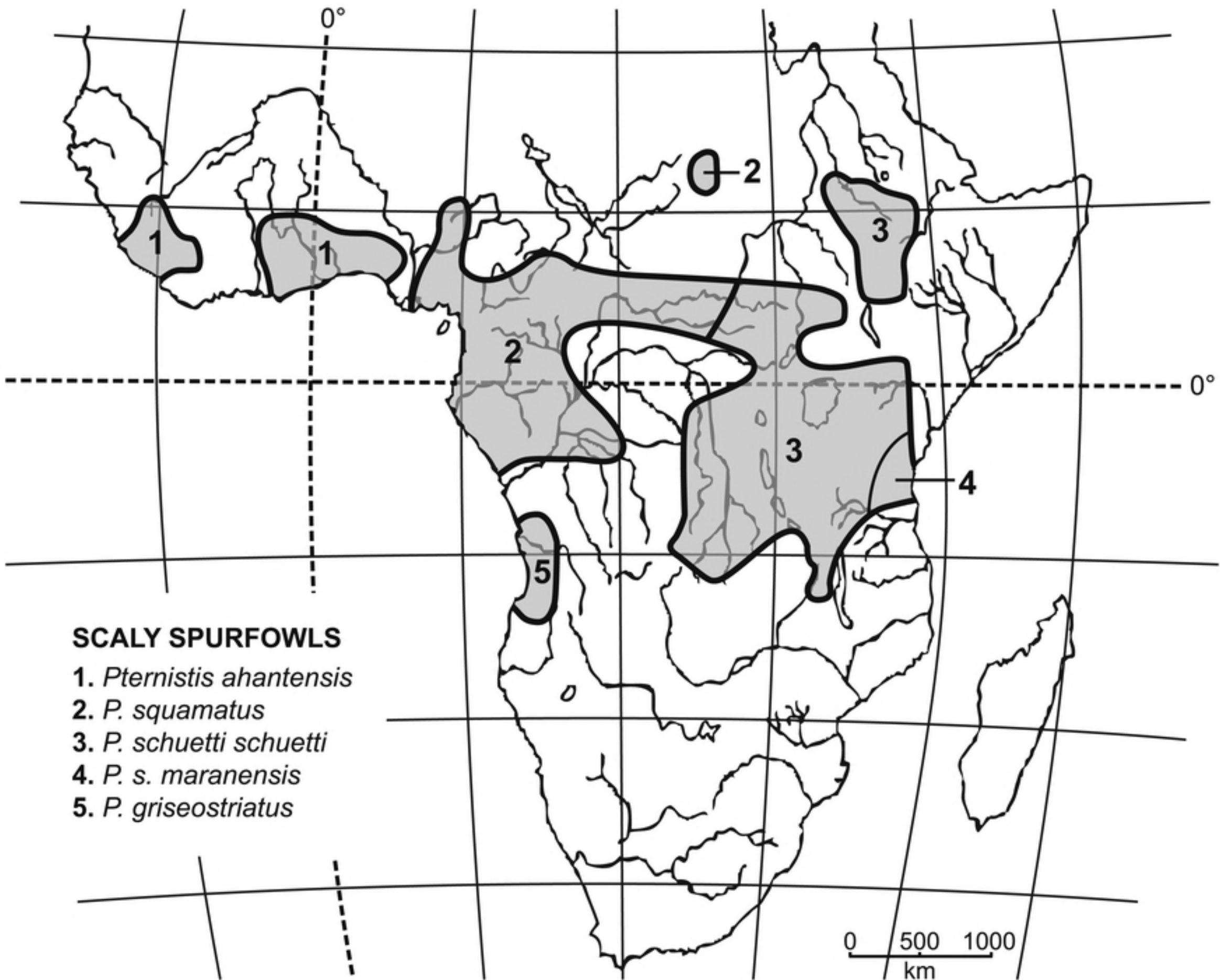
* subspecies elevated to species

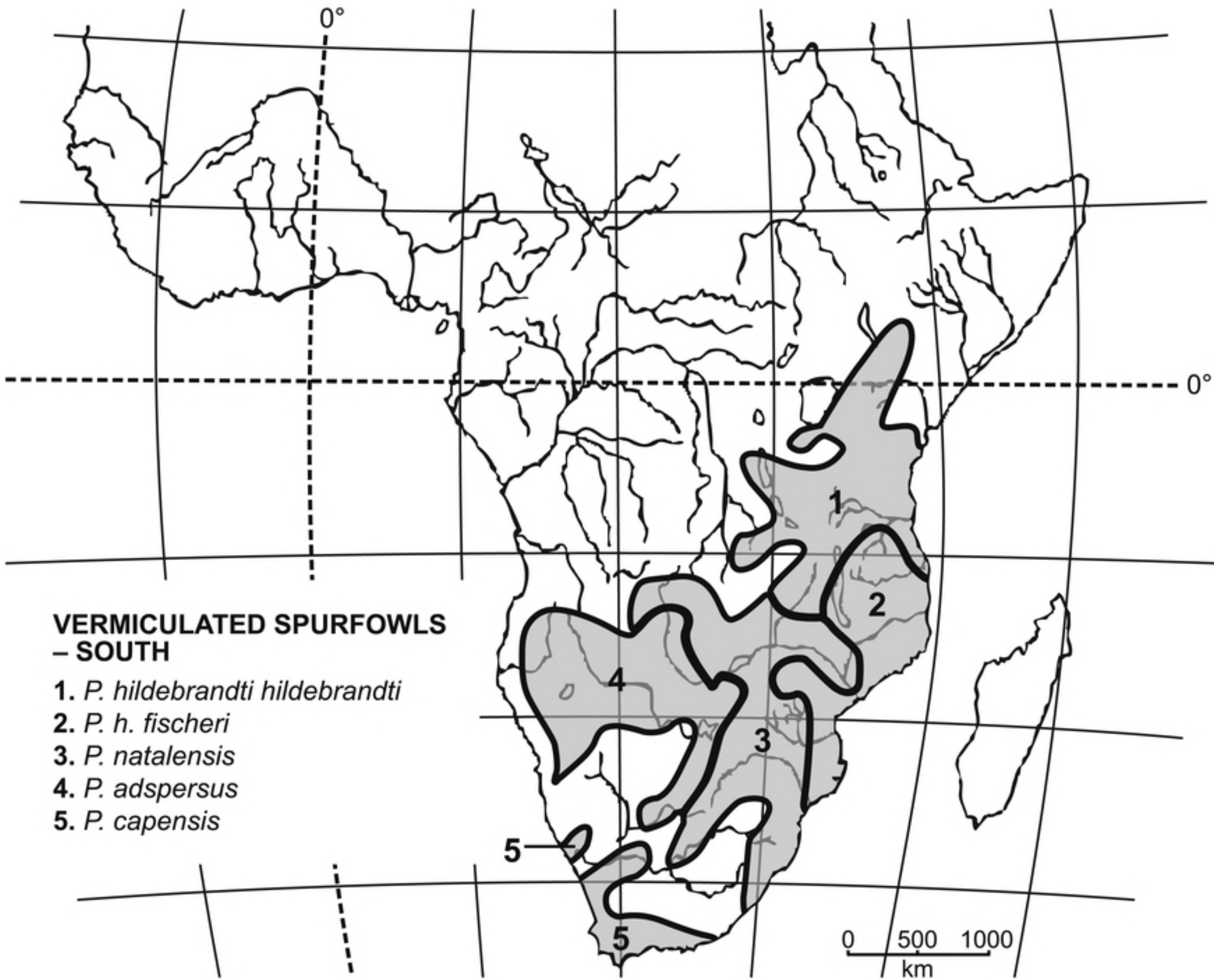


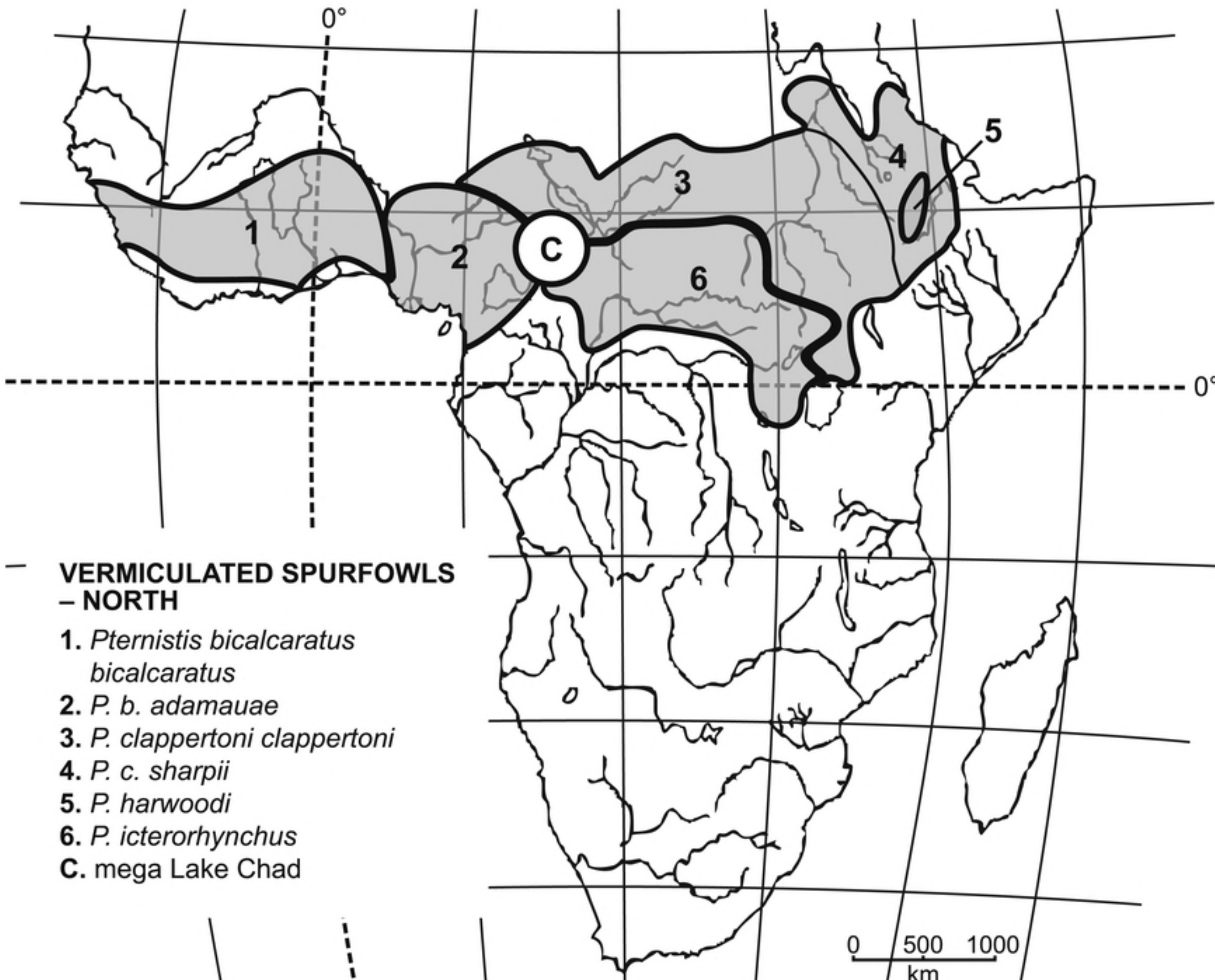


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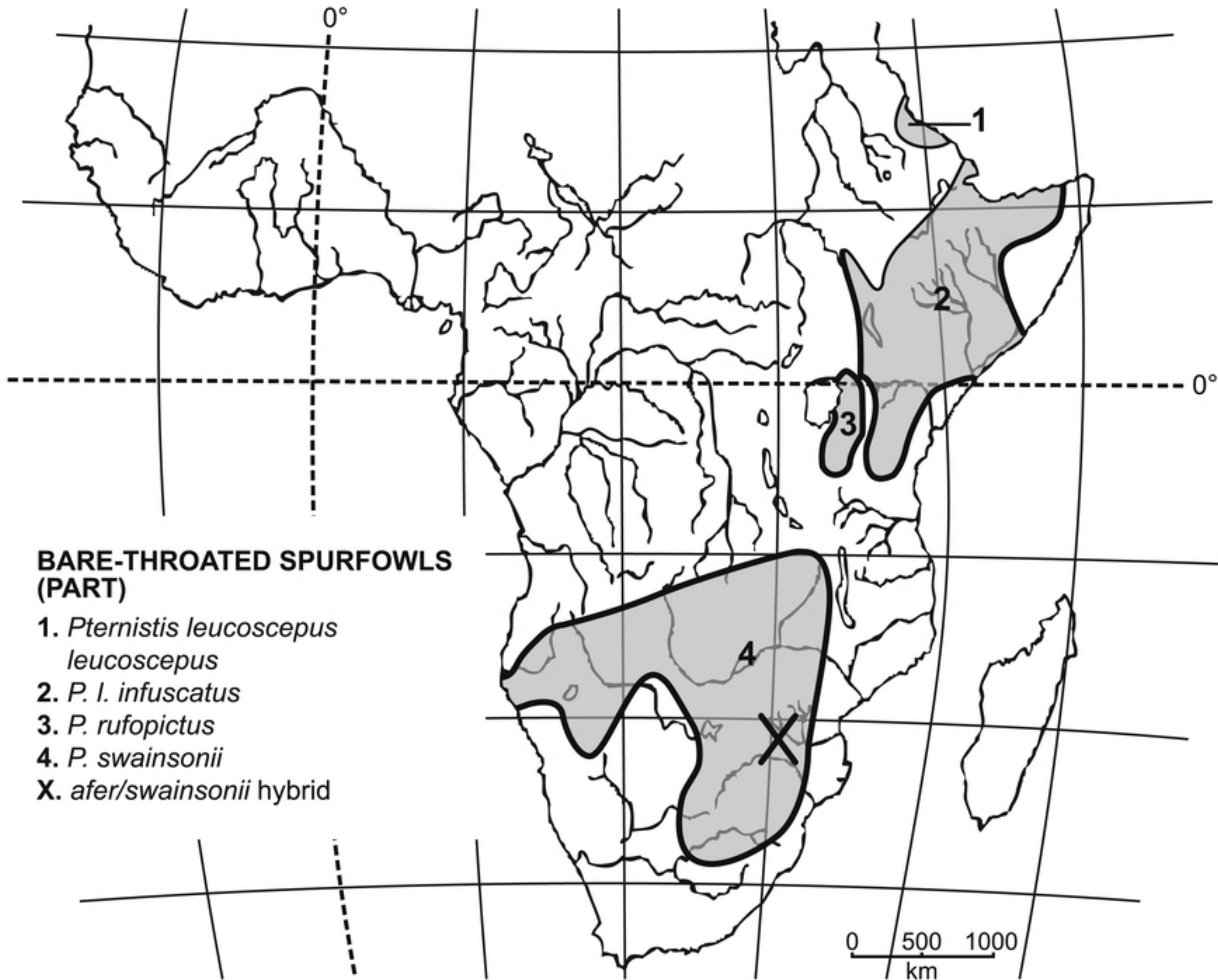






**VERMICULATED SPURFOWLS
– NORTH**

- 1. *Pternistis bicalcaratus*
bicalcaratus
- 2. *P. b. adamauae*
- 3. *P. clappertoni clappertoni*
- 4. *P. c. sharpii*
- 5. *P. harwoodi*
- 6. *P. icterorhynchus*
- C. mega Lake Chad



**BARE-THROATED SPURFOWLS
(CONCL.)**

1. *Pternistis cranchii*

2. *P. a. humboldtii*

3. *P. afer afer*

4. *P. a. castaneiventer*

H1. *cranchii/afer* hybrids

H2. *cranchii/humboldtii* hybrids

