



Above: Adult male Burmese Grey Chinquis *Polyplectron b. bicalcaratum* in its native habitat. Note multiple metatarsal kicking thorns.
Photo P. Kittipinyowat.

PEACOCK-PHEASANTS AND ASIATIC SPURFOWL

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PART 1

INTRODUCTION TO PEACOCK-PHEASANTS

In this article, we examine in detail several tropical Asian galliforms frequently mentioned in technical ornithological literature but rarely discussed at length, the peacock-pheasants, those members of the genus *Polyplectron*, conventionally considered ^{*a} as deep forest-adapted, evolutionary prototypes of the larger and even more elaborately plumaged argus and peafowl. A theory that's become a matter of tradition places the peacock-pheasant as a phylogenetic link between pheasants and peafowl. In this article we will have an additional look at some obscure galliforms even more poorly known than peacock-pheasants, namely the mysterious, Crimson-headed partridge (*Haematortyx sanguiniceps*) endemic to the mountains of Borneo and the Indian Subcontinent's enigmatic Asiatic spurfowl of the genus *Galloperdix*. These two genera share a number of unusual features with peacock-pheasants that may suggest a monophyletic origin.

Nine peacock-pheasant species are presently recognised, all united within the genus *Polyplectron*. Two forms once identified as subspecies by some authors are currently regarded as distinct species. The Hainan peacock-pheasant *P. katsumatae* and the Bornean peacock-pheasant *P. schleiermacheri* were both treated as distinct species until Jean

Delacour's reclassification scheme circa 1977, when each were demoted to subspecific status; the Hainan as subspecific of the Grey and the Bornean as a subspecies of the Malayan. Biogeographical, molecular, morphological and phenotypic data have re-established their species status. ^{*b}

Right: Young chick of the Bornean peacock-pheasant *Polyplectron schleiermacheri*. Note well-developed wings. While Peacock-pheasants are highly precocial like other galliforms they are more similar to peafowl in their delayed maturity, requiring extensive care from their parents for a prolonged period.

Photo Robert at PBase.



The Latin name of the genus *Polyplectron* means "many to strike with" in reference to the multiple posteriorly projecting thorn-like metatarsal spurs in males and in some species exhibited in females as well. This curious trait is shared with Asiatic spurfowl and the Crimson-headed partridge. This may be evidence that multiple spurs are a plesiomorphic trait, one that is shared with a common ancestor.

Left: Legs of a (mounted) Crimson-headed Partridge *Haematortyx sanguiniceps*. Note multiple metatarsal kicking thorns.

Photo: Kermit Blackwood.



Another unusual physical characteristic exhibited in the males of some species is the perpetual development of especially thickened tarsal scales at the front of the legs that resemble shin guards.

Likewise, peacock-pheasants and their proposed allies possess proportionally long necks, lengthy gracile legs and slender toes. The bodies of peacock-pheasants are surprisingly modest in weight and proportion given the impressive size their exquisite and expansive plumage may suggest.

While we tend to see a bit of the pheasant and a bit of the peafowl in some of their superficial characteristics, *Polyplectron* are truly unique unto themselves and as we will examine further, the probable closest relatives of peacock-pheasants the *Galloperdix* and *Haematortyx* are sufficiently partridge-like that they've been classified as members of the anachronistic *Perdicinae* subfamily in which quail and partridge were traditionally placed, while *Polyplectron* were placed within the *Phasianinae* which has likewise been shown to be a paraphyletic grouping.



Left: Family of Aravalli Red Spurfowl *Galloperdix spadiceus caurina*. The female is the more boldly patterned of the sexes. Photo: Sharad Sridhar. India.

Peacock-pheasants possess long squarish wings, substantial in terms of body mass to wing ratios. The trailing edge notch is much-reduced or non-existent, evidence of the capacity for sustained, flapping flight. Primary feathers

exhibit strongly rounded tips. Unlike those of pheasants or peafowl, the wings of peacock-pheasants are barely audible in flight. The voluminous tails of most species appear disproportionate in length to their diminutive bodies. In most, the majority of rectrices remain roughly the same width along their entire length. The highly expansive tails of these birds are a most prominent feature utilised in social and anti-predatory display behaviors as well as in sustained flight.

Peacock-pheasants forage amongst deadfall in lowland forest, generally in regions predominated by outcroppings and rocky ravines. They tend to frequent those places where the terrain is very broken and hilly, often on slopes where dense stands of thorny vegetation and bamboo forest predominate. They prefer to haunt the peripheries of sparsely illuminated places with deep shadow interspersed with strongly dappled light.

Peacock-pheasants are extremely wary birds, hardly a moment passes without males stopping to stand at stationary alert, carefully scanning the environment for the slightest sense of danger. As their primary source of nutrition are invertebrates these birds are obliged to forage actively making it difficult to remain undetected. Consequently, they tend to travel and hunt beneath closed canopy especially where woody limbs and trunks grow more or less horizontally and as a rule in close proximity to running water. Often times the places where they come to drink are also important foraging zones and these micro-habitats will characteristically be dominated by boulders and rocks. According to documentation of crop contents collected in the wild, peacock-pheasants are highly invertivorous. They derive the bulk of their nutrition from small mollusks, isopods, insects, spiders and other arthropods. Small drupes and other fruits, rootlets and sprouts are very important in their diets as well. Green vegetation is mostly ignored by the birds and given their deep-forest habitats, grain is unknown to them. Seeds of many plants, in particular bamboo are significant in their diets. Peacock-pheasants actively hunt for food larders which are far from common and difficult to detect. Consequently, they will gorge themselves on seeds and termites, insect larvae and small fruits. Some species appear to be particularly fond of fern spores.

The principle means of locomotion for most species of peacock-pheasant is neither running nor flying but rather a curiously fluid saunter. Their deliberate halting steps will periodically quicken into a laterally positioned gait with rectrices half fanned. This might be best described as "oblique mincing". This curious pace is generally accompanied by guttural warning notes and with one slightly spread wing held above the back. On these occasions, peacock-pheasants accentuate their size by displaying an expanded surface area of the upper wing and a portion of the tail. Lateral saunter and its accelerated version oblique mincing tends to occur with frequency when a social unit of peacock-pheasants is foraging

together or when the birds are traveling any span of distance that brings them through unfamiliar surroundings/ situations. Tail flicking occurs intermittently while the birds are walking as well.

Apparently males act as sentinels as it is this gender that stops and studies the surroundings with the most frequency, uttering guttural warning calls when warranted. When crossing open spaces or beneath tall trees with scant cover, they may suddenly scurry with necks held parallel to the ground and rectrices fanned widely. This behavior occurs when some member of their widely-spaced foraging party or another creature in the near-vicinity sounds out an alarm note.

Tropical bay owls, small felines and civets are probably important predators of peacock-pheasants. These normally nocturnal hunters may hunt during daylight hours in the shadowy understory beneath the closed canopy of slope forest and ravines. Any number of diurnal forest-adapted birds of prey are likely a constant threat. Perhaps most significantly, the ever-present menace of lurking monitor lizards and pythons can never be underestimated. An intimate arms race between endothermic theropod dinosaurs/ birds and ectothermic reptiles has been underway since the dawn of their existence. Substantially smaller, less powerful opportunistic predators like tree snakes, forest squirrels, tarsiers and hornbills, will take eggs, chicks and juveniles. Predation by non-obligatory predators is of great significance in the natural selection of Galliform birds acting upon the capacity of adults at avoiding/ fending off attacks as well as on the precocity of the chicks themselves.

Right: Northern Grey peacock-pheasant *Polyplectron bicalcaratum bakeri* at stationary alert sounding a warning call. Note elevation of semi-plumes normally concealing bare skin of the gular region. If warning call proves to be unwarranted, these micro-plumes will return to their typical, neatly compacted positions. Photo: P. Stubbs.



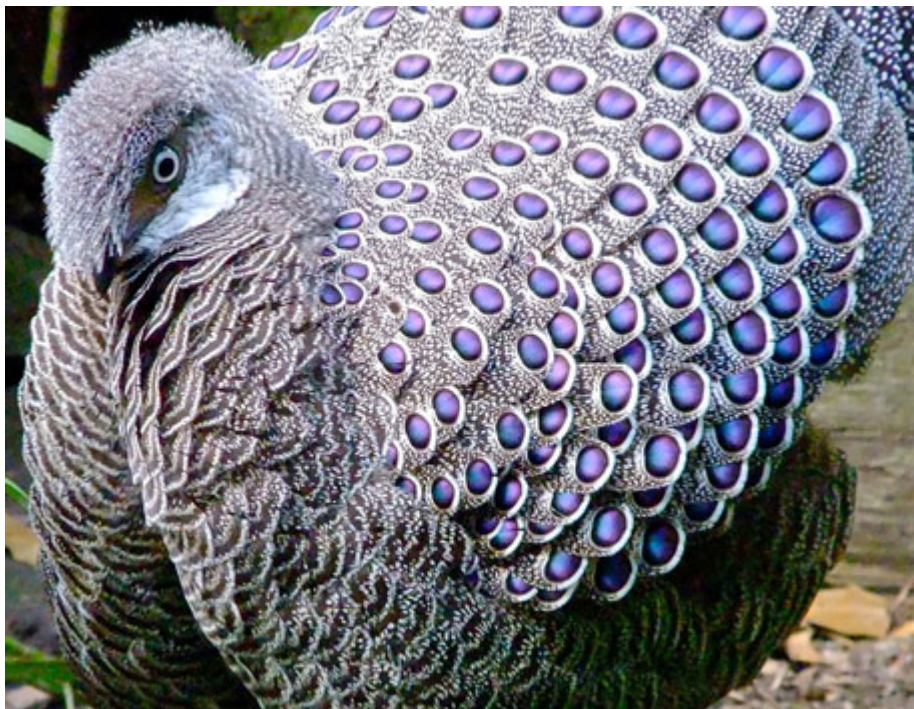
In the majority of peacock-pheasant species the contour plumage is soft and lax, muted, warm earthen and mineral hues, from warm sepia to sterling silver; from a sooty bark grey to pewter and bronze.

Peacock-pheasants are finely vermiculated, speckled, spotted and/ or barred and highly cryptic in pattern and colouration. An exception to the rule is the electric violet blue and shadow black mantle and upper wings of the male *P. emphanum*.

As suggested by their descriptive name, peacock-pheasants are best-known for their long rectrices, prominently marked in several species, with highly iridescent, metallic blue, violet or greenish ocelli. Unlike peafowl, the peacock-pheasants' dorsal plumage is likewise ocellated. As the iridescent portions of each feather are highly light-reflective, peoples in their native haunts refer to them as mirror fowl eg: "*chinquis*", jewelled fowl and glass fowl.

Right: Grey peacock-pheasant *P. p. bakeri* male preliminary threat posture. Note the bird is in motion, positioning tracts of ocellated dorsal plumage according to emotional state and intention. Photo Peter Stubbs.

Depending on ambient light levels, and the position of the plumes themselves, these orbs of metallic pigment may be made to appear to stand out in three dimensions, like droplets of water. This creates the illusion of what could be described as holographic spheres. Some of these curious traits give peacock-pheasants a unique aesthetic unlike that of any other living bird, though reminiscent in one attribute or another with those of insects, reptiles and aquatic animals.



Left: Male *P. e. emphanum*. Note marked elongation and specialization of crown plumage. Photo: Frank Lin.

The hypothesis that an evolutionary runaway processes led to ever more elaborate ornamentation in these birds has long been the most popular model for their evolution (Charles Darwin's Works: The Descent of Man and Selection in relation to Sex) and is consistent with the theory that peafowl and similar showy animals are 'display machines' that have simply become showier over time. However, this is completely contradicted by molecular data: according to Kimball *et al.*'s (2001) ground-breaking

molecular phylogenetic work, the least-ornamented Sumatran peacock-pheasant *P. chalcurem* and Mountain peacock-pheasant *P. inopinatum* are not old members of the group closer to the peacock-pheasants' common ancestor, but rather, very young ones that have only emerged quite recently.

While genus *Polyplectron* is surprisingly old, apparently emerging during the mid to late Miocene some 4 million years ago, molecular clock analysis indicates that both the montane-adapted species *P. chalcurem* and *P. inopinatum* (together with a third: the hill forest-adapted Grey peacock-pheasant *P. bicalcaratum*) are less than 1.5 million years old,



with the Sumatran and Grey peacock-pheasants perhaps being less than 0.7 million years old.

Left: Adult Male Mountain peacock-pheasant *P. inopinatum*.
Photo: P. Stubbs.

These results are significant for several reasons. They may indicate that some species of peacock-pheasants are evolutionary novelties; in fact, they are so young, geologically speaking, their speciation events may not have been driven by geographic events like changing sea levels or tectonic movement. The overall picture is a dynamic one in which these birds have moved extensively about south-east Asia,

whereby species that occur in close proximity are not necessarily close relatives.

Right: Adult male Bornean peacock-pheasant *Polyplectron schleiermacheri*. Note specialized microplumes of the crown, nape and upper-neck. These plumes, the *ephemeral ruff* serve a purpose much more significant than decoration. They are utilised as highly-advanced form of *vibrissae*, utilised to detect the slightest movement.

Photo: Robert at PBase.



It would appear that dates of recent species diversification within the peacock-pheasants may roughly coincide with major volcanic events believed to have had catastrophic impact on forests throughout the region. [citation](#)

On a strictly theoretical level, if terrestrial deep forest-adapted birds like peacock-pheasants are basically incapable of long-distance dispersal, e.g. via flight, periodic major volcanic events in Indonesia and New Guinea may have presented certain ecological challenges and consequently a contributing factor in the diversification and speciation of these birds. Some species may have diverged from more typical virgin forest species in unusually challenging habitats, for example amongst landscapes buried in masses of woody debris consequent of wide scale volcanic catastrophism. Pockets of refugia forest in deep ravines and steep mountain slopes not affected by the ash field, will have theoretically survived volcanic events that would have extinguished a great diversity of life elsewhere within the ash field. Viable populations of peacock-pheasants would have survived in these fragmented forests where their predators and/or competitors may have either vanished or expanded in number. Surrounding these refugia zones, novel ecosystems would theoretically emerge within assumedly large considerable expanses of deadfall and in some regions miles of standing dead and dying old growth forest. In a matter of years the chaotic landscape is bustling with invertebrate life as populations of arthropods like termites and isopods together with fungi, algae and mold expand in equilibrium with the disintegration of deadfall.

Invertebrates including peacock-pheasants exploit novel microhabitats within these post – catastrophe forests. As vegetation grows through ash layers, maturing into slope and hill forests in deadfall zones, optimal habitats for these birds grows exponentially.

It may be that populations of the oldest of the three most recently derived species, *P. inopinatum*, the Mountain peacock-pheasant, survived the first of three major Pleistocene-era Indonesian volcanic events more or less intact though thoroughly fragmented in range.

Founder populations of *P. chalcurus*, the Sumatran Bronze-Tailed peacock-pheasant, the first of the two most recently derived species, emerging from its *P. inopinatum* forebearers in the mountains of Sumatra along the shadow zone of the Mount Toba supervolcano.

Founder populations of *P. bicalcaratum*, the Grey peacock-pheasant, the second of the two most recently derived species taking refuge surviving in biogeographically semi-protected regions of montane refugia forest not unlike the habitats of the theoretical progenitive species, subsequently dispersing into deadfall zones and eventually diversifying into the species with the largest geographical range.

Logically, predators of the lowland species will have returned to more sizeable populations and radiated into the habitats of the proto-grey. Perhaps this is a factor in their morphological and behavioral specializations resembling more closely the primitive species than the montane forms. Theirs must have been a most surreal landscape dominated by the enormity of countless fallen giants. Given the chaotic landscape of these ecosystems it would be highly challenging for all but the smallest forest denizens to navigate.

The relative date of the most recently derived peacock-pheasant clade (e.g. *P. inopinatum*, *P. bicalcaratum*, *P. chalcurus*) appears to concur with the eruption of Mount Weh and the first of [three major eruptions of Mount Toba in Sumatra](#).

Below: Deadfall. A period of marked volcanic activity throughout Indonesia including the eruption that formed Weh Island, formerly a part of Sumatra, began about 2 million years ago. This is approximately when the Mountain peacock-pheasant *P. inopinatum* emerges from its progenitive branch which is occupied by *P. germaini*. Photo: John Davidson.



The first, major eruption to effect the diversification of these birds would theoretically be that of Mount Weh, which occurred ~2 Million Years ago. The second eruption took place ~ 800,000 years ago about the same time catastrophic volcanic eruptions were also taking place in New Guinea. A second major eruption occurred at Mount Toba ~ 500,000 years ago. The most recent major volcanic eruption in the region was that of the supervolcano Mount Toba ~ 78,000 years ago. The consequences of the latter were likely one of the most catastrophic episodes in the history of modern vertebrates.

Theoretically speaking intervals between events presented sufficient time and suitable habitat for invertivorous species like peacock-pheasants to exploit regenerating forest habitats within deadfall zones. It's believed that heavy blankets of volcanic ash from the Mount Toba supervolcanic event destroyed upwards of 60% Asia's subtropical forests. The earlier events at Mount Toba are not considered to have been as powerful but major eruptions nonetheless laying deep ash layers throughout Asia, mostly to the west, greatly impacting India. Late Miocene and Mid-Pliocene aged volcanism may be partially responsible for the diversification of the Crimson-headed Partridge and *Galloperdix* spurfowl from peacock-pheasant ancestors.

Right:

Theoretically, one consequence of volcanic catastrophism would be the wholesale extirpation of most reptilian predators. Due to the relative absence of a significant class of predators, complex anti-predatory adornments like eye spots were no longer required. Chicks matured without the level of reptilian predation of lowland species as well. Consequently, secondary sexual characteristics we associate with ornamentation would eventually be lost.

This juvenile Northern Grey peacock-pheasant *P. b. bakeri*, may resemble Pleistocene progenitors of the Mountain Clade species.

Photo: P. Stubbs.



Recent major eruptions like those of Weh and Mount Toba in Indonesia may have isolated populations of a *Polyplectron germaini* related species, which subsequently diverged into the *P. inopinatum* clade that includes *P. chalcurus* and *P. bicalcaratum*.



Right: Sumatran Bronze-Tailed peacock-pheasant. Photo: Jeff Berger.

It's intriguing that the only known species of peacock-pheasant to inhabit Sumatra is likewise the most divergent in terms of morphology and behavioral ecology, is only ~ 800,000 years old, inhabiting mountainous slope forests potentially the most flighted peacock-pheasant species, one that is sexually mature earlier than other species. As an adult it resembles the half-grown chick or "keat" of the older, more ornately-plumaged species. As Mount Toba erupted ~ 80,000 years ago, the Sumatran Bronze-tailed is evidently well-suited for long-term survival in an active volcanic zone.



Left: Mountain peacock-pheasant *P. inopinatum*.

Photo: P. Stubbs.

The lineage *Polyplectron*, *Haematortyx* and *Galloperdix* evolved from may have diversified as early as the Late-Miocene ~ 9 MYA. The oldest clade of surviving species, which includes the Bornean *P. schleiermacheri*, Palawan *P. emphanum* and Malayan *P. malacenseis* began its diversification ~ 4,000,000 years ago.

Of this "primitive" clade the Palawan is the most sexually dichromatic species with distinctive juvenile and subadult plumage phases. Males are sexually mature generally in the second or third year. Compellingly of this most ancient clade, *P. emphanum* is apparently the least disinclined to make sustained flights beyond vegetative cover. The Palawan is often described as the most adorned of the peacock-pheasants. It is the most peacock-like in appearance, resembling a miniature version of the more familiar creature it has been so aptly named after.

The Malayan is apparently strictly lowland forest adapted species, which may occasionally inhabit slope forest. Both Davison and McGowan have written excellent papers on the range ecology of the Malayan species.



Right: Malayan peacock-pheasant male, recognition posture.

Photo: Vernon Denton.

Perhaps most importantly, these phylogenetic results may suggest that the poorly-ornamented plumage of the Sumatran and Mountain peacock-pheasant is not 'primitive': instead, these species simply must have evolved from highly ornamented ancestors. In fact, in Kimball et al.'s (2001) phylogenetic tree, the Palawan peacock-pheasant clade – are the most elaborate of the whole group – was found to be the sister-species to all other peacock-pheasants, a position suggesting that it is closest in anatomy and biology to the peacock-pheasant's late Miocene-aged common ancestor. We need to keep this idea in mind (that the showy species are sometimes the older, 'more ancestral' ones, and that plainer species are very new on the evolutionary tree and have evolved from them), since as we will revisit this topic.

Right: Adult pair White-Cheeked Palawan peacock-pheasant, *P. e. emphanum*. Note projection screen properties of dorsal plumage. Photo: P. Stubbs.



Why do we see such fantastically elaborate plumage in these birds, and why is there such variation within the group? As mentioned above, the conventional explanation behind all elaborate plumage in gallinaceous birds is that it has evolved via sexual selection pressure: that is, that the males with the showiest, most elaborate plumage have been selected as mates by females since they are the ones carrying the best genes. Observations of males displaying their showy feathers to females, combined with the fact that obvious sexual dimorphism is present in some species, seemingly supports the assumption that sexual selection is behind plumage evolution in these birds.



However, we know exceedingly little about the natural behaviour of these birds in the wild and there are indications from observed behaviour that other factors may have been at play, and may still be at play, as goes the plumage evolution in peacock-pheasant and other elaborate gallinaceous birds.

Left: Adult male Bornean peacock pheasant, *P. schleiermacheri*. Amongst the *Polyplectron*, this species exhibits the least elongated tail. It's relatively modest length and semi-vaulted morphology are reminiscent of *Galloperdix*. Photo: Robert at PBase.

Given the prominence of eye-like spots in deterring predators – such markings are seen widely among insects and in frogs, lizards, snakes and even some mammals – the possibility exists that these remarkable, dazzling structures serve an anti-predator function. After all, as noted above, we know that these birds inhabit tangled, cluttered environments with low ambient light. We know that they go to great lengths to avoid detection, prefer not to fly and are obliged by the nature of their principle source of nutrition (arthropods) to move about actively while foraging. Finding adequate food in subtropical forests can be quite challenging even for ecological specialists like peacock-pheasants. Locating food larders, for instance, swarming termite nests and fallen fruit is a preoccupation of a pair, especially those with juvenile progeny. We can postulate that these birds probably encounter many different creatures in a given day, creating critical scenarios that require interspecific communication. Peacock-pheasants will typically encounter potential predators at close quarters, and in spaces where there is frequently little possibility of effective escape. What is possibly of still greater significance is the likelihood that the majority of creatures it comes into contact with during its daily excursions are rarely predators of the adult males but rather the smaller, less-ornamented females and their young. Other species like may be competitors at a food larder and still others entirely unknown to it. An adult male peacock-pheasant that's encountered a young, squirrel-sized monitor lizard or tree snake is in little danger of serious injury. It may use its plumage to avoid conflict and when necessary to defend itself from intrusion or harm. This hypothesis has been mentioned over the years for peafowl and other gallinaceous birds but has yet to be adequately tested.



Above: Pair bonding display in White-Cheeked Palawan pair. As peacock-pheasants are strictly monogamous, pairs remaining together indefinitely, with males participating in nest defense and chick-rearing, these showy display behaviors are probably better referred to as demonstrative intention display behavior. The male is demonstrating to the female his capacity to defend her and their chicks. His performance mimics the extremely ritualized display behaviors males utilise to interrupt the advance of interspecifics. See also this very special [video](#) Photo and video by [P. Stubbs](#).

Following C. W. Beebe's work of 1914, many ornithologists of the early 20th Century thought that peacock-pheasants should be classified within two genera: *Chalcurus* housing the two least-ornamented species (the Sumatran peacock-pheasant and Mountain peacock-pheasant *P. inopinatum*), and *Polyplectron* for the more ornamented ones (Beebe 1914). This view fell out of favour during the 1970s (Delacour 1977), the assumption soon becoming that the least-ornamented peacock-pheasants are 'more primitive' – that is, more similar to the ancestral condition – that are the more ornamented ones. As we have just seen, the opposite now seems to be the case. Could it be that montane-adapted species inhabit ecosystems outside the reproductive range of certain reptile species?

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In our next issues: Part 2, On the evolutionary history and morphology of peacock-pheasants, Galloperdix spurfowl and crimson-headed partridge - with some observations of the daily round of life of semi-captive free-ranging peacock-pheasants over a five year period. Part 3 will be on their aviculture Part 3 will focus on developmental growth phases, their aviculture and conservation.

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