



OVERVIEW

PALEOGENE FOSSILS AND THE RADIATION OF MODERN BIRDS

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MODERN GENERA of birds arose mainly in the Neogene Period (1.8–23.8 mya), and modern species mainly in the Plio-Pleistocene (0.08–5.3 mya). Neogene fossil birds generally resemble modern taxa, and those that cannot be attributed to a modern genus or species can usually be placed in a modern family with a fair degree of confidence (e.g. Becker 1987, Olson and Rasmussen 2001). Fossil birds from earlier in the Cenozoic can be more challenging to classify. The fossil birds of the Paleogene (23.8–65.5 mya) are clearly attributable to the Neornithes (modern birds), and the earliest well-established records of most traditional orders and families of modern birds occur then. But the fossils tend to be primitive and more difficult to seat phylogenetically within the Neornithes (Dyke and van Tuinen 2004).

Not a few early Paleogene fossils have been said to exhibit a mosaic of characters associated with two or more traditional families or orders (e.g. Peters 1992, Feduccia 1999, Mayr 2003a). An excellent example is an Eocene bird referred to the Psittaciformes that lacks the specialized skull of parrots (Mayr 2005a). Paleontologists sometimes resort to describing primitive fossils as “petrel-like” or “hoopoe-like” (for instance) without referring them to the corresponding modern families (e.g. Houde and Olson 1992; Feduccia and McPherson 1993; Mayr 2000a, 2003b). Nevertheless, the primitive fossils of the Paleogene provide the earliest firm records of such diverse modern radiations as ratites (Houde 1988), owls (Mourer-Chauviré 1987, Peters 1992), waterfowl (Ericson 1997, Olson 1999, Dyke 2001), ibises (Peters 1983), penguins (see Clarke et al. 2003), galliforms (Mourer-Chauviré 1992, Mayr 2000b, Dyke and Gulas 2002), passerines (Mourer-Chauviré et al.

1989, Mayr and Manegold 2004), and others. Paleogene fossils also document diverse extinct branches of the neornithine tree, ranging from large pseudotoothed seabirds to giant flightless land birds to small zygodactyl perching birds (Ballmann 1969, Harrison and Walker 1976, Andors 1992).

Before the Paleogene, fossils of putative neornithine birds are sparse and fragmentary (Hope 2002), and their phylogenetic placement is all the more equivocal. The Paleogene is thus a crucial time period for understanding the history of diversification of birds, particularly with respect to the deeper branches of the neornithine tree.

EARLY NEORNITHES OF EUROPE

One ornithologist who has energetically taken up the challenge of Paleogene birds is Gerald Mayr of the Forschungsinstitut Senckenberg in Frankfurt, Germany. Mayr has published more than 70 papers on Paleogene birds and related topics since 1998 (for a recent summary, see Mayr 2005a). Notably, last year he described a hummingbird, *Eurotrochilus inexpectatus*, from the early Oligocene of Europe (Mayr 2004). Fossils with hummingbird-like characters had been known from the Oligocene of Eurasia, but only from wing bones that appeared to be very primitive and perhaps transitional between hummingbirds and other apodiform birds (Karhu 1999, Mayr 2003a). *Eurotrochilus inexpectatus* is based on a well-preserved fossil skeleton with striking similarities to modern hummingbirds, including tiny size; long, thin bill; short humerus; and deep carina of the sternum. This was a bird that hovered to sip nectar from flowers, and it did so approximately 30–35 mya in Germany.

On page 1055 of this issue of *The Auk*, Mayr (2005b) introduces a genus and species of tiny barbet-like bird from the near-shore marine

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deposits of Frauenwiler, Germany, the same locality where the fossil hummingbird was found. The new taxon is known from a single associated skeleton lacking the skull. The fossil is not sufficiently well preserved to support a detailed cladistic analysis of its evolutionary relationships, though it shows a specialized morphology of the distal end of the tarsometatarsus and other characters diagnostic of the Pici (woodpeckers, Picidae; honeyguides, Indicatoridae; and barbets and toucans, Rhamphastidae). In other characters, it appears to be plesiomorphic with respect to all modern members of the Pici, and Mayr concludes that it is probably outside the crown group defined as the common ancestor of all modern species and its descendants. The fossil is thus the oldest substantial record of the Pici, if the definition of Pici is expanded to accommodate a stem group. Postcranial bones from the Miocene of Europe have also been referred to the barbets (Ballmann 1969). The fossil record thus supports a deep history for the Pici in the Old World, in consonance with recent molecular evidence (Johansson and Ericson 2003, Moyle 2004).

The new hummingbird and piciform bird are just two recent additions to the very rich Paleogene fossil record of Europe (Mlíkovský 2002, Mayr 2005a). Mayr's work has emphasized the Middle Eocene oil shales of Messel, where complete but often crushed skeletons represent diverse land and water birds (Peters 1988, Mayr 2005a). Other important Paleogene sites of Europe include the Upper Eocene to Lower Oligocene fissure fills of Quercy in France (Mourer-Chauviré 1982); the Lower Eocene London Clay, especially the exposures at Walton-on-the-Naze, United Kingdom (Feduccia 1999); and the Upper Paleocene to Lower Eocene marine deposits of the Fur Formation in Denmark (see Kristoffersen 2002).

All told, Europe boasts a richer Paleogene avifauna in terms of number and taphonomic variety of fossil localities and diversity of avian taxa compared with other continents. One assessment estimated that 55 families of birds are represented in the major localities of the European Paleogene (Feduccia 1999). Second to Europe is North America, where the Green River and Willwood formations provide important early Eocene records of approximately 25 families of birds. The dearth of similarly productive Paleogene localities in Asia and on southern

landmasses, particularly for the Eocene and Paleocene, is a longstanding obstacle to interpretation of the biogeographic history of birds.

SYSTEMATICS AND FOSSILS

Phylogenetic analysis.—Revisionary work in systematics of fossil birds is now commonly based on cladistic character analysis, and taxonomic descriptions of new taxa are sometimes accompanied by such analyses (e.g. Bourdon et al. 2005). Paleontologists prefer to work with complete associated skeletons and multiple individuals of each terminal taxon, but often make do with isolated or fragmentary specimens. To the extent that confidence is judged by the quantity of supporting character evidence, it follows that confidence in the phylogenetic placement is more variable for fossils than for modern birds. Interpretations of the fossil record need to take that variability into account.

Considerable effort is being devoted to resolving the deeper branches of phylogeny for the Neornithes through DNA sequencing and coding of morphological characters in modern birds (Livezey and Zusi 2001, Cracraft et al. 2004). Paleogene fossils appear to represent diverse early stages in the development of those very clades. Consequently, there is great potential for reciprocal illumination between modern and fossil phylogenetic evidence. On the other hand, the current lack of consensus on the higher-level relationships of modern birds is a hindrance to interpretation of the fossil record. The polarity and frequency of homoplasy for osteological characters of Paleogene fossils could be better understood in the context of a robust phylogenetic hypothesis.

Phylogenetic analyses at lower taxonomic levels (within orders and families) have generally been more successful for birds. Phylogenetic results are always richer when cast in the light of the fossil record, as in the examples of the barbets, hummingbirds, and rollers discussed here.

Stem versus crown groups.—Use of fossils to calibrate molecular rates has brought to prominence the distinction between crown and stem group fossils. Crown group fossils can provide minimum ages of diversification within modern clades, but stem group fossils may be older than those clades. In the past, stem group fossils that are classified in modern orders and families of birds may have been used unwittingly as

calibration points for the corresponding crown groups, providing age estimates that are erroneously too old. Simple misidentification of fossils can also invalidate calibrations. Therefore, it is important to begin taking the potential for error in phylogenetic placement of fossils into account when performing rate calibrations (Graur and Martin 2004, van Tuinen and Dyke 2004).

An example of reconciliation between fossil and molecular evidence is that of the Madagascan ground rollers, Brachypteraciidae. Eocene fossils from the Messel oil shales had been classified as members of the family. Kirchman et al. (2001), however, found levels of molecular divergence between ground rollers and true rollers (Coraciidae) that are too low to support an Eocene origin of ground rollers. Independently, Mayr and Mourer-Chauviré (2000, 2003) performed a cladistic character analysis that supported removing the fossils from the Brachypteraciidae and placing them basal to Brachypteraciidae + Coraciidae.

AVIFAUNAL DYNAMICS

Tertiary radiation.—The weak molecular genetic signal found so far for relationships among many higher-level taxa of birds could be explained if there was an early, explosive radiation of birds into diverse ecological niches. Just such an explosion has been hypothesized based on the early Paleogene fossil record of Europe and North America (Feduccia 1995, 2003). In Europe, where the record is best, there were more family-level taxa of birds in the Eocene than at present (Blondel and Mourer-Chauviré 1998). By contrast, the global fossil record for Cretaceous Neornithes is surprisingly slim—49 bones that are for the most part too fragmentary for confident identification (Hope 2002). Fountaine et al. (2005) studied the quality of the Mesozoic fossil record of birds and found that, when extinct non-neornithine taxa are included, it has grown to be quite respectable. It is thus uncontroversial that the Neornithes became much more diverse and ecologically dominant after the Cretaceous–Tertiary extinction event, but there is still lively debate over just how many lineages originated in the Cretaceous and survived that event (Cracraft 2001).

Biogeography.—Many Paleogene fossil birds of Europe have their closest modern relatives on southern landmasses today (e.g. species

with affinities to the African mousebirds, South American seriéamas, and Australian frogmouths). Avian taxa were probably more widely distributed during the Eocene, when global climate was equable. Certainly, there was greater faunal similarity between Europe and North America, which were connected by land in the early Eocene (Blondel and Mourer-Chauviré 1998, Mayr and Weidig 2004). The retreat of some taxa to the tropics and subtropics is partly explained by climatic cooling beginning in the Oligocene. Differentiation of the Eurasian and North American avifaunas took place in the Oligocene through Miocene as the continents became isolated (Blondel and Mourer-Chauviré 1998).

Debate continues over the biogeographic context of diversification of the Neornithes. The high number of early Paleogene birds that appear to be basal to modern radiations suggests that the diversification of many crown groups came after those epochs (Mayr 2005a). Biogeographic analysis of the same crown groups supports the alternative hypothesis that they arose earlier in the Cretaceous in Gondwana and were initially dispersed by continental drift (Cracraft 2001). Questionable molecular-rate calibrations favor the latter hypothesis, which is otherwise in conflict with the fossil evidence (Feduccia 2003, Mayr 2005a).

Grande Coupure.—The Grande Coupure marking the Eocene–Oligocene transition (33.7 mya) was a time of great faunal turnover in European mammals, and apparently in birds as well. Mayr's (2005a) intensive study of Paleogene birds has led him to conclude that there were no neornithines in family-level crown groups in Europe before the Grande Coupure. Fossils that belong within family-level crown groups begin to appear in the Oligocene. The implication is that most or all of the diversity within modern families of birds has evolved since the Grande Coupure.

Paleontologists concur that the Passeriformes originated in the south and invaded the Northern Hemisphere in the late Eocene or early Oligocene (Olson 1988, Mourer-Chauviré 1995). The earliest fossils in Europe are from the Lower Oligocene of Frauenwiler and nearby France (Mayr and Manegold 2004). Fossil passerines do not become prevalent until the Miocene. Food competition with passerines is believed to have been a factor in the extinction of diverse small nonpasserine birds that had been present

in the Paleogene of the Northern Hemisphere (Mayr 2005b, c).

SUMMARY

We have a picture of the Paleogene of Europe in which flowers are pollinated by hummingbirds, mosaic psittaciform birds that lack the specialized heads of parrots fly about, and what is now the most species-rich order of birds arrives on the scene quite late. The geographic distributions and phenotypes of some Paleogene birds would be beyond our capacity to imagine or to reconstruct without the solid evidence of fossils.

Careful study of the fossils has led to the hypothesis that the diversity within traditional modern families of birds arose after the Eocene. Although the record is strongest for Europe, the hypothesis also applies to North America, where the Eocene avifauna is very similar. Indeed, Mayr indicates that his hypothesis may apply globally. This is a significant insight that can be further tested with morphological, molecular, and fossil data.

Perhaps the greatest unsolved problem in avian systematics is the evolutionary relationships among modern higher-level taxa. Thanks to collaboration among systematists to resolve the avian tree of life, large morphological and molecular character matrices for neornithine birds are nearing completion (Livezey and Zusi 2001, Cracraft et al. 2004). Smaller molecular data sets for subclades of Neornithes are appearing regularly. The resulting trees become much more interesting if they can be correlated with a time scale and a fossil history. Adding osteological characters as a data partition in molecular phylogenetic databases would permit interactive analyses of genetic, morphological, and fossil evidence. Some of the odd phenotypes of the Paleogene might then be placed on the new phylogenetic trees that are emerging. The rich Paleogene fossil record provides a perspective on the evolutionary history of birds that cannot be reconstructed from studies of modern taxa alone. I urge greater effort to fully integrate that record in our modern reassessment of avian evolutionary history.

ACKNOWLEDGMENTS

I thank G. Mayr and S. L. Olson for comments on the manuscript.

LITERATURE CITED

- ANDORS, A. V. 1992. Reappraisal of the Eocene groundbird *Diatryma* (Aves: Anserimorphae). Pages 109–126 in *Papers in Avian Paleontology Honoring Pierce Brodkorb* (K. E. Campbell, Jr., Ed.). Natural History Museum of Los Angeles County Science Series, no. 36.
- BALLMANN, P. 1969. Die Vögel aus der altburdigalen Spaltenfüllung von Wintershof bei Eichstätt in Bayern. *Zitteliana* 1:5–61.
- BECKER, J. J. 1987. *Neogene Avian Localities of North America*. Smithsonian Institution Press, Washington, D.C.
- BLONDEL, J., AND C. MOURER-CHAUVIRÉ. 1998. Evolution and history of the western Palaearctic avifauna. *Trends in Ecology and Evolution* 13:488–492.
- BOURDON, E., B. BAÂDI, AND M. IAROCHENE. 2005. Earliest African neornithine bird: A new species of Prophaethontidae (Aves) from the Paleocene of Morocco. *Journal of Vertebrate Paleontology* 25:157–170.
- CLARKE, J. A., E. B. OLIVERO, AND P. PUERTA. 2003. Description of the earliest fossil penguin from South America and first Paleogene vertebrate locality of Tierra Del Fuego, Argentina. *American Museum Novitates* 3423:1–18.
- CRACRAFT, J. 2001. Avian evolution, Gondwana biogeography and the Cretaceous–Tertiary mass extinction event. *Proceedings of the Royal Society of London, Series B* 268:459–469.
- CRACRAFT, J., F. K. BARKER, M. BRAUN, J. HARSHMAN, G. J. DYKE, J. FEINSTEIN, S. STANLEY, A. CIBOIS, P. SCHIKLER, P. BERESFORD, AND OTHERS. 2004. Phylogenetic relationships among modern birds (Neornithes): Toward an avian tree of life. Pages 468–489 in *Assembling the Tree of Life* (J. Cracraft and M. J. Donoghue, Eds.). Oxford University Press, Oxford.
- DYKE, G. J. 2001. The fossil waterfowl (Aves: Anseriformes) from the Eocene of England. *American Museum Novitates* 3354:1–15.
- DYKE, G. J., AND B. E. GULAS. 2002. The fossil galliform bird *Paraortygoides* from the Lower Eocene of the United Kingdom. *American Museum Novitates* 3360:1–14.
- DYKE, G. J., AND G. MAYR. 1999. Did parrots exist in the Cretaceous period? *Nature* 399:317–318.

- DYKE, G. J., AND M. VAN TUINEN. 2004. The evolutionary radiation of modern birds (Neornithes): Reconciling molecules, morphology and the fossil record. *Zoological Journal of the Linnean Society* 141:153–177.
- ERICSON, P. G. P. 1997. Systematic relationships of the Paleogene family Presbyornithidae (Aves: Anseriformes). *Zoological Journal of the Linnean Society* 121:429–483.
- FEDUCCIA, A. 1995. Explosive evolution in Tertiary birds and mammals. *Science* 267: 637–638.
- FEDUCCIA, A. 1999. *The Origin and Evolution of Birds*, 2nd ed. Yale University Press, New Haven, Connecticut.
- FEDUCCIA, A. 2003. “Big bang” for tertiary birds? *Trends in Ecology and Evolution* 18: 172–176.
- FEDUCCIA, A., AND A. B. MCPHERSON. 1993. A petrel-like bird from the late Eocene of Louisiana: Earliest record for the Procellariiformes. *Proceedings of the Biological Society of Washington* 106:749–751.
- FOUNTAIN, T. M. R., M. J. BENTON, G. J. DYKE, AND R. L. NUDDS. 2005. The quality of the fossil record of Mesozoic birds. *Proceedings of the Royal Society of London, Series B* 272: 289–294.
- GRAUR, D., AND W. MARTIN. 2004. Reading the entrails of chickens: Molecular timescales of evolution and the illusion of precision. *Trends in Genetics* 20:80–86.
- HARRISON, C. J. O., AND C. A. WALKER. 1976. A review of the bony-toothed birds (Odontopterygiformes): With descriptions of some new species. *Tertiary Research Special Paper*, no. 2.
- HOPE, S. 2002. The Mesozoic record of Neornithes (modern birds). Pages 339–388 *in* *Over the Heads of the Dinosaurs* (L. M. Chiappe and L. M. Witmer, Eds.). University of California Press, Berkeley.
- HOUDE, P. W. 1988. Paleognathous birds from the early Tertiary of the Northern Hemisphere. *Publications of the Nuttall Ornithological Club*, no. 22.
- HOUDE, P. W., AND S. L. OLSON. 1992. A radiation of coly-like birds from the Eocene of North America (Aves: Sandcoleiformes new order). Pages 137–160 *in* *Papers in Avian Paleontology Honoring Pierce Brodkorb* (K. E. Campbell, Jr., Ed.). Natural History Museum of Los Angeles County Science Series, no. 36.
- JOHANSSON, U. S., AND P. G. P. ERICSON. 2003. Molecular support for a sister group relationship between Pici and Galbulae (Piciformes sensu Wetmore 1960). *Journal of Avian Biology* 34:185–197.
- KARHU, A. A. 1999. A new genus and species of the family Jungornithidae (Apodiformes) from the late Eocene of the northern Caucasus, with comments on the ancestry of hummingbirds. Pages 207–216 *in* *Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution* (S. L. Olson, P. Wellnhofer, C. Mourer-Chauviré, D. W. Steadman, and L. D. Martin, Eds.). Smithsonian Contributions to Paleobiology, no. 89.
- KIRCHMAN, J. J., S. J. HACKETT, S. M. GOODMAN, AND J. M. BATES. 2001. Phylogeny and systematics of ground rollers (Brachypteraciidae) of Madagascar. *Auk* 118:849–863.
- KRISTOFFERSEN, A. V. 2002. An early Paleogene trogon (Aves: Trogoniformes) from the Fur Formation, Denmark. *Journal of Vertebrate Paleontology* 22:661–666.
- LIVEZEY, B. C., AND R. L. ZUSI. 2001. Higher-order phylogenetics of modern aves based on comparative anatomy. *Netherlands Journal of Zoology* 51:179–205.
- MAYR, G. 2000a. Tiny hoopoe-like birds from the Middle Eocene of Messel (Germany). *Auk* 117:964–970.
- MAYR, G. 2000b. A new basal galliform bird from the Middle Eocene of Messel (Hessen, Germany). *Senckenbergiana Lethaea* 80: 45–57.
- MAYR, G. 2003a. Phylogeny of early Tertiary swifts and hummingbirds (Aves: Apodiformes). *Auk* 120:145–151.
- MAYR, G. 2003b. A new Eocene swift-like bird with a peculiar feathering. *Ibis* 145: 382–391.
- MAYR, G. 2004. Old World fossil record of modern-type hummingbirds. *Science* 304: 861–864.
- MAYR, G. 2005a. The Paleogene fossil record of birds in Europe. *Biological Reviews* 80: in press.
- MAYR, G. 2005b. A tiny barbet-like bird from the lower Oligocene of Germany: The smallest species and earliest substantial fossil record of the Pici (woodpeckers and allies). *Auk* 122:1055–1063.

- MAYR, G. 2005c. A new cypselomorph bird from the Middle Eocene of Germany and the early diversification of avian aerial insectivores. *Condor* 107:342–352.
- MAYR, G., AND A. MANEGOLD. 2004. The oldest European fossil songbird from the early Oligocene of Germany. *Naturwissenschaften* 91:173–177.
- MAYR, G., AND C. MOURER-CHAUVIRÉ. 2000. Rollers (Aves: Coraciiformes s.s.) from the Middle Eocene of Messel (Germany) and the Upper Eocene of the Quercy (France). *Journal of Vertebrate Paleontology* 20:533–546.
- MAYR, G., AND C. MOURER-CHAUVIRÉ. 2003. Phylogeny and fossil record of the Brachypteraciidae: A comment on Kirchner et al. (2001). *Auk* 120:202–203.
- MAYR, G., AND I. WEIDIG. 2004. The Early Eocene bird *Gallinuloides wyomingensis*—A stem group representative of Galliformes. *Acta Palaeontologica Polonica* 49:211–217.
- MLÍKOVSKÝ, J. 2002. *Cenozoic Birds of the World, part I: Europe*. Ninox Press, Praha.
- MOURER-CHAUVIRÉ, C. 1982. Les oiseaux fossiles des Phosphorites du Quercy (Éocène supérieur à Oligocène supérieur): Implications paléobiogéographiques. *Geobios Memoire Special* 6:413–426.
- MOURER-CHAUVIRÉ, C. 1987. Les Strigiformes (Aves) des phosphorites du Quercy (France): Systématique, biostratigraphie et paléobiogéographie. Pages 89–135 in *L'Évolution des Oiseaux d'Après le Témoignage des Fossiles* (C. Mourer-Chauviré, Ed.). Documents des Laboratoires de Géologie de Lyon, no. 99.
- MOURER-CHAUVIRÉ, C. 1992. The Galliformes (Aves) from the Phosphorites du Quercy (France): Systematics and biostratigraphy. Pages 67–95 in *Papers in Avian Paleontology Honoring Pierce Brodkorb* (K. E. Campbell, Jr., Ed.). Natural History Museum of Los Angeles County Science Series, no. 36.
- MOURER-CHAUVIRÉ, C. 1995. Dynamics of the avifauna during the Paleogene and the Early Neogene of France. Settling of the recent fauna. *Acta Zoologica Cracoviensia* 38:325–342.
- MOURER-CHAUVIRÉ, C., M. HUGUENEY, AND P. JONET. 1989. Découverte de Passeriformes dans l'Oligocène supérieur de France. *Comptes Rendus de l'Académie des Sciences Série II* 309:843–849.
- MOYLE, R. G. 2004. Phylogenetics of barbets (Aves: Piciformes) based on nuclear and mitochondrial DNA sequence data. *Molecular Phylogenetics and Evolution* 30:187–200.
- OLSON, S. L. 1988. Aspects of Global Avifaunal Dynamics during the Cenozoic. Pages 2023–2029 in *Acta XIX Congressus Internationalis Ornithologici* (H. Ouellet, Ed.). National Museum of Natural Sciences, Ottawa.
- OLSON, S. L. 1999. The anseriform relationships of *Antalavis* Olson and Parris (Anseranatidae), with a new species from the Lower Eocene London Clay. Pages 231–243 in *Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution* (S. L. Olson, P. Wellnhofer, C. Mourer-Chauviré, D. W. Steadman, and L. D. Martin, Eds.). Smithsonian Contributions to Paleobiology, no. 89.
- OLSON, S. L., AND P. C. RASMUSSEN. 2001. Miocene and Pliocene birds from the Lee Creek Mine, North Carolina. Pages 233–265 in *Geology and Paleontology of the Lee Creek Mine, North Carolina* (C. E. Ray and D. J. Bohaska, Eds.). Smithsonian Contributions to Paleobiology, no. 90.
- PETERS, D. S. 1983. Die "schnepfenralle" *Rhynchaetes messelensis* Wittich 1898 ist ein ibis. *Journal für Ornithologie* 124:1–27.
- PETERS, D. S. 1988. Die Messel-vögel—eine lanvogelfauna. Pages 137–151 in *Messel Ein Schaufenster in die Geschichte der Erde und des Lebens* (S. Schall and W. Ziegler, Eds.). Kramer, Frankfurt am Main.
- PETERS, D. S. 1992. A new species of owl (Aves: Strigiformes) from the Middle Eocene Messel oil shale. Pages 161–169 in *Papers in Avian Paleontology Honoring Pierce Brodkorb* (K. E. Campbell, Jr., Ed.). Natural History Museum of Los Angeles County Science Series, no. 36.
- VAN TUINEN, M., AND G. J. DYKE. 2004. Calibration of galliform molecular clocks using multiple fossils and genetic partitions. *Molecular Phylogenetics and Evolution* 30:74–86.