



Modern avian radiation across the Cretaceous-Paleogene boundary

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Use of skin from the feet of museum specimens as a source of DNA.—Mundy et al. (1997:126) stated that “because the sole of the foot has not to our knowledge been used as a taxonomic character in birds, the damage done to the specimens for future research is negligible.” Although not commonly used, foot soles can provide systematically important morphological characters.

Characters on the plantar surface of the feet of birds have been used with success in recent studies. Lennerstedt (1973, 1974, 1975a, b, c) described such characters, their interspecific and individual variation, and their variation at different seasons, and also carried out a functional study. Mann et al. (1978) used such characters, among others, to erect a new genus of babbler (Timaliidae), viz. *Kakamega*. Characters on the plantar surface of the foot were intensively examined by Mann (1979, 1988) in taxonomic studies of passerine birds.

I would urge researchers who wish to use such tissue to remove small pieces from either the large pad on the hind digit or from the central pad, avoiding the edges and any folds or furrows. In this way, sufficient tissue can be made available for DNA studies without destroying the basic morphology.

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Modern avian radiation across the Cretaceous–Paleogene boundary.—The pattern of modern avian radiation across the Cretaceous–Paleogene (K-P) boundary has been debated for more than a decade (e.g., Feduccia 1995, Cooper and Penny 1997, Dyke and van Tuinen 2004, Clarke et al. 2005) and was discussed in a recent review in *The Auk* by James (2005). Here we show, using a comprehensive compendium of temporal, phylogenetic, and geological data (Fountain et al. 2005; full data set available on request from the authors), that the bulk of sediments yielding fossil birds from the earliest Paleogene (65–49 mya) are aquatic: marginal marine or lacustrine. This does not reflect preservation potential; older birds from the Mesozoic (146–65 mya), where there are lower volumes of aquatic rocks, are known from all sedimentological environments (Fountain et al. 2005). Because global sea level is known to have fallen from the Cretaceous to the Paleogene (Fara 2002), leading to an increase in terrestrial rock volume with respect to marine, the presence of more birds in aquatic environments is likely independent of preservation potential. This suggests that either taphonomic effects bias the interpretation of avian evolution across the K-P boundary or that more “waterbirds” were actually present in the early Paleogene. Thus, our geological and paleontological data set supports a “shorebird” or “waterbird” transition in prevailing environments of preservation in the aftermath of the K-P extinction,

albeit in the absence of clear phylogenetic control. Previous proposals for avian “survivorship” across the K-P boundary have explicitly defined a “shorebird or waterbird morphotype” for modern avian ancestry (Feduccia 1995); our data do not address this, having bearing only on environments of preservation.

We compiled a database of fossil bird records for the Mesozoic ($n = 117$) and collated a comprehensive sample of named taxa from the early Paleogene (Paleocene–Eocene; $n = 132$) (Mlikovsky 2002, Fountaine et al. 2005). Whereas Mesozoic birds appear in equal numbers in aquatic and terrestrial sediments, our Paleogene data set is strongly aquatic, from nonmarine sediments. Only 7% of named birds from the early stages of the Paleogene are from terrestrial sediments (Fig. 1); almost all (>90% of records) named taxa of Paleogene birds are from lacustrine or marginal marine sediments, independent of their preservation potential (Fountaine et al. 2005).

In the Cretaceous, the rarity of modern birds may reflect actual contemporary abundance: the paucity of known fossils ($n = 27$) does not necessarily imply patchy preservation (Fountaine et al. 2005). Indeed, all but two modern bird fossil records are from aquatic

environments and just two are represented by partial skeletons. By contrast, >30 species from nonmodern clades of Cretaceous age are known from complete skeletons (Fountaine et al. 2005). This dramatic difference in relative preservation could be an artifact of a smaller sample size, or it could be real.

Why not a biological explanation for these data? There is no *prima facie* reason to expect a difference in the relative preservation potential of modern and nonmodern avian clades: data show that specimens within each broad subdivision span similar size ranges (Fountaine et al. 2005). Comparing our data with similar compilations of other Cretaceous vertebrate groups (Fara and Benton 2000) further demonstrates that preservation likelihood is independent of body size. Instead, the clear taphonomic bias evident in these data may suggest that modern birds were simply more prevalent in aquatic environments before and after the K-P boundary.

Fossil representatives of several of the modern avian clades are now known from the late stages of the Cretaceous (Clarke et al. 2005; see also Dyke and van Tuinen 2004); indeed, this period boasts some of the best-preserved avian records from the entire Mesozoic,

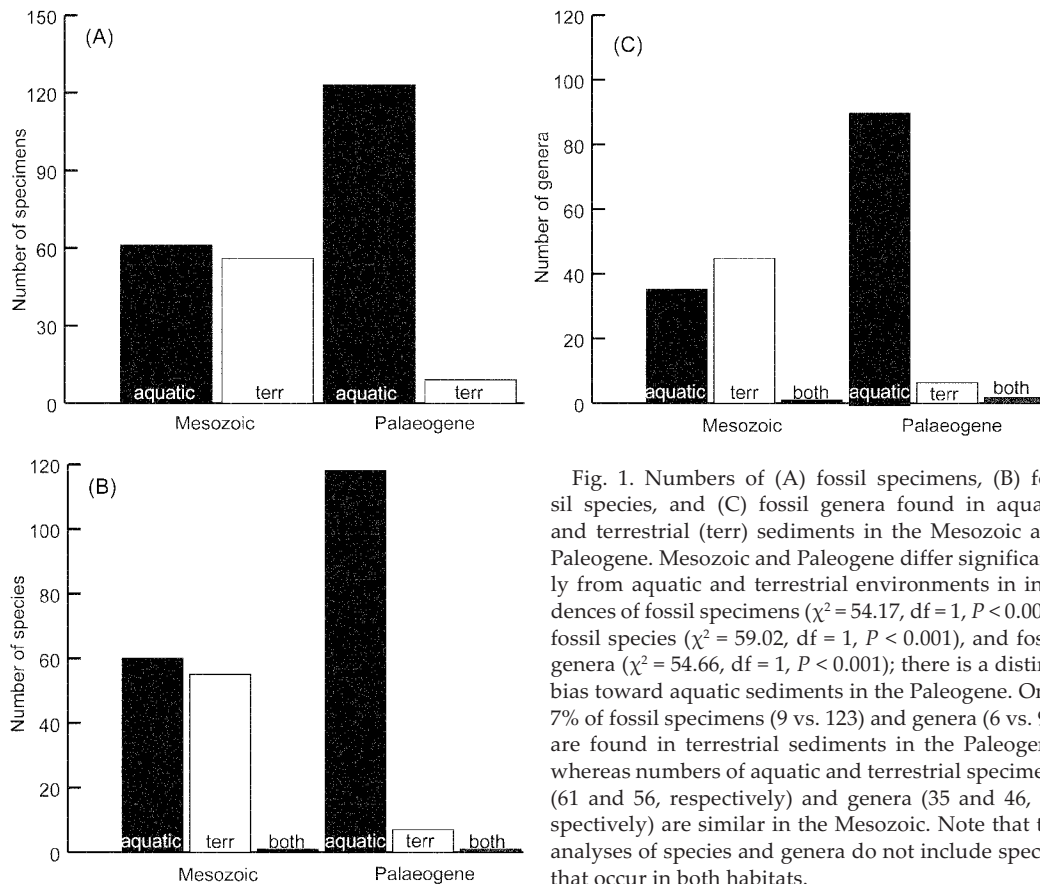


Fig. 1. Numbers of (A) fossil specimens, (B) fossil species, and (C) fossil genera found in aquatic and terrestrial (terr) sediments in the Mesozoic and Paleogene. Mesozoic and Paleogene differ significantly from aquatic and terrestrial environments in incidences of fossil specimens ($\chi^2 = 54.17$, $df = 1$, $P < 0.001$), fossil species ($\chi^2 = 59.02$, $df = 1$, $P < 0.001$), and fossil genera ($\chi^2 = 54.66$, $df = 1$, $P < 0.001$); there is a distinct bias toward aquatic sediments in the Paleogene. Only 7% of fossil specimens (9 vs. 123) and genera (6 vs. 91) are found in terrestrial sediments in the Paleogene, whereas numbers of aquatic and terrestrial specimens (61 and 56, respectively) and genera (35 and 46, respectively) are similar in the Mesozoic. Note that the analyses of species and genera do not include species that occur in both habitats.

from a wide range of sedimentary environments (Fountaine et al. 2005). Because other extinct clades of similarly sized taxa (e.g., Enantiornithes, Ichthyornithiformes) have been recovered globally from the Cretaceous, we consider it unlikely that modern birds were present but were “morphologically cryptic” (i.e., hard to identify on the basis of morphology alone). Our data set strongly supports the contention that the fossil record of birds across the K-P boundary is well enough understood to extract biological patterns—aquatic environments of preservation dominate the early Palaeogene avian fossil record, because these were the habitats in which more modern birds lived at the time of the transition.

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