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Molecular evolution of the Asian francolins (*Francolinus*, Galliformes): A modern reappraisal of a classic study in speciation

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ABSTRACT

We investigated the evolution of the Asian francolins, five little known species in the genus *Francolinus* (Phasianidae). Evolutionary affinities of two of these species, *F. gularis* (swamp francolin) and *F. pondicerianus* (grey francolin), has long remained unclear. In contrast, the other three species, *F. pintadeanus* (Chinese francolin), *F. pictus* (painted francolin) and *F. francolinus* (black francolin) have been cast among the "spotted francolins" on a morphological and ecological basis. Previous molecular DNA investigations including Asian francolins mostly relied upon partial gene sequencing of one specimen per species (no more than three species and with the exclusion of *F. pictus*). Therefore, fundamental questions do persist. What relationship exists among the spotted and the other Asian francolins? What is the geographic origin of the black francolin, the species with the largest distribution range? How did the geological history influence the diversification of francolins across Asia? We sequenced the entire Control Region of the mitochondrial DNA in 228 samples of all five Asian francolin species, which were collected in 16 countries (from East Europe to East Asia). We constructed a molecular phylogeny according to four different procedures. We showed the monophyly of each of the Asian francolins and the spotted group, while that of the entire Asian group was presumed according to a biogeographical model we proposed. The splitting of the genus *Francolinus* occurred ~17.4 Ma (95% HPD: 13.4–22.1) while the spotted francolins diverged ~10.5 Ma (7.0–14.9). We resolved the most recent common ancestor to painted and black francolin as being in the Indian sub-continent, thus suggesting a westwards adaptive radiation of the latter. In Pakistan, we identified *F. f. asiae* representatives in the Northern Areas and in the Sindh. The latter represents a relict population of Indian fauna within the Pakistani range of the Great Rann of Kachchh.

1. Introduction

The francolins (Phasianidae) are medium-sized galliforms included in the genus *Francolinus*, which traditionally comprised 41 species (but see below): 36 distributed throughout Africa and five throughout Asia (Hall, 1963). In his classic study on the speciation of this large group of birds, Hall (1963) hypothesized an Asian origin and a successive radiation across Africa of the genus *Francolinus*, which would have diverged from other phasianids during Oligocene. Conversely, Crowe and Crowe (1985) suggested an African origin, with a nomadic or migratory ancestor that became sedentary in Asia. On the basis of morphological and ecological data, Hall (1963) also proposed the monophyly of the genus *Francolinus* as well as that of eight groups including the very large majority of species. Of these eight groups, seven are represented in Africa, and one in Asia. The Asian group included *F. pintadeanus* (Chinese francolin), *F. pictus* (painted francolin) and *F. francolinus* (black francolin), collectively referred to as "spotted francolins". *Francolinus gularis* (swamp francolin) and *F. pondicerianus* (grey francolin), the other Asian francolins, were considered of uncertain evolutionary affinities.

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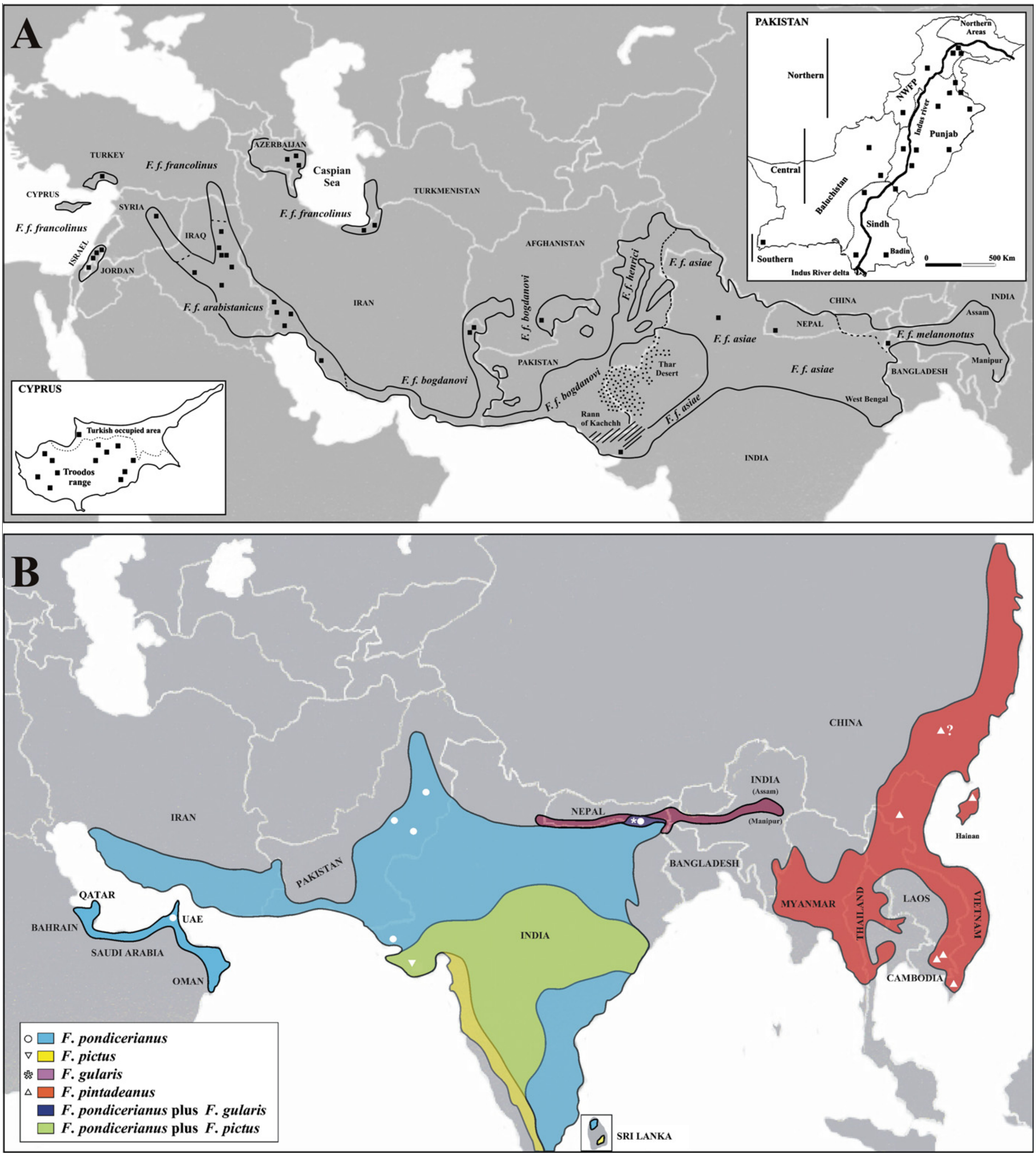

Fig. 1. Distribution map and sampling localities of the Asian francolins. (A) The black francolin (*F. francolinus*) distribution range is shown (black thick line); dotted lines delineate known boundaries among the different subspecies (see text for details). Black solid squares indicate the sampling localities (Table S1). Relevant geographic features mentioned in the main body of the text are also indicated. (B) The distribution map of grey, painted, swamp and Chinese francolin are given together with the sampling localities indicated by white symbols (? unknown locality of Chinese francolin GenBank entry: Table S1); overlapping areas among different distribution ranges are highlighted (see legend).

Recent studies mostly based on mitochondrial DNA (mtDNA) rejected monophyly of the genus *Francolinus*, while confirmed that of the spotted francolins (Crowe and Crowe, 1985; Milstein et al., 1987; Crowe et al., 1992, 2006; Bloomer and Crowe, 1998). According to this, in the latest taxonomy provided by the International Ornithological Committee (IOC), only the Asian species were included in the genus *Francolinus* while those inhabiting the African continent were assigned to the genera *Dendroperdix*, *Peliperdix*, *Pternistis* and *Scleroptila* (Gill and Donsker, 2012). Nevertheless, fundamental questions regarding evolution and biogeography of