



Above: Endemic to mature mountain forests of Borneo, the mysterious crimson-headed wood-partridge, *Haematortyx sanguiniceps*, has traditionally been classified as an aberrant relative of the hill-partridge and grouped accordingly within the *Arborophilinae*. A pivotal piece in a complex taxonomic puzzle, *Haematortyx* was considered a phylogenetic link between the multiple-spurred ferruginous wood-partridge *Caloperdix oculus* and the enigmatic crested wood-partridges *Rollulus rouloul*. It has been recently revealed that *Haematortyx sanguiniceps* is one of the peacock-pheasant's nearest relatives. *Caloperdix* has been established as a close relative of *Rollulus*. Could it be that the crimson-headed wood-partridge links *Polyplectron* with the wood-partridges? Photo: Ichimura Katsuya.

*For the seed doth not reveal what tree it contains.  
The tree reveals what is within the seed.*  
- Ancient Egyptian proverb

## PEACOCK-PHEASANTS AND ASIATIC SPURFOWL

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### PART 3

With these natural history essays I've intended to explore taxonomic roots of galliform birds, analysing the proverbial trunk (geological age) of their order's phylogenetic tree. I've touched on the greater basal limbs: that belonging to the megapode dividing from that of the cracid ~100 million years ago (!) and between them emerge the slightly younger major branchings those of the toothed quail and guineafowl splitting ~ 50 million years ago.



Recent finding on the phylogeny and systematics of the junglefowl and francolin groups, like those of the pheasant and grouse groups are fairly thoroughly discussed in academic papers. This is of great benefit for further analysis of some newly defined parameters emerging from the ashes of a different era's conventional wisdom. This level of focus on the big picture eventually pans out as we reach the younger branches where individual genera within respective monophyletic lineages divide upon themselves. And finally we arrive at those outermost stems, the species and subspecies of each genera. Every theory brought forward here is product of a growing comprehension of the subject matter but I must reiterate that I am in no way masquerading as a lettered scientist. Like some of you it's all I can do to get through many of the research papers referenced here. My synopses are purely my own and while I run the risk of being misread as some pseudo-scientist I am confident of my knowledge of these birds. Like your own the exploration of all things gallinaceous is a dynamic process. Thank you for your patience and understanding.

A reiteration:

We've explored theoretical scenarios of the K-Pg impact winter's effects on the archetypal progenitors of those most basal of living gallinates, the megapodes and their fascinating reproductive strategies, with particular emphasis placed on the egg defense behaviors of mound building species that coexist with varanid lizards. This was contrasted with the diminished egg defense and lack of morphological specialization exhibited amongst cracids, the next oldest lineage of Galliformes, which evolved in ecosystems free of those predatory nest specialist lizards. We've discussed the issue of monogamous reproductive strategies that appear to be the rule amongst the oldest limbs of the Galliformes family tree and the significance of male territorial defense amongst these ancient terrestrial birds.

In this installation we touch on the evolutionary histories of the toothed quail and Asiatic wood-partridges, which together with the guineafowl form a set of slightly younger branches in the phylogenetic tree, still many millions of years older than the earliest grouse or typical pheasant. Reproductive strategies of the two former groups compel a consideration that perhaps the curious nest mounds of toothed quail and Asiatic wood-partridges are a plesiomorphic trait accrued from an archaic ancestor even older than the megapodes.

In this installation we will also cover some of the problems associated with a long tradition of apparent oversimplification of galliform taxonomy. As we will be discussing the fairly obscure genus *Galloperdix*, a partridge-like bird formerly classified amongst the perdicines and based primarily on morphology, has sometimes been associated with the junglefowl, (as a sort of phylogenetic link between *Gallus* and partridges) I'll apply some focus on the taxonomy of former perdicines and junglefowl. As *Galloperdix* has been recently established as the nearest living relative of *Polyplectron* the enigma of the peacock-pheasants' taxonomic placement has only grown more compelling. This narrative thread leads to an examination of a theoretical locus between great branches (guineafowl and toothed quail) where peacock-pheasants emerge either from a peafowl lineage or potentially, from the Asiatic wood-partridges/hill-partridges aka Arborophilids.

## **EVOLUTIONARY RELATIONSHIPS OF PEACOCK-PHEASANTS AND THEIR ALLIES**

### **A Tradition of Galliform Taxonomy based upon Phenetic Analysis**

Historically, two large families, *Phasianidae* and *Perdicipidae* were considered separate and monophyletic branches within the Galliformes: Phasianidae included such diverse species as junglefowl, peafowl, peacock-pheasants, tragopans and typical pheasants. Perdicipidae included quails, partridges and francolins.

Data sets that support this theoretical arrangement emphasize general morphology and plumage ornamentation, as well as purported reproductive strategies: The mostly unadorned partridge family were considered strictly monogamous whilst the famously adorned pheasants were assumedly polygamous or even promiscuous, especially those elaborately-ornamented species like the argus and peafowl (Johnsgard 1986). Species exhibiting morphological traits of both phasianids and perdicines such as stone partridge, blood pheasants, spurfowl, and monal partridges defied neat classification into either of the traditional assumedly monophyletic families. This handful of oddities were generally considered more or less intermediate between these two families and placed more or less together in their own amorphous group.

Subsequent to the inclusion of molecular data more recent reclassification schemes ostensibly simplified the taxonomic arrangements dealing with both groups. The Phasianidae and Perdicionidae families were lumped together into a single all-encompassing, assumedly monophyletic family, Phasianidae. Nevertheless, morphology, assumed reproductive biology, phenotype and zoogeography would continue to distinguish partridge-like birds from pheasant-like birds. As genera formerly classified in one of the two monophyletic families were still maintained as separate groups though demoted into respective subfamilies, *Phasianinae* and *Perdicioninae* chief amongst them and including additional subfamilies including those of peafowl *Pavoninae* (assumedly including peacock-pheasants), hill-partridges, *Arborophilinae*, tragopans, grouses and so on. There's a great deal of further research required to further define lineages that are neither partridge, pheasant, tragopan or peafowl.

One example of a phylogenetic conundrum presents itself in the peafowl (crested argus, great argus, Congo peafowl & typical peafowl) which have consistently been described as an ancient and highly-isolated group generally classified in their own subfamily Pavoninae. As my next natural history essay series focuses on peafowl mention of them here is only perfunctory. For the intents and purposes of this essay peafowl are distinguished from pheasants on a family level and referred to here as pavonids. Peacock-pheasants have consistently been classified within the peafowl clade, however substantiation of this taxonomic arrangement hasn't proved to be readily attainable or reached much consensus amongst researchers. Plumage characteristics and display behaviors are principle characteristics included in data sets that group *Polyplectron* with pavonids. Nevertheless, it has been recently determined that two genera of unadorned species formerly classified as perdicines are actually the nearest genetic relatives of peacock-pheasants. This presents us with a bit of a taxonomic conundrum. The debate had always been about whether the peacock-pheasant was a peafowl or a pheasant. How can a peafowl-like pheasant/ pheasant-like peafowl be more closely related to tropical partridges? Where does this leave the peafowl in all of this? Surely peafowl are closer to pheasants than to partridges- right?

Obviously traditional phenetic analysis missed some of the more obvious characteristics shared between the three genera *Polyplectron*, *Galloperdix* & *Haematortyx* if only because females of the different species were never compared with one another. There has been a long tradition of inadvertent bias whereby males of gallinate species are the primary focus of investigation.

Of course the elaborately adorned peacock-pheasant male differs markedly from the non-descript male Asiatic spurfowl yet a casual glance reveals how similar the females actually are and once osteology, morphology, vocalizations, ethology, reproductive strategy and molecular biology are included in the analysis it becomes readily apparent how closely-related they are. If we include independently evolved nest defense strategies in the analysis the notion that any resemblance between peacock-pheasants and peafowl can probably be attributed to convergence attains a bit more credibility.

Plate 1  
 OLDEST BRANCHES OF THE GALLIFORMES



Left:  
**Cracidae.**  
 Plain  
 Chachalaca.  
 Photo: Gary  
 Kinard.



Above:  
**Odontophoridae.**  
 Partridge  
*Ptilopachus*  
 female.  
 Photo: Nancy  
 Johnston.



Right: **Numididae.**  
 Black *Phasidus*.  
 Photo: Brian Schmidt  
 © Smithsonian Institution



Left: **Megapodiidae.**  
 Philippine Scrubfowl.  
 Photo: Atze den Ouden & Yvonne Stevens.



Right: **Arborophilidae.**  
 Roul roul.  
 Photo: Bill Fleites.

## A Dissolution of Perdicines

Contemporary studies have shown that subdivisions delineating so-called phasianines and perdicines are not consistent with the evolutionary history of the group (Crowe et al. 2006a, 2006b; Eo et al. 2009, Kimball et al. 2011; Wang et al. 2013). It's now accepted that neither phasianines nor perdicines are monophyletic. Just how the different groups are related to one another is still in the process of being sorted out. A few findings have shaken classification schemes. For example it's been established that toothed "New World" quail (Odonts) are not related to most "Old World" perdicines and are nearly as ancient as cracids. They are now placed in their own family the Odontophoridae which is evidently derived from the slightly older Numididae. The branching including toothed quail and guineafowl derives from a lineage ancestral to both megapodes and cracids and is itself basal to the remaining gallinates. Toothed quail are more related to cracids and guineafowl than to true partridges and as such are no longer classified as perdicines. Similarly, though Grouse and turkeys were traditionally classified in their own distinct families or subfamilies within the Phasianidae accordingly, they have proven to be one another's closest living relatives and clade together. They form a sibling group to typical pheasants with which they share a common ancestor. Compellingly, the true partridge *Perdix* also clades with typical pheasants and grouses but is essentially unrelated to hill-partridge, true quail or francolins. Likewise, bamboo partridges (*Bambusicola*) provide another example of this problem of phenetic classification of gallinates. In this case, Akishino Fumihito, Tetsuo Miyake, and their colleagues discovered that *Bambusicola* is neither partridge or pheasant. New data sets (based primarily on molecular biology) have revealed that the diminutive bamboo partridge shares a common monophyletic ancestor with the world's most populous and economically important livestock species (*Gallus domesticus*), the common chicken. At the time of this revelatory finding Junglefowl were still considered pheasants, classified in a subfamily Gallusinae within the Phasianidae. Though the bamboo partridge, the true partridge and the true quail share similar morphologies and life histories they are not one another's nearest genetic relatives by a long shot. Each of these unadorned monogamous species is more closely related to an adorned species than to each other. The bamboo partridge, junglefowl and true quail share a monophyletic ancestor, with each belonging to one of two well-demarcated groups. The true partridge *Perdix* shares a monophyletic ancestor with typical pheasants, including such ornate species as those of the genus *Chrysolophus* and grouses. The two respective groups are only distantly related, no closer to one another than bovids to deer.

### What's the definition of a Perdicine?

If partridge, quail and francolin don't form a single monophyletic group just what are they taxonomically? We had grown accustomed to the notion that peacock-pheasants were intermediate between typical pheasants and the peafowl. Now we have to ask if the peacock-pheasant and its Asiatic spurfowl allies form a phylogenetic link between pheasants and *Perdicines*? That's a spot that's already been occupied by francolins for just about as long as anyone's been pondering this topic. But the taxonomy of francolin is just as complex as that of the partridge and pheasant. They're not monophyletic either!

Chiefly African in zoogeographical range, though a very few species also inhabit regions of South Asia, those large quail to grouse-sized, cryptically coloured and patterned fowl known collectively as francolins have proven to be a compelling group unto themselves. Francolin literally means "little hen", which as we shall come to appreciate is an apt description given their genetic proximity to *Gallus*. Their modern classification (heavy splitting) drawn largely from molecular data is pertinent to our discussion as we bore our way through problematic phenetic classification schemes of previous centuries.

It has been recently established that the ~ 40 species comprising the genus *Francolinus* are paraphyletic. Just as some "partridge", for example - the bamboo partridge, hill-partridge and rock partridge are not actually related to true partridges of the genus *Perdix* (which proves to be a small pheasant!), the francolins have apparently derived from three major radiations, each with its own respective evolutionary history and from basically unrelated ancestors.



***Pternisted erkeli* Eritrean Francolin. Photo: Donald Metzner.**

Formerly classified within *Francolinus*, *Pternistes* is the most populous genus within the Coturnix group. Described as "partridge-francolins", there are 23 species in total. Unlike quail-francolins, which are related to junglefowl, bamboo-partridges and Asiatic francolins, partridge-francolins are endemic to Africa. Their nearest relatives are the diminutive junglebush quail *Perdicula* and the *Alectoris* rock-partridges.

Partridge-francolins have traditionally been called spurfowl in reference to their powerful kicking thorns. This trait of multiple spurring is shared with *Acryllium*, *Phasidus*, *Ithaginis*, *Caloperdix*, *Haematortyx*, *Galloperdix* & *Polyplectron*. Double spurs have very unusually been exhibited by individual specimens of *Guttera plumifera*, *Rheinardia nigrescens* & *Gallus lafayette*. These genera appear to have independently evolved this trait of multiple metatarsal spurs as each has closer relatives that are either non-spurred or single-spurred. It may be the case that multiple spurring is a plesiomorphic trait accrued from a common Eocene ancestor to many extant gallinates.

These three lineages of “little hens” are not one another’s closest relatives by a long shot. Though by and large they outwardly resemble one another quite closely, the three respective groups of francolins have evidently arrived at their conservative morphologies and phenotypes via evolutionary convergence. We can readily envision consequences of gradual global climate change subsequent of the Miocene epoch when the entire planet cooled substantially and frequently aridified. Assumedly subtropical forest adapted ancestors of these different francolin lineages adapted to wide-scale ecological challenges presented by environments transforming from jungle to shrubland and savanna. Apparently, all along their respective evolutionary histories they’ve shared similar, if not the identical predators while eking out their survival in similar habitats for many of the same foods. It should be mentioned that there are ecological differences that prevent some level of competition between different species. For example, some of the “partridge-francolins” uncover food by digging into the earth with decurved and powerfully reinforced bills similar to those of eared pheasants. Conversely, some “quail-francolin” procure their food largely above the surface of the ground. The bills of the surface foragers are outwardly more reminiscent of those of the junglefowl, which also procures most of its food on the surface of the ground versus deep within root bases of perennial grasses. Many environments host more than one species of francolin. This is likely made possible by their divergent foraging strategies. Though the different francolins largely look and behave alike (at first glance) they have evidently come to resemble one another via evolutionary convergence. Their phenetic classification has proven artificial.

## A Monophyly of Gallocoturnixids

Based on molecular biology and osteology, francolin species formerly lumped together in the anachronistic genus *Francolinus* either share monophyletic ancestors with a clade that includes true quails, *Coturnix*, or a sibling lineage that clades closely with the junglefowl *Gallus*. Likewise, according to the latest research, bamboo partridges (genus *Bambusicola*) prove to be closely related to the newly defined group (endemic to Africa) referred to as “quail-francolins”. This group includes the genera *Scleroptila*, *Dendroperdix* and *Peliperdix* collectively. Junglefowl (*Gallus*) have been established to be closely-related to Asiatic francolins of the genus *Francolinus* and as discussed earlier, with the bamboo partridges *Bambusicola* and their sister the long-billed partridge *Rhizothera*. The quail, partridge, Asiatic francolin and bamboo partridge form a single monophyletic group. For the purposes of this article (and with full disclosure that I am of the “splitter” school of taxonomy and an undergraduate at that), this monophyletic grouping are hitherto described as ***gallusinids***.

**Right: Swamp Francolin female.**  
**Photo: Sharad Sridhar.**

The gallusinids’ geographical range is expansive, encompassing African and Indo-Malayan [ecozones](#), which were apparently contiguous throughout the Miocene and Pliocene epochs ~ 20-5 MYA. Fossil species evidently belonging to this newly defined grouping suggest that a region (radically different in geography and ecology) encompassing what is now northwestern Eurasia may have been an original centre of distribution of gallusinids including rather surprisingly, the now strictly subtropical Asian junglefowl.



The gallusinids are not completely phylogenetically isolated as they have a sibling lineage forming a second monophyletic branching, hitherto defined as the "coturnixids", with which they apparently share a late Oligocene ancestor. The most populous genus of this group *Pternistes* currently described as "partridge-francolins" consists of 23 species formerly classified within the *Francolinus*. Unlike gallusinid quail-francolins, partridge-francolins are endemic to Africa. The term used to distinguish them from other francolins is a slightly convoluted and potentially confusing descriptor given that *Pternistes* is not closely related with true francolins (now described as quail-francolins), which they outwardly resemble. Indeed *Pternistes* has a closer genetic relative in the true quail *Coturnix* than to quail-francolins. Their nearest allies appear to be the diminutive bush-quails of the genus *Perdicula*, which are endemic to Southern Asia. Other members of the coturnixid assemblage include rock partridges of the genus *Alectoris* and perhaps most significantly, the true quail, *Coturnix* which has the largest range of any galliform bird. The massive snowcock *Tetraogallus*, once considered the largest of the anachronistic perdicines, as well as that smallest of all Galliformes, the painted quail, *Excalfactria*, the Madagascar partridge, *Margoroperdix*, as well as the ghostly see see and sand partridges of the genus *Ammoperdix* are also coturnixids.

These two sister groups, that of the junglefowl/quail-francolins/bamboo partridges (gallusinid) and that of the true quail/jungle bush quail/partridge-francolins/rock partridges/snowcocks/sand partridges (coturnixid) form one large assemblage, described in this essay, as the Gallocoturnixids.

### **The Curious Case of the Stone Partridge**

One supposed francolin species represents a lineage that at least morphologically would appear to link the Asiatic spurfowl with francolins. The so-called Nahan's forest francolin, formerly *Francolinus nahani*, has been revealed to be a very near relative and deep forest equivalent of the erstwhile monotypic stone partridge of the genus *Ptilopachus*. So here we have a forest-adapted "francolin" that has proven to belong to a genus that has been revealed to be so isolated phylogenetically speaking, from its African congeners, it's proven to be a major discovery in of itself. This is important to keep in mind because *Ptilopachus* has, on morphological grounds, traditionally been grouped with *Galloperdix* and *Bambusicola* as being the least partridge-like of the perdicines. Regardless, *Ptilopachus* is not a close relative of *Bambusicola* nor *Galloperdix*. Rather counter-intuitively, *Ptilopachus* has very recently been established as sole representative of the toothed quail family (Odontophoridae) inhabiting the African continent. This is a major development. Clearly, *P. nahani*, the forest stone partridge, is not a francolin after all, indeed *Ptilopachus* and *Francolinus* (+ other francolin genera) are entirely unrelated. Its placement within the odonts is basal suggesting that it is the least-derived of the family. As the Odontophoridae are older than geographic autonomy of the African continent we have to wonder if it represents a lineage that would eventually diversify into not only the odonts of North, Central and South America but in addition, perhaps the Arborophilids.

With this one exception, Odontophoridae are endemic to the "New World" a bioregion, not incidentally, which experienced some of the most acute effects of the K-T impact winter. Epicentres of the space rock impact zones that doomed the vast majority of life on earth are located within the Yucatan Peninsula, the apparent centre of distribution of the odonts. This suggests that archetypal progenitors of toothed quail not unlike *Ptilopachus* probably colonized a regenerating dead zone in what is today Central America while their still older cousins the stone partridge maintained a presence on the newly born continent of Africa. It is entirely plausible that Arborophilids emerged from this same stock, a supposition which I will return to shortly. This is a critical topic in the context of a possible phylogenetic link between Arborophilids and peacock-pheasants. Indeed, I suspect the peacock-pheasant is more closely allied with Arborophilids than to other gallinates.



Plate 2  
STONE PARTRIDGE & TOOTHED QUAIL



From top, left:  
a. Stone Partridge keats. Photo: Krzysztof Blachowiak.  
b. *Odontophorus*. Photo: Dario Sanches.  
c. Hogan Nest Mound. Photo: Antero Topp.  
d. Scrubland Stone Partridge *Ptilopachus petrosus*.  
Photo: Klaus Rudlof.  
e. Forest Stone Partridge *Ptilopachus nahani*.  
Photo: Pete Morris.  
f. *Colinus* male incubating within Hogan Nest Mound.  
Photo: Bud Bostick.

## Hill-Partridges, Wood-Partridges & Palaeortyx

Just as neotropical cracids, odontophorids, and Africa's guineafowl diversified from archetypal gallinates related to *Eulipoa* and *Macrocephalon* (primitive megapodes), another major branching theoretically emerged from the same curious KT impact winter survivors. This fourth monophyletic grouping is that of the hill-partridges & wood-partridges, e.g., arborophilids, which may be amongst the nearest living relatives of the fossil genus *Palaeortyx*. This extinct species appears to have descended from a post KPg impact winter scrubfowl intermediate morphologically between odonts and arborophilids. First appearing some 30 million years ago during the Oligocene epoch, *Palaeortyx* is believed to have diversified throughout the sub-tropical forested land mass that would eventually become Eurasia. Most species of arborophilids are collectively known as hill-partridges belong to the genus *Arborophila*.

From Wikipedia (unfortunately outdated):

*Arborophila* is a genus of bird in the Phasianidae family.[1] It is a very diverse genus, having the second most members within the Galliformes after *Francolinus*. These are fairly small, often brightly marked partridges found in forests of eastern and southern Asia.[1] Some species in this genus have small ranges, and are threatened by habitat loss and hunting.

### Species

While most species in this genus are highly distinctive and their taxonomic treatment is settled, there are three complexes where the species limits have not been entirely resolved and to various degrees are disputed:

*A. orientalis*–*sumatrana*–*campbelli*–*rolli* complex,  
*A. cambodiana* complex,  
and  
*A. chloropus*–*merlini*–*charltonii* complex.[1]

*A. torqueola* is always called the hill partridge or common hill-partridge, but in all other species "hill" is often disregarded (for example, *A. rufipectus* is variously known as the Sichuan hill-partridge or Sichuan partridge)

The crested wood-partridge or roul roul, *Rollulus* is possibly the nearest proximation of an Eocene epoch proto-arborophilid. Hill-partridges evidently derived from wood-partridges (probably speciating during the Miocene) which are morphologically and behaviorally reminiscent of both toothed quail and guineafowl. Three phylogenetically basal genera of this diverse group are the gemstone hued *Rollulus* and its close cousins, the multiple-spurred *Caloperdix* and heavy-billed black partridge, *Melanoperdix*. The center of distribution of the Arborophilidae appears to be Indo-Malayan. Every species of hill-partridge and Asiatic wood-partridge are Indo-Malayan with one exception. *Xenoperdix*, the Udzwunga forest-partridge is native to the African continent. Just as *Ptilopachus* is sole representative of the odonts in Africa so too is *Xenoperdix* the one arborophilid on the continent. The relationship between these two enigmatic genera is not close but further research may explore this topic further.

Arborophilids are reminiscent of their incubator bird antecedents (and some odonts) in the integral role males play in nest construction and clutch safeguarding. Arborophilids construct mounded nesting chambers or "shanties" within which the females, and occasionally the males themselves, incubate small clutches of eggs. Both odont and arborophilid males/pairs construct domed nests of leaf litter, though the toothed quail family's mounded "hogans" are sometimes multi-chambered, more complex affairs than the often superficially subterranean appearing "shanties" of the arborophilid.

Curiously, *Ptilopachus* is the only known galliform species to be truly polyandrous. Though generally monogamous, in captivity stone partridge females will frequently associate with two or more males to the exclusion of other females. Males fashion nests in grass tussocks (with three or more grass tunnels providing ready exits) within which the female deposits her eggs. In situations where there are multiple males, the female deposits a clutch in the nest of each male which alone incubate the eggs and are the primary caretakers of chicks. In captivity, stone partridge reproduce more or less continually throughout the year.

Plate 3  
ROUL ROUL



*Rollulus rouloul*  
Photos:  
Huub Dijcks.

**Plate 3** - Crested wood-partridge, *Rollulus rouloul*, occupy a basal phylogenetic position within the hill-partridge group Arborophilidae. Whereas the genus *Arborophila* diversified primarily during the mid-late Pleistocene beginning ~ 1 MYA Rollulus and its nearest relatives probably began to diversify during the mid-late Miocene ~ 9-2 MYA. The roul roul, as it is colloquially known, is a highly gregarious species joining in flocks of up to 20 birds, which separate into pairs during nesting. Both parents (and unpaired 'helpers') are equally invested in the rearing of progeny, which is substantial as the keats require bill feeding for several weeks. Like other Arborophilids, Rollulus is chiefly invertivorous, though an opportunistic gleaner of seeds, sprouts and fruit. Photos: Huub Dijcks.

Could these reproductive strategies be plesiomorphic? Perhaps the arborophilids and odontophorids accrued this habit of nesting, where males essentially bury/conceal their eggs and incubating mate beneath leaf litter, from the earliest archetypal gallinates. The *Ptilopachus* polyandrous nesting behaviors appear somewhat intermediate between those of the mound building male megapode, which tends to its homeothermic incubators year round and the toothed quail/ arborophilid male nest mound construction where females or both sexes share incubation duties. Is this the developmental stage from which megapodes began their mound building? It may be the case that only odonts and arborophilids have maintained this original reproductive strategy, one that was lost in the megapode, which may have evolved its unusual form of egg incubation consequent of the K-Pg impact winter's ecological cataclysm which obliged the birds to protect their eggs within homeothermic mounds. I suspect *Ptilopachus* may actually be a still closer approximation of the *Palaeortyx* lineage than Asiatic wood-partridges. Perhaps it represents an evolutionary stage intermediate between a Paleocene aged scrubfowl and the earliest guineafowl precursor that would eventually diversify into toothed quail in one hemisphere during the late Oligocene and later, further diversifying during the Eocene, into Asiatic wood-partridges in another.

Like cracids and numids, both odont and arborophilid evolved in lock step with a new class of endothermic carnivore, the placental mammal, only recently emerged from the ashes of the Eocene. We can envision a cracid/odont evolutionary history free of varanids in contrast with that of the megapode and peafowl forever locked in arms races with this class of nest predator. Compellingly, only those galliform species inhabiting regions where varanids remain in ecosystems but little changed for many tens of millions of years ( i.e., argus and peacock-pheasant), tend to exhibit highly ornate plumage used in aggressive nest defense. This is a topic to be revisited later. [Reference Arborophilid Nesting](#)

### **A More Modern Phylogenetic Arrangement**

Several different, competing views have been published on the possible evolutionary relationships of these groups. There are literally dozens of theories and ideas that cannot be further extrapolated upon without more substantial data. Nevertheless, it's generally accepted that there are at least four monophyletic groups formerly classified as either pheasants or partridges sufficiently distinctive to warrant some level of taxonomic distinction. The following monophyletic assemblages traditionally classified as either perdicines or phasianines are established:

1. Roul Roul, Wood-Partridges & Hill-Partridges ("Arborophilids")
2. Peafowl & Argus ("Pavonids")
3. Monophyletic group with sibling branches ("Gallocoturnixids")
  - True Quail, Chukar, Partridge-Francolins, Junglebush Quail, Snowcocks & Sand Partridges ("Coturnixinae")
  - Junglefowl, True Francolins, Quail-Francolins, Crested Francolins, Bamboo Partridges and Long-Billed Partridges ("Gallusinae")
4. Monophyletic assemblage with sibling branches ("Tetraophasinids")
  - Blood Pheasants ("Ithaginisinae")
  - Tragopans, Monal-Partridges & Monals ("Tragopaninae")
  - Koklass, Grouses & Turkeys ("Tetraoninae")
  - True Partridges & Typical Pheasants ("Phasiperdixinae")

Plate 4  
PAVONIDS

***Pavoninidae* Genera**

*Rheinardia* (Crested Argus, 2 species)

*Argusianus* (Great Argus, 2 species)

*Afropavo* (Congo Peafowl, monotypic)

*Pavo* (Typical Peafowl, 4 species)

From top:

*Rheinardia*.

Photo: Tomáš Najer.

*Argusianus*.

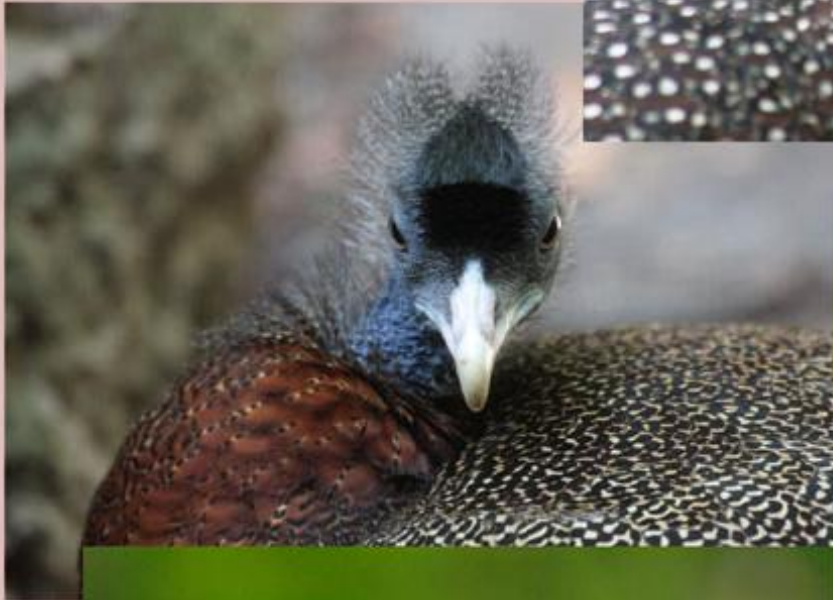
Photo: Nathan Rupert.

*Afropavo*.

Photo: Artis Zoo-Netherlands.

*Pavo*.

Photo: Dale Forbes.



## Asiatic Spurfowl a Phylogenetic Conundrum

While some consensus is emerging with respect to the position of many genera with regard to each other, several genera have not yet been included in these analyses and persist as enigmatic affinities.

As stated earlier, the possibility exists that the mostly plumage-based support for the inclusion of *Polyplectron* within the peafowl clade is the result of convergence. It should also be noted that peacock-pheasants possess several unusual features in common with a small handful of poorly known galliform species that have rarely been included within evolutionary analyses, namely the Asiatic spurfowl, which have, based upon their outward similarity to partridges, been traditionally classified as members of the anachronistic perdicine group.

*Galloperdix* and *Haematortyx*, e.g. the Asiatic spurfowl, are poorly known galliforms, rarely photographed, often only briefly mentioned in books, and usually not included in studies on the evolution of diversity within the galliforms.

Sun et al. have recently established that these two genera are indeed the peacock-pheasants nearest molecular relatives (. 2014)

Before the advent of molecular biology it was traditionally assumed that the hen-like Asiatic spurfowl of the genus *Galloperdix* was a perdicine that formed a phylogenetic link between junglefowl and tropical species like the crested wood-partridge of the genus *Rollulus* (an Arborophilid). Indeed two monotypic species intuitively considered as each other's closest relatives, the ferruginous wood-partridge *Caloperdix* and the crimson-headed wood-partridge *Haematortyx* both exhibit those curious multiple metatarsal spurs characteristic of *Galloperdix*. Both share the general morphology and behavioral ecology of *Rollulus*. What appeared to be a neat assemblage of medium-sized, tropical partridge-like birds traditionally classified as members of the anachronistic *Perdicinae* have proven to belong to two distinct evolutionary lineages. Despite its multiple spurs, *Caloperdix* clades closely with *Rollulus* & *Melanoperdix*. *Galloperdix* & *Haematortyx* clade together closely with *Polyplectron*. The notion that peacock-pheasants might be allied to any of these obscure species was entirely overlooked for all these centuries due to the size, morphology and colouration of male *Polyplectron*. But what of the relationship between the ferruginous wood-partridge and crimson-headed wood-partridge? Is this another example of convergent evolution? Isn't it possible that *Haematortyx* is a phylogenetic bridge between the wood-partridges and peacock-pheasants?

Without their characteristic armory of visually arresting accretions, the peacock-pheasants are difficult to distinguish from *Galloperdix*, particularly in voice. While the plumage of males of the two genera differ markedly, females of the two genera correspond rather closely. In the hand similarities in overall morphology between *Polyplectron*, *Galloperdix* & *Haematortyx* are striking. What is immediately obvious is how the crimson-headed wood-partridge is basically analogous with Asiatic spurfowl and peacock-pheasants in anatomical morphology, vocalizations and behavioral ecology but couldn't be more dissimilar in plumage. This may be attributed to the elevation these montane forest birds frequent and nest within. Of the peacock-pheasant/Asiatic spurfowl (hitherto *Polyplectron*) group, only the bronze-tailed peacock-pheasant inhabits similar altitudes. If the nesting habitats of montane-adapted Asiatic spurfowl are above the elevational limits for reproduction of certain predatory reptiles perhaps they have secondarily lost their ornamentation as has been demonstrated in *P. chalcurus*. In the case of *Haematortyx* it may have never developed to begin with, especially if most of the species' evolutionary history has taken place in the mountains.

### Kicking Thorns

While the presence of two spurs, one on each leg, is present in various galliform groups, peacock-pheasants are remarkable in possessing as many as four sharply pointed spurs on each hindlimb, though three or just two per leg seem to be more typical. Asiatic spurfowl are similar to peacock-pheasants in that their spurs are long, slender, and generally straight and sharply pointed.

Plate 5  
COTURNIXINAE



Coturnixinae (from top left)

- a. *Alectoris*. Rock-Partridges. Photo: Vladimír Motyčka.
- b. *Pternistes*. Partridge-Francolins. Photo: Lindsay Hansch.
- c. *Perdicula*. Junglebush Quails. Photo: Subharghya Das.
- d. *Ammoperdix*. Sand Partridges. Photo: Soner Bekir.
- e. *Tetraogallus*. Snowcocks. Photo: Rebecca Schlofne.
- f. *Coturnix*. True Quails. Photo: Bernard Dupont.

Plate 6  
GALLUSININAE



From top, left to right:

- a. *Bambusicola*. Mountain Bamboo Partridge. Photo: Mikael Nord.
- b. *Dendroperdix*. Crested Francolin. Photo: Michael Van de Kamp.
- c. *Gallus*. Sri Lanka Junglefowl. Photo: Chandana Witharanage.
- d. *Francolinus*. Swamp Francolin. Photo: Sharad Sridhar.
- e. *Scleroptila*. Shelleys Francolin. Photo: Lane Dirk.
- f. *Peliperdix*. Coqui Red-tailed Francolin. Photo: Ariadne van Zandbergen.
- g. *Rhizothera*. Long-billed Partridge. Photo: Gerald Cubitt.



Furthermore, the lowermost spur is about half the length of the adjacent one, an unusual feature only present in *Polyplectron*, *Galloperdix*, *Haematortyx*, and most compellingly *Caloerperdix*; which exhibits clear molecular and morphological affinities with the arborophilids with which it is classified. The ferruginous wood-partridge is the only known species of the arborophilid group exhibiting this metatarsal spurring.

The presence and characteristics of metatarsal spurs on the legs of gallinates is worthy of its own paper. It should suffice to say that birds so armed are highly invested in nest and chick defense, and these weapons are effective in interspecific encounters. Multiple spurred species, with the exception of *Galloperdix lunulata*, are longer legged than those with single spurs. The birds use them defensively when a predator attempts to subjugate them, as well as when a creature trespasses against them, be that a competitor or potential predator of eggs or chicks.

Other galliform species exhibiting multiple spurs include the mysterious *Phasidus niger* of Central Africa (and presumably its Eocene-aged Asiatic relative *Telecrex*). The vulturine guineafowl of the genus *Acryllium* exhibits multiple knobs analogous with those of the spurs of *Phasidus*. Curiously, the white-breasted guineafowl only sports single spurs. I have read of two documentations of individual *Guttera plumifera* guineafowl males exhibiting double spurs on a single leg. These weapons grow directly from the bone.

Interestingly, the crested argus, *Rheinardia* has been documented exhibiting multiple vestigial spurs on a single leg (Beebe 1919). This is the only member of the peafowl documented as exhibiting the trait.

Several species within the coturnix group exhibit multiple spurring. Partridge-francolins of the genus *Pternistes* are often referred to as African spurfowl due to their multiple metatarsal kicking thorns. There are apparently no examples of multiple spurring amongst the Gallusinids, the clade that includes bamboo partridges, junglefowl and African francolin genera (to the exclusion of *Pternistes*).

Of all the prominently spurred pheasants and tragopans belonging to the monophyletic "Tetraophasid" group, the sole genus to exhibit multiple spurring is the enigmatic blood pheasant, *Ithaginis*, a primitive relative of the tragopan and hence allied with the common ancestor of all grouses and true pheasant genera. Interestingly, the blood pheasant has evolved in a region once inhabited by the subtropical, Eocene-aged fossil species *Telecrex* synonymous with the black guineafowl *Phasidus*. There are fossil Galliformes in Florida from the early to mid-Miocene, (*Rhegminornis* if memory serves me correctly) that evidently sported multiple spurs.

**Red-breasted Partridge *Arborophila hyperythra*. Photo: Dubi Shapiro.**



As a rule, authors discuss galliform birds primarily in relation to their sexual behavior and reproductive biology. Character traits useful in anti-predatory applications are seldom discussed. As galliforms evolved largely in the Eocene, it would be interesting to explore if metatarsal spurring may prove to be a plesiomorphic character. However, like eyespots on the plumage of peacock-pheasants and pavonines, this trait may be derivative of a similar challenge and thus the result of convergence. It has been hypothesized that metatarsal spurs have arisen independently amongst Galliformes and likewise lost secondarily in some groups. As each of the multiple-spurred representatives of the five respective groups are considered basal within their monophyletic lineages, it could be inferred that with geographic ranges and distribution of Galliform birds expanding over time these groups encountered similar interspecific threats. Perhaps multiple metatarsal spurring in these five ancient lineages provided some form of selective advantage at the onset of their speciation, but the need for this trait was subsequently lost. I tend to think multiple spurring is a plesiomorphic trait though it remains to be seen if this can be substantiated.

Plate 7  
ARBOROPHILIDS



**Arborophilids**

From top, left to right:

- a. Archetypal Megapode (*Eulipoa*) similar to hypothetical ancestral Arborophilid. Photo: Sam Woods.
- b. *Melanoperdix*. Photo: Untung Sarmawi.
- c. *Rollulus*. Photo: Stefan Koeder.
- d. *Arborophila*. Photo: Graham Ekins.
- e. *Caloperdix* (keat). Photo: Mark Herand.
- f. *Xenoperdix*. Painting by Martin Woodcock.
- g. *Palaeortyx miocaena* ~ 25 MYA. Photo: Michael Wuttke.
- h. *Palaeortyx major* ~ 10 MYA. Photo: commons Wikipedia.

Plate 7a  
ARBOROPHILID NEST SHANTIES



***Rollulus***  
**nest shanties**

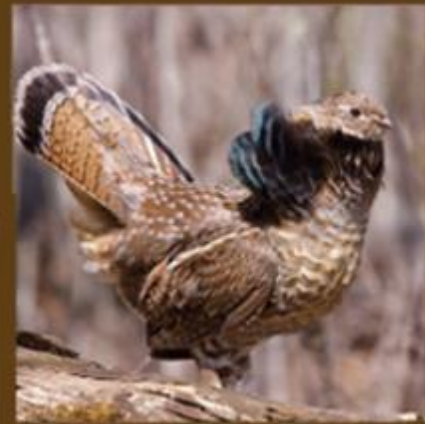
Top photo:  
Huub Dijcks.  
Second one:  
Peter Stubbs.  
Bottom, right:  
Jan Akkeson.

Though strictly monogamous, roul roul tend to toward facultative social polyandry. When in the wild and at liberty within large flight aviaries, up to three unpaired males will occasionally associate with a breeding pair, assisting in construction of the large mound nest, e.g. "shanty" within which the female alone incubates a small clutch of up to 5 eggs.

Nest Shanties can be complex affairs and may be maintained throughout the year. A flock may construct several shanties within which the males draw their mates before egg laying commences. Only one nest will be used. While females will participate in the construction of these mounds it males provide most of the labour. In some instances an entire social unit constructs mounds cooperatively. Socially bonded females often nest within the same mound and generally on separate nests. Occasionally males take up incubation duties and generally do so at dusk.

Though highly precocial at hatching, Rollulus chicks, e.g., "keats" perch within the nest for several days and may also take cover within these structures during rainstorms. Curiously, it is the male that generally remains with chicks when they roost overnight with their mounds, while the female perches arboreally near by.

Plate 8  
TETRAOPHASIANIDS



**Tetraophasianids**  
family Tetraophasianidae

- a. subfamily *Phasiperdixinae* (Genus: *Phasianus*) Photo: David Fenwick
- b. subfamily *Tetraoninae* (Genus: *Pucrasia*) Photo: Satyendra Sharma
- c. subfamily *Tetraoninae* (Genus: *Perdix*) Photo: Tarmo Lampinen
- d. subfamily *Phasiperdixinae*. (Genus: *Lagopus*) Photo: Jose Hlasek
- e. subfamily *Tragopaninae*. (Genus: *Ithaginis*) Photo: Cheng Qing Ka Cho
- f. subfamily *Tetraoninae*. (Genus: *Bonasa*) Photo: Rod Planck
- g. subfamily *Phasiperdixinae*. (Genus: *Crossoptilon*) Photo: Scott Vowers
- h. subfamily *Meleagrisminae*. (Genus: *Agriocharis*) Photo: Lynn McBride
- i. subfamily *Tragopaninae*. (Genus: *Tragopan*) Photo: Francy Hermans

## Introducing the Asiatic Spurfowl and the Crimson-Headed wood-partridge

From Johnsgard,

*"The spurfowl are medium-sized, tropical scrub and woodland species of the Indian subcontinent having long tails of 14 rectrices that are about 80% as long as the wing. The wing is rounded, with the fifth and sixth primaries the longest. The sexes are dimorphic, but in two of the three species both sexes have a considerable area of bare red skin around the eyes. The tail is somewhat vaulted, and in males of one species is slightly iridescent. Males have one to three tarsal spurs, and females usually few or none.*

*The usual social unit is from two to six birds, which typically are of family groups, and it has been suggested that mating is permanent. The male's advertisement call is a chuckle-like crowing. The alarm call is a quickly repetitive guttural rattling like those of guineafowl.*

*Painted and Sri Lanka spurfowl utter whistling and buzzing contact notes.*

*Three species are recognized.*

*Galloperdix spadicea (Gmelin) 1789: Red Spurfowl*

*G.s. spadicea*

*G.s. caurina*

*G.s. stewarti*

*G. lunulata ( Valenciennes) 1825: Painted Spurfowl*

*G. bicalcarata (J.R. Forster) 1781: Sri Lanka Spurfowl*

*Polyplectron* and *Galloperdix* are strictly monogamous, with males selecting nests and guarding them. Furthermore, their chicks are very similar in appearance, as is the manner in which species of both genera require the long-term investment of two bonded parents for their chicks to survive into adulthood and presumably inherit optimal home ranges. Unlike the chicks of quail, pheasants, or grouses, those of Asiatic spurfowl, peacock-pheasants, pavoines, and hill partridges beg incessantly when not reared appropriately.

In the aviculture section of this collection of essays, we will discuss how this dependence on parental care and thus its absence oftentimes leads to preventable stress-related illness and mortality. The aforementioned traits of multiple spurring, smooth bare facial skin, monogamous reproductive strategies, aggressive nest site defense, occasional male incubation and extensive bi-parental care are also shared with the crimson-headed wood-partridge, *Haematortyx*.

### Red Spurfowl

The red spurfowl, *Galloperdix spadicea*, has by far the largest geographic range. There are three apparently clinal races known, *G. s. caurina*, *G. s. spadicea* and *G. s. stewarti*. The latter may be further isolated geographically and systematically from other red spurfowl forms. In this species, it is the female that is more boldly patterned and visible of the sexes. The females' contour plumage exhibit a distinctive colour palette that includes mineral greys, bright ochrous buff, and sepias. The dorsal plumage is generously starred with inumbrations analogous with those of female peacock-pheasants, particularly those of the Bornean and Hainan.

The males of two of the red races are handsome, subtly scalloped in grey or pinkish vermillion over a tawny vermillion background. The one subspecies, *G. s. stewarti*, exhibits a distinctly maroon tint with less obvious scalloping on a comparatively uniform dark-cinnamon red and burned orange hue background. *G. s. caurina* and the nominate *G. s. spadicea* exhibit varying degrees of comparatively pale fulvous, mouse grey, and oak brown.

The females of *caurina* appear to be somewhat greyer than *spadicea*, which appears to be the palest form. *G. s. stewarti* sports a dark grey head and upper neck and dark tipped crest of moderate length. The female *stewarti* is likewise considerably darker than the females of *caurina* and *spadicea*, whereas the male is more or less uniformly coloured. The hen of this form exhibits more prominent inumbration, brighter bolder ochres, and tawny brindle.

Red spurfowl inhabit rocky foothills and dense bamboo jungle. It may often be found in gullies thickly wooded with thorn scrub. During the dry season it is regularly encountered in deciduous forest. The lowest elevation it has been documented at is approximately 300 m (1000 feet). The highest elevation this species is found occurs during the wet season at approximately 2300 m (7,500 feet), where it is often observed in small groups. It appears to nest primarily between 600-1200 m (2,000-4,000 feet).



**Female Kerala Red Spurfowl *Galloperdix s. stewarti***

Photo: [P.J. Vansanthan](#)

Red spurfowl usually forage in small parties of three to five. While in motion, the tail is generally held horizontally and only slightly expanded. It does not flick its tail in the manner of peacock-pheasants. When alarmed the tail is held in a more vertical manner and strongly vaulted as in junglefowl. Red Spurfowl are quite silent during most hours

of the day but vocalize frequently during crepuscular hours.

Asiatic spurfowl, peacock-pheasants included, are highly invertivorous. The natural diet of *Galloperdix* is higher in fallen seeds, berries and rootlets than peacock-pheasants. Like their deep forest adapted cousins, the spurfowl are adept mollusk hunters foraging amongst rocks in creek bottoms during the dry season. Like peacock-pheasants, the *Galloperdix* are highly selective of the tiny stones and bits of gravel they ingest to aid digestion. Pairs will offer one another choice bits of grit as if they were edible food items. This shared behavior amongst the Asiatic spurfowl may be an evolutionary response to the challenges of digesting the calcium-rich shells of the tiny mollusks they are so attracted to.

When flushed, red spurfowl usually only fly into the closest dense vegetation. When hard-pressed they are capable of sustaining themselves over considerable distances. Falconers have reported that these birds have a greater endurance than francolins. Theirs is a more rapid and typically a flapping flight like that of the peacock-pheasant. They are reportedly pugilistic when flown on and present an unnecessary risk in their penchant for injuring the eyes and nares of birds of prey.

Red spurfowl stay in well-defined territories throughout the year. They roost in the branches of thorny evergreentrees and in the crowns of palms. <sup>[5]</sup>

They are highly communicative with vocalizations that include a distinct kerwick...kerwick... and harsh karr...karr... notes. The Marathi name Kokatri is echoic in origin. <sup>[6]</sup>

The breeding season is January to June, mainly before the rains. A ground nesting bird, it deposits 3-5 eggs in carefully selected nest sites generally abutting roots, logs or boulders.

Males are monogamous but generally do not incubate. The males occasionally deposit twigs and leaf litter around the females. An interesting observation was made in a captive pair inhabiting a large flight aviary. Keepers had inadvertently hosed the substrate around the setting female to the extent that not only had her nest come to be discovered it had been made vulnerable to opportunist nest predators sharing the flight, hornbills and jays chief amongst them. While the keepers struggled with just what to do with the quandary the male showed up and began kicking substrate right onto the female until she was fairly buried. Some old desiccated banana leaves were strewn in the direction of the nest and the male made use of them.

Males are known to perform diversionary distraction behaviors to draw attention when females with chicks are nearby. <sup>[9]</sup>

Plate 9  
CALOPERDIX



Photo: P. De Chabane.



Photo: Xiu Hong Lin She.



Photo: Nicholas Tan.



Photo: Alex Vargas.

**Ferruginous wood-partridge *Caloperdix oculus***

Ferruginous wood-partridges are reminiscent phenotypically of hill partridges (*Arborophila*) and to some extent, the crimson-headed wood-partridge (*Haematortyx*). On a molecular level it is evidently closely related to the crested wood-partridge (*Rollulus*) and a third species the black wood-partridge.

Ecologically *Caloperdix* is quite unlike any of these species as it frequents rivulets coursing through hill forest on the sunny sides of slopes. It is not particularly shy and in some respects reminiscent of the pitta in its mode of life. The birds are always on the move, highly invertivorous, puddle hunters with that courageous presence- that bold behavior, perhaps it's not quite so skulking as its close relatives. In captivity they get along well with crested wood-partridge.

What is perhaps most unusual about ferruginous partridge is the presence of two short spurs on each leg of males. This trait is unknown in other members of the hill and wood-partridge family.

Its hind-toe is approaching that of *Rollulus* in that it is slightly abbreviated - hallmarks of highly cursorial species, for instance tinamou and bustards.

Its bill is unusually long for an Arborophilid though wide like that of crested wood-partridge. *Polyplectron*, *Galloperdix bicalcarata* and *Haematortyx* share this trait. This is a typical bill type of the Megapodius scrubfowl, which may live almost entirely on mollusks on volcanically active islands.

These species exploit termite nests in deadfall and forage for insect larvae within decaying fruit.

And they have in common with the *Caloperdix* the habit of puddle hunting, which involves wading through floating leaf tea in pursuit of invertebrates.

Like *Rollulus*, *Caloperdix* is a dome nester.

Feruginous Wood-Partridge  
*Caloperdix o. oculus*. Photo: N. Hill.





## Sri Lanka Spurrowl

Perhaps at least partially due to the surreal landscapes of its island home as much as its striking plumage and haunting voice, the Sri Lanka spurrowl, *G. bicalcarata*, is a most compelling species. Its vocalizations seem ventriloquial and include tonal whistles, guttural warning calls and on occasion, males broadcast repetitious announcement calls not unlike those of male Palawan and Malayan peacock-pheasants. Curiously, female Sri Lanka spurrowl are essentially similar in phenotype to the male red spurrowl, differing only slightly in their comparatively less vivid bare facial skin, lack of a prominent crest, and absence of scalloping or barring on dorsal plumage and tail. As the red spurrowl is native only to the Indian subcontinent and the Sri Lanka spurrowl endemic to that island, confusing the two isn't likely. What is still stranger is how the male Sri Lanka spurrowl's spangled scalation corresponds with the ocellated inumbriations of the female red spurrowl. Judging from preserved study skins in hand, perhaps the most obvious traits that immediately distinguish the female *bicalcarata* from the male *spadiceus* is its overall darker, cooler colouration, the reddish regions exhibiting a distinctly maroon hue. The head and neck of the Sri Lanka spurrowl female are dark mouse grey. The dorsal plumage of the female Sri Lanka spurrowl are a tawny sepia and chestnut hue.

Male Sri Lanka spurrowl are perhaps the most striking of the *Galloperdix* species, with their dark ebony contour and ventral plumage disruptively marked with dramatically contrasting centres of vivid white. The breast and frontal neck appear primarily white with wide black perimeters, while the lateral breast coverts and mantle sport comparatively narrow and long vertical white stripes on a black violet and sepia background. The throat and sub auricle regions of the male *bicalcarata*'s face are whitish grey. The crown and occiput show distinct freckles in tiny white spots. From a distance, in certain light conditions, the head and face appear bluish grey. In the hand, the presence of a dark, slightly glossy & iridescent band from crown to nape is apparent. Intensely red facial skin, beak and legs are particularly vivid in the males, which may also be the most prominently spurred of all the Asiatic spurrowl and peacock-pheasants.

This species inhabits more verdant habitat than the red spurrowl and prefers jungle forested hillsides and tangled brakes along rivers. It is most common during the wet season at about 1500 m (5,000 feet). This species is a bit more vocal than other spurrowl and possibly more pugilistic. Sri Lanka spurrowl roost nocturnally in giant trees well above the forest, a trait shared with mountain and Palawan peacock-pheasants. Other spurrowl species habitually perch substantially lower in dense thickets tangled with viney vegetation and amongst bamboo.

## Painted Spurrowl

The painted spurrowl, *G. lunulata*, inhabits the Eastern Ghats and central southern India. The females of this species are particularly stunning. At time their overall colouration and patterning appears essentially similar to that of a juvenile peacock-pheasant, in the tawny umber and ochreous chestnut palette of the head, and the warm mineral and pale stone brown hues of the body plumage.

The female *lunulata* is the only species of Asiatic spurrowl that exhibits prominent patterns demarcating the head and face. The top of the crown of the female is darker than all but the terminal ends of the rectrices. Its bare facial skin is a dark umber grey. A striking ochreous vanilla band extends from the base of the bill in a parallel line with the rich tawny chestnut of the sub auricle region, which is repeated in thick lines extending from the base of the culmen, over the eyes and concluding abruptly with dark greyish umber occipital and upper neck plumage. This gives the impression of a mask, especially when in flight.

The male painted spurrowl is in some ways reminiscent of both sexes of the mountain peacock-pheasant in its dark sepia colour pallet, which appears to plummet into flat-shaded plumbeous hues, peppered with tiny stars and orbs of dazzling white. It is also reminiscent of the male Sri Lanka spurrowl in that the head and upper neck appear grizzled for the plethora of chaotic freckling, and like that species, the outline of the male's head

often seems diffuse against the background of its preferred habitat. As in the male Sri Lanka spurfowl, secondary and marginal wing coverts of *lunulata* are prominently spotted in white.

The male *G. lunulata* compares with the female red spurfowl in the presence of swaths of prominent ochreous breast plumage, though clearly the female *spadicea*'s yellowish hues are quite muted in direct comparison. While each of the *Galloperdix* spurfowl show a subtle iridescent sheen (like that of the Sumatran bronze-tailed peacock-pheasant) in low light, none but the male *lunulata* exhibit wide glossy surfaces distinctly metallic in appearance. The rectrices and wings of this species gleam dark bronze with coppery purple and greenish pink gloss.

Peacock-pheasants and Asiatic spurfowls prefer grossly similar terrain. Optimal habitat for both genera is hilly, rocky country with frequent outcroppings and steep landscapes. As a rule, Peacock-pheasants differ from spurfowl in that they inhabit moist, closed canopy jungle ecosystems rather than the spurfowl's seasonally semi-arid, mostly deciduous, scrub forest. The Sri Lanka spurfowl's habitat is intermediate in character between the two basic ecosystems. Unlike peacock-pheasants and other spurfowl, *lunulata* is attracted to broken outcroppings amongst windswept hilltops covered in dense grasses and stunted thorn scrub. In this habit it is more reminiscent of a toothed quail like the cotton top (*Callipepla squamata*) than a member of the peacock-pheasant, Asiatic spurfowl clade.



**Bar-backed Partridge.**  
**Photo: Christer Sundström.**

Like the mountain peacock-pheasant, which too is rather exceptional in its behavioral ecology and habitat use, painted spurfowl are unusual in their partiality for landscapes very much shaped by the elements, wind in particular.

Like the aforementioned peacock-pheasant species, the painted spurfowl is occasionally to be found foraging or trekking through exceedingly steep and rocky places far from cover. They are unusually short in leg and like montane-adapted species like the monal and chir pheasant, their carriage is decidedly horizontal on a flat surface. The legs are positioned further back in the carriage than other peacock-pheasants and spurfowl, which give the birds a decided advantage as they race along amongst outcroppings, climbing vertically along ravine walls.

The wing morphology of *lunulata* confirms that, like *P. inopinatum*, it is regularly obliged to make sustained ascending flights. The wing formula of the painted spurfowl and mountain peacock-pheasants are both similar in some respects with that of the sage grouse, especially in the shape and length of the primaries. This may suggest the birds have in common the capacity to fly with agility and endurance through powerful air currents.

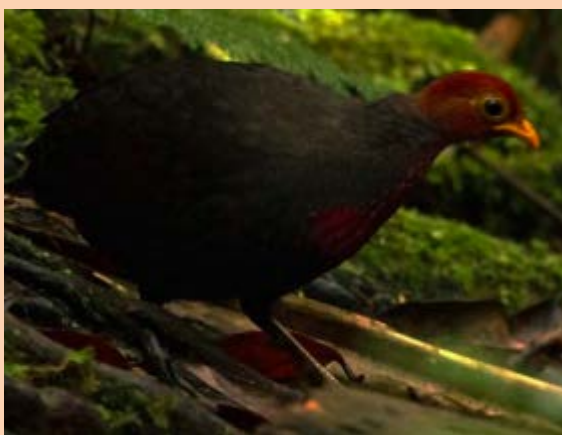
**Plate 10  
HAEMATORTYX**



From top left:

**Adult male crimson-headed wood-partridge.** Note multiple kicking thorns, long slender legs and toes and the outermost tail coverts.  
Photo: Adam Riley.

**Adult female**  
Note length and shape of bill for comparison with that of Polyplectron. Some areas of plumage of the female crimson-headed wood-partridge are more visually arresting than those of the males. This is true of the Congo peafowl as well. In that species too, it is the female that is more immediately visible in direct light. Photo: Joakim Johansson.



**Adult male**  
The crimson-headed wood-partridge is an ecological specialist. Its colouration and morphology are the result of millions of years of adaptation in the dark and frequently wet conditions of the moss forests they frequent. Mollusks and other semi-aquatic invertebrates are important food items for the species. Photo: C.K. Leong.

**Adult male.**  
Birds of prey are probably a constant source of menace to these diminutive fowl. Several species of small owls are known to hunt periodically during daylight in the closed canopy old forest where *Haematortyx* dwells. Small forest hawks are common in these habitats as well.  
Photo: Eugene Cheah.

**The male subadult *Haematortyx*** is apparently tolerated within close proximity of the parents even at this late stage of development (assumedly a two or three year old). As is typical with peacock-pheasants, female progeny are encouraged to disperse at this developmental stage. Photo: Dave Irving.

**Adult female *Haematortyx*** exhibiting vivid pink vermillion breast and head and vivid pink crimson undertail coverts. This species is curious in that its body plan is like that of other montane adapted gallomorphs in that the body is somewhat elongated. The birds maintain a fairly horizontal posture through their daily round of life. This is analogous with what is observed in bronze-tailed peacock-pheasants, painted spurfowl and mountain peacock-pheasants. Note the length of wing and shape of secondary wing quills. Wing morphology can provide clues as to how often landfowl fly and if they are capable of prolonged flight or only short bursts. In general, though walking and climbing are the principle means of locomotion peacock-pheasants and Asiatic spurfowl are capable of sustained flapping flight for considerable distances. Given the topography of their preferred habitat crimson-headed wood-partridges are probably capable of sustained ascending flights that enable them to travass mossy escarpments that so dominate the landscape. There is anecdotal evidence that this species may migrate altitudinally every few years. It purportedly abandons its montane moss forest habitat during the wet season for slope forests in the lowlands. This has also been suggested for crested wood-partridge and Bornean white-tailed pheasants.  
Photo: Rob Hutchinson.

## **Crimson-Headed Wood-Partridge**

The crimson-headed wood-partridge *Haematortyx sanguiniceps* is a medium-sized, tropical forest-adapted species endemic to Borneo, having, a rounded tail of 12 rectrices less than half as long as the wing. The wing is rounded, with the sixth primary the longest. The sexes are slightly dimorphic, but both are distinctly crimson-rufous on the head, neck and breast. Males have from one to three tarsal spurs; females have none. The bill is relatively weak. A single monotypic species is recognized:

*Haematortyx sanguiniceps* Sharpe 1879.

This species is most common in montane moss forests, but unlike hill-partridge it also occurs on leached-out sandy forests of the valley bottoms and in primary forests (Smythies 1968)

***Haematortyx* mature subadult male. Photo: Azahari Reyes.**

The crimson-headed wood-partridge lacks elaborate plumage and like a quail is basically missing a functioning tail altogether. The overall hue of both sexes is a deep blackish sepia, decidedly ashen in the female. The contour plumage of juveniles is barred transversely in a manner reminiscent of that of the adult Sumatran bronze-tailed peacock-pheasant and of a similar though more chestnut hue. While it is often written that the female is a paler, washed out version of the male, they are in my estimation, if anything more complex in hue and colour. The head of the female is decidedly more striking in that it is an even more visually arresting crimson hue than that of the male but with rich vermillion and Naples orange neck and throat plumage bleeding into a vivid rust at the breast.



In some respects the female crimson-headed wood-partridge is subtly reminiscent of the female painted spurfowl. Like that species, the female *Haematortyx*'s head is separated chromatically at the sub auricle region towards the upper neck.

I've studied this species in primary moss forests in the mountains of Sabah at the Mount Kinabalu National Park. Their favorite haunts are typically quite dark and as such they're difficult to see. It's always interesting to see intense red plumage in those birds that are active during crepuscular hours and during overcast days. It's important to keep in mind that most species of predator are red-blind (cannot see in the red spectrum).

The *Ithaginis* blood partridge and tragopans are similar shades. Each have much to fear in aerial predators, especially nocturnal ones, which generally hunt most actively during crepuscular hours. Likewise, their mammalian predators, though typically nocturnal, remain quite active for many hours of the day in primary forest and other closed canopy habitats. Trying to follow these birds proved exceedingly difficult. Even those of us that are not colour blind had a very rough time seeing these birds even with state of the art binoculars, unless they were in motion, and even then it was challenging. Running across the dark substrate in moist shadowy places amongst giant decaying leaves, creeping along the inclines of roots and rivulets through shadowy spaces.

Plate 11  
GALLOPERDIX



***Galloperdix***

From top:

- a. **Red spurfowl** *Galloperdix spadicea spadicea*, male. Photo: Harsha J.
- b. **Indian red spurfowl** *Galloperdix s. stewarti*, female. Photo: P.J. Vasanthan.
- c. **Sri Lanka spurfowl** *G. bicalcarata*, female. Photo: W M C Narampanawa.
- d. **Kerala red spurfowl** *G. s. stewarti*, female. Photo: Anil Nediara.
- e. **Sri Lanka spurfowl** *G. bicalcarata*, male. Photo: W M C Narampanawa.
- f. **Painted spurfowl** *G. lunulata*, pair. Photo: Jainy Kuriakose.

Using recordings of peacock-pheasants and spurfowl, I discovered I could draw the *Haematortyx* in and this revealed something I had never suspected. This little group at least occasionally frequented high reaches well above the forest floor; In this instance their little troop sunned themselves after a long downpour somewhere along a great mossy limb of a forest giant decaying into the steep slope about twenty or thirty yards from the trail and a few hundred feet above. After calling in response to my recordings for half an hour or so and only once the sun had sufficiently dried off enough moisture they fairly dropped to the ground. Their flight was more reminiscent of a falling leaf or mini-rugby ball than a bird's descending flight. Upon alighting each bird went to crouching and spinning about in precisely the same manner one observes in the grey and bronze-tailed peacock-pheasants.

There are some really exciting vocalizations of crimson-headed wood-partridge at [xeno-canto](#). Compare and contrast recordings of *Galloperdix* and *Polyplectron* with those of *Haematortyx*, you may be surprised at how similar they are to one another.

The crimson hue the species is so aptly described by is a hue to be seen in only a very few instances amongst all the gallinates. It's difficult to describe, but if you've seen a blossom-headed parakeet you'll have a clearer image of the density of plush velvet micro plumes present in *Haematortyx sanguiniceps*. From a distance the female's head appears the most sumptuous hue of pink.

Being highly invertivorous, the crimson-headed wood-partridge is forever on the move. When suddenly excited or alarmed, the crown feathers are lifted in the manner we see in other gallinate birds and it's surprising how long these feathers actually are. Simultaneously, the miniscule, round-tipped tail feathers are spread laterally, exposing the eye popping crimson undertail coverts which seem to double the size of the bird. When the male goes to zipping around a hen or juveniles, with its crimson pom-pom exposed to its fullest, lateral tail coverts normally concealed by the wings become apparent. Here is the one spot on the entire body of the bird exhibiting the sort of iridescent colouration we come to expect amongst the peacock-pheasants. However, this one discrete spot is confined to a thumbnail sized patch of metallic gloss bridging the normally developed sepia-hued base of the elongated tail covert with the disintegrated crimson portion of the plumes' terminal edges. There, a single ocelli-like marking, divided just barely in two by the vane of each feather. The male makes a great deal of this window, a sort of bulls eye as he contorts and shape-shifts around his mate who sometimes pecks at him when he intermittently crouches at her feet as if begging for food.

I twice observed them foraging on tiny snails in a rivulet along the trail which led to some interesting pair bonding rituals reminiscent of roul roul, and yet strangely similar to what one sees with peacock-pheasant pairs, particularly the Palawan.

The last image I have of the crimson-headed wood-partridge is of a group of five birds including a single subadult standing on the wide expanse of a huge mossy limb of a forest giant growing from hundreds of feet down the slope of a ravine well beyond the path of my daily pilgrimage. It was damp, and gloomy quite cold really, my last day at Kinabalu. I knew the birds flew from the slope where the trail climbed up a steep hillside every evening, but the low light and perpetual fog made it too difficult to see them clearly.

On this day, the sun was streaming down on a moist bank just fifteen or so feet away. Steam was rising and I knew the birds were probably sunning there amongst the mossy roots. A noisy group of birdwatchers were winding their way along the path, disturbing the little group of mountain buntings that so often seemed to be in close proximity or actually with the wood-partridges.

With the alarm call of a tree shrew, crimson heads of three male wood-partridges popped up, followed by the pink vermillion of the female and juvenile male. They let out their staccato scolding alarm note, part roul roul, part peacock-pheasant. It was just beginning to rain when the male made itself visible. The sentinel male perched above the rest began running back and forth, prompting the rest to follow in kind. They walked single file along a great limb that bridged the divide between the mountain slope and steep drop below.

Plate 12  
COMPARATIVE FEMALES



**Female Asiatic Spurfowl**

**Haematortyx** Wood-partridge female. Photo: Dae- Hyun.

**Galloperdix** Painted spurfowl female. Photo: Udayan Rao Pawar.

**Polyplectron** Palawan peacock-pheasant female. Photo: Tomasz Doron'

**Polyplectron** Mountain peacock-pheasant female and juvenile. Photo: [Mike Birder](#)

**Galloperdix** Red spurfowl female. Photo: Aranya Parva.

**Polyplectron** Malayan peacock-pheasant female. Photo: Huub Dijks.

Without so much as opening a single wing, they threaded their way amongst the waving branches in the direction of a sheltered portion of the slope. Here, many great tree ferns crowded the steep mountain's inner elbow. They disappeared amongst the heavy leaves but I'm fairly certain they went to roosting within the crown of a tree fern. Then the sky really began to pour. I turned back around and finished my long descent to the hot springs at the foot of the mountain below.



Above: *Chinquis* stunning hill partridge. Photo: Huub Dijcks.

### Toward a New Theory of the Evolutionary History of Polyplectron

When we examine the ranges of *Galloperdix* and *Polyplectron*, it's striking how the two genera replace one another zoogeographically. The red spurfowl, *Galloperdix spadicea*, is somewhat analogous with the grey peacock-pheasant, *Polyplectron bicalcaratum*, in that these species are by far the most populous and diverse of their respective genera. They almost meet one another's ranges but there appears to be no overlap. It is also curious that the red spurfowl inhabits some of the same regions of India as the painted spurfowl, *Galloperdix lunulata*, however, the two occupy different habitats and different elevations. In this their overlapping ranges are analogous with the situation of Malayan and mountain peacock-pheasants.

Given the ecological history of the Indian subcontinent in regards to Pleistocene-aged volcanic winters, replete with their deadly ash fields, could it be the case that the *Galloperdix* are simply *Polyplectron* that found their ecosystems collapsing? Surviving populations, stranded in refugia forests, adapted for life in far more arid habitats with greater swings in temperature than their peacock-pheasant antecedents? Perhaps the Asiatic spurfowl is a peacock-pheasant that has become more partridge-like due to evolutionary pressure that required the birds to constantly move across wide, open areas in search of food and water, especially during the dry season? If birds of prey are a more important predators of spurfowl than they are for peacock-pheasants, which may well be the case given that spurfowl inhabit far dryer and more open habitat, perhaps these spurfowl have traded in their elaborate armaments for a body plan that enables them to fly with greater speed and more efficiency.



As for the crimson-headed wood-partridge, I suspect that it may have diverged from the same branch as *Rollulus* and *Caloperdix*, which presumably derived from some *Palaeortyx*-like lineage intermediate between the proto-odont and proto-guineafowl. I am currently collaborating with researchers with a great comprehension of galliform evolutionary history and taxonomy. One of the foremost objectives is to explore similarities and differences between arborophilids and the peacock-pheasant/ Asiatic spurfowl group.



**Left: *Chalcurus* and hill partridge.**

**Photo: Huub Dijcks.**

For now, in my own notes and current thinking I'm theorizing that the latter group is more or less synonymous with the former. For the intents and purposes of this series of natural history essays I will refer to peacock-pheasants and their allies as arborophilids.

*There is much yet to learn.*

My synopses brought forward here are purely my own and while I run the risk of being misread as some pseudo-scientist I am aware of how badly referenced this draft is. I'm experimenting with natural history writing and haven't quite got the execution of it. There is an ebook publication of these essays on the evolutionary history of Asiatic Spurfowls { Polyplectron group in the works. It will be referenced exactly and have undergone a comprehensive editing to shorten paragraphs, clarify and axe laborious sentences. For now I'm sharing observations and insights of the steady stream of consciousness variety, with the intention of publishing this work in a more formal matter-very shortly. Like your own, my exploration of all things gallinaceous is a dynamic process. Drink lots of water lest you get salt poisoning with all the salt you'll need to read through my assertions. Thank you for your patience.

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In the next installation the biology of peacock-pheasants, their natural history, conservation and aviculture will be covered.

Below: *Nisaetus cirrhatus* eating *Gallus sonneratii* (Bandipur). Photo: Yathin S Krishnappa, Wikipedia Commons.



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