Avian Research

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The phylogeny of francolins (*Francolinus, Dendroperdix, Peliperdix* and *Scleroptila*) and spurfowls (*Pternistis*) based on chick plumage (Galliformes: Phasianidae)

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Abstract

Background: This paper describes the chick plumage of spurfowl (*Pternistis*) and francolin (*Francolinus*, *Dendroperdix*, *Peliperdix* and *Scleroptila*) chicks, tests its significance for phylogenetic relationships and also explores the patterns of character evolution in the francolin and spurfowl lineages. Previously regarded as monophyletic, the two evolutionarily distant clades are now divided into five genera. Questions considered were whether chick plumage supports the dichotomy between spurfowls and francolins and what role habitat matching plays.

Methods: The study was based mainly on photographs of chick skins from the American Museum of Natural History and the Natural History Museum at Tring. Eight plumage characters were selected for comparative scoring, summarised in a matrix. These characters were subsequently analysed phylogenetically and their evolution was traced on the existing molecular phylogeny using a parsimony approach.

Results: Based on chick plumage the phylogeny of species groups among francolins and spurfowls, was largely unresolved possibly ascribed to a high degree of symplesiomorphy inherent among the Phasianids. This possibly could have resulted in a high degree of polytomy particularly among the spurfowls and francolins. Furthermore, the ancestral state reconstructions revealed high prevalence of symplesiomorphic states and reversals which do not help in the classification of groups. Although the differences are described that separate some African francolins from spurfowls, other francolins (in Asia and Africa) share remarkably similar characteristics with spurfowls. Plain dark dorsal plumage is probably advantageous for avoiding detection by predators in forests, while facial stripes optimise the breaking of body shapes in dense grass cover (as in *Scleroptila* spp.) and semi-striped faces are advantageous for stationary camouflage under tree and bush cover (as in *Pternistis* spp.).

Conclusions: Although symplesiomorphy is a hereditary explanation for downy colours and patterns, the traits relevant for habitat matching are combined in a manner which is determined (adaptation) by natural selection.

Keywords: Spurfowl, Francolin, Phasianidae, Chick plumage, Phylogeny, Ancestral state reconstruction, Habitat

Background

Melanin is the most common pigment in plumage. Two classes of melanin form the basis of the colours typically seen in birds namely eumelanins which is responsible for black and brown hues and phaeomelanins which is responsible for reddish-brown colours, but birds often possess a mixture of the two melanin types. These colours are not strongly influenced by environmental conditions but instead these pigments are produced in cells (Paxton 2009). It is predicted that the downy patterns of chicks have adapted to match habitat. The typical combination of lighter and darker chick plumage on chicks is a matter

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of pigmentation and dilution of pigment (lighter coloured plumage) respectively.

Plumage colouration and patterning can be used to infer evolutionary relationships (Vázquez and Gittleman 1998; Paxton 2009), and chick plumage patterns and colours have often been used to test phylogenetic relationships among bird taxa (Whetherbee 1957; Bertelli et al. 2002). Chicks of related species generally appear particularly similar, which is ascribed to the lack of known selective pressures for rapid divergence in chick plumage patterns during speciation, and therefore lends itself to a phylogenetic analysis that reveals evolutionary relationships. Chick plumage patterns can therefore often provide more valuable clues to phylogenetic relationships than adult plumage patterns (Milstein and Wolff 1987; Johnsgard 2008).

Gamebird chicks are highly cryptic, since they are flightless and avoid predation on the ground (Milstein and Wolff 1987). It would therefore make sense that inheritable traits and crypsis would interact, since natural selection also plays a role (Peichel 2014). Habitat matching, which refers to the consequence of natural selection where plumage colour and pattern matches the colour and texture of occupied habitats, enable birds to avoid detection and capture by predators (Short 1967; Frost 1975; Merilaita and Lind 2005; Stevens and Merilaita 2008).

Chick plumage has been found to have phylogenetic signal to delineate families and to differentiate between sub-families and species. Chick plumage studies indicate that the cassowaries (Casuaridae) and emu (Dromiceiidae) are closely related, and suggest that ostriches (Struthioniformes), cassowaries and emu (Casuariiformes) may be closely related (Jehl 1971). Bertelli et al. (2002) reviewed the chick plumage studies by Jehl (1971) and disputed the division of the tinamous (Tinamidae) into sub-families. In their response Bertelli et al. (2002) acknowledged that forest-dwelling chicks are generally dark in colour with a distinctive forehead, while the steppe tinamou species are striped. While this was used by Jehl (1971) as a cue to describe two sub-families, Bertelli et al. (2002) argued that these chicks possess plesiomorphic character states found in the family. In other words, the tinamous remain a monophyletic family.

Phylogenetic analysis of 157 characters of definitive plumages and soft parts, chick plumage, tracheae, and non-tracheal skeletons of 59 Anatini provided a phylogenetic hypothesis of high consistency (Livezey 1991). The heads of duckling species show different patterns which are particularly evident from the side of the face (laterally). Chicks of closely related species, such as *Anas fulvigula*, *A. castanea* and *A. acuta* are distinguishable based on head patterns (Livezey 1991). Duck chicks are the only group of non-passerine birds studied to date that show differentiation at the species level based on chick plumage. This is unlike the results arrived at by Jehl (1971) and Livezey (1991), whose chick plumage studies reached only sub-family level.

The chick plumage colour patterns of grouse (Tetraoninae) vary within the range of patterns revealed by other Phasianids, found for example in *Perdix perdix* and *Colinus virginianus.* Indeed, a significant pattern identified within the sub-family Tetraoninae included a variegated back, with longitudinal rufous stripes stretching forward onto the crown, a variety of facial marks and distinctive yellowish or greyish white under parts. The Tetraoninae possess a distinctive streak at the base of the mandible (Short 1967). According to Short (1967), the broad black crown cap, trimmed by a thinner black line on the crown, is ancestral to grouse such as *Lagopus*, and all crown markings of *Centrocercus* and *Dendragapus* species are remnants of the full crown cap and trimmings of ancestral forms. This suggests that there is an evolutionary relationship between the head markings within the Tetraoninae.

What do we know about francolin and spurfowl chick plumage relationships?

Hall (1963) placed all spurfowls (occurring in Africa only) and francolins (occurring in Asia and Africa) under one genus, *Francolinus*, and described differences between chicks based on chick plumage. She divided the "monophyletic francolins" into eight taxonomic groups and mentioned that the chicks of the Bare-throated, Montane, Scaly, Vermiculated (all in the genus *Pternistis*), Striated (*Dendroperdix*) and Spotted (*Francolinus*) groups have a single conspicuous brown longitudinal band (with side lines) on the back through the crown (the crown cap) and a solid blackish stripe from the bill through the eye to the neck (extended eye stripe). The Red-winged (*Scleroptila*) group also have a variegated back, but with a narrower longitudinal band, and a narrower and darker crown patch than the spurfowls, with eight alternate black and white stripes on the sides of the crown, through and under the eyes.

Within the Red-tailed (*Peliperdix*) group, the female *P. coqui* chick is similar to the chicks of the Red-winged group in that it has a crown patch with lateral dark brown and buffy coloured stripes arranged across the back through the crown and stripes under the eyes. Conversely, the male *P. coqui* chick displays a similar pattern to the basic patterns displayed by the chicks of the Bare-throated, Montane, Scaly, Vermiculated, Striated and Spotted groups, namely a broad crown cap and a single conspicuous rufous longitudinal band across the back through the crown cap and a solid blackish eye line. This difference between male and female *P. coqui* constitutes sexual dimorphism at the chick stage (Hall 1963).

In the Red-winged group the striped facial pattern (disruptive plumage) becomes a permanent cryptic feature in the adults, but in spurfowls the facial eye stripes often disappear, resulting in a plain colour in many species (Little and Crowe 2011). Although Hall (1963) mentioned that some variation was evident among sub-species of *F. francolinus* and *F. shelleyi*, she did not elaborate on this. Overall, she concluded that small variations existed among species and groups.

Francolins and spurfowls are not monophyletic

Crowe et al. (1992, 2006) reviewed the monophyletic genus "*Francolinus*" proposed by Hall and found that it represents two distant clades split among five genera: spurfowls (*Pternistis*) and francolins (*Francolinus*, *Scleroptila*, *Peliperdix* and *Dendroperdix*). In other words, based on DNA and morpho-behavioural studies, francolins and spurfowls do not share a common evolutionary path (Milstein and Wolff 1987; Crowe and Little 2004; Crowe et al. 2006). Bloomer and Crowe (1998) included the genetic material of several species, and Mandiwana-Neudani et al. (2014) analysed the genetic material (in conjunction with vocalisations) of 40 species (18 francolins and 22 spurfowls) to demonstrate the dichotomy between spurfowls and francolins. Mandiwana-Neudani et al. (2011) described the syringeal features that separated the two groups. However, none of these authors assessed chick plumage in any depth.

We assessed the chick plumage characters of chicks of traditionally recognised spurfowl and francolin species, in conjunction with a broad selection of outgroup species, to (1) describe the chick plumage of spurfowls and francolins; (2) phylogenetically confirm or dismiss the dichotomy between spurfowls and francolins; (3) investigate the patterns of evolution of chick plumage characters which are diagnostic traced on a molecular phylogeny and (4) evaluate habitat matching of spurfowl and francolin chicks.

Methods

We conducted phylogenetic analyses with common set of character states for francolin and spurfowl chicks in conjunction with a relatively large outgroup (Additional file 1: Fig. S1). A wide selection of outgroup species was important to determine the role that plesiomorphic character states play during the evolution of colours and patterns as suggested by existing literature (Short 1967; Jehl 1971) (Table 1).

Representative species from the groups described by Hall (1963) were examined, totalling 11 francolin species and 16 spurfowl species. All the chicks of francolins and spurfowls as well as a wide outgroup in the collections of the Natural History Museum at Tring and the American Museum of Natural History in New York were photographed to capture the dorsal and lateral characteristics of the head and the dorsal characteristics of back plumage (Milstein and Wolff 1987, Table 1). This data set was augmented with photographs from searches on the internet, drawings in reference books and unpublished photographs and sketches by the author (e.g. Milstein and Wolff 1987; Little and Crowe 2011; Little 2016). A photograph of a pair of *Pternistis hartlaubi* chicks was provided by Joris Komen. A day-old *P. adspersus* and *P. natalensis* hybrid chick was photographed by the author (JHvN unpublished). Although it was not possible to age the chick skins (age of chicks in days), spurfowl and African francolin chicks revealed head and facial markings and longitudinal bands on their backs which were generally consistent with the description of downy chick plumage, separating them from juveniles, in the literature (Crowe et al. 1986; Little 2016). Four *Pternistis swainsonii* chicks raised by a free ranging bantam *Gallus domesticus* hen on a farm in South Africa retained these markings for at least 5 weeks (JHvN unpublished). However, a study conducted by Little and Crowe (1992) showed that the back feathers of the *Scleroptila afra* chick disappears after about 14 days. Since all *Scleroptila* spp. had clear back bands, it is accepted that all *Scleroptila* spp. assessed were less than 14 days old. The plain state, or plain brownish or reddish chick plumage, was assumed as the ancestral root for the phylogenetic trees. In keeping with this, the Maleo (*Macrocephalon maleo*) is regarded as the oldest taxon among Galliformes; the chick possesses plain colours (not cryptic) (Crowe et al. 2006). The elected character states and the scores (0–2) allocated to 8 characters (and 25 states) are shown in Table 3. Figure 1 shows the parts (characteristics) of the head and back plumage that were used to compile the character matrix in Table 3. The taxa in Table 3 follow the nomenclature presented by Crowe et al. (2006), Little and Crowe (2011), and Mandiwana-Neudani et al. (2014) except the specific epithets which follow Gill and Donsker (2017). The mitochondrial Cytochrome *b* (mt Cyt*b*) sequences including those of francolins, spurfowls and the selected outgroups were sourced from GenBank (Table 2).

Phylogenetic analyses—chick plumage and molecular characters

Parsimony analysis was performed on both chick plumage and Cyt*b* characters in Windows-based PAUP* ver. 4.0b10 (Swofford 2002) with the following tree search parameters considered: full heuristic search with all characters unordered and with equal weight, starting tree(s) obtained via stepwise addition;

Table 1 List of museum downy chick skins and photographs within Phasianidae evaluated to study the phylogenetic relationships of spurfowls and francolins

Common name	Scientific name	No. of specimens	Reference
Maleo	*Macrocephalon maleo*	1	Internet[1]
Crested Guineafowl	*Guttera pucherani*	2	AMNH
Black Guineafowl	*Agelastes meleagrides*	1	AMNH
Vulturine Guineafowl	*Acryllium vulturinum*	1	Internet[2]
Helmeted Guineafowl	*Numida meleagris*	6	Author and NHM at Tring
Western Capercaillie	*Tetrao urogallus*	2	AMNH
Blue Grouse	*Dendragapus obscurus pallides*	9	AMNH
Willow Grouse	*Lagopus lagopus*	9	AMNH
Greater Prairie-chicken	*Tympanuchus cupido*	2	AMNH
Ring-necked Pheasant	*Phasianus colchicus*	4	AMNH
Red Jungle Fowl	*Gallus gallus*	6	NHM at Tring, AMNH
Latham's Francolin	*Peliperdix lathami*	1	NHM at Tring FWNB 1548
Coqui Francolin	*Peliperdix coqui*	8	NHM at Tring, AMNH, author 416173/5, 261918, 416174
White-throated Francolin	*Peliperdix albogularis*	1	Little (2016)
Crested Francolin	*Dendroperdix sephaena*	5	Internet and authors
Swamp Francolin	*Francolinus gularis*	1	Internet[3]
Grey Francolin	*Francolinus pondicerianus*	7	NHM at Tring, Bishop Museum, and AMNH 454656/7/8, 63492, 63484
Black Francolin	*Francolinus francolinus*	3	Internet[4]
Orange River Francolin	*Scleroptila gutturalis*	3	Authors
Red-winged Francolin	*Scleroptila lavaillantii*	1	NHM at Tring
Grey-winged Francolin	*Scleroptila afra*	2	Little (2016)
Shelley's Francolin	*Scleroptila shelleyi*	1	NHM at Tring
Chukar Partridge	*Alectoris chukar*	1	NHM at Tring
Common Quail	*Coturnix coturnix*	1	Internet[5]
Hartlaub's Spurfowl	*Pternistis hartlaubi*	2	Joris Komen
Handsome Spurfowl	*Pternistis nobilis*	1	AMNH 763926
Chestnut-naped Spurfowl	*Pternistis castaneicollis*	1	AMNH 541450
Erckel's Spurfowl	*Pternistis erckelii*	4	NHM at Tring, AMNH 541460/1/2
Scaly Spurfowl	*Pternistis squamatus*	5	NHM at Tring, AMNH 156952, 541381
Ahanta Spurfowl	*Pternistis ahantensis*	1	Crowe et al. (1986)
Red-billed Spurfowl	*Pternistis adspersus*	1	NHM at Tring
Cape Spurfowl	*Pternistis capensis*	10	Author and NHM at Tring
Natal Spurfowl	*Pternistis natalensis*	2	NHM at Tring, AMNH
Hildebrandt's Spurfowl	*Pternistis hildebrandti*	2	NHM at Tring, AMNH 541354
Heuglin's Spurfowl	*Pternistis icterorhynchus*	6	NHM at Tring, AMNH 156931/2/3, 156935, 156930
Swainson's Spurfowl	*Pternistis swainsonii*	5	Berruti (2011), authors
Grey-breasted Spurfowl	*Pternistis rufopictus*	2	NHM at Tring, internet[6]
Yellow-necked Spurfowl	*Pternistis leucoscepus*	5	NHM at Tring
Red-necked Spurfowl	*Pternistis afer*	6	NHM at Tring, AMNH 763932, 763934, 428598, 763936, 541486

AMNH American Museum of Natural History (New York); *NHM at Tring* Natural History Museum at Tring (Britain). Common and scientific names follow the IOC list (Gill and Donsker 2017). The specimens for *Peliperdix coqui* include four males and four females

Internet[1] https://images.search.yahoo.com/yhs/search?p=macrocephalon+maleo&fr=yhs-visicom-weatherno

Internet[2] https://images.search.yahoo.com/yhs/search?p=vulturine+guinea+fowl+chicks+images+download

Internet[3] https://www.google.com/search?q=sWAMP+fRANCOLIN+CHICK&enablesearch=true

Internet[4] https://www.youtube.com/watch?v=CWFvUf3sj_cha

Internet[5] https://images.search.yahoo.com/yhs/search?p=coturnix+coturnix+images+of+chicks+hatching&fr

Internet[6] https://images.search.yahoo.com/yhs/search?=gREY-BREASTED+sPURFOWL+IMAGES+OF+CHICK&fr

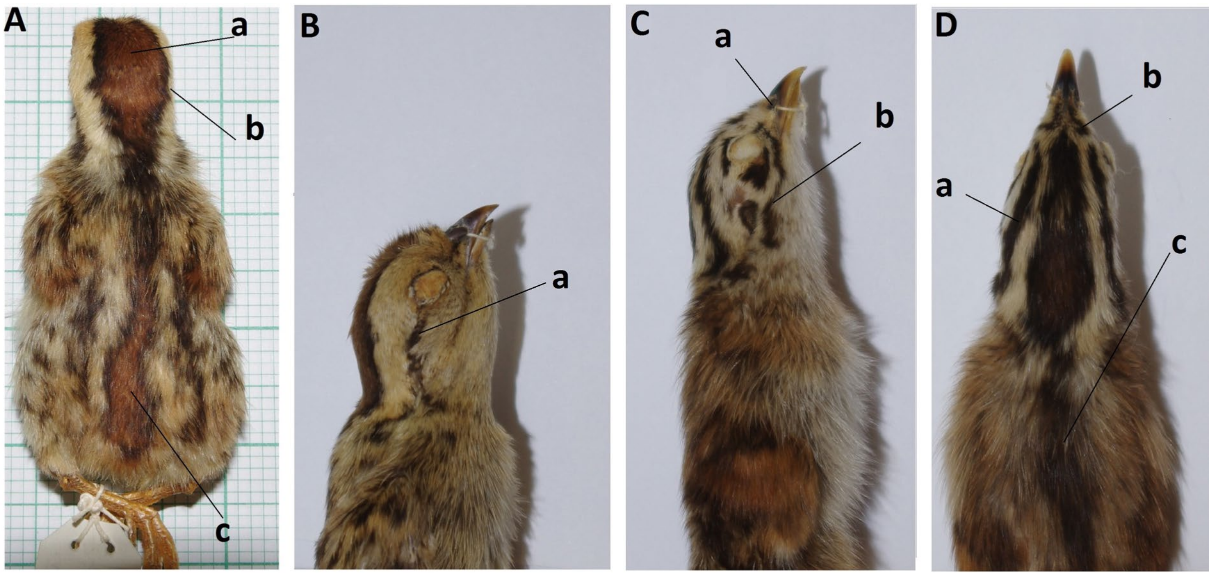

Fig. 1 Back, crown and facial markings of spurfowl and francolin chicks used as character states for phylogenetic analysis. **Aa** shows the typical broad crown cap associated with spurfowl (*Pternistis afer*) with a thin darker trimming (**Ab**). In francolins this trimming is separated from the crown as a loose-standing crown stripe. **Ac** shows the longitudinal band with variegated lateral stripes. **Ba** shows the eye stripe of *P. adspersus*, which is typical of spurfowls. It often stretches in front of the eye to the nares. **Ca** and **Cb** show the nare spot and facial stripes respectively of *Scleroptila levaillantii*, which is typical of *Scleroptila* spp. **Da** and **Db** show the orbital stripe and nare spot of *S. levaillantii*, which are typical of *Scleroptila* spp. **Dc** shows the central back stripe of *S. levaillantii*; in *Scleroptila* this is normally narrower than the central longitudinal band of spurfowls

tree-bisection-reconnection branch-swapping option was in effect, and 1000 random additions of taxa (Maddison 1991). One tree was held at each step during stepwise addition, with branches collapsed (creating polytomies) if the maximum branch-length was zero. Multiple, equally parsimonious cladograms were recovered and strict consensus cladograms were constructed. Bootstrap resampling (Felsenstein 1985) with 1000 pseudoreplicates and five random additions of taxa per bootstrap pseudoreplicate was used to determine the degree of support for each node. Both the natal downy and Cyt*b* phylogenies were rooted on *M. maleo*. Three measures of phylogenetic signal were gained by estimating consistency index (CI), which measures how well the data and the tree fit with each other, that is, the consistency of the tree to the dataset; the retention index (RI), which measures how well synapomorphies explain the tree; and the homoplasy index (HI), which measures the amount of homoplasy observed on a tree relative to the maximum amount of homoplasy that could theoretically exist. These metrics reveal the amount of phylogenetic signals inherent in both character matrices.

Ancestral state reconstruction

The ancestral state reconstructions were made on the existing mt Cyt*b* phylogeny for eight natal downy characters (Table 3) using Parsimony approach implemented in Mesquite ver. 3.2 (Maddison and Maddison 2017). All character states were unordered and the analysis employed the Markov k-state 1 parameter (mk1) model (Lewis 2001) where any particular change from one state to the other is equally probable.

Results

Broad groups of chick plumage

From the outgroup it was possible to select three broad groups of chick plumage colours and patterns by which to categorise the francolin and spurfowl chicks.

Plain: The darkish chicks of megapodes (Megapodiidae) are plain dorsally without stripes. The chick plumage of guineafowl species that live in the open understory of forests, such as *Guttera pucherani* and *Agelastes meleagrides*, are vaguely striped (rather blotchy) compared with the prominent striped patterns of guineafowl species that raise their chicks in grass, such as *Numida meleagris* and *Acryllium vulturinum* (Madge and McGowan 2002) (Fig. 2). The chick plumage of the forest-living *A. niger* is mainly dark rufous and black above (Little 2016).

Semi-striped: Grouse (Tetraonidae), *Gallus gallus* and *Phasianus* chicks have a variegated pattern with a central longitudinal band that proceeds through the crown to the forehead (Fig. 3). The rufous crown stripe often forms a single broad crown cap, with thinner trimmings on either side of the crown cap.

Table 2 Taxa for which mitochondrial Cytochrome *b* sequences were sourced from GenBank

Common name	Scientific name	GenBank No.
Maleo	*Macrocephalon maleo*	AM236881.1
Crested Guineafowl	*Guttera pucherani*	AM236882.1
White-breasted Guineafowl	*Agelastes meleagrides*	AM236884.1
Vulturine Guineafowl	*Acryllium vulturinum*	FJ752436.1
Helmeted Guineafowl	*Numida meleagris*	AP005595.1
Western Capercaillie	*Tetrao urogallus*	AB120132.1
Dusky Grouse	*Dendragapus obscurus*	AF230178.1
Willow Ptarmigan	*Lagopus lagopus*	KX609784.1
Greater Prairie-chicken	*Tympanuchus cupido*	AF230179.1
Common Pheasant	*Phasianus colchicus*	KY246295.1
Red Junglefowl	*Gallus gallus*	AF028795.1
Latham's Francolin	*Peliperdix lathami*	AM236893.1
Coqui Francolin	*Peliperdix coqui*	FR691633.1
White-throated Francolin	*Peliperdix albogularis*	FR694145.1
Crested Francolin	*Dendroperdix sephaena*	FR694141.1
Swamp Francolin	*Francolinus gularis*	U90649.1
Grey Francolin	*Francolinus pondicerianus*	FR691632.1
Black Francolin	*Francolinus francolinus*	AF013762.1
Orange river Francolin	*Scleroptila gutturalis*	AM236900.1
Red-winged Francolin	*Scleroptila lavaillantii*	AM236900.1
Grey-winged Francolin	*Sclerotptila afra*	AM236897.1
Shelley's Francolin	*Scleroptila shelleyi*	FR691620.1
Chukar Partridge	*Alectoris chukar*	FJ432715.1
Common Quail	*Coturnix coturnix*	EU839461.1
Hartlaub's Francolin	*Pternistis hartlaubi*	FR691618.1
Handsome Spurfowl	*Pternistis nobilis*	FR691592.1
Chestnut-naped Spurfowl	*Pternistis castaneicollis*	AM236903.1
Erckel's Francolin	*Pternistis erckelii*	FR691589.1
Scaly Spurfowl	*Pternistis squamatus*	AM236904.1
Red-billed Spurfowl	*Pternistis adspersus*	FR691623.1
Cape Spurfowl	*Pternistis capensis*	AM236909.1
Natal Spurfowl	*Pternistis natalensis*	AM236911.1
Hildebrandt's Spurfowl	*Pternistis hildebrandti*	FR691595.1
Heuglin's Spurfowl	*Pternistis icterorhynchus*	FR691601.1
Swainson's Spurfowl	*Pternistis swainsonii*	U90634.1
Grey-breasted Spurfowl	*Pternistis rufopictus*	FR691588.1
Yellow-necked Spurfowl	*Pternistis leucoscepus*	AM236906.3
Red-necked Francolin	*Pternistis afer*	AM236908.2

Striped: These chicks possess multiple stripes on the sides of their faces and are striped longitudinally across the crown right to the nares. Their back patterns are also variegated, but with a prominent central longitudinal band. *Numida meleagris* and *A. vulturinum* are typical examples of striped chicks (Fig. 2C, D). *Coturnix coturnix* chicks also display multiple stripes. The well-defined thin stripes across the crown and on the sides of the face of *N. meleagris* compared with the weakly defined stripes and blotches (fluidity) of *A. meleagrides* and *G. pucherani* suggest that the well-defined stripes emerged from a darkish plainer ancestor (see *A. niger)*, with its black plain dorsal chick plumage. The latter three guineafowl species live in forests.

Chick plumage of spurfowl chicks

The 15 spurfowl chicks for which data were captured show a marked degree of similarity in terms of the selected character states (Table 3, Additional file 1: Table S1). The chick plumage of spurfowl chicks is regarded as semi-striped, since they lack the multiple disruptive stripes on the face and crown. The chick plumage of a hybrid *P. adspersus* and *P. natalensis* chick did not vary from this typical pattern. The back bears a broad, dark brown (rufous) central longitudinal band flanked by thinner and lighter-coloured stripes (otherwise known as a variegated back pattern). The crown has a broad rufous crown cap which is often trimmed by a thin, darker stripe on the edges. This crown cap is essentially an extension of the longitudinal band across the back. The face has an eye stripe which extends for a short distance in front of the eye (it often resembles a blotch in front of the eye). Some species, such as *P. icterorynchus*, *P. nobilis* and *P. erckelii*, generally have a reddish appearance, but their patterns (structurally) remain like the rest. *P. hartlaubi* is like the rest, with limited facial stripes and a variegated back pattern with a central longitudinal band on the back.

Chicks from two species showed prominent diagnostic features. *Pternistis nobilis* has a bold, thicker eye stripe, which is more prominent than the rest of the spurfowls, with a relatively thick frontal eye stripe. *Pternistis erckelii* has a solid, longish jaw stripe which in other species is faint or absent (Fig. 4).

Spurfowl chicks differ from their closest evolutionary relatives. Both the spurfowl chicks and *Coturnix coturnix* chicks are semi-striped on their heads but *Alectoris chukar* chicks possess stripes. Dorsally, only spurfowl chicks have a broad crown cap compared to scattered or banded crowns in the other two species (Table 3).

Chick plumage of francolin chicks

Data were captured for 11 species representing all four genera (Table 3).

Asiatic francolins: *F. pondicerianus*, *F. francolinus* and *F. gularis* are semi-striped. Like the spurfowls, they possess a rufous crown cap. The sides of their faces often have a few blotch-like blackish markings (probably remnants of stripes from an ancestor that was fully striped) behind the eye and on the neck. Like spurfowls, they also have a longitudinal band on the back with thinner, lighter-coloured

Table 3 A character matrix of chick plumage with scores used for the phylogenetic analysis of Phasianidae chicks

Taxon	Characters							
	1	2	3	4	5	6	7	8
Macrocephalon maleo	0 (F)	0 (F)	0 (F)	0 (F)	0 (F)	0 (F)	0 (F)	0 (F)
Guttera pucherani	2 (F)	0 (F)	3 (F)	2 (F)	0 (F)	0 (F)	2 (F)	1 (F)
Agelastes meleagrides	2 (F)	0 (F)	3 (F)	2 (F)	0 (F)	0 (F)	?	1 (F)
Acryllium vulturinum	1 (C)	2 (C)	1 (C)	1 (C)	0 (C)	2 (C)	2 (C)	0 (C)
Numida meleagris	1 (C)	2 (C)	1 (C)	1 (C)	0 (C)	2 (C)	2 (C)	0 (C)
Tetrao urogallus	0 (F)	2 (F)	2 (F)	2 (F)	0 (F)	0 (F)	1 (F)	0 (F)
Dendragapus obscurus	1 (F)	1 (F)	2 (F)	2 (F)	0 (F)	1 (F)	1 (F)	1 (F)
Lagopus lagopus	2 (O)	1 (O)	3 (O)	2 (O)	0 (O)	1 (O)	1 (O)	0 (O)
Tympanuchus cupido	2 (O)	2 (O)	2 (O)	2 (O)	2 (O)	1 (O)	1 (O)	1 (O)
Phasianus colchicus	1 (O)	2 (O)	3 (O)	2 (O)	0 (O)	2 (O)	1 (O)	0 (O)
Gallus gallus	2 (F)	2 (F)	3 (F)	3 (F)	0 (F)	0 (F)	2 (F)	0 (F)
Peliperdix lathami	0 (F)	0 (F)	3 (F)	3 (F)	0 (F)	0 (F)	0 (F)	0 (F)
Peliperdix coqui	2 (O)	2 (O)	3 (O)	3 (O)	0 (O)	2 (O)	2 (O)	0 (O)
Peliperdix albogularis	2 (O)	2 (O)	3 (O)	3 (O)	1 (O)	2 (O)	2 (O)	?
Dendroperdix sephaena	2 (O)	2 (O)	3 (O)	3 (O)	0 (O)	2 (O)	2 (O)	0 (O)
Francolinus gularis	2 (O)	2 (O)	1 (O)	3 (O)	0 (O)	2 (O)	?	?
Francolinus pondicerianus	2 (O)	2 (O)	3 (O)	3 (O)	0 (O)	2 (O)	1 (O)	0 (O)
Francolinus francolinus	2 (O)	2 (O)	1 (O)	3 (O)	1 (O)	2 (O)	1 (O)	0 (O)
Scleroptila gutturalis	1 (C)	2 (C)	1 (C)	1 (C)	1 (C)	2 (C)	1 (C)	0 (C)
Scleroptila lavaillantii	1 (C)	1 (C)	1 (C)	1 (C)	1 (C)	2 (C)	1 (C)	1 (C)
Sclerotptila afra	1 (C)	1 (C)	1 (C)	1 (C)	1 (C)	1 (C)	1 (C)	0 (C)
Scleroptila shelleyi	1 (C)	0 (C)	1 (C)	1 (C)	2 (C)	?	1 (C)	1 (C)
Alectoris chukar	2 (O)	1 (O)	2 (O)	3 (O)	0 (O)	1 (O)	2 (O)	0 (O)
Coturnix cotunix	1 (C)	2 (C)	1 (C)	3 (C)	1 (C)	2 (C)	2 (C)	1 (C)
Pternistis hartlaubi	2 (O)	0 (O)	3 (O)	3 (O)	0 (O)	0 (O)	2 (O)	1 (O)
Pternistis nobilis	2 (O)	0 (O)	3 (O)	3 (O)	0 (O)	0 (O)	2 (O)	?
Pternistis castaneicollis	2 (O)	0 (O)	3 (O)	3 (O)	0 (O)	?	?	0 (O)
Pternistis erckelii	2 (O)	0 (O)	3 (O)	3 (O)	1 (O)	0 (O)	2 (O)	1 (O)
Pternistis griseostriatus	2 (O)	2 (O)	3 (O)	3 (O)	0 (O)	2 (O)	?	?
Pternistis squamatus	2 (O)	2 (O)	3 (O)	3 (O)	2 (O)	0 (O)	2 (O)	0 (O)
Pternistis ahantensis	2 (O)	2 (O)	3 (O)	3 (O)	0 (O)	?	?	0 (O)
Pternistis adspersus	2 (O)	2 (O)	3 (O)	3 (O)	0 (O)	2 (O)	2 (O)	0 (O)
Pternistis capensis	2 (O)	2 (O)	3 (O)	3 (O)	0 (O)	0 (O)	2 (O)	0 (O)
Pternistis natalensis	2 (O)	2 (O)	3 (O)	3 (O)	0 (O)	2 (O)	2 (O)	0 (O)
Pternistis hildebrandti	2 (O)	2 (O)	3 (O)	3 (O)	0 (O)	2 (O)	2 (O)	0 (O)
Pternistis icterorhynchus	2 (O)	0 (O)	3 (O)	3 (O)	0 (O)	0 (O)	2 (O)	0 (O)
Pternistis swainsonii	2 (O)	2 (O)	3 (O)	3 (O)	0 (O)	2 (O)	2 (O)	0 (O)
Pternistis rufopictus	2 (O)	2 (O)	3 (O)	3 (O)	0 (O)	2 (O)	1 (O)	0 (O)
Pternistis leucoscepus	2 (O)	1 (O)	3 (O)	3 (O)	2 (O)	0 (O)	?	0 (O)
Pternistis afer	2 (O)	2 (O)	3 (O)	3 (O)	0 (O)	2 (O)	2 (O)	0 (O)

This table also shows associations between habitat and character states of spurfowls and francolins (read scores for states from Additional file 1: Fig. S1). Micro-habitat is the immediate habitat structure in which the bird is typically observed (Madge and McGowan 2002). *Numida meleagris* and *Acryllium vulturinum* breed and raise their chicks in grass but adults live in open micro-habitats, hence they were categorised as closed micro-habitat species. (O) open micro-habitat (e.g. bush or edges of forests). (C) closed micro-habitat (grasslands and/or low growing shrubs). (F) forest. Only the male *Peliperdix coqui* was used for analysis and it is expected that *C. albogularis* chicks also possess sexual dimorphisms but it was not confirmed

lateral stripes (in other words, variegated back markings). Interestingly, only some *F. pondicerianus* chicks have a striped crown, showing intra-specific variability.

Dendroperdix sephaena is semi-striped, and shows resemblance to the spurfowls and Asiatic francolins. It has a rufous, crown cap with a solid eye line behind the

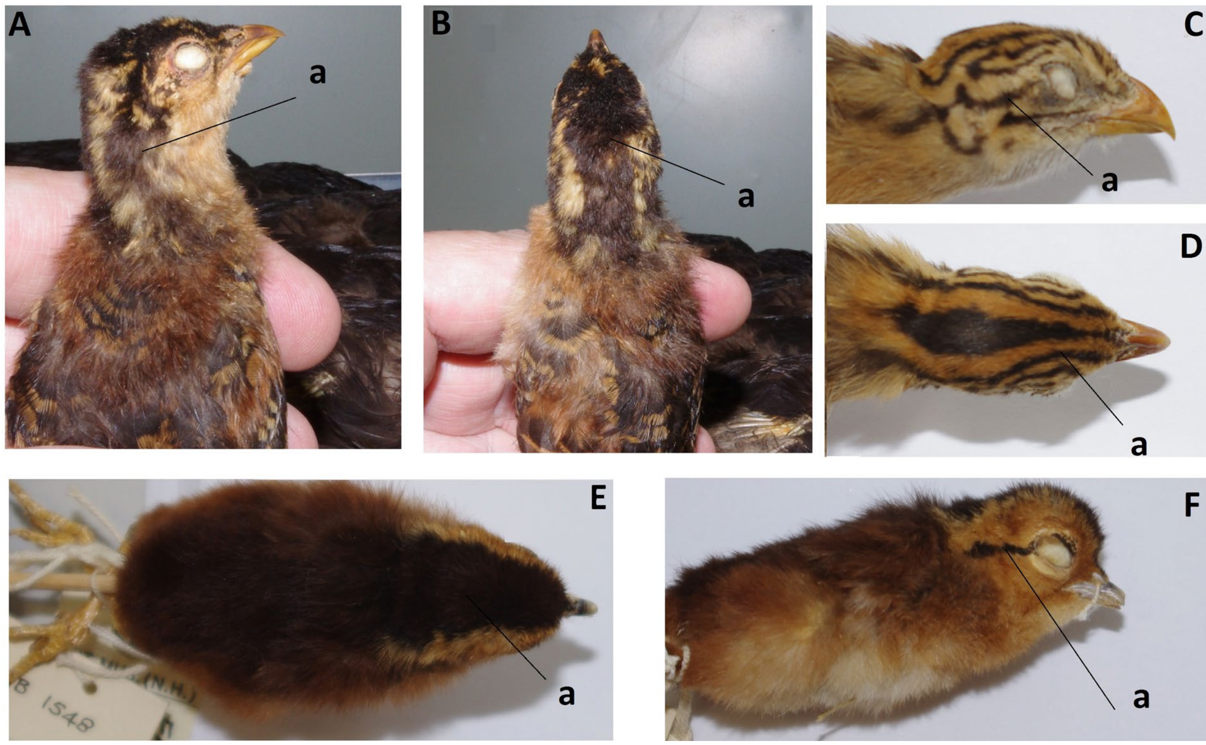

Fig. 2 **Aa** and **Ba** show the blotchy marks of the *Agelastes meleagrides* chick, which live in forests, compared with the striped markings, **Ca** and **Da**, of the *Numida meleagris* chick, which live in the open habitats. *Agelastes meleagrides* is regarded as plain, and *N. meleagris* as striped. **Ea** and **Fa** show the plain dorsal patterns and lateral eye stripe respectively of the *Peliperdix lathami* chick, which live in forests. Note that the latter possesses an eye stripe which is similar to the spurfowls. In fact, structurally, it is only the plain back that differentiates it from the spurfowls

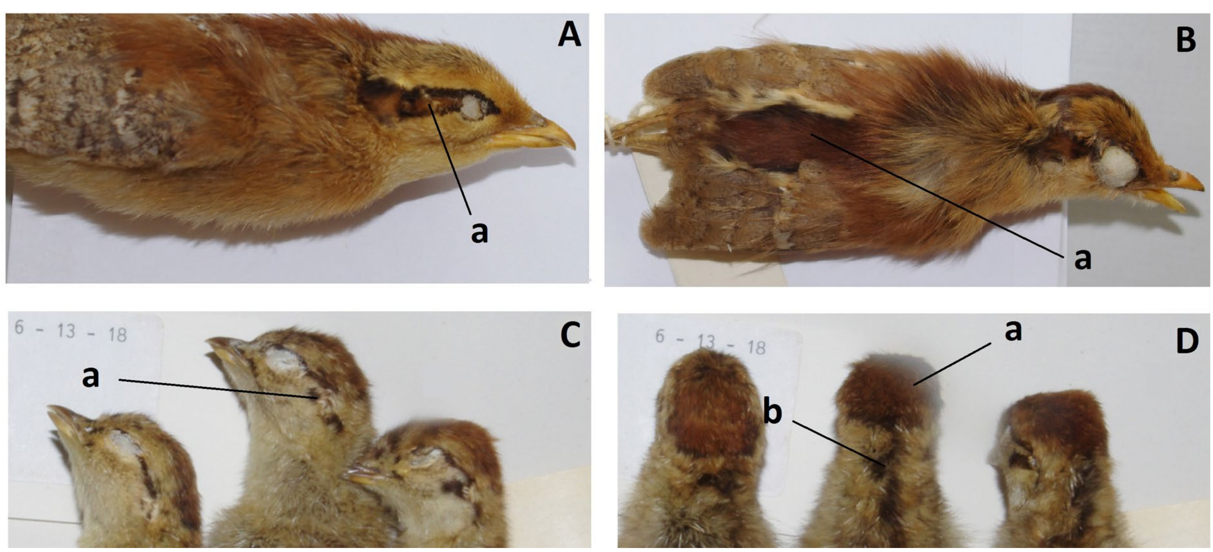

Fig. 3 **Aa** and **Ba** show the eye stripe and a broad longitudinal band on the variegated back respectively of the *Gallus gallus* chick, which is similar to spurfowls. **Ca** and **Da** show the broken facial marks (i.e. disconnected remnants of stripes) and crown respectively of *Tetrao tetrix* chicks, which are also often found in Asian francolins. **Db** shows the connectivity of the central dorsal line from the crown across the back, which is often associated with the subfamily Tetraoninae

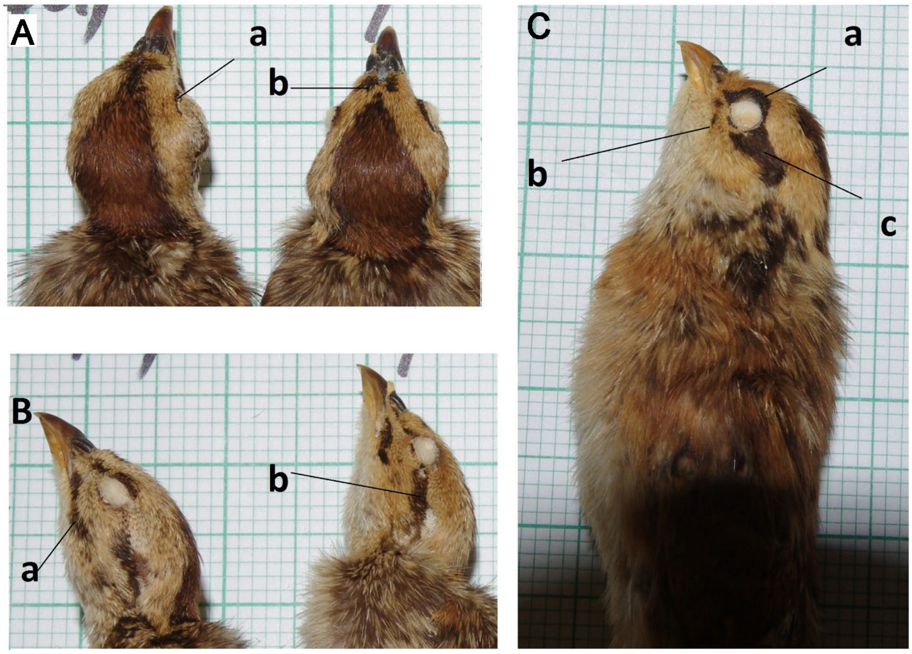

Fig. 4 **Aa** shows remnants of a fuller orbital stripe of *Pternistis erckelii*. By comparison, among *Scleroptila* this orbital stripe arches over the orbit and is well defined. **Ab** shows the nare spots which were, in its ancestral stage, probably connected to the crown cap of *P. erckelii*. **Ba** and **Bb** show the remnants of a fuller jaw stripe, which is well defined in some francolin species (e.g. *Scleroptila*) and the eye line respectively, which is typical of all spurfowls. **Ca** shows the pronounced eyebrow, **Cb** shows the remnants of a jaw stripe and **Cc** shows the thick eye stripe respectively of *P. nobilis* which are typically also found on *G. gallus*

eye, stretching down along the neck which is also typical for spurfowl chicks. It has a distinctive round dark spot on the neck, which it shares with *F. francolinus* and *F. gularis* (Fig. 5). The back also has a broad, dark brown central longitudinal band flanked with thinner, lighter-coloured stripes (in other words, variegated back markings) similar to spurfowl chicks.

The male *P. coqui* chick is semi-striped, with a rufous crown cap and a solid eye stripe behind the eye, a broad, dark brown longitudinal band on the back flanked by

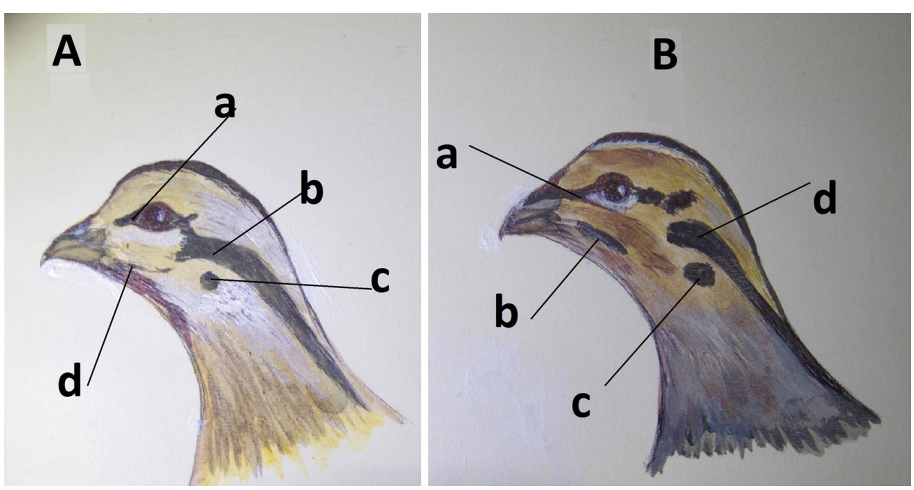

Fig. 5 *Francolinus gularis* and *Dendroperdix sephaena* are similar in many ways. **Aa** shows the eye line in front of the eye; **Ab** shows the long eye stripe behind the eye and along the neck; **Ac** shows the isolated round dot; **Ad** shows the thin jaw stripe of *F. gularis*. **Ba** shows the eye line in front of the eye; **Bb** shows a thicker jaw stripe; **Bc** shows the isolated black dot and **Bd** shows the disconnected eye stripe behind the eye down the neck of *D. sephaena*

lighter lateral stripes reminiscent of spurfowl chicks (Fig. 6A, B). A female chick collected at Shangabue (Zimbabwe) shows a typical spurfowl crown and back, but the sides of the face have multiple stripes, which is typical of *Scleroptila* spp. (Fig. 6C). A similar female chick specimen is kept in the Ditsong National Museum of Natural History in South Africa. The distinction between female and male chicks is also evident at the juvenile stage, when the male has a clean buffy coloured face and the female multiple facial stripes; this is eventually carried through to adulthood. The male chicks resemble spurfowl chicks and are more closely related to the Asiatic chicks than to the striped chicks of *Scleroptila* spp.

Scleroptila gutturalis has a broad rufous crown cap, with multiple stripes on the face and a broad central longitudinal band on the back with thinner, light-coloured lateral stripes. *Scleroptila levaillantii*, *S. shelleyi* and *S. afra* have striped heads (instead of a well-defined crown cap) and facial markings, and the head colours are distinctively white and black, revealing a chevron pattern.

The Asiatic francolins, *D. sephaena* and the male *P. coqui* chick possess broad crown caps and semi-striped faces which are like their closest evolutionary relative *G. gallus*. *Scleroptila* species do not share these characteristics with *G. gallus*.

Chick plumage and Cyt*b* phylogeny

The natal downy (Table 3) and Cyt*b* data sets consisted of eight and 1,143 characters, consisting of eight and 430 parsimony informative characters, respectively. The matrices had a CI of 0.405, RI of 0.734 and HI of 0.595 whereas Cyt*b* yielded a CI of 0.50, RI (of 0.521) and HI of 0.5, respectively. The Cyt*b* phylogeny confirms the francolin-spurfowl dichotomy (Fig. 7) with francolins, spurfowls, grouse and allies (Tetraoninae) all in the family Phasianidae. Numididae is also recovered. The number of taxa included in this analysis had to match those for which the natal downy characters were available and this possibly could have resulted in the topology and nodal support that is slightly different from that in Crowe et al. (2006). The Asian/African linking lineage consisting of *F. francolinus pondicerianus*, *F. gularis* and *D. sephana* was recovered even though the branch from which these species arose is unresolved. The natal downy phylogeny (Fig. 8) shows poor phylogenetic structure which is largely polytomous and therefore no inferences can be made.

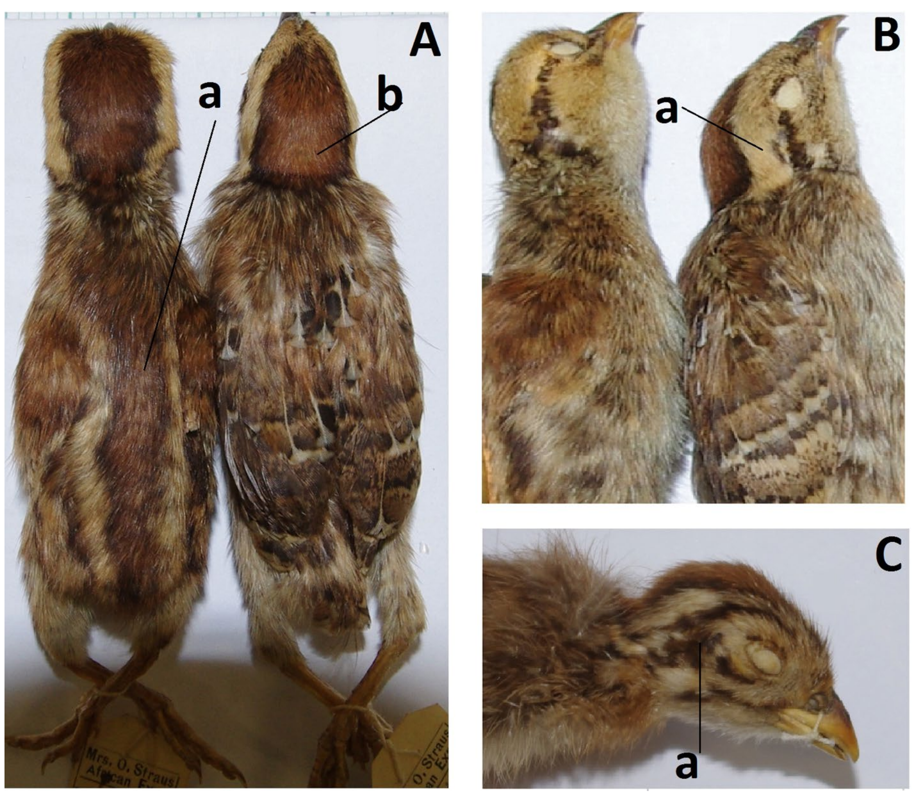

Fig. 6 **Aa** and **Ab** show the broad longitudinal band on the back and the crown cap respectively of *Peliperdix coqui*; these features are typically associated with the spurfowls. **Ba** shows the facial patterns of a male chick that are also similar to spurfowl chicks, while **Ca** shows the facial stripes of a female chick that aligns itself with *Scleroptila* in this regard. This species shows sexual dimorphism at the chick stage

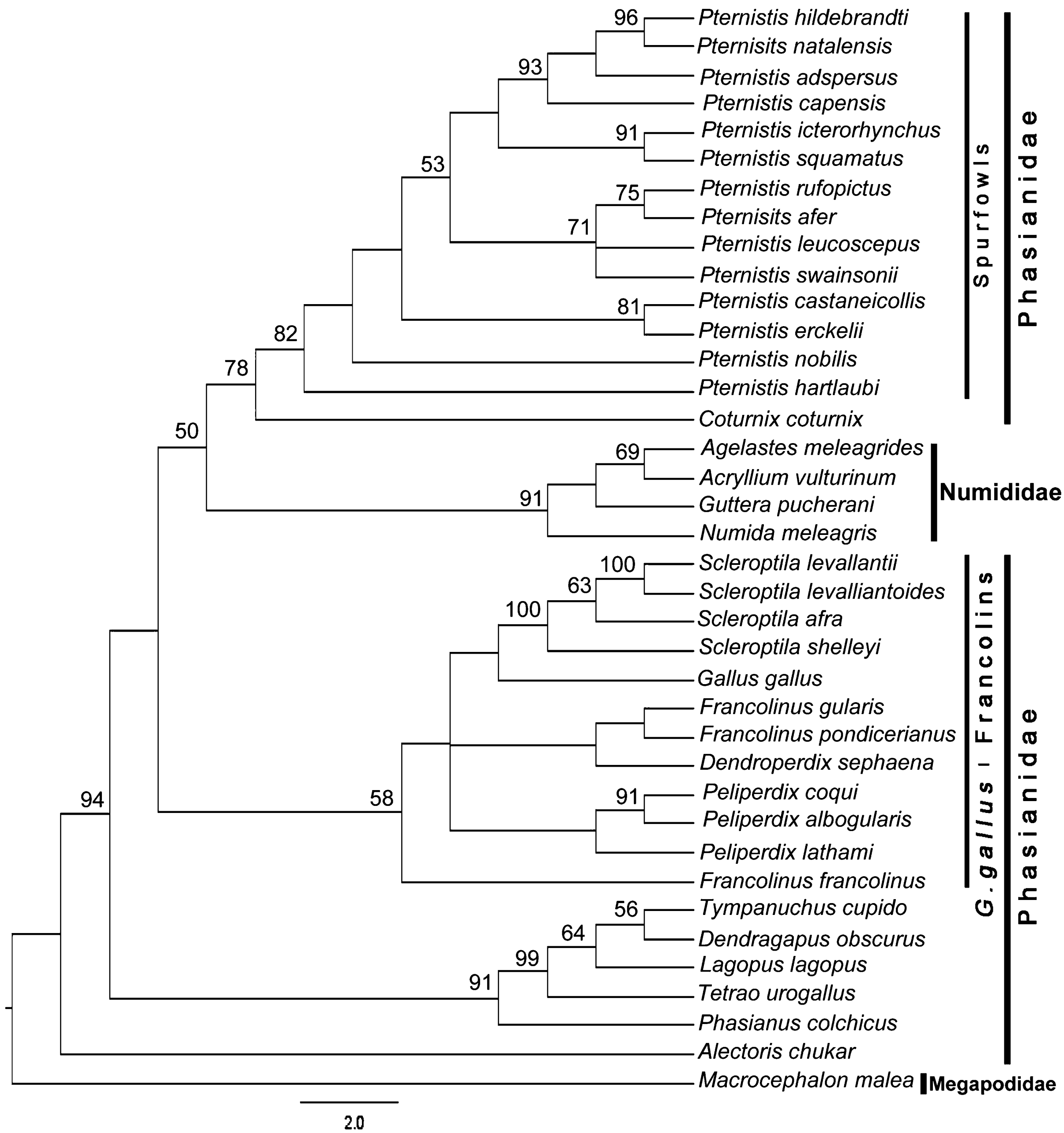

Fig. 7 A strict consensus Parsimony tree reconstructed from mitochondrial Cytochrome *b* characters. Numbers shown above branches (≥ 50%) are bootstrap support values. The scale bar represents the number of character state changes of which branch lengths are proportional to the number of character state changes

Symplesiomorphy underlying spurfowls

Ancestral characters form the "building blocks" that shape the colours and patterns of downy chicks. The broad longitudinal central rufous longitudinal band on the back and crown of spurfowl chicks (variegated) are also evident in *G. gallus* and grouse. The solid eye line of spurfowls, with the rest of the face often clean, is also evident in *G. gallus*, and is particularly similar between *P. nobilis* and *G. gallus* (see Figs. 3, 4). The prominent jaw stripe of *P. erckelii* (and to a lesser extent by other spurfowls) is also evident in *Coturnix coturnix*, *N. meleagris* and *V. acryllium* chicks.

Symplesiomorphy underlying francolins

The Asian francolins have a rufous central longitudinal band on the back and crown, like *G. gallus*. The blotches

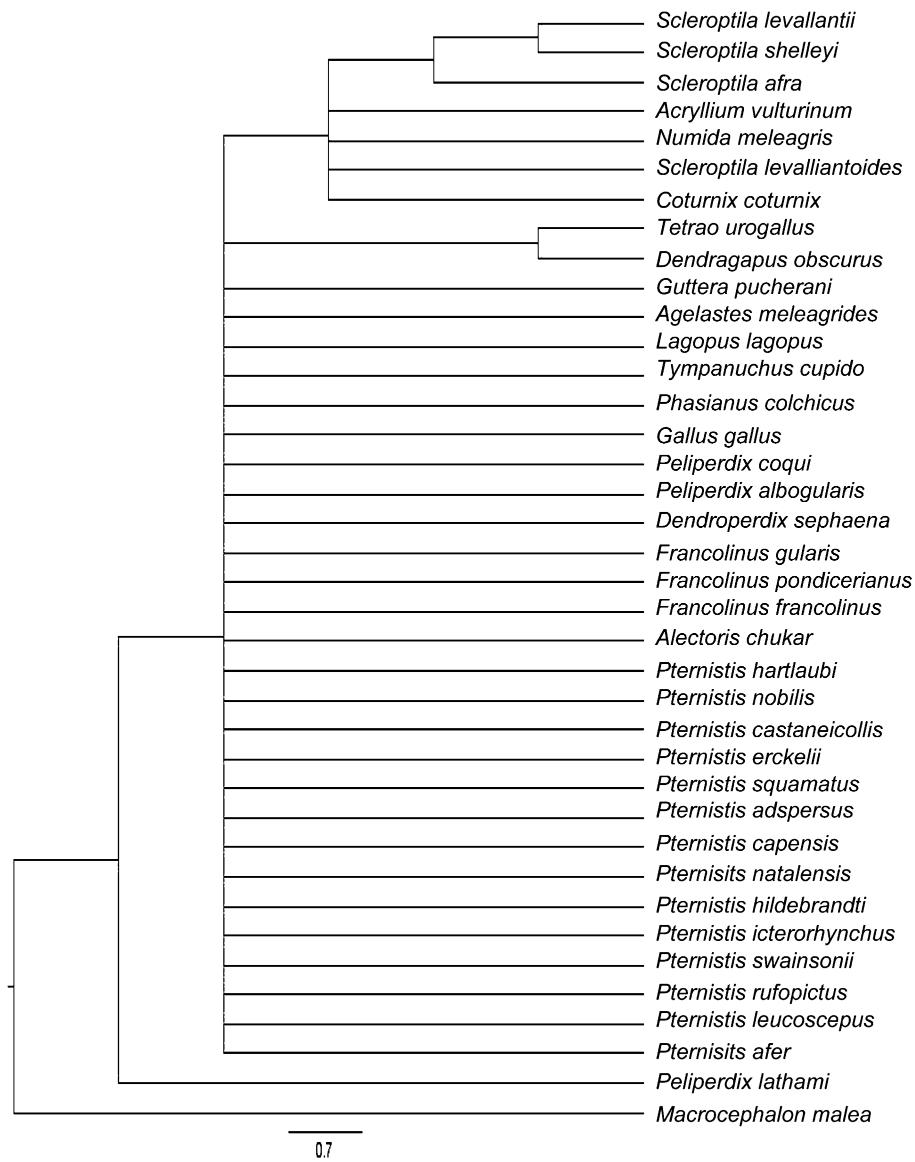

Fig. 8 A strict consensus parsimony tree based on the natal downy characters. Most parts of the tree were supported with low bootstrap values and are not shown. The scale bar represents the number of character state changes of which branch lengths are proportional to the number of character state changes

behind the eye (as in *F. gularis*) are like some Tetraonidae spp., being especially evident in *D. obscurus pallides* and *L. lagopus. Dendroperdix sephaena* has all the characteristics of the *G. gallus* chick. However, the single diagnostic isolated spot on the neck is similar to a spot recorded in the same area of the neck of *F. gularis* and *F. francolinus* (Fig. 5). *Peliperdix coqui* chicks also have the characteristics of *G. gallus*, but the female chick's striped facial parts are similar to those of the *N. meleagris* chick. *Scleroptila gutturalis* falls in the same category as the female *P. coqui* chicks. It has a crown and back feather pattern like *G. gallus*, but the facial parts resemble *N. meleagris* chicks.

The chicks of *S. afra*, *S. lavaillantii* and *S. shelleyi* are similar to the striped pattern seen in *N. meleagris*, *A. vulturinum* and *Coturnix coturnix* chicks. However, the black lateral facial patterns of the latter three francolins stand out and could be related to the black facial parts of an Asiatic ancestor such as *F. gularis.* This is unlike *S. gutturalis*, which does not fall in this category and does not have black-coloured stripes. The plain colours of *P.*

lathami chicks resemble the plain colours found in *P. pucherani*, *A. meleagrides* and *A. niger.*

Correlations between micro-habitat and chick plumage character states

Micro-habitat refers to the immediate environment of the bird within a broader landscape. Generally, species clades live in uniform micro-habitats for most of the year (Fig. 9). Some, such as *N. meleagris* and *A. vulturinum* live out in the open but breed in closed habitat, in other words in grass. *Peliperdix lathami* is an exception as it lives in forests but its close relatives, *P. coqui* and *P. albogularis* move into open micro-habitats (Fig. 9).

Most species that live in open micro-habitats (*Peliperdix*, *Dendroperdix*, *Francolinus* spp., *Pternistis* spp., *L. lagopus*, *T. cupido* and *G. gallus*) are semi-striped compared to *Scleroptila* spp., *C. coturnix*, *N. meleagris* and *A. vulturinum* that live in closed micro-habitats and are all multi-striped (more cryptic) (Additional file 1: Table S2). Most species that live in open micro-habitats possess rufous variegated colour combinations but species that live in closed micro-habitats have dark reddish and rufous colour combinations. Most forest species possess reddish colours (Additional file 1: Table S2).

Most species that live in open micro-habitats possess rufous caps on their crowns compared to all species living in closed micro-habitats that possess banded crowns. Forest species possess caps as well (Additional file 1: Table S2).

Most species that live in open micro-habitats possess a distinct eye band and comparatively most species that live in closed micro-habitats possess multiple facial stripes. Most forest species possess spots on the sides of their faces. Most species that live in open micro-habitats do not have jaw stripes whereas species that live in closed micro-habitats have partly or fully developed jaw stripes. Forest species do not possess any markings on the sides of their faces (Additional file 1: Table S2).

The back colours of species that live in open micro-habitats are rufous and most species that live in closed micro-habitats also possess rufous colours. Comparatively forest species possess dark reddish colours on their backs (Additional file 1: Table S2).

Most species that live in open micro-habitats possess broad stripes on their backs and species that live in closed micro-habitats possess thin and broad stripes. Comparatively forest species possess both but do not show any preference for any pattern (Additional file 1: Table S2).

Most species that live in open habitats possess no nose spots and for species that live in closed and forest habitats no preference was revealed. They both have spots or no spots. Generally, species of closed micro-habitats are more cryptic than species in open micro-habitats (Additional file 1: Table S2).

Ancestral state reconstruction

Disruptive markings

The ancestral state is inconclusive that is, the ancestor could have either been semi-striped or plain (with no markings). It seems semi-stripe is a plesiomorphic state among francolins and spurfowls with independent evolution of stripes in the grassland *Scleroptila* lineage, the spurfowls' closest phylogenetic relative (*Coturnix coturnix*) and twice within Numididae and the sub-family Tetraoninae (Additional file 1: Fig. S2). There were two reversions to plain plumage in *P. lathami* and *Tetrao urogallus*.

Colour combinations of head

Generally, the ancestral states are inconclusive with the probability of all states (blackish brown, blackish, rufous variegated) having been present in the earlier ancestor. The colours of the head of *M. maleo* is plain black-brownish. This ancestral state together with the two diverged colour forms, rufous variegated and blackish colours, are found among the chicks of both *Pternistis* and *Scleroptila* spp. However, the head is consistently rufous variegated among *Francolinus* spp. (Additional file 1: Fig. S3).

Dorsal patterns

Generally, the ancestral states are inconclusive with the probability of all states (unchanged pail, banded, scattered, capped) having been present in the earlier ancestor. In *M. maleo* the dark head forms a continuous dark unchanged colour with the rest of the head and facial parts. The plain dorsal crown of *M. maleo* diverged into a well-defined capped crown found among *Pternistis* and *Francolinus* spp. but with a longitudinally banded pattern across the crown of *Scleroptila* species (Additional file 1: Fig. S4).

Side view patterns

The ancestral state is inconclusive, that is the ancestor may have had either plain or eye band/stripe. Francolins and spurfowls have eye band with independent evolution of multiple patterns in the grassland *Scleroptila* lineage and spots in the grouse and allies, *Lagopus*/*Phasianus* (Tetraoninae) lineage with an inconclusive ancestral state in members of Numididae. Unlike *Scleroptila* spp., the eye-stripes also evolved in *Francolinus* species (Additional file 1: Fig. S5).

Jaw stripe

With regard to this character, the ancestral state is plain (no distinguishable jaw stripe). Even though most of the

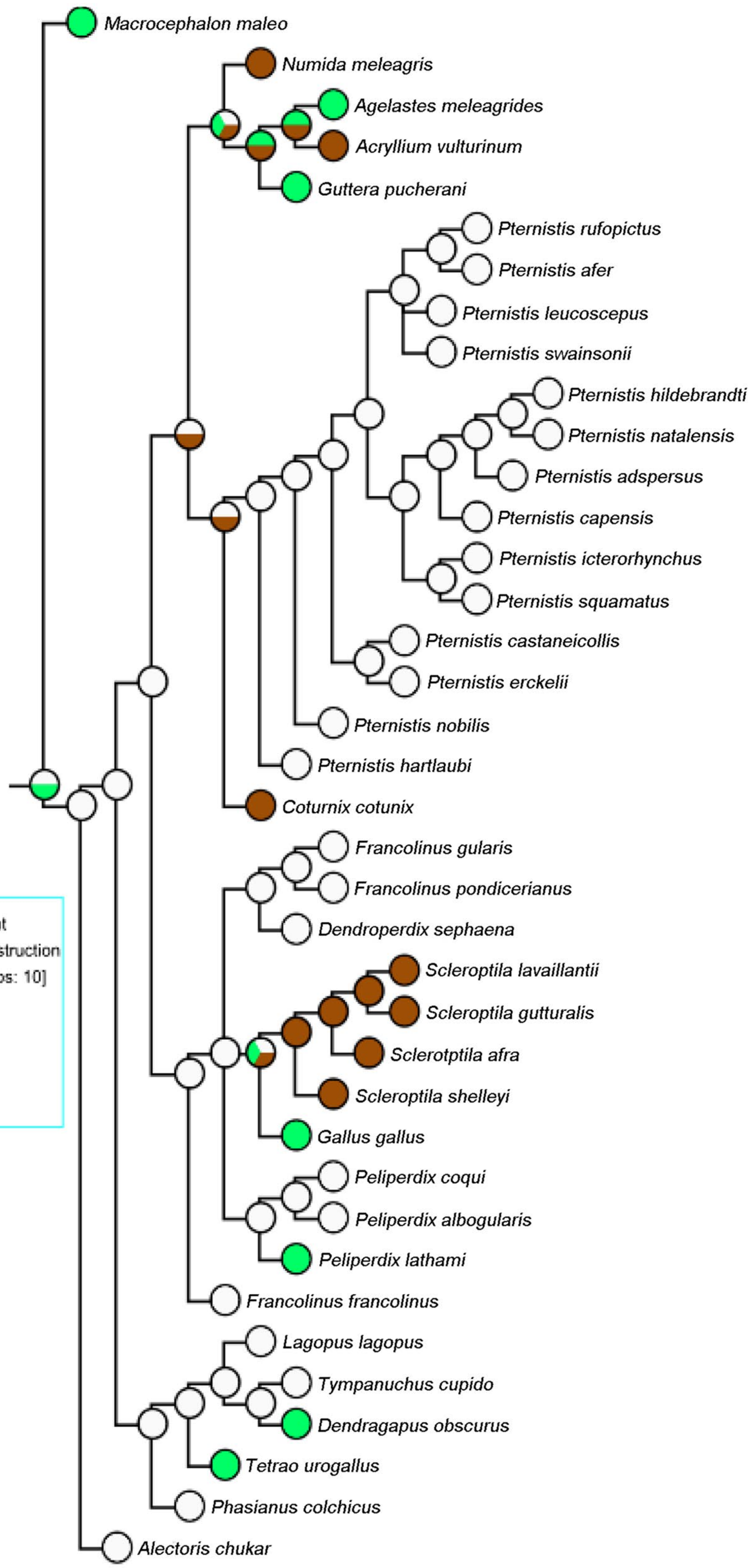

Fig. 9 Ancestral character state reconstruction for francolins and spurfowls based on Parsimony optimisation of habitat traced on mitochondrial Cytochrome *b* phylogeny. Habitat of taxa were traced on their mitochondrial Cytochrome *b* characters (see Fig. 7)

deeper node states are inconclusive, the francolins and spurfowls generally have a plain state, the independent evolution of full (jaw stripe) occurred six times (thrice among francolins and once among spurfowls). The state "partly" stripe independently evolved one among francolins and twice among spurfowls. The grouse and allies is the lineage where the ancestral plain state persisted as well as in the linking lineage between Asian and African francolins (Additional file 1: Fig. S6).

Back colours

Generally, the ancestral states are inconclusive with the probability of all states (blackish-brown, blackish, rufous variegated) having been present in the earlier ancestor. The general back colour of the *M. maleo* chick is plain black-brownish. This ancestral character state plus a diverged rufous variegated pattern became characteristic among *Pternistis* spp. but *Francolinus* spp. only attained the rufous variegated patterns. *Scleroptila* spp. possess these variants but also include a blackish tone that is often revealed in the chicks of grouse and allies in the subfamily Tetraoninae. In short, all the ancestral states are consistently distributed across the tree. The exception if the independent evolution of a state shown by a white ball with black lines leading to a montane species *P. castaneicollis* and *S. shelleyi* which indicates that the observed state is undecided while the most parsimonious state is black brownish and rufous variegated, respectively (Additional file 1: Fig. S7).

Back patterns

Generally, the ancestral states are inconclusive with the probability of all states (plain, narrow, broad) having been present in the earlier ancestors. The *M. maleo* chick is black-brownish plain. This state diverged into two clear patterns. Most *Pternistis* spp. possesses a broad central back band flanked by two thinner but lighter coloured stripes (dilution of pigmentation) on either side. All *Scleroptila* spp. have markedly narrower back stripes which evolved independently and this is observed in *P. rufopictus*. *Peliperdix lathami* experienced a throw-back of plain colours on their backs as found in *M. maleo.* The re-appearance of plain back is also observed in *T. cupido* and *A. meleagrides* (Additional file 1: Fig. S8).

Nose spot

The ancestral state is plain (no distinguishable nose spot). *Macrocephalon maleo* does not possess a nose spot since the nose and crown consist of a continuous black-brownish plain colour. The absence of a nose spot prevails throughout the francolin and spurfowl lineage (pleisiomorphic state) with independent evolution of nose spots within the Red-winged grassland *Scleroptila* subclade, among spurfowls that is, among the Montane, Vermiculated species as well as in the most basal spurfowl species *P. hartlaubi*. Importantly, the plain state of ancestors such as *M. maleo* is due to full pigmentation while the plain state among francolin and spurfowl is due to the dilution of pigmentation (Additional file 1: Fig. S9).

Discussion

Phylogeny

From a cladistics point of view, the topology of the natal downy phylogeny of francolins and spurfowls is largely unsatisfactory or polytomous. This could be due to the high degree of symplesiomorphy within Phasianidae (Johnsgard 2008) (Fig. 8). It was therefore not possible to delimit species satisfactorily based on plumage characters. These results are incongruent with the spurfowland francolin phylogeny built on DNA and adult morpho-behavioural characters wherein resolved species relationships were determined with a high nodal support (Mandiwana-Neudani et al. 2014). The latter refutes Hall's (1963) hypothesis and confirm that spurfowls (*Pternistis*) and francolins (*Francolinus, Dendroperdix, Peliperdix* and *Scleroptila*) do not form a monophyletic group (Crowe et al. 2006). Thus, the spurfowl and francolin phylogeny based on natal chick plumage characters does not support this dichotomy.

Inter-specific comparisons

Dendroperdix sephaena and *F. gularis* have a clear isolated dark spot on the side of the neck, a discontinued break between the eye stripe and the neck stripe, a faint jaw stripe and an eye liner which supports the view of Mandiwana-Neudani et al. (2014) that *D. sephaena* phylogenetically resembles the Asiatic francolins and might be considered a linking form between the Asiatic and African francolins (Fig. 5, Table 3).

Female *P. coqui* chicks have the disruptive eye stripes seen in *S. gutturalis*, and the male has limited facial markings as seen in the spurfowl chicks, which places this species between the two clades based on chick plumage. Hartlaub's Spurfowl *P. hartlaubi* is regarded as the most basal species of all extant spurfowls, but has a mating system and vocalisations which differ substantially from all other spurfowls (Komen 1987; Van Niekerk 2013). There is some debate as to whether this species belongs to the genus *Pternistis*, but based on chick plumage it is similar to all spurfowls (J. Komen in litt). It was expected that the spurfowl chicks of *P. ahantensis*, *P. squamatus* and *P. griseostriatus* that live on the fringes of forests would have attained forest-like character states such as a dark, reddish, rufous, plain dorsal plumage or at the least vague blotches, instead of variegated stripes fusing into a darker background plumage colour. In other words, it was expected that the forest species would resemble other forest-living birds such as *A. meleagrides*, *G. pucherani* and *P. lathami* and the forest-dwelling tinamous chicks (Jehl 1971), all of which have plumage patterns which are not contrasting and generally darker. Instead they are very like all the other savannah-living spurfowls. Lack of forest-living characteristics among the spurfowls that live on the fringes of forests could be ascribed to a relatively recent speciation event, leaving these taxa in a state of flux, engaged in finding and refining habitat niches which may, in evolutionary time scales, imprint on chick plumage patterns and colours (Milstein and Wolff 1987). This lack of deviation from unity is supported by the polytomous structures in the cladograms (Fig. 8).

No character captured from spurfowl or francolin skins could be described as "derived" (not observed in any ancestor), which confirms the strong role that symplesiomorphy plays in natal chick plumage within Phasianidae, as was demonstrated within grouse (Short 1967) and which also seems applicable to other families such as that of the tinamous (Bertelli et al. 2002). In fact, at the outset it was demonstrated that spurfowls and francolins could each be divided into three broad plumage categories found in the wider Phasianidae family, namely plain, striped and semi-striped chicks, which confirms the role played by symplesiomorphy.

Field identification

It was possible to separate subsets according to plumage characteristics. *Scleroptila* show strong signs of disruptive lateral facial patterns. Conversely, the spurfowls have limited facial stripes, but a broader longitudinal band running from the crown down the neck and through the centre of the back. These differences have also been reported in the literature (Little 2016). The Asian francolins have a broad longitudinal band on the back like the spurfowls, but have black spots or blotches (speckled remains of stripes) just behind or below the eye, which is more in accordance with the spurfowls than for *Scleroptila* spp. Asian francolins are similar to *D. sephaena*, which has a single round dark spot just below the ear.

Pternistis erckelii is similar to the rest of the spurfowls, but has a distinct jaw line which is only partly visible on the jaws of a few other spurfowls. The plain back plumage of *Peliperdix lathami* (formerly *F. lathami*; Hall 1963; Madge and McGowan 2002) is at variance with the spurfowls and francolins that have dorsal stripes. These plain dorsal features on the back could be an adaptation for life in forest conditions to break the bird's outline in shade, whereas semi-striped or striped plumage might be detected by predators under these conditions (Stevens and Merilaita 2008). A more complete set of francolin and spurfowl skins than what is currently available may reveal useful diagnostic features for individual species, but it is doubtful whether it would reveal derived traits that would assist in describing speciation based on chick plumage.

Habitat matching

Generally, species that live in open micro-habitats possess less cryptic markings than species that live in closed micro-habitats or forests. *Coturnix coturnix* is closely related to *Pternistis* spp. but unlike *Pternistis* spp. they live in grasslands and therefore possess cryptic multiple stripes over their faces and crowns like the chicks of *Scleroptila* spp. to which they are not as closely related phylogenetically (Fig. 7).

Scleroptila species. are not closely related to *Numida meleagris* or *Acryllium vulturinum* but as the latter species raise their chicks in grass like *Scleroptila* spp., they all possess cryptic stripes like *Scleroptila* spp. *Peliperdix lathami* lives in forests and therefore does not possess an eye stripe like *Peliperdix coqui*, *Peliperdix algularis*, *Francolinus* spp. and *Pternistis* spp. that live in open micro-habitats. *Peliperdix* spp., *Dendroperdix sephaena* and *Francolinus* spp. are more closely related to *Scleroptila* spp. but unlike *Scleroptila* spp. they live in open macro-habitats and therefore unlike *Scleroptila* spp., they do not possess multiple stripes across their faces and crowns, but instead possess a single wide eye stripe like *Pternistis* spp. which live in open micro-habitats. *Gallus gallus* are more closely related to *Scleroptila* spp. but their chicks look like the chicks of *Pternistis* spp. since they also live in open micro-habitats. It is therefore concluded that habitat matching is a likely driving force that determines the natal down of francolin and spurfowl chicks.

Does the chick plumage of spurfowl and francolin chicks have any significance for camouflage? Why don't these chicks simply have plain colours like *A. meleagrides* or *Peliperdix lathami* that live under the canopy of forests? The limited facial stripes of spurfowl chicks probably assist the chicks to blend in with a bushier type habitat with limited ground cover such as grass. Should these chicks possess multiple stripes it would be conspicuous under these open conditions as it would define the outline of the head (Merilaita and Lind 2005; Stevens and Merilaita 2008). On the other hand, the multiple facial stripes of *S. afra*, *S. levaillantii* and *S. levaillantoides* chicks possibly break the outline of the shape of the chick's head in grass cover. A non-striped head will be more detectable in grass than is a striped head (Merilaita and Lind 2005). In both francolins and spurfowls, the variegated back stripes probably provide countershading, making it difficult for a predator to distinguish the shape of the chick from its physical surroundings (Caro 2014).

In summary, although symplesiomorphy is a hereditary explanation for downy colours and patterns, the traits relevant for habitat matching are combined in a manner which is determined (adaptation) by natural selection (Frost 1975; Paxton 2009; Peichel 2014).

Evolution of downy patterns

Macrocephalon maleo is the most basal outgroup species to spurfowl and francolin within the Galliformes. Its downy chick plumage is basically uniformly black-brownish. The divergence of other downstream variants is basically a dilution of darker pigment (Mills and Patterson 2009). While speciation continued dark plain colours became limited but patterned on certain body parts of descendants, particularly on the crown, face and back. *A. meleagrides* and *Guterra pucherani* are proximate descendants to *M. maleo* and here it is evident that the uniformly dark plumage of downy chicks possesses whitish (diluted) blotches, but not yet particularly sharply defined features (e.g. striped).

Further down the evolutionary pathway two overriding morphological forms emerged with less black-brownish pigmentation in certain areas revealing dark stripes on their heads and back that are symmetrical and orderly arranged on a buff-coloured (diluted) background. These patterns are observed among many Phasianidae but particularly among *Pternistis* spp. where it emerged as semi-stripes (fewer stripes) compared to *Scleroptila* spp. where the remaining rufous stripes emerged as multiple stripes, giving the bird a disruptive chick plumage.

The presence of nose spots happened when most darker pigmentation receded leaving two isolated spots (or short stripes) on either side of the base of the upper mandible (nares). Indeed, in some species such as *Lagopus lagopus*, *Scleroptila afra* and *Numida meleagris* there are continuous stripes from the nose across the orbit on both sides of the head showing that dilution emerged along stripes. The presence of jaw stripes and multiple stripes on the face is ascribed to the evolution of darker pigmentation in this area. An ancestral bird like *M. maleo* has uninterrupted dark plain colours all over the head but the darker pigmentation diluted on the lower facial areas, but leaving no distinguishable jaw stripe (Additional file 1: Fig. S1).

There are more stripes on the side of the face of *Pternistis erckelii* than in other spurfowls, such as having a distinct jaw stripe and a thin stripe above the orbit which is more bold and typical of *Scleroptila* spp. and female *P. coqui*. The jaw stripe is only faintly visible on some other spurfowls. Ostensibly, while this seems to be a logical course of evolutionary events, for instance that *P. erckelii* could link the spurfowls and *Scleroptila* spp., it is more likely that the ancestors of extant francolins and spurfowls moved back and forth between striped and semi-striped chick plumage, which was probably determined by exposure to different habitats.

Conclusions

In summary, the following evolutionary pathways of *Pternistis* spp., *Francolinus* spp. and *Scleroptila* spp. might have played out: plain facial colours (see *M. maleo*) was followed by limited stripes, forming an eye-stripe in ancestral Phasianidae and was particularly deposited throughout *Pternistis* spp., *Francolinus* spp. and *Peliperdix* spp., followed by the emergence of some pigmentation in the form of multiple dark facial stripes in *Scleroptila* spp. In other words, when birds moved into grass, facial stripes became prominent. The scattered spots in grouse and allies (Tetraoninae) might be a breakdown of eye-stripes (divergence of eye stripes) since these spots are in that area of the neck towards where the eye stripe extends. However, from a dorsal point of view all variants (full pigmentation, cap and banded) were present among earlier ancestors of spurfowls and francolins. The facial sides of gamebird chicks (around eyes) are important for survival. The chick invariably uses his head as look-out point and will therefore adapt its morphological appearance to match the micro-habitat for camouflage and still allow maximum vigilance, while the rest of body is lower and often hidden. It is understandable that ancestral states diverged into multiple forms (that is the inconclusive linking of the ancestral states to *Pternistis* and *Scleroptila* spp.) because this is ascribed to habitat matching. Despite that the symplesiomorphic states hinders the use of downy characters to its full potential for the purpose of classification, this study revealed the evolutionary patterns of various characters and also how they associate with habitat. This had never been explored.

Additional file

Additional file 1: Table S1. Characters, associated states and their scores as given in Table 3. **Table S2:** Counts of character states associated with species arranged under three micro habitats to demonstrate association of species with habitat type. **Figure S1:** Facial, crown and dorsal feather patterns of the chick selected for this study. **Figure S2:** Ancestral state reconstruction for francolins and spurfowls based on Parsimony optimisation of disruptive markings traced on mitochondrial Cytochrome *b* phylogeny. **Figure S3:** Ancestral state reconstruction for francolins and spurfowls based on Parsimony optimisation of colour combination of head traced on mitochondrial Cytochrome *b* phylogeny. **Figure S4:** Ancestral state reconstruction for francolins and spurfowls based on Parsimony optimisation of dorsal patterns (crown) traced on mitochondrial Cytochrome *b* phylogeny. **Figure S5:** Ancestral state reconstruction for francolins and spurfowls based on Parsimony optimisation of side view patterns traced on mitochondrial Cytochrome *b* phylogeny. **Figure S6:** Ancestral state reconstruction for francolins and spurfowls based on Parsimony optimisation of jaw stripe traced on mitochondrial Cytochrome *b* phylogeny. **Figure S7:** Ancestral state reconstruction for francolins and spurfowls based on Parsimony optimisation of back colours traced on mitochondrial Cytochrome *b* phylogeny. **Figure S8:** Ancestral state reconstruction for francolins and spurfowls based on Parsimony optimisation of back patterns traced on mitochondrial Cytochrome *b* phylogeny. **Figure S9:** Ancestral state reconstruction for francolins and spurfowls based on Parsimony optimisation of nose spots traced on mitochondrial Cytochrome *b* phylogeny.

Authors' contributions
JHvN produced the research design including conceptualisation, museum assessments and character analysis. TGMN conducted the phylogenetic analysis and the ancestral state reconstructions as well as the interpretations. Both authors have read and approved the final manuscript.

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Acknowledgements
We thank Petra van Niekerk for assisting with the selection and photography of museum skins and Melissa van Niekerk for drawing the chicks' sketches.

Competing interests
The author declares that they have no competing interests.

Availability of data and materials
The datasets used and/or analysed during the current study are available from the corresponding author and are available for public access on GenBank.

Consent for publication
Not applicable.

Ethics approval and consent to participate
Not applicable.

Funding
Not applicable.

Received: 22 May 2017 Accepted: 11 December 2017
Published online: 08 January 2018

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