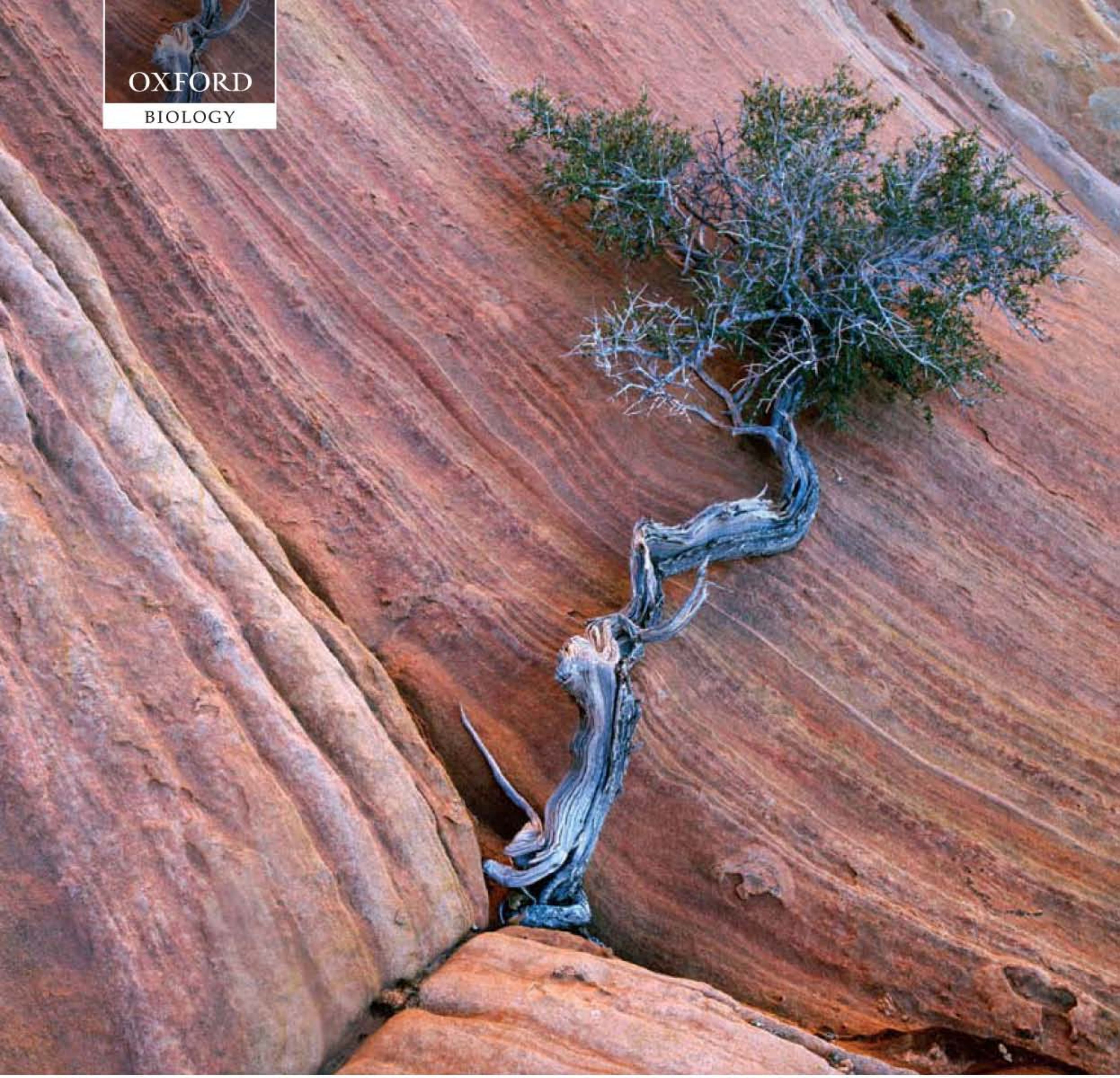
OXFORD
BIOLOGY



the TIMETREE of LIFE

edited by S. BLAIR HEDGES and SUDHIR KUMAR

foreword by James D. Watson

Diurnal birds of prey (Falconiformes)

Joseph W. Brown[a,*] *and David P. Mindell*[a,b]
[a]Department of Ecology and Evolutionary Biology & University of Michigan Museum of Zoology, 1109 Geddes Road, University of Michigan, Ann Arbor, MI 48109-1079, USA; [b]Current address: California Academy of Sciences, 55 Concourse Drive Golden Gate Park, San Francisco, CA 94118, USA
*To whom correspondence should be addressed (josephwb@umich.edu)

Abstract

Diurnal birds of prey (~313 species) are traditionally grouped into five families, constituting the neoavian Order Falconiformes. No consensus has been reached as to whether the group is natural because of uncertainty concerning inclusion of the falcons (Falconidae) and the New World vultures (Cathartidae). However, a clade of "core falconiforms" is supported which includes Sagittariidae (Secretary Bird) and closely related families Pandionidae (Osprey) and Accipitridae (hawks, eagles, kites, and Old World vultures). The Falconiformes timetree suggests that "core falconiforms" diverged in the early Paleogene about 62 million years ago (Ma), but that Cathartidae and Falconidae originated in late Cretaceous 76 Ma.

The diurnal birds of prey constitute the Order Falconiformes, and are generally classified into five reciprocally monophyletic families (*1*): Cathartidae (New World vultures, seven species; North and South America), Sagittariidae (Secretary Bird, one species; Africa), Pandionidae (Osprey, one species; cosmopolitan), Accipitridae (hawks, eagles, kites, and Old World vultures, ~240 species; cosmopolitan) (Fig. 1), and Falconidae (falcons and caracaras, ~64 species; cosmopolitan). Falconiform taxa are generally characterized by morphological adaptations to predation, be it active hunting (hooked bills and strong talons) or eating carrion (long necks and unfeathered heads), although extensive specialization exists in the order. Here, the relationships and divergence times of the families of Falconiformes are reviewed.

Among the traditional avian orders, the controversy currently surrounding the status of Falconiformes as a natural (monophyletic) group is eclipsed only by that of Pelecaniformes (tropicbirds, boobies and gannets, cormorants and shags, anhingas, pelicans, and frigatebirds) and Caprimulgiformes (nightbirds). Falconiformes has been variously considered monophyletic, polyphyletic, and paraphyletic (*2*). The basis for this debate involves both the possible inclusion of traditionally nonfalconiform taxa (owls) into Falconiformes, and the possible exclusion of families traditionally thought to belong to the order.

A close affinity between the diurnal (Falconiformes) and predominantly nocturnal (owls; Order Strigiformes) birds of prey was hypothesized as early as Linnaeus (*3*), who placed both (among others) in his Order Accipitres. This scheme was refuted by the influential classifications of Fürbringer (*4*) and Gadow (*5*), who found the two groups to be only distantly related, and most subsequent taxonomic treatments have followed suit (*1*). Cracraft (*6*) provocatively diverged from this practice by proposing a classification scheme where a monophyletic owl clade is nested among falconiform families, rendering Falconiformes paraphyletic. However, this classification has been criticized (*7*), and the few subsequent morphological studies (*8, 9*) recovering this

Fig. 1 A Rough-legged Hawk (*Buteo lagopus*), Family Accipitridae, from Nunavut, Canada. Credit: G. Court.

J. W. Brown and D. P. Mindell. Diurnal birds of prey (Falconiformes). Pp. 436–439 in *The Timetree of Life*, S. B. Hedges and S. Kumar, Eds. (Oxford University Press, 2009).

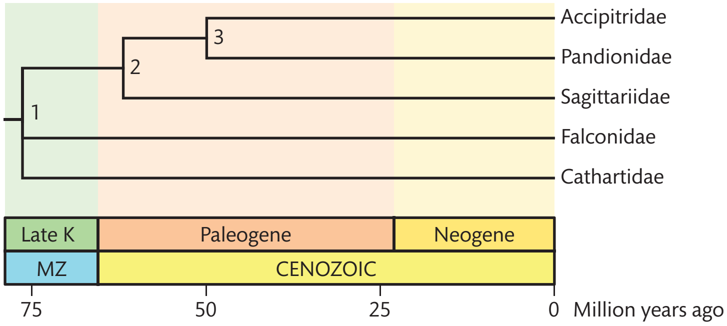


Fig. 2 A timetree of diurnal birds of prey (Falconiformes). Divergence times are from Table 1. *Abbreviations*: MZ (Mesozoic) and K (Cretaceous).

arrangement have had only weak statistical support. The recent comprehensive morphological analysis of Neornithes (*10*) instead strongly supports a close relationship for Falconiformes and Strigiformes, forming the proposed Superorder "Falconimorphae." Published molecular genetic studies with broad taxon and character sampling fail to ally falconiform and strigiform taxa in any arrangement (*2, 11–14*). Regardless of whether or not "Falconimorphae" proves to be a natural grouping, it appears we may safely exclude strigiforms in our discussion of the tempo of falconiform diversification.

Although the monophyly of the traditional Order Falconiformes has been supported (*10, 15*), diverse data sets have suggested it as polyphyletic. Karyological (*16*), morphological (*17*), and mitochondrial (mt) gene order data (*14*) have repeatedly emphasized the marked heterogeneity of Falconiformes relative to that found in other traditional avian orders, and have called to question whether such heterogeneity could arise in a natural group. At the extreme (*17*), Falconiformes has been regarded as an artificial aggregation of four separate (and possibly unrelated) orders: Sagittariiformes, Cathartiformes, Falconiformes, and Accipitriformes (possibly including *Pandion*). However, phenetic *dissimilarities* cannot establish the case for polyphyly, and subsequent authors studying the *affinities* of falconiform and non-falconiform taxa have localized taxonomic uncertainty to individual falconiform families.

Chief among the taxa thought not to belong to Falconiformes is the Family Cathartidae. This family is generally regarded as being the most distinct falconiform lineage, and recent mtDNA data (*14*) show that cathartids have a different and less-derived gene order than other falconiform taxa sampled. Both morphological (*18*) and DNA–DNA hybridization (*2*) data have suggested an alliance between Cathartidae and storks (Family Ciconiidae, Order Ciconiiformes), an arrangement first suggested a century earlier (*19*). Although subsequent research generally supported the separation of Cathartidae from other falconiform taxa, neither morphological (*17*) nor genetic (*20, 21*) studies aimed at discerning cathartid affinities have succeeded in recovering the Cathartidae–Ciconiidae pairing. An early mtDNA study (*22*) repeatedly cited in support of a Cathartidae–Ciconiidae relationship included erroneous sequences (*23, 24*), and has long since been retracted. In morphological studies that recover a monophyletic Falconiformes (*10, 15*), Cathartidae is found to be the basal-most lineage in the clade. Of particular note, there is also no support for a close relationship between New World (Cathartidae) and Old World (Accipitridae) vultures, and thus ecological similarities between them provide a striking example of evolutionary convergence.

Lineages represented by a single living species have often been difficult to classify in ornithology, presumably because long branches (time) and/or extreme ecological specialization confound the identification of homologous character states. Two falconiform families, Pandionidae and Sagittariidae, are in this category and each has experienced some minor taxonomic turbulence. However, no character data have convincingly excluded them from Falconiformes or placed them elsewhere. Some morphological similarities between the secretary bird and seriemas (Family Cariamidae, Order Gruiformes) have been used to suggest a gruiform ancestry for *Sagittarius* (*19*), but this has not been supported in recent analyses. Gadow (*5*) appears to have been the first to recognize the distinctiveness of the piscivorous osprey (*Pandion haliaetus*) from accipitrid taxa by placing the former in a separate Family Pandionidae. Recent classifications variously consider the osprey as either the basal-most "extreme" member of Accipitridae, or the closest relative

Table 1. Divergence times (Ma) and their confidence/credibility intervals (CI) among falconiform birds.

Timetree		Estimates							
Node	Time	Ref. (*2*)	Ref. (*11*)	Ref. (*12*)		Ref. (*29*)		Ref. (*32*)	
		Time	Time	Time	CI	Time	CI	Time	CI
1	76.3	71.1	72.8	81.1	94–67	91.3	113–76	65.1	72–58
2	61.8	46.8	50.4	73.1	87–59	77.0	96–63	–	–
3	49.9	35.1	42	56.8	70–37	65.5	83–52	–	–

Note: Node times in the timetree represent the mean of time estimates. When multiple time estimates were available from the same study, then the mean of reported times and CIs is used as the representative estimate. For the unresolved Node 1, the representative estimates presented are averages of the divergence of Falconidae and Cathartidae from the remaining falconiform families. Results in ref. (*2*) are derived from DNA–DNA hybridization data; divergence times for Nodes 1 and 3 were not published in the original study, but are derived from melting temperatures presented there, as well as the same calibration factor used to estimate the divergence time for Node 2. The estimate from ref. (*32*) is derived from complete mtDNA genome sequences and employing a Bayesian autocorrelated model of rate evolution (only Falconidae and Accipitridae were sampled). The estimate presented from ref. (*11*) is derived from an analysis of five nuclear genes using two different rate-smoothing dating methods: closest-relative smoothing and ancestor-descendant smoothing. Ref. (*29*) reports a reanalysis of the data from ref. (*33*) using the same tree topology, but improved fossil calibrations and a dating method that employs a Bayesian autocorrelated model of rate evolution. Ref. (*3*) constitutes an average estimate from analyses of ~5 kb of mtDNA under eight combinations of different dating methods (*n* = 5: ancestor-descendent rate smoothing, closest-relative rate smoothing, Bayesian autocorrelated model of rate evolution, overdispersed clock, and Bayesian non-autocorrelated model of rate evolution) and tree topologies (*n* = 3).

of that family. Regardless, this difference is semantic, and does not influence evolutionary interpretations.

Curiously, the namesake family of the order, Falconidae, may also not be closely related to any of the remaining falconiform taxa. Nuclear DNA studies support this notion (*11, 13*), but do not give a consistent indication as to where Falconidae lies within the neoavian tree. The inconsistent placement of Falconidae in mtDNA studies has been hypothesized to be a result of insufficient taxon sampling (*25*). However, broad taxonomic sampling (*11, 12*) and strategically sampled mitochondrial genome sequences (*14*) have failed to support a close relationship between Falconidae and other falconiform families. A recent morphological study (*10*) that recovers a monophyletic Falconiformes unites Pandionidae with Falconidae (rather than with Accipitridae); however, this hypothesis is novel and unsupported elsewhere. Notably, given the rules of taxonomic precedence the ordinal name "Falconiformes" must include the Family Falconidae; if falcons are demonstrably shown to be unrelated to the remaining falconiform families, then the grouping of these latter families will be raised to the rank of a novel order.

In summary, at present there is no overwhelming evidence that Falconiformes is monophyletic, but also no convincing evidence for an alternative phylogenetic placement of the five traditional falconiform families. Present knowledge therefore suggests refraining from taxonomic modifications until new data are examined. However it seems prudent at this juncture to focus discussion of divergence times to the "core falconiforms" family set of ((Accipitridae, Pandionidae), Sagittariidae) that is supported as a clade by most studies (*2, 11, 13, 15, 26*), and consider the relationships of Falconidae and Cathartidae to the "core falconiforms" as unresolved (Fig. 2).

Few molecular studies have yet estimated divergence times among all traditional falconiform families (Table 1). Early DNA–DNA hybridization analyses assuming the average rate of change in genome-wide DNA–DNA hybridization analyses was 4.7 million years per degree (centigrade) of DNA–DNA melting temperature lowered (*2*) suggested that the living lineages of the "core falconiforms" originated in the Eocene about 47 Ma, a scenario supported by a strict interpretation of the fossil record (*27*). However, doubts surrounding the validity of the vicariance event dating used in calibrating the DNA–DNA hybridization analyses (*28*), together with the assumption of rate constancy across the entire avian tree, renders this time estimate suspect. Surprisingly, a recent study of five nuclear genes with broad taxonomic sampling (*11*) yielded even younger estimates in some divergence time analyses. However, this study was found to contain several problems surrounding divergence time estimation (*29*). Most important in the context of the present chapter, the inferred age of Pandionidae at 29 Ma using a closest-relative rate smoothing procedure (*11*) significantly postdates the oldest known fossil of that taxon at 37 Ma (*30*), a fossil that was supposedly used as a minimum age constraint in the dating analyses. A reanalysis of these data (*29*) using a Bayesian modeling of rate evolution together with improved fossil constraints yielded much older divergence time estimates, with Cathartidae and Falconidae diverging from the remaining falconiform lineages at about 91 Ma, followed by the divergence of Sagittariidae at 77 Ma and the Accipitridae–Pandionidae split at 65 Ma (Fig. 2).

These nuclear DNA results agree closely to those generated from various dating analyses of ~5 kb of mtDNA for 135 avian taxa (*12*), despite considering very different tree topologies outside of "core falconiforms." In the latter study, different assumptions about how substitution rate variation evolves produced a range of falconiform divergence time estimates, the Accipitridae–Pandionidae split ranging from 69 to 50 Ma, the origin of Sagittariidae ranging from 91 to 61 Ma, and the divergence of Cathartidae and Falconidae ranging from 105 to 61 Ma. A study of complete mtDNA genomes employing a Bayesian modeling of rate evolution yielded a slightly younger (but overlapping) mean estimate of about 65 Ma for the first divergence within the traditional Falconiformes; however, sparse taxon sampling likely contributed to this younger estimate (*31*). The generally close agreement of date estimates across genomes, tree topologies, and dating methods lends credence to the ancient origin of falconiform taxa. However, interpretation of the fossil record in light of these molecular date estimates requires the existence of extensive "ghost lineages" beyond the oldest falconiform fossil, belonging to a living lineage, at ~37 Ma (*30*).

Acknowledgments

J.W.B. thanks R. Pollard for assistance. Support was provided by the University of Michigan to J.W.B. and US National Science Foundation to D.P.M.

References

1. A. Wetmore, *Smithson. Misc. Coll.* **139**, 1 (1960).
2. C. G. Sibley, J. E. Ahlquist, *Phylogeny and Classification of Birds* (Yale University Press, London, 1990).
3. C. Linnaeus, *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species cum Characteribus Differentiis, Synonymis, Locis*, 10th ed. (Laurentii Salvii, Holmiae, 1758).
4. M. Fürbringer, *Untersuchungen zur Morphologie und Systematik der Vögel* (von Holkema, Amsterdam, 1888).
5. H. Gadow, in *Klassen und Ordnungen des Thier-Reichs*, H. G. Bronn, Ed. (C. F. Winter, Leipzig, 1893), pp. 259–270.
6. J. Cracraft, *Auk* **98**, 681 (1981).
7. S. L. Olson, *Auk* **99**, 733 (1982).
8. G. Mayr, J. Clarke, *Cladistics* **19**, 527 (2003).
9. M. C. McKitrick, *Misc. Publ., Mus. Zool., Univ. Mich.* **179**, 1 (1991).
10. B. C. Livezey, R. L. Zusi, *Zool. J. Linn. Soc.* **149**, 1 (2007).
11. P. G. P. Ericson *et al.*, *Biol. Lett.* **4**, 543 (2006).
12. J. W. Brown, J. S. Rest, J. García-Moreno, M. D. Sorenson, D. P. Mindell, *BMC Biol.* **6** (2008).
13. M. G. Fain, P. Houde, *Evolution* **58**, 2558 (2004).
14. G. C. Gibb, O. Kardailsky, R. T. Kimball, E. L. Braun, D. Penny, *Mol. Biol. Evol.* **24**, 269 (2007).
15. C. S. Griffiths, *Auk* **111**, 787 (1994).
16. L. E. M. de Boer, *Genetica* **46**, 77 (1976).
17. M. T. Jollie, *Evol. Theory* **1**, 285; **2**, 115; **3**, 1 (1976–1977).
18. J. D. Ligon, *Occasional Papers/University of Michigan, Museum of Zoology* **651**, 1 (1967).
19. A. H. Garrod, *Proc. Zool. Soc. Lond.* **1874**, 339 (1874).
20. M. Wink, *Zeitschrift der Naturforschenden* **50**, 868 (1995).
21. I. Seibold, A. J. Helbig, *Phil. Trans. Roy. Soc. Lond. B Biol. Sci.* **350**, 163 (1995).
22. J. C. Avise, W. S. Nelson, C. G. Sibley, *Proc. Natl. Acad. Sci. U.S.A.* **91**, 5173 (1994).
23. S. J. Hackett, C. S. Griffiths, G. P. Bates, N. L. Klein, *Mol. Phylogenet. Evol.* **4**, 350 (1995).
24. A. J. Helbig, I. Seibold, *Mol. Phylogenet. Evol.* **6**, 315 (1996).
25. K. E. Slack, A. Janke, D. Penny, U. Arnason, *Gene* **302**, 43 (2003).
26. H. R. L. Lerner, D. P. Mindell, *Mol. Phylogenet. Evol.* **37**, 327 (2005).
27. A. Feduccia, *Trends Ecol. Evol.* **18**, 172 (2003).
28. M. van Tuinen, C. G. Sibley, S. B. Hedges, *Mol. Biol. Evol.* **15**, 370 (1998).
29. J. W. Brown, R. B. Payne, D. P. Mindell, *Biol. Lett.* **3**, 257 (2007).
30. C. J. O. Harrison, C. A. Walker, *Zool. J. Linn. Soc.* **59**, 323 (1976).
31. H. P. Linder, C. R. Hardy, F. Rutschmann, *Mol. Phylogenet. Evol.* **35**, 569 (2005).
32. K. E. Slack *et al.*, *Mol. Biol. Evol.* **23**, 1144 (2006).
33. P. G. P. Ericson *et al.*, *Biol. Lett.* **4**, 543 (2006)