THE SIGNIFICANCE OF THE DISTRIBUTION OF THE MEGAPODIIDAE

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SUMMARY

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An analysis of the zoogeography of the Megapodiidae and Phasianidae shows these families to have a mutually exclusive and complementary distribution. This probably results from the ability of the Phasianidae to displace megapodes while being unable to cross water barriers. Megapodes, on the other hand, are excellent overwater colonizers and persist in areas inaccessible to phasianids. Despite their great differences in morphology and behaviour, the distributional pattern of megapodes and phasianids seems to indicate that they interact as ecological counterparts.

The megapodes or mound-builders (Megapodiidae) are, in their behaviour and morphology, the most distinctive family of Galliformes. Within that order, despite their specialized breeding, they are structurally primitive and are almost universally regarded as such (*pace* Clark 1964). The present distribution of the megapodes lies almost entirely within Australasia. It is instructive to examine the northern limits of distribution of megapodes in some detail, because this reveals a previously unnoted pattern suggesting significant interaction with the Phasianidae.

The Phasianidae (*sensu stricto*) is the largest, most diverse and probably the most advanced family of Galliformes and has its centre of taxonomic diversity in Asia. The members of this group are notably poor at crossing water barriers. As a consequence, phasianids are practically absent from the islands east of Wallace's Line, which partially demarcates the Asian and Australian faunas, and from the Philippines, the geological history of which is that of an oceanic archipelago. The only exceptions to this generalization are found in the *Coturnix* group and in the genus *Gallus*.

In Australasia the *Coturnix* group is represented by *Coturnix chinensis*, *C. novaezelandiae* (including *pectoralis*), *C. ypsilophora* and *Anurophasis monorthonyx*. The first three of these are very small forms, clearly derived from Eurasian members of the genus *Coturnix*, which contains the only truly migratory forms in the Phasianidae. *Anurophasis* is a partridge-sized bird confined to the highlands of New Guinea. Although it was first considered to be related to the francolins (Mayr *in* Peters 1934), it too is now thought to be derived from the small *Coturnix*-type quails (Rand and Gilliard 1967). In this regard it is pertinent to note that the only endemic galliform bird in Madagascar, the partridge *Margaroperdix*, is now thought to have been derived from *Coturnix* (Frost 1975). Considering their migratory propensities, it is not surprising that the *Coturnix* quails have advanced successfully into Australasia. For this reason, and because all these forms are small and therefore unlikely to interact significantly with the Megapodiidae, they are of little importance in the present analysis. For the purposes of the remaining discussion, all references to the Phasianidae and phasianids may be taken to exclude the *Coturnix* quails and their derivatives.

Because man and species of the genus *Gallus* have been intimately associated for a long time, any unusual distribution patterns of the latter are to be regarded with great suspicion. For obvious zoogeographical reasons the populations of Red Jungle Fowl *Gallus gallus* in the Philippines and Celebes have traditionally been considered to have been introduced by man. To my knowledge, no one has seriously questioned that *Gallus gallus* was introduced to Celebes but Parkes (1962) has argued that the Philippine populations are probably natural because they are recognizably distinct from mainland populations and exhibit clinal variation within the archipelago. This conclusion is plausible but not compelling, considering that in North America the House Sparrow *Passer domesticus* has developed clinal geographical variation in the little more than one hundred years since its introduction there (Johnston and Selander 1964), a period considerably less than the 3,000 years during which the Malays have occupied the Philippines. Here, I shall regard the populations of *Gallus gallus* in the Philippines and Celebes as having been introduced.

The above exceptions having been noted, there remains only a single species of phasianid occurring east of Wallace's Line, this being the Green Jungle Fowl *Gallus varius*, which extends from Java and Bali across to Lombok and the remainder of the Lesser Sunda Islands. Here again, the possibility of human intervention is not above suspicion, as Beebe (1921) reports a fairly long association between this species and man. On the other hand, Beebe also records a family group of *Gallus varius* on the coast of Java that each evening was seen to fly across seventy-five metres of open water to roost on a small mangrove islet. This, and the fact that the distribution of *G. varius* is entirely insular to begin with, makes *G. varius* the only reasonable candidate among the Phasianidae, apart from *Coturnix*, for having crossed Wallace's Line unaided.

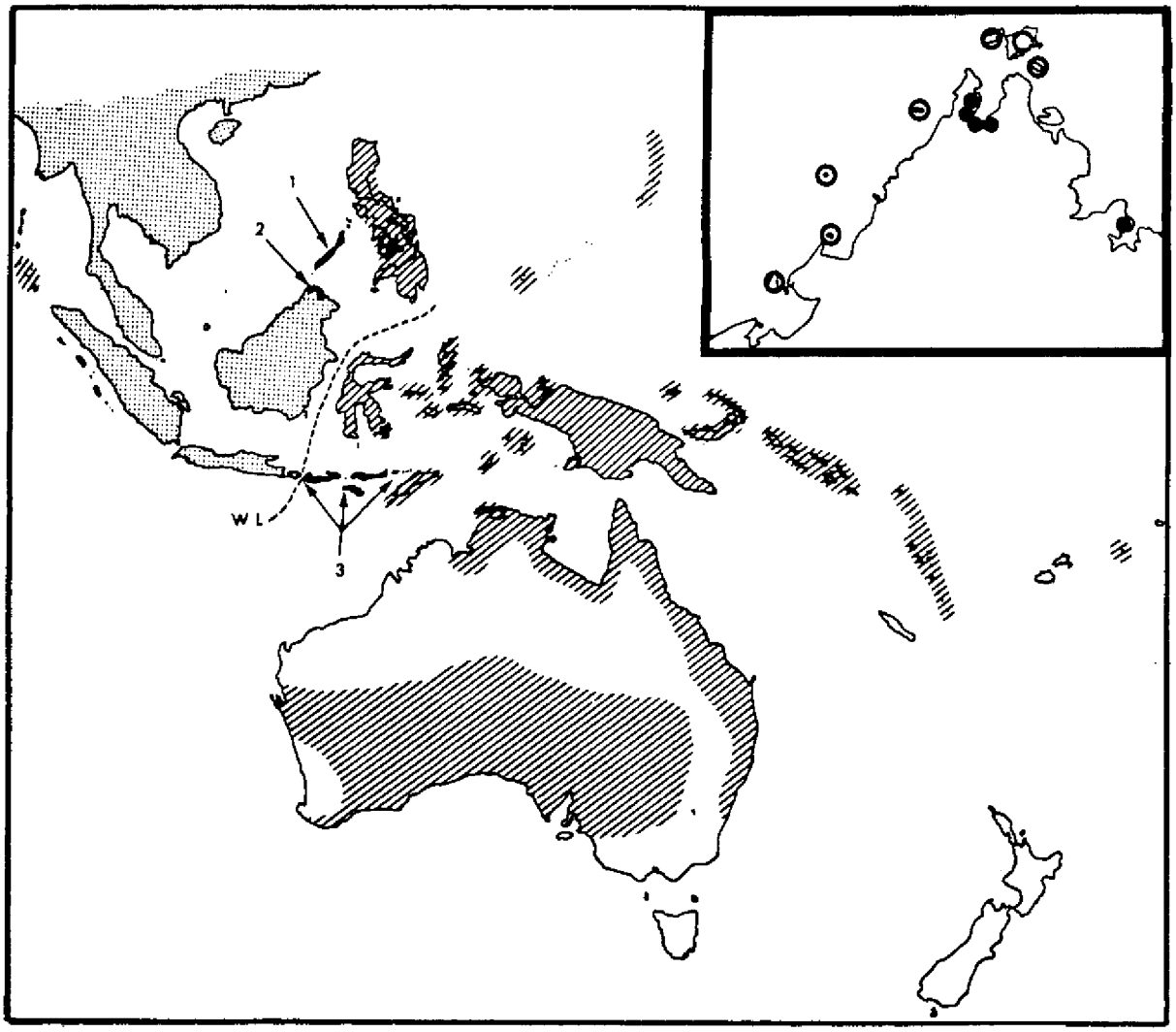

Figure 1. Natural Australo-Malaysian distribution of the Phasianidae (stipple), excluding *Coturnix* and derivatives, contrasted with the distribution of the Megapodiidae (diagonal hatching). Blackened areas with numbered arrows indicate the only regions of apparent natural overlap between the two families: 1, Palawan; 2, northern Borneo; 3, Lesser Sunda Islands. WL= Wallace's Line. Inset: Distribution of *Megapodius freycinet* in northern Borneo (adapted from data in Smythies 1968); dots show mainland records, circles show island populations.

In marked contrast to the Phasianidae, the megapodes are quite capable of dispersing over water for considerable distances (Fig. 1). Most of the various genera and species are concentrated east of Wallace's Line in Celebes, the Moluccas, New Guinea and Australia. Forms of *Megapodius* extend eastward through the Bismarck Archipelago, the Solomons, the New Hebrides and, evidently skipping Fiji (an artefact of human intervention?), find their most remote outpost in *M. pritchardii* endemic to the island of Niuafou. Endemic forms of *Megapodius* occur also in the Palau Islands and in the Mariannas. North and west of Wallace's Line, populations of *Megapodius* are found in the Philippines, on Palawan and northernmost Borneo. Particularly noteworthy populations, divisible into two races, occur in the Nicobar Islands in the Indian Ocean.

From Figure 1 it can be seen that the ranges of the Phasianidae and the Megapodiidae are, with minor exceptions, not only mutually exclusive but perfectly complementary.

There are only three areas of apparent overlap. In the Lesser Sunda islands *Gallus varius* and *Megapodius* both occur. On Palawan a single species of phasianid, *Polyplectron emphanum*, evidently co-exists with *Megapodius*. Borneo harbours a diverse variety of phasianids. According to Smythies (1968), *Megapodius* occurs on mainland Borneo only in a few localities at the northern tip and is otherwise confined to adjacent offshore islets (Fig. 1, inset), thus effectively avoiding interaction with phasianids. Megapodes are perfectly capable of crossing the water barriers between Lombok and Bali, Bali and Sumatra, or between Celebes and Borneo. If they reached the Nicobars in the first place, then it is only reasonable that they should be able to disperse to Java, Sumatra or mainland Asia; yet none is found there now. The perfectly complementary distribution of the Phasianidae and Megapodiidae is thus a strong indication that these families, despite their great differences in structure and habits, are ecological counterparts that cannot co-exist. Given this, it becomes obvious that phasianids are excluding megapodes and preventing their expansion northward.

Regarding the origins of megapodes, Cracraft (1973:508) in discussing continental drift and plate tectonics, has hypothesized that the 'distribution of primitive galliforms across Gondwanaland in the Cretaceous could have produced isolation of ancestral megapodes in Australasia and protocracids in South America.' Farther on (p. 529), he states more positively that the Megapodiidae 'almost certainly had a trans-Antarctic dispersal history.'

There is a certain attractiveness in the idea that megapodes, like the marsupials with their similarly 'aberrant' mode of reproduction, were part of an ancient fauna that inhabited Australia when the southern continents were connected or more close to each other. However, Cracraft's (1973:507) major assumption, that the megapodes and the Cracidae, at present a Neotropical family, were both derived from an ancestral galliform group inhabiting Gondwanaland in the Cretaceous, is almost certainly erroneous.

The cracids have a well-documented fossil record in the Tertiary of North America extending at least as far back as the early Oligocene (Tordoff and Macdonald 1957). Because cracids have not been able to reach the West Indies, it is unlikely that they gained access to South America until the land connexion between North and South America was effected in the late Pliocene. Vuilleumier (1965) considered the South American species of cracids to be of post-Pliocene origin. The impressive evidence assembled by Haffer (1974) correlates major speciation events in South American birds with Pleistocene climatic changes. It seems almost certain that the Cracidae, or their ancestors, would not have been in South America in the Tertiary at a time appropriate for dispersal across Antarctica.

Rich (1975:104) did not rule out the possibility that megapodes might have 'moved south across the Indomalaysian route and been isolated there at some time during or after the mid-Tertiary.' She indicates that Australia was within 10° of its present position by the Miocene. Furthermore, 'during the Miocene, a southward migrating island arc system collided with the northern edge of the Australian crustal plate, adding the final, northern segment, to form modern New Guinea' (Rich 1975:72). There would seem to have been ample opportunity for the megapodes, with their capability of dispersal over water, to have colonized Australia from Asia by the Miocene. This would allow more than enough time for the modest diversification of the family observed in Australia today.

Thus, the geographical origins of the megapodes remain equivocal. Nevertheless, it can hardly be gainsaid that these birds must have been isolated in Australasia for a considerable time. By the late Tertiary, the Australian plate had moved up to its present position, resulting in the juxtaposition of its fauna and that of Asia. But because the two areas were never connected, a marked faunal discontinuity was preserved, marked in part by Wallace's Line. With the possible exception of *Gallus varius*, non-migratory phasianids have not been able to cross this gap and the megapodes have remained secure as relicts in Australasia. With its ability to disperse over water, *Megapodius* reached the Philippines and was able to persist because these islands have never been part of the Asian mainland and hence were inaccessible to phasianids. A single species of phasianid, *Polyplectron emphanum*, is found on Palawan, which in contrast to the Philippines is a continental island. This species has not yet supplanted *Megapodius*, if it is capable of doing so.

The forms of *Megapodius* in the Nicobars might be interpreted as relicts left after phasianids had displaced continental populations of megapodes. But because these forms are only subspecifically distinct from the nearest populations 1,600 kilometres eastward, it seems more likely that *Megapodius* reached the Nicobars directly across the sea or perhaps by dispersing along islets off the southern coasts of Sumatra and Java.

Regardless, the most important observation to be made here is that the distribution of megapodes and phasianids indicates that there is interaction between members of the two families that is suggestive of competitive exclusion. This may be used to account for the current absence of the Megapodiidae from the Asian mainland.

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