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Rapid diversification of falcons (Aves: Falconidae) due to expansion of open habitats in the Late Miocene

Jérôme Fuchs [a,b,c,*], Jeff A. Johnson [d], David P. Mindell [e,f]

[a] Department of Ornithology and Mammalogy, California Academy of Sciences, 55 Music Concourse Drive, San Francisco, CA 94118, United States
[b] UMR7205, Institut de Systématique, Evolution, Biodiversité, CNRS MNHN UPMC EPHE, Département Systématique et Evolution, Muséum National d'Histoire Naturelle, 57 Rue cuvier, Case Postale 51, F-75231 Paris Cedex 05, France
[c] UMS MNHN/CNRS 2700, Outils et Méthodes de la Systématique Intégrative (OMSI), Muséum National d'Histoire Naturelle, 57 rue Cuvier, F-75231 Paris Cedex 05, France
[d] Department of Biological Sciences, Institute of Applied Sciences, University of North Texas, 1155 Union Circle #310559, Denton, TX 76203, United States
[e] Department of Biochemistry & Biophysics, University of California San Francisco, San Francisco, CA 94158, United States
[f] Division of Environmental Biology, National Science Foundation, 4201 Wilson Blvd., Arlington, VA 22230, United States

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ABSTRACT

Understanding how and why lineages diversify is central to understanding the origins of biological diversity. The avian family Falconidae (caracaras, forest-falcons, falcons) has an uneven distribution of species among multiple well-supported clades, and provides a useful system for testing hypotheses about diversification rate and correlation with environmental changes. We analyzed eight independent loci for 1–7 individuals from each of the 64 currently recognized Falconidae species, together with two fossil falconid temporal calibrations, to assess phylogeny, absolute divergence times and potential shifts in diversification rate. Our analyses supported similar diversification ages in the Early to Middle Miocene for the three traditional subfamilies, Herpetotherinae, Polyborinae and Falconinae. We estimated that divergences within the subfamily Falconinae began about 16 mya and divergences within the most species-rich genus, *Falco*, including about 60% of all Falconidae species, began about 7.5 mya. We found evidence for a significant increase in diversification rate at the basal phylogenetic node for the genus *Falco*, and the timing for this rate shift correlates generally with expansion of C4 grasslands beginning around the Miocene/Pliocene transition. Concomitantly, *Falco* lineages that are distributed primarily in grassland or savannah habitats, as opposed to woodlands, and exhibit migratory, as opposed to sedentary, behavior experienced a higher diversification rate.

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> "*The Late Miocene or early Pliocene would seem to have been about the right time, just when things were starting to go well for another group of open-country inhabitants, the early hominids. It is musing and somehow prophetic to think that falcons and men both derive from the same evolutionary stimulus – the creation of open grasslands and savannahs with new and unexploited opportunities for both winged and bipedal hunters... Thus it appears that the association between men and falcons is deep rooted indeed. What did "Lucy" and her kin* (Australopithecus afarensis) *experience when they looked up into the azure sky over the Afar Plains and saw hunting falcons?*"
>
> [p. 15, *The Falcons of the World*, Cade and Digby, 1982]

1. Introduction

Understanding when, how and why lineages diversify over time is a central question in evolutionary biology (Eldredge and Gould, 1972; Nee, 2006). Analyses of many higher level clades show that diversification rates vary through time, often showing a burst of speciation events followed by a slowdown in diversification (e.g., Lovette and Bermingham, 1999; Weir and Schluter, 2004; McPeek, 2008; Rabosky and Lovette, 2008b; Phillimore and Price, 2008; Rabosky, 2009; Hardy and Cook, 2012 but see Cusimano and Renner, 2010). Both intrinsic traits (e.g., adaptation to a new diet or habitat) and extrinsic events (e.g., climatic or tectonic changes) may explain variation in diversification rates through time. Consequently, the early speciation burst may be considered adaptive (Schluter, 2000; Gravilets and Vose, 2005), through a key innovation or colonization of a new area, or non-adaptive per se if the diversification is best explained by vicariance only.

* Corresponding author at: UMR7205, Institut de Systématique, Evolution, Biodiversité, CNRS MNHN UPMC EPHE, Département Systématique et Evolution, Muséum National d'Histoire Naturelle, 57 Rue cuvier, Case Postale 51, F-75231 Paris Cedex 05, France.
E-mail address: fuchs@mnhn.fr (J. Fuchs).

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The subsequent slowdown in diversification rate is then often explained as resulting from a perceived reduction in opportunity for speciation due to a density dependent niche-filling process (Schluter, 2000; Gravilets and Vose, 2005 but see Moen and Morlon, 2014).

Two recent studies on birds challenged the pattern of slowdown in diversification rates after an initial burst of diversification. Derryberry et al. (2011) found that the species rich Neotropical radiation of ovenbird-woodcreeper (Furnariidae) sustained high and nearly constant speciation rates despite having started to diversify more than 30 million years ago (mya). Jetz et al. (2012) suggested a hypothesis for birds in which diversification rates have increased steadily over the last 50 million years within a variety of temperate zone birds, including various songbirds, waterfowl, gulls and woodpeckers. Jetz et al. (2012) suggested that the observed heterogeneity in diversification rate was best explained as hemispheric rather than latitudinal, as traditionally thought, with radiations in Asia, North America and southern South America largely driven by changes in habitat, including mountain uplift and landscape dynamics related to glacial cycles.

Analyses identifying the timing and primary drivers of diversification within particular clades can help evaluate these ideas, and delineate factors important for the process of speciation. New analytical methods have been developed for identifying particular nodes on a phylogeny where shifts in diversification rate have occurred (Chan and Moore, 2005; Rabosky et al., 2007; Moore and Donoghue, 2009; Alfaro et al., 2009) and for testing alternative models of diversification rate change (Rabosky, 2006a,b; Rabosky and Lovette, 2008a).

The Falconidae is a broadly distributed family of avian predators that began to diversify during the late Oligocene–early Miocene (Fuchs et al., 2011a, 2012). Sixty-four species, divided into eleven genera, are currently recognized (Dickinson, 2003). Species range in size from sparrow-sized *Microhierax* falconets to the large hawk-sized members of the genus *Falco* (falcons). Habitat preferences vary from forests to arid savannah and steppes, and diet breadth ranges from the specialized *Ibycter* and *Herpetotheres* species feeding on Hymenoptera and snakes, respectively, to the more generalist *Phalcoboenus*. Three subfamilies (Herpetotherinae, Polyborinae and Falconinae) are widely recognized and their relationships and generic limits are well established (Griffiths, 1999; Griffiths et al., 2004; Fuchs et al., 2011a,b, 2012; Noriega et al., 2011). The former two subfamilies are endemic to the New World, whereas the Falconinae is more widespread with a large proportion of species in the Old World. The species level relationships within the Herpetotherinae (eight species) and Polyborinae (eleven species) have been recently addressed (Fuchs et al., 2011a, 2012), but the relationships within Falconinae, the most species-rich subfamily (46 species), remain to be resolved.

The Falconinae includes three genera. Two are restricted to the Old World, *Polihierax* (two species, Ethiopian and Oriental regions) and *Microhierax* (five species, Oriental), whereas the genus *Falco* (39 species) is cosmopolitan. Generic limits within the Falconinae are generally well understood, and debates focus more on species level relationships and sub-generic limits within the species-rich genus *Falco* (e.g., Cade and Digby, 1982; Wolters, 1975–1982) and whether the Oriental species of *Polihierax* (*P. insignis*) merits its own genus (*Neohierax*; Wolters, 1975–1982). The genus *Falco* is often divided in few well defined super-species or closely related species (e.g., Kestrels, Old World Hobbies; *Hierofalco* Wolters, 1975–1982). Within *Falco*, kestrels (17 species) are often considered as the ancestral lineage (Cade and Digby, 1982); kestrels have their center of diversity in the Afrotropics and the Indian Ocean islands (seven species) with additional species in the Palearctic (two species), Oriental (one species), Australasia (one species) and the New World (one species). Five atypical kestrels ('gray kestrels', 5 species: *F. ardosiaceus*, *F. dickinsoni*, *F. zoniventris*, *F. amurensis*, *F. vespertinus*) occur in the Ethiopian and Palearctic bioregions. Cade and Digby (1982) identified several species for which relationship within the genus were unclear due to atypical morphology (e.g., brown falcon *F. berigora* and merlin *F. columbarius*). Recent work has suggested that most of traditionally delimited superspecies or species groups are monophyletic (e.g., 'typical kestrels', Groombridge et al., 2002; members of the *Hierofalco* clade: *F. biarmicus–F. cherrug–F. jugger–F. rusticolus*, and *F. subniger*, Nittinger et al., 2005) but no phylogeny that includes all currently recognized species is available.

Due to the highly uneven distribution of species diversity among sister subfamilies (e.g., Polyborinae 11 species, Falconinae 46 species), the Falconidae provides an ideal group to test the potential correlation between change in diversification rates for sister clades and putative adaptations to new habitats and/or diets (key innovations). Here, using a new phylogeny reconstructed with DNA sequence data from eight nuclear and mitochondrial loci and over 140 individuals including all Falconidae species, we assess the biogeographic history of Falconidae, reconstruct the evolution of habitat, diet and migration traits, and assess correlation between these three eco-ethological traits and diversification rates. We also propose several changes for the classification of the Falconidae.

2. Material and methods

2.1. Sampling

We sampled 1–7 individuals for all currently recognized species of Falconidae ($n = 64$, Dickinson, 2003; Supplementary Table 1). We sought to sample the broad geographic distribution for polymorphic species (e.g., *Falco peregrinus*, *F. columbarius*) to better explore potential divergences within species. Sequences from representatives of several avian orders (Accipitriformes, Passeriformes, Piciformes, Strigiformes) were used as outgroups (Supplementary Table 1).

We analyzed DNA sequences from eight loci: a continuous mitochondrial fragment of about 2.4 kb (encompassing the $tRNA_{Leu}$, ND1, $trNA_{Ile}$, $tRNA_{Gln}$, $tRNA_{Met}$ and ND2 region) and seven autosomal loci (Myoglobin intron-2 – MB, β-Fibrinogen intron-5 – FGB, Transforming Growth Factor beta2 intron-5 – TGFb2, Phosphoenol Pyruvate CarboxyKinase intron-9 – PEPCK, Vimentin intron-8 – VIM, Period Homolog 2 intron-9 – PER, and Recombination Activating Gene 1 – RAG1).

DNA was extracted from fresh tissues (muscles, liver, kidney, blood, feathers) using the Qiagen DNeasy extraction kit (Valencia, CA) following manufacturer's protocols. For 13 species, we extracted DNA from museum toe-pad samples (historic) in a dedicated ancient DNA lab and used a phenol–chloroform extraction protocol and 20 µl of dithiothreitol (DTT, 0.1 M) per sample.

The primer sequences used for PCR-amplification and sequencing are detailed in Supplementary Tables 2 (fresh samples) and 3 (historic samples). For fresh samples, we amplified the mitochondrial region in one fragment using the primers L3827 and H613 using the TaKaRa LA Taq (TaKaRa Co. Ltd., Tokyo, Japan). The thermocycling conditions for the mitochondrial fragment included a hotstart at 94 °C, an initial denaturation at 94 °C for 3 min, followed by 40 cycles at 94 °C for 40 s, 56 °C for 40 s, and 72 °C for 3 min, and was completed by a final extension at 72 °C for 15 min. The thermocycling conditions for the nuclear loci included a hotstart at 94 °C, an initial denaturation at 94 °C for 3 min, followed by 35–40 cycles at 94 °C for 40 s, 55–60 °C for 30–45 s, and 72 °C for 30–45 s, and a final extension at 72 °C for 10 min.

Nuclear introns were amplified using the Recombinant Invitrogen Taq (Invitrogen Co., Carlsbad, CA).

For toe pads, sequencing was performed in a stepwise fashion obtaining overlapping sequences using primers designed in succession after each set of sequences were obtained and analyzed. For some species where only toe pad samples were available, we could only amplify four loci (mtDNA, MB, FGB and TGFb2). Primers for the mtDNA fragments were designed specifically for particular species or species group. For *F. jugger*, previously shown to be part of the *Hierofalco* clade (Nittinger et al., 2007) and where we detected the presence of pseudogenes (see Section 3), we designed primers that were specific to mtDNA fragments by targeting the conserved 3′ base of the primer to avoid a amplification of the putative pseudogene.

Purified PCR products were cycle-sequenced in both directions using Big Dye terminator chemistry (ABI, Applied Biosystems) with the same primers used for PCR amplification, and run on an ABI 3100 DNA sequencer. We used an additional set of primers to sequence the mitochondrial fragment (see Supplementary Material Table 3). Heterozygous sites in the nuclear loci (double peaks) were coded using the appropriate IUPAC code. Apparent length polymorphisms were cloned using the TOPO TA cloning kit with pCR2.1 vector and Mach1 cells (Invitrogen Co., Carlsbad, CA) or resolved by eye. In the latter case, we compared the ambiguous 5′-end with the unambiguous 3′-end of the forward and reverse sequences to resolve the placement and composition of gaps and the linkage of polymorphisms to those gaps (Peters et al., 2007). When cloning was required, between four and ten colonies were sequenced per individual.

Alignment was performed by eye for all loci using Sequencher 4.2 (Gene Codes Corporation, Ann Arbor, MI, USA). Sequences newly generated for this study have been deposited in Genbank (www.ncbi.nlm.nih.gov; accession numbers KM875731–KM876667). The alignments were straightforward, owing to the low number of insertion–deletions events and the conserved flanking sequences of each indel. All alignments are available from the first author upon request.

2.2. Phasing

We used the program Phase v2.1.1 (Stephens et al., 2001; Stephens and Donnelly, 2003) to infer the allelic phase for each nuclear locus. Several runs, using different seed values were performed. We used the recombination model (*-MR option*) and ran the iterations of the final run 10 times longer than the other runs (*-X10 option*). We considered the estimate from Phase v2.1.1 as the best estimate for phase probability.

2.3. Phylogenetic analyses: individual gene trees

Separate phylogenetic analyses for each locus were conducted using maximum likelihood (RAxML v7.0.4; Stamatakis, 2006; Stamatakis et al., 2008) and Bayesian inference (MrBayes 3.1.2; Ronquist and Huelsenbeck, 2003; Huelsenbeck and Ronquist, 2003). We only retained unique alleles/haplotypes for the single locus phylogenetic analyses. The models of nucleotide substitution for each locus were determined with TOPALi v2.5 (Milne et al., 2009) and the Bayesian Information Criteron (BIC). For the mitochondrial data set and RAG-1, we also evaluated the support of different *a priori* partitioning strategies (e.g., by gene and/or by codon position) using the Bayes Factors (B_F; Nylander et al., 2004). A value greater than 4.6 for $\ln B_F$ was considered as strong evidence against the simpler model (Jeffreys, 1961); this value is similar to the threshold proposed by Kass and Raftery (1995) for strong support for the more complex model ($2 \ln B_F = 10$). All Bayes Factor calculations were performed in Tracer v1.5 (Rambaut and Drummond, 2007). The list of selected substitution models are indicated in Supplementary Table 4.

For MrBayes 3.1.2, we used default priors for the base frequency and substitution models. We ran several sets of analyses by changing the branch length priors, from *unconstrained: exp (10)* (default value) to *unconstrained: exp (50)*, *unconstrained: exp (100)* and *unconstrained: exp (150)* and the temperature from 0.2 to 0.1. We then compared the likelihood of each analysis with different branch length priors using the Bayes Factor. In every MrBayes analyses, four Metropolis-coupled Markov Chains Monte Carlo, one cold and three heated, were run for ten to fifty million iterations with trees sampled every 1000 iterations. Four independent Bayesian runs initiated from random starting trees were performed for every set of analyses, and the log-likelihood values and posterior probabilities were checked to ascertain that the chains had reached the posterior distribution. We ensured that the potential scale reduction factor (PSRF) approached 1.0 for all parameters and that the average standard deviation of split frequencies converged toward zero. We used Tracer v1.5 (Rambaut and Drummond, 2007) to ensure that our sampling of the posterior distribution had reached a sufficient effective sample size (ESS > 200) for meaningful parameter estimation.

2.4. Phylogenetic analyses: partitioned

Analyses of the concatenated data sets (eight loci) were performed using the phased nuclear data. Hence, for each nuclear locus and individual bird, we randomly selected one of the two possible phased alleles. For species where more than one individual was available, we excluded the individuals for which fewer than six loci could be sequenced. The exceptions involved toe pad samples for which we included representatives for every species even if fewer than six loci were available. Consequently, one species was represented by mitochondrial data only (*F. jugger*), and a few other species had only three nuclear loci (e.g., *N. insignis*, *F. moluccensis*). This heterogeneous matrix due to the use of toe-pads as a source of DNA prevented us from using species tree algorithms. Based on the length of the concatenated data set, the amount of missing data (including gaps) ranged from 4% (*F. sparverius*, *H. cachinnans*, *M. chimachima*) to 69% (*F. jugger*), with an average of 13%.

Concatenated maximum likelihood and Bayesian analyses were performed allowing the different parameters of the substitution model to vary among loci (i.e., partitioned analyses – see results, Nylander et al., 2004). The loci we analyzed have very different optimal branch length priors, based on Bayes Factor comparisons. Thus, for the Bayesian analyses, we used different branch length priors and compared topologies, support values and convergence values.

2.5. Divergence time estimates

We used Beast 1.6.2 (Drummond et al., 2006; Drummond and Rambaut, 2007) to estimate lineage divergence times within Falconidae. Because sampling was comprehensive, we used a Yule speciation process as a tree prior. Similar to previous studies (Fuchs et al., 2011a, 2012), the divergence between Falconinae and Polyborinae was used as a calibration point, estimated to have occurred at least 16.3 myrs ago. This estimate is based on the South American fossil *Pediohierax ramenta* (Wetmore, 1936) which has been suggested to be the earliest Falconinae (Becker, 1987; Late Burdigalian; Gradstein et al., 2004) We used a lognormal distribution (offset 16.3, lognormal mean: 0.8, lognormal standard deviation: 0.61); the 95% credibility interval of the prior distribution was 17–23.7 myrs ago corresponding to the beginning of the Miocene. We also compared the divergence time estimates obtained using *Pedohierax* with divergence times using the

re-assigned fossil *Thegornis musculosus* (Noriega et al., 2011). The South American fossil *Thegornis* was initially assigned to the Falconidae, based on a distal tarsometatarsi, before being moved to the Accipitridae, either close to *Circus* harriers or *Buteo* hawks (reviewed in Noriega et al. (2011)). A cladistic analysis based on a newly discovered complete specimen suggested that *Thegornis* is in fact sister to the genus *Herpetotheres* (Noriega et al., 2011). For this reason, we used *Thegornis* here as the earliest possible split between the genera *Herpetotheres* and *Micrastur*. We used a lognormal distribution (offset 16.3, lognormal mean: 0.8, lognormal standard deviation: 0.61); the 95% credibility interval of the prior distribution was 17–23.7 myrs ago corresponding to the beginning of the Miocene epoch. For each of the eight loci, we compared the likelihood values of a model assuming a strict molecular clock and a model assuming an uncorrelated lognormal clock model using a Bayes Factor. Tracer v1.5 was used to visualize the posterior distributions for every parameter. For the partitioned analyses we assigned each locus its own specific substitution model and uncorrelated lognormal clock model, and used uniform priors for the rate matrix (0, 5) and for the gamma parameter (0, 50). MCMC chains were run for 10^8 steps and were sampled every 10,000 steps.

2.6. Biogeography

We used the Bayesian Binary MCMC (BBM) and the Dispersal-Extinction-Cladogenesis (DEC, Ree et al., 2005; Ree and Smith, 2008) algorithms, as implemented in Rasp 2.1b (Yu et al., 2010, 2012; http://mnh.scu.edu.cn/soft/blog/RASP), to reconstruct the biogeographic history of the Falconidae. Based on White et al. (1994), we coded the ranges using seven biogeographic units: Australasia, Ethiopian, Oriental, Palearctic, Neotropics, Nearctic and Madagascar. Definitions and limits of the biogeographic units followed Newton (2003) with three modifications, Oceania and Antarctica are not included in the analyses (as Falconidae are absent from those units) and Madagascar (including the Seychelles and Mauritius) is considered distinct from the Ethiopian region.

We performed two sets of analyses, one only considering the breeding ranges and the second also considering the wintering ranges for migratory species. We set the maximum number of ancestral areas to seven, which corresponds to the largest number of areas occupied by a Falconidae species (*F. peregrinus*). We used 1000 trees sampled from the posterior distribution from the Beast analyses of the eight loci data set with the combination of the two calibration points (*Pedohierax* and *Thegornis*) to account for phylogenetic uncertainty and used the Maximum Clade Credibility tree as a template to map the results.

For the BBM analyses, we selected the F81 model, to allow different rates of change among ancestral areas model, and ran 10 chains for 100,000 generations with reconstructions being saved every 100 generations.

For the DEC analyses, we considered the dispersal rates across regions to be equal and set the possible ancestral ranges to adjacent areas.

2.7. Diversification rates analyses

Evolution of diversification rates through time was analyzed using the Ape (Paradis et al., 2004), Geiger (Harmon et al., 2008), and Laser v2.2 (Rabosky, 2006a,b) packages, as implemented in R2.15 (http://www.r-project.org/). Because we sampled several individuals per species when possible, we pruned conspecific individuals from the diversification rate analyses. The number of species retained for the diversification rates analyses was 66, including the 64 species currently recognized (Dickinson, 2003) plus two taxa that may warrant species status (*F. aesalon*/*F. columbarius*, *F. rupicolus*/*F. tinnunculus*) based on the results from this study (see Section 3). We estimated the empirical gamma (γ) statistic (Pybus and Harvey, 2000) on the Maximum Clade Credibility (MCC) tree and a 10,000 trees subset of the posterior distribution obtained from the Beast analyses using the *GamStat* command.

We tested for temporal variation in diversification rates using the ΔAICrc statistic as implemented in Laser v2.2 (Rabosky, 2006a,b). This ΔAICrc represents the difference in AIC scores between the best rate-constant and rate-variable models. Because selecting the model with the lowest AIC criterion results in a high Type I error rate (Rabosky, 2006a), we generated 10,000 phylogenies under the Purebirth model using the *YuleSim* function. For the latter simulations, we used the empirical speciation rate for each data set. We then compared the percentage of ΔAICrc values that were greater than our observed value. If less than 5% of the simulated ΔAICrc values were greater than our observed value, we considered the hypothesis of constancy in diversification rates to be rejectable (when the variable rate model was selected first). We also calculated the AIC of a model with (i) a linear time-varying speciation rate and constant extinction through time (*SPVAR*), (ii) a model assuming constant speciation rates but time varying extinction rates (*EXVAR*), and (iii) a model with both time-varying speciation and extinction rates (*BOTHVAR*). We compared AIC values from the three later models to the AIC of the best fit model estimated for each data set (ΔAIC*ts* statistic, Rabosky and Lovette, 2008a,b). For each data set, we ran fifteen analyses using the *SPVAR*, *EXVAR* and *BOTHVAR* functions with different starting parameter values, and checked the likelihood scores to determine their convergence.

We used Turbo-Medusa v0.1 (https://github.com/josephwb/turboMEDUSA), a recently updated version of Medusa (Alfaro et al., 2009) to identify nodes in the tree where a rate shift could have occurred. We performed the analyses on the MCC tree and allowed eight possible rate shifts in the birth–death model parameters throughout the Falconidae tree. We selected the best model concerning the number of rate shifts based on a corrected threshold which consisted of a decrease in information theoretic score of −3.681292 units (AICc).

2.8. Reconstructing ancestral states for migration behavior, habitat and diet

For three variables (migration behavior, habitat, and diet), we reconstructed the ancestral states for each node on 1000 trees sampled from the posterior distribution obtained from the Beast analyses using the Maximum Likelihood approach and the Brownian motion model of character change implemented in BayesTraits (Pagel et al., 2004). Migration was scored as present or absent; a species was considered to be migratory if seasonal movements to another biome are involved. Two discrete characters were coded for habitat (forest/woodland and grassland/tundra) and four discrete characters for diet (arthropods, birds, mammals and amphibian/reptiles). Character coding was based on White et al. (1994). For diet and habitat, multistate coding was performed (e.g., for omnivorous species). We tested for possible correlation between the evolution of diet and habitat characters using a likelihood ratio test (Pagel and Meade, 2006), with the degree of freedom set to four and a significance threshold of 0.05. To perform the correlation test, we reduced the number of character states for diet to two (invertebrates versus vertebrates).

2.9. Relationships between diet, habitat, migratory behavior and diversification rates

We tested for character-state associated diversification using the BiSSE approach (Maddison et al., 2007) implemented in Mesquite (Maddison and Maddison, 2007). To perform the BiSSE

analyses, we reduced the number of character states for diet to two (invertebrates versus vertebrates). A multistate extension of BiSSE has recently been developed (MuSSE, FitzJohn, 2012) but it is not currently possible to code multiple states for one taxon. For example, the diet of the European Hobby could not be coded as consisting of vertebrates and insects; the other options were either to create a third state ('generalist') or code diet for multistate species as unknown but we considered the latter two options unsatisfactory.

We used the MCC trees from the three possible combinations of calibration derived from the eight loci analyses using multiple individuals as a template for the maximum likelihood calculation. We optimized the parameters on eight different models and we selected the best fit model using the Akaike Information Criterion. To assess the robustness of our conclusions, we simulated 1000 trees under the birth–death model, using the parameter values obtained from the most constrained model (three parameters with equal speciation rates, extinction rates and transition rates). We then calculated the null distribution for likelihood differences between the tested and the most constrained models. If 5% of the values were higher than the empirical value derived from the MCC tree, we considered the most constrained models as not rejected.

3. Results

3.1. Phylogenetic analyses

3.1.1. mtDNA gene tree

For the mtDNA analyses, we only included Falconidae individuals for which the complete fragment ($tRNA_{Leu}$ to ND2) was available ($n = 167$). This included representatives for all species recognized in this study. The sequence length varied from 2328 bp (*Herpetotheres cachinnans*) to 2354 bp (*Ibycter americanus*). We excluded intergenic sequences and stop codons for the phylogenetic analyses and only unique haplotypes were retained ($n = 130$, including the three putative pseudogenes detected in *F. biarmicus*, *F. cherrug* and *F. rusticolus*, all part of the Hierofalco clade). Two species pairs shared haplotypes (e.g., *P. albogularis*/*P. megalopterus* and *F. peregrinus*/*F. pelegrinoides*).

An exponential branch-length prior with a mean of 50 was the best fit after Bayes Factor comparisons ($B_{F\ 50\ over\ 100} = 54.075$; $B_{F\ 50\ over\ 10} = 0.689$). A partitioning scheme with independent substitution models for each codon position for each of the two protein coding genes and the tRNAs (seven partitions) was strongly favored over schemes with four partitions (codon positions of the two coding loci and tRNAs; $B_F = 1312.2$), three partitions (ND1, ND2 and tRNAs; $B_F = 1011.6$), two partitions (protein-coding and tRNA; $B_F = 1030.8$) and one partition ($B_F = 1095.8$).

Several rare genetic changes support the mtDNA topology (Fig. 1). For example, the Falconinae/Polyborinae clade is supported by the change of an AGG/AGA stop-codon system in ND1 for the outgroups and Herpetotherinae to a TAA stop-codon in other Falconidae species. The clade comprising all *Falco* species but excluding the Old World kestrels is supported by a unique single nucleotide insertion in the $tRNA_{Met}$. In one case, a homoplasious one base pair deletion, shared between the Accipitridae, Picidae and Strigidae outgroups and the *F. dickinsoni*/*F. ardosiaceus* clade was observed in the $tRNA_{Ile}$; all other Falconidae as well as the representative of the Passeriformes did not have this deletion.

The three subfamilies were monophyletic with maximum support values (ML: 100, BI: 1.0) and the Polyborinae were sister to the Falconinae (ML: 100, BI: 1.0). Relationships among members of the Herpetotherinae and Polyborinae are identical to those reported elsewhere (Fuchs et al., 2011a,b, 2012). Within the Falconinae, the Oriental genus *Microhierax* was monophyletic (ML: 100, BI: 1.0) and sister to the Ethiopian species *Polihierax semitorquatus* (ML: 100, BI: 1.0). In contrast to traditional hypotheses, the white-rumped pygmy-falcon (*Polihierax insignis*) was sister (ML: 100, BI: 1.0) to a monophyletic genus *Falco* (ML: 100, BI: 1.0) and not directly related to the African pygmy-falcon (*Polihierax semitorquatus*). The relationships among the *Falco* species received only moderate support in most cases but a few clades received strong support. Those include (1) the typical Old World kestrels (ML: 100, BI: 1.0) and the latter clade plus *F. zoniventris* (ML: 96, BI: 1.0), (2) a clade consisting of the Old World hobby falcons (*F. concolor*, *F. cuvieri*, *F. eleonorae*, *F. longipennis*, *F. severus*, *F. subbuteo*) and the New World species pair *F. rufigularis*/*F. deiroleucus* (ML: 100, BI: 1.0; hereafter referred as the 'hobby clade'), (3) a clade with *F. chicquera. F. mexicanus*, *F. hypoleucos*, peregrine-like falcons (*F. pelegrinoides*, *F. peregrinus*, *F. fasciinucha*) and the Hierofalcons *sensu stricto* (*F. biarmicus*, *F. cherrug*, *F. jugger*, *F. rusticolus*, *F. subniger*) (ML: 100, BI: 1.0). The aplomado falcon (*Falco femoralis*), primarily distributed in Central and South America, was the sister group to the New Zealand falcon (*Falco novaezeelandiae*) (ML: 96, BI: 1.0).

Low genetic divergences among a number of species within *Falco* were observed (e.g., 0.2% between *F. moluccensis* and *F. tinnunculus*, 0.5% between *F. araea* and *F. newtoni*). In some cases, one species was nested within another, with low maximum divergence among haplotypes (*F. cuvieri* within *F. subbuteo*, divergence among haplotypes 0.5%; and *F. fasciinucha* within *F. peregrinus* divergence among haplotypes 0.4%). In other cases, species possessed very low divergence, and appeared polyphyletic (0.09% between *F. cherrug* and *F. rusticolus*). In contrast, relatively high divergence was shown between *Falco columbarius* individuals from different sides of the Atlantic Ocean. The differentiation between the Old World and New World *F. columbarius* samples was substantial (2.2%), about four times more than what was found in some closely related but undisputed falcon species (*F. newtoni*/*F. araea*: 0.5%, *F. cherrug*/*F. subniger* 0.3%; *F. cuvieri*/*F. subbuteo*: 0.3–0.6%).

3.1.2. Individual nuclear gene trees

For most historic samples using toe-pad tissues, we were able to amplify and obtain sequences from three introns (MB, FGB, TGFb2) but not the remaining four loci (PEPCK, PER, VIM, RAG1).

Analyses of the phased nuclear alleles for each locus indicate that alleles were often shared among closely related species, especially in the genus *Falco*. For example, *Falco biarmicus*, *F. fasciinucha*, and *F. peregrinus* share one PEPCK allele, *Phalcoboenus carunculatus*, P. *megalopterus* and *P. albogularis* share a MB allele, and *Falco rufigularis*, *F. subbuteo* and *F. eleonorae* shared a RAG1 allele. One exception involved the sharing of a TGFb2 haplotype between distantly related species, *F. cenchroides* and *F. vespertinus*. The number of alleles per locus that were shared among species varied from 6 (PER) to 15 (MB) with an average of 10.6 shared alleles, which corresponds to about 9% of the total number of alleles for each locus.

The gene trees obtained from the nuclear loci were unevenly resolved but support for the primary clades (Herpetotherinae, Polyborinae–Falconinae, Polyborinae, Falconinae, *Polihierax semitorquatus-Microhierax*, *Microhierax*, *Polihierax insignis-Falco*, *Falco*) were found in all nuclear gene trees, usually with bootstrap values or posterior probabilities greater than 95 and 0.95, respectively. The few exceptions involved the support for the monophyly of the *P. semitorquatus-Microhierax* clade, which was paraphyletic in the PEPCK gene tree, as *Microhierax* was more closely related to *Falco* (ML: 72 BI: 0.85). The Oriental *P. insignis* was the sister-group of the genus *Falco* in all gene trees where sequences could be obtained (FGB: ML: 93 BI: 1.0; MB: ML: 76 BI: 0.82, TGFb2: ML: 100 BI: 0.99). Relationships among *Falco* species always involved

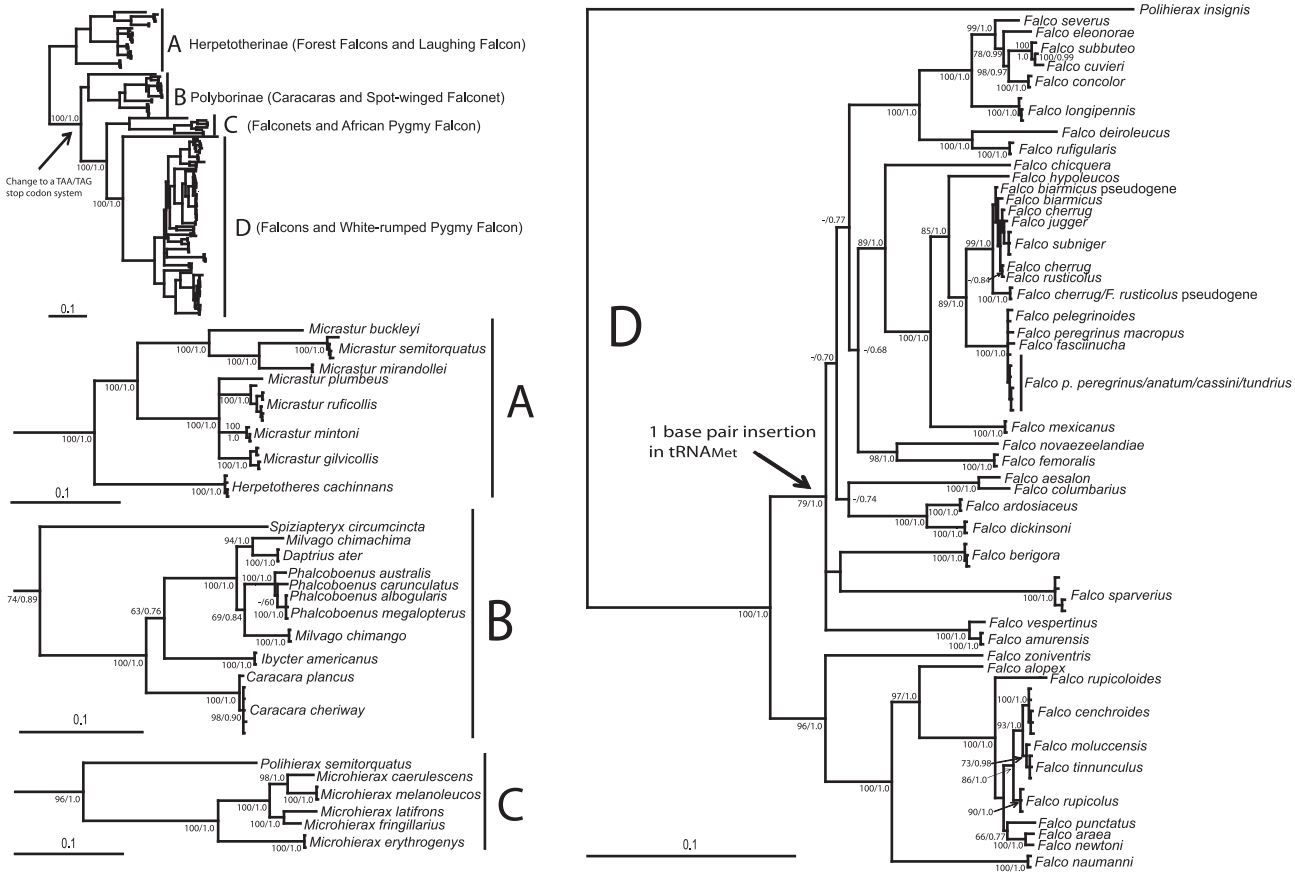

Fig. 1. 50% Majority consensus rule tree resulting from the Bayesian analyses of the mitochondrial data set (seven partitions). Numbers close to the nodes refer to posterior probabilities and maximum likelihood bootstrap support values higher than 0.95 and 70%, respectively. Only unique haplotypes were included in the analyses.

large polytomies or limited bootstrap values and posterior probabilities (Supplementary Figs. 1–7).

3.1.3. Partitioned nuclear loci

The concatenated analyses of the nuclear loci were based on 176 OTUs and seven loci (5124 bp total). We performed separate analyses for: (1) the three loci for which toe pad tissues could be sequenced (FGB, MB, TGFb2); (2) all seven loci excluding individuals for whom limited data was available; and (3) the same seven loci, but including all individuals despite limited data being available for some.

In the concatenated analyses of the three loci for which all species could be sequenced, all primary lineages within the Falconidae (e.g., Herpetotherinae, Falconinae/Polyborinae, Polyborinae, Falconinae, *Microhierax*/*Polihierax*, *Falco*/*P. insignis*, *Falco*) were supported by bootstrap values or posterior probabilities equal to or greater than 90% or 1.0, respectively (Fig. 2). There were few well supported topological differences relative to the mitochondrial tree. One involved the relative position of *M. buckleyi* with respect to *M. mirandollei* and *M. semitorquatus* (previously reported in Fuchs et al., 2011a). However, three noticeable differences relative to the mitochondrial tree were observed: (1) the striking lack of resolution for the genus *Falco*, (2) the basal position of the American kestrel (ML: 83%, BI: 1.0), and (3) the lack of support for the monophyly of 17 of the 39 *Falco* species (44%).

The topology resulting from the analyses of the seven autosomal loci, including the toe pads samples, was very similar, both in terms of topology and nodal support, to the topology obtained in the analyses of the three autosomal loci where data could be obtained for all species (*F. jugger* excepted). In the seven loci analyses, there was a tendency for a decrease in the number of *Falco* species that were not monophyletic ($n = 12$).

3.1.4. Partitioned mitochondrial and nuclear loci

The analyses performed on the concatenated data set (7431 bp) was well supported with most of the interspecific nodes within the Falconidae being supported by bootstrap values or posterior probabilities greater than 70% or 0.95 (Fig. 3). The concatenation of the mitochondrial and nuclear loci did not improve the resolution of the tree but some relationships were more strongly supported than in the mitochondrial or nuclear analyses. For example, the hobby clade was recovered as the sister group of the clade formed by the New Zealand/aplomado falcons and the large clade involving the peregrine-like falcons and hierofalcons (ML: 75%, BI: 1.0).

3.1.5. Divergence time estimates

The divergence time estimates were obtained using the concatenated data set (10 partitions) with (1) the *Pedohierax* fossil, (2) the *Thegornis* fossil, and (3) both fossils together, and a sampling strategy with several individuals per species. A summary of the divergence time estimates for the primary clades is given in Table 1.

The 95% HPD for divergence time estimates using the two fossil calibrations independently were usually overlapping (Table 1; e.g., *Pedohierax* fossil: *Microhierax*: 3.4 myrs, 95% HPD: 2.4–4.5; *Thegornis* fossil: *Microhierax*: 5.1 myrs, 95% HPD: 3.4–7.1), but the basal nodes tend to have non-overlapping estimates (Table 1; e.g., *Pedohierax* fossil: Falconidae: 22.3 myrs, 95% HPD: 19.6–25.6; *Thegornis* fossil: Falconidae: 34.2 myrs, 95% HPD:

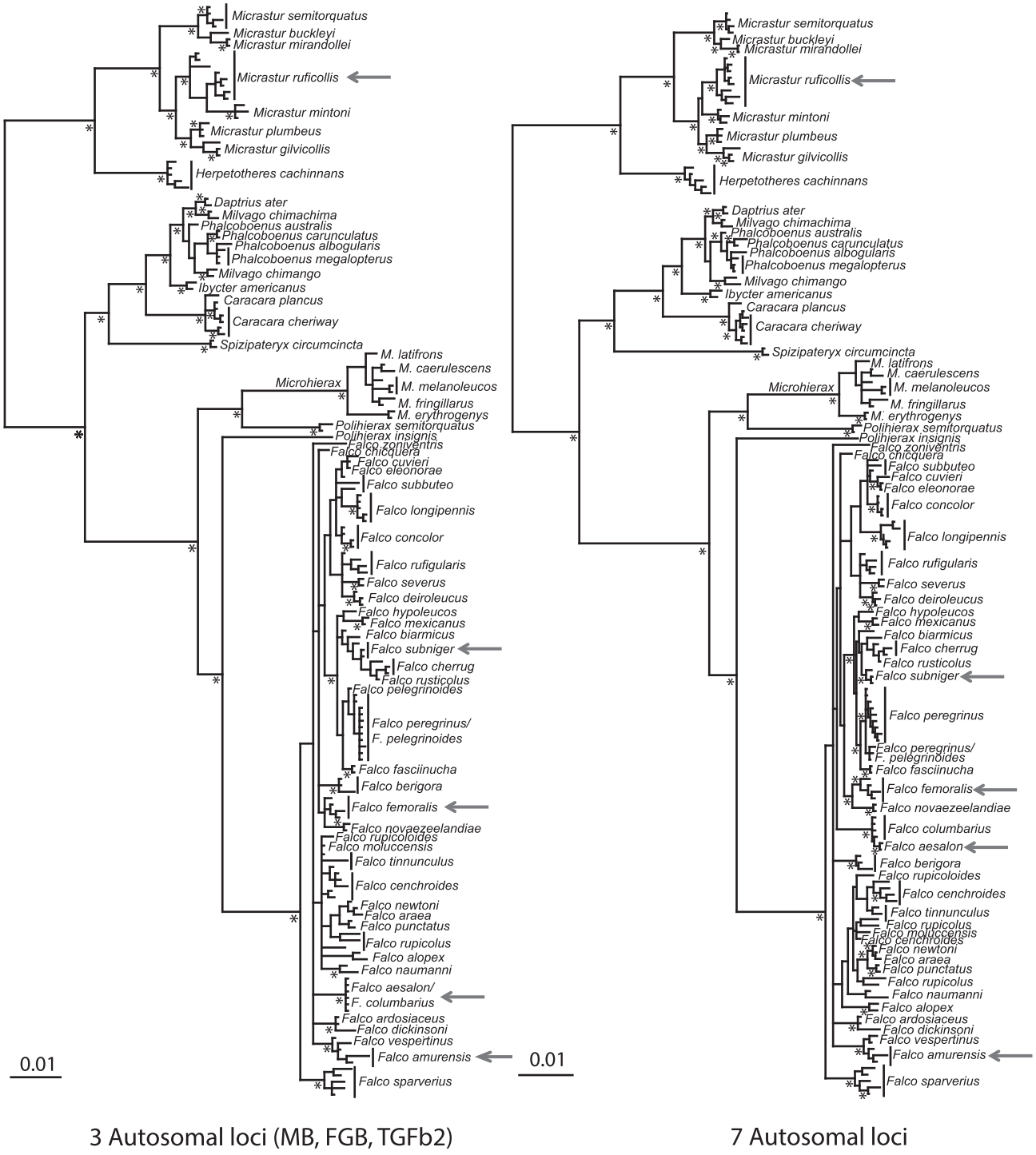

Fig. 2. 50% Majority consensus rule tree resulting from the Bayesian analyses of the nuclear data sets using (1) only the three loci (MB, FGB and TGFb2, left) for which sequences were available for all species but *F. jugger* and (2) the seven loci sequenced for this study (right). An Asterisk indicates nodes that received posterior probabilities and maximum likelihood bootstrap support values higher than 0.95 and 70%, respectively. Arrows indicate taxa that were non-monophyletic in the 3 loci analyses and monophyletic in the 7 loci analyses.

26.2–43.2). The divergence time estimates using the *Thegornis* fossil were about 1.5 times older than the divergence time estimates using the *Pedohierax* fossil (Table 1). Combining the two calibration points yielded estimates that were intermediate (Table 1; e.g., Falconidae: 28.8 myrs, 95% HPD: 23.1–34.8; *Micrastur*: 4.9 myrs, 95% HPD: 3.0–6.1).

The divergence time estimates we obtained using the fossil data for some nodes are slightly older than estimates we obtained in our previous studies (Fuchs et al., 2011a, 2012), although the 95% HPD are overlapping. Given the small but existing differences between analyses that used the two fossil calibration points, we will consider the extreme estimates as being equally plausible.

The extant Falconidae started to diversify in the late Eocene to Late Miocene (*Thegornis* fossil 34.2 mya 95% HPD: 26.2–43.2; *Pedohierax* fossil 22.3 mya 95% HPD: 19.6–25.6). The Falconinae started to diversify during the Middle Miocene, between 12.6 (95% HPD:

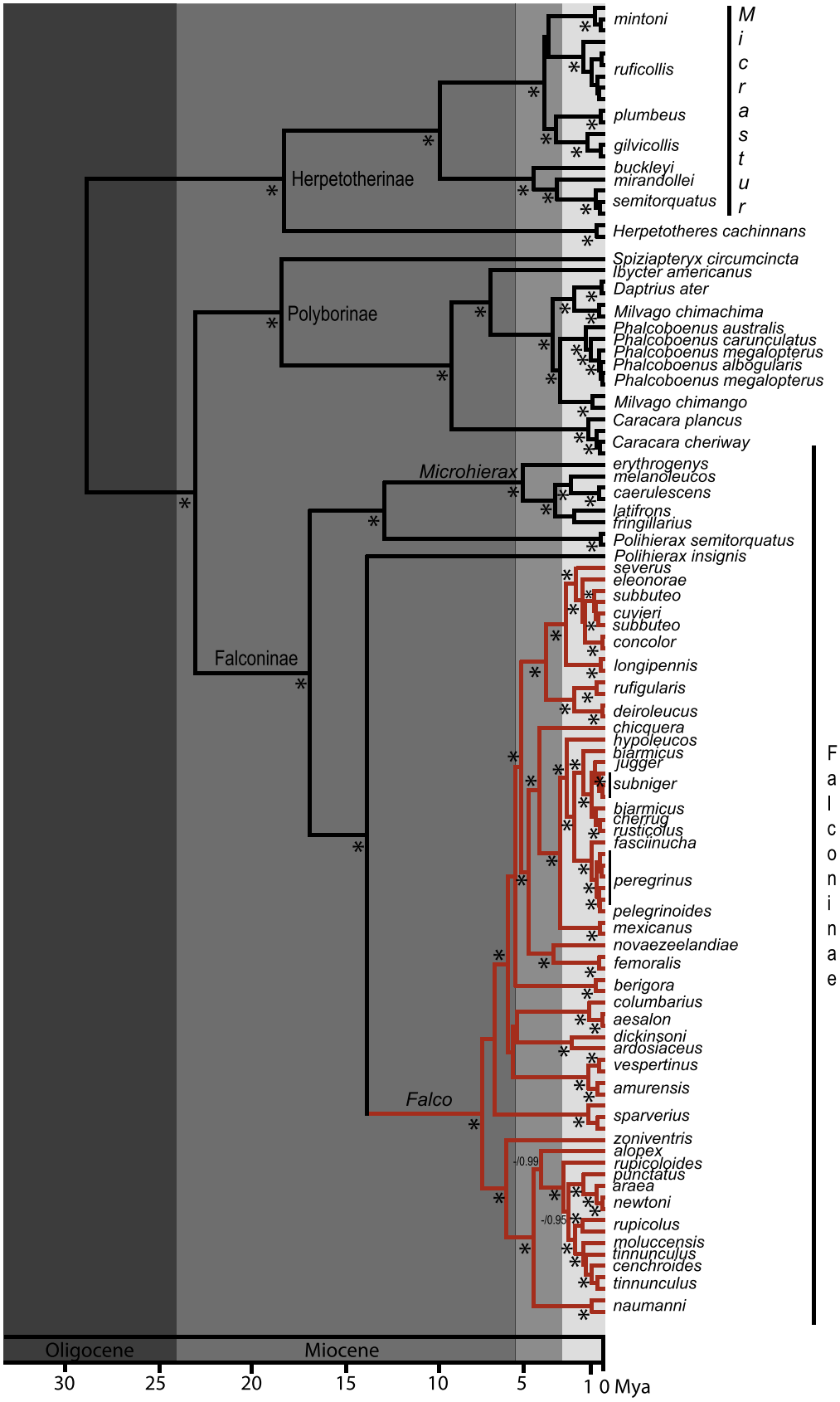

Fig. 3. Chronogram obtained using the eight loci data set and the two fossil calibration points (*Pedohierax* and *Thegornis*). We assumed an Uncorrelated Lognormal clock model for all loci and used the best fit substitution model for each partition. Asterisks indicate posterior probabilities and maximum likelihood bootstrap support values higher than 0.95 and 70%, respectively. The different shades of gray indicate different geological epochs. The different branch colors indicate the two parts of the tree with different diversification rates. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Divergence times for selected clades in Falconidae (in mya) depending on fossil calibration (*Pedohierax*, *Thegornis*, or both) using the 10 partitions data set (tRNA, ND1, ND2, MB, FGB, TGFb2, VIM, PER, PEPCK, RAG1) and including multiple individuals per species when possible. Numbers between brackets represent the 95% Highest Posterior Density. Values in bold indicate the calibration points.

Clade	*Pedohierax*	*Thegornis*	Both fossils
Falconidae	22.3 (19.6–25.6)	34.2 (26.2–43.2)	28.6 (23.1–34.8)
Herpetotherinae	10.0 (7.5–12.8)	**18.0 (16.6–19.8)**	**18.0 (16.6–18.3)**
Micrastur	6.0 (4.3–7.8)	10.1 (7.3–13.0)	9.0 (6.5–11.7)
Polyborinae/Falconidae*	**18.0 (16.7–19.8)**	27.2 (20.8–34.8)	**22.6 (17.9–27.6)**
Polyborinae	14.1 (11.4–16.9)	21.3 (14.7–27.8)	17.8 (13.3–22.6)
Basal split 'caracaras'	6.2 (4.6–8.0)	9.6 (6.5–12.8)	8.4 (5.8–11.2)
Falconinae	12.6 (10.6–14.7)	19.3 (14.6–24.6)	16.2 (12.7–20.2)
Polihierax/*Microhierax*	9.3 (7.2–11.3)	14.3 (10.0–18.6)	12.1 (9.0–15.5)
Microhierax	3.4 (2.4–4.5)	5.1 (3.4–7.1)	4.5 (3.0–6.1)
Neohierax/*Falco*	10.1 (8.0–12.2)	15.3 (10.9–20.1)	13.0 (9.5–16.6)
Falco	5.0 (4.0–6.1)	7.7 (5.6–9.8)	6.7 (5.0–8.4)

10.6–14.7) and 19.3 mya (95% HPD: 14.6–25.6). The divergence between the Ethiopian *Polihierax* and the Oriental *Microhierax* occurred between 9.3 mya (95% HPD: 7.2–11.3) and 14.3 (95% HPD: 10.0–18.6), at the same time as the divergence between the Oriental *P. insignis* and the cosmopolitan genus *Falco* about 10.1 mya (95% HPD: 8.0–12.2) and 15.3 mya (95% HPD: 10.9–20.1). The genus *Microhierax* diversified during the Late Miocene–Early Pliocene (*Pedohierax*: 3.4 mya 95% HPD: 3.4–5.1; *Thegornis*: 5.1 mya, 95% HPD: 3.4–7.1). The species-rich genus *Falco* started to diversify in the Late Miocene, between 5.0 mya (*Pedohierax*: 95% HPD: 4.0–6.1) and 7.7 mya (*Thegornis*: 95% HPD: 5.6–9.8).

3.1.6. Biogeography

The biogeographic analyses performed using RASP indicated a general pattern of diversification across different biomes through dispersal, although the relative contribution of dispersal and vicariance depended on the algorithm (Supplementary Fig. 8). The DEC algorithm had a tendency to favor more vicariance events than the BBM algorithm. The ancestral area for the Falconidae was either the Neotropics (BBM) or a combination of all seven biogeographic areas (DEC).

The most diverse subfamily, the Falconinae was either inferred to be of Oriental origin (BBM) or a combination of all seven biogeographic areas (DEC). Within the genus *Falco*, complex histories were inferred by both algorithms with multiple extant ancestral areas. The most likely origin for Old World kestrels (Supplementary Fig. 8) was either Madagascar (breeding range only coding, BBM and DEC) or Ethiopian (breeding and wintering range coding, BBM and DEC). Greater probability for an Ethiopian origin was given in analyses accounting for wintering ranges, due to the different coding of the lesser kestrel (*F. naumanni*). Extinction, or range shift, was also detected in some lineages, with an interesting example involving New Zealand falcon (*F. novaezeelandiae*; Australasia) and aplomado falcon (*F. femoralis*; Neotropics and Nearctic), suggesting a Palearctic ancestral area for the node.

The exact reconstruction of the ancestral area for each node does not necessarily appear similar between the two methods, however, suggesting that some uncertainty exists concerning the ancestral area occupied by the Falconidae. Importantly, both methods recovered a trend where the relative role of dispersal across bioregions for speciation was more important during the last 6 myrs than in the early history of the Falconidae. This shift in the relative contribution of dispersal and vicariance appears to be linked to the diversification of the genus *Falco*.

3.1.7. Diversification rates

To conclude that there is a significant decrease in the diversification rate in a clade, the threshold for the γ statistic, with an exhaustive sampling scheme at the species level, must be smaller than −1.645 (Pybus and Harvey, 2000). For the Falconidae, no decrease in diversification rates were detected on the Maximum Clade Credibility trees (*Pedohierax*: $\gamma = 3.012$, $p = 1.0$; *Thegornis*: $\gamma = 3.029$, $p = 1.0$; both fossils –: $\gamma = 2.673$, $p = 1.0$) and the posterior distributions of the γ statistics do not include zero.

The diversification rate analyses performed using Laser indicated that a yule-2-rate diversification model had a better fit to the data than any of the constant rate models ($\Delta AICrc_{Pedohierax\ fossil} = 2.605$, $\Delta AICrc_{Thegornis\ fossil} = 2.818$; $\Delta AICrc_{Both\ fossils} = 3.334$). Yet, after simulations, a constant rate model for the whole family could not be statistically rejected ($p = 0.11$). It is worth noting, however, that the estimated time for the shift in the yule-2 rate model, as estimated by Laser, corresponds to the first diversification event for *Falco* ($st_{Pedohierax} = 4.5$ mya; $st_{Thegornis} = 7.6$ mya; $st_{Both\ fossils} = 6.3$ mya).

The *AICc* values, obtained from the Turbo-Medusa analyses, favored a model with two rates in the Falconidae tree, with a shift in diversification rates occurring at the basal node for the genus *Falco* (Table 2). The shift in net diversification rate was due to both a two fold increase in speciation rate and a drop in extinction rate to zero in *Falco* when compared to the other Falconidae (Table 2, Supplementary Table 5).

3.1.8. Estimation and correlation of habitat and diet changes

Preliminary analyses on 1000 trees from the posterior distribution, assuming either equal or unequal state transitions for the three characters, indicated that an equal state transition model was rejected for migration (average $\Delta Ln > 4$, Pagel et al., 2004) but was not rejected for habitat and diet (average $\Delta Ln < 2$). The posterior distribution ($n = 1000$ trees) of twice the difference in log-likelihood scores for the correlated and uncorrelated models of character evolution for habitat and diet indicates that the correlated model had a significantly better fit than the uncorrelated model (degree of freedom = 4, $p < 0.001$, χ^2 range: 10.77–17.43). The latter correlation was not found between habitat and migration (degree of freedom = 4, $p = 0.41$–0.70, χ^2 range: 2.15–3.97)

Table 2
Likelihood comparisons for models with different number of rate shifts (obtained using Turbo-Medusa) using different chronograms (MCC trees) as templates (all obtained using the eight loci data set and with the sampling of multiple individuals per species to reconstruct the phylogeny). The Birth–Death model was considered in all analyses. Abbreviations are: r, net diversification rate; epsilon, proportion of surviving species; b, speciation rate; d extinction rate. Only the best-fit model is presented (see Supplementary Table 5 for the parameter values for the other models).

	N rate shifts	Ln	Parameters	AIC	r, epsilon, b, d	AICc
Thegornis	1	−161.2841	5	332.5682	[1] 0.04813015, 7.384675e−01, 0.18403123894, 0.13590108894 [2] 0.33152867, 2.834539e−07, 0.33152876397, 9.4e−08	333.0482
Pedohierax	1	−133.6876	5	277.3753	[1] 0.07289855, 7.454207e−01, 0.28634908651, 0.21345053651 [2] 0.50793436, 3.435723e−06, 0.50793610512, 1.74511e−6	277.8553
Both fossils	1	−153.0072	5	316.0145	[1] 0.06125818, 7.007466e−01, 0.20470337179, 0.14344519179 [2] 0.37275694, 1.017213e−07, 0.37275697791, 3.791e−8	316.4945

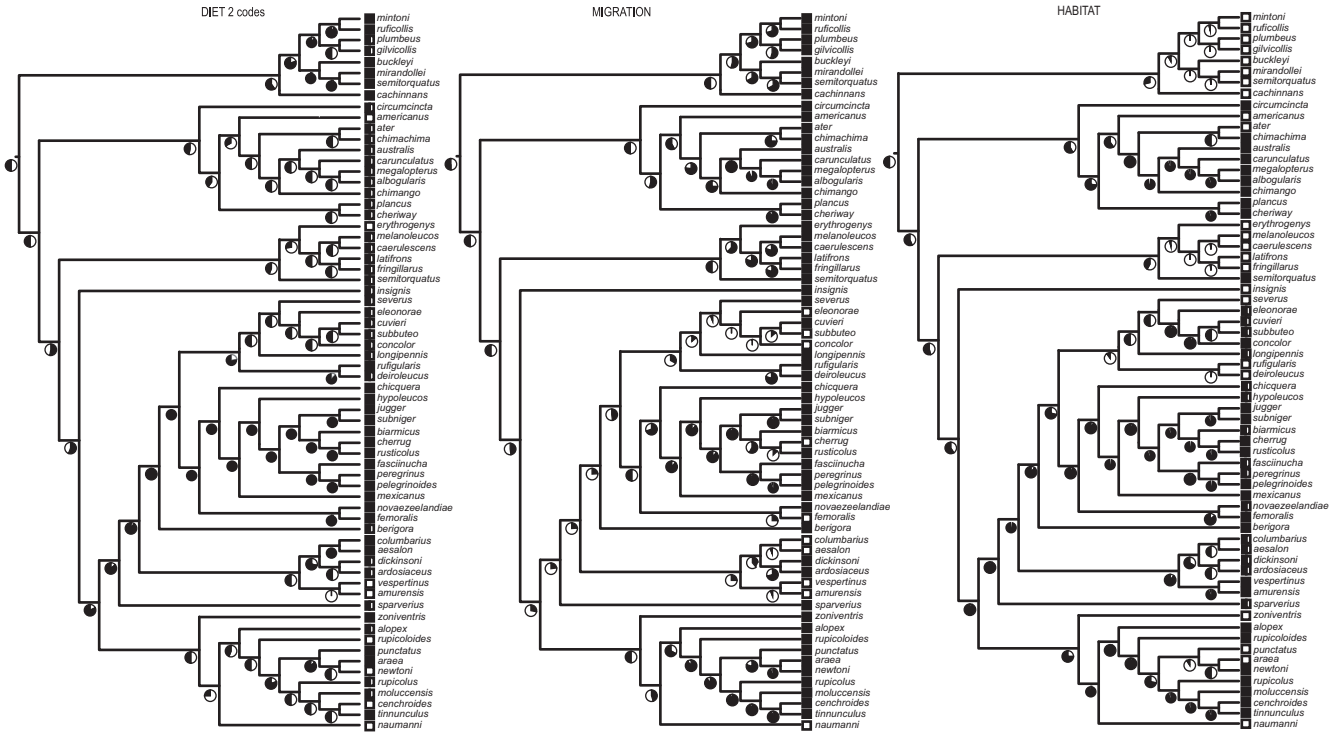

Fig. 4. Reconstruction of ancestral character states for three eco-ethological characters (diet migration and habitat) using the maximum likelihood algorithm in BayesTraits. We used 1000 trees samples from the posterior distribution of tree using the 10 loci data with multiple individuals per species and both calibration points). Color codes are: Diet: black: vertebrates, white: insectivorous. Migration black: sedentary, white: migrating. Habitat: black: open savannah/grassland/tundra, white: forest/woodland.

or between migration and diet (degree of freedom = 4, $p = 0.36–0.90$, χ^2 range: 1.01–4.29).

Reconstructions of the ancestral states indicated substantial uncertainty at the base of the phylogeny as state probabilities were close to 0.5 for the three characters (Fig. 4). For diet, estimation of a broad diet spectrum was found for the family and specialization in a vertebrate diet evolved independently in the Herpetotherinae and *Falco* clades (Old World kestrels excluded). Migration evolved independently multiple times in the genus *Falco*, but reconstruction of this character's evolution showed much more uncertainty than the two other characters, even for non-migratory clades (e.g., Herpetotherinae). One factor that may have biased the analyses is the fact that migration is a rare state, and estimation of its transition rate is not robust. With this caveat, migration appears to have evolved in two primary clades, the Old World hobbies and the clade formed by *F. aesalon*/*F. columbarius*/*F. ardosiaceus*/*F. dickinsoni*/*F. amurensis*/*F. vespertinus* (Fig. 4). Adaptation to more open habitats (grassland/xeric habitat) appears to have evolved in the Polyborinae and genus *Falco* (Fig. 4).

3.1.9. Relationships between migratory, diet, and habitat and diversification

The BiSSE analyses indicated that character state for habitat and migration are associated with diversification rate parameters, mostly with higher speciation rates, whereas diet does not show this association (Supplementary Tables 6a, 6b, 6c).

For migration, the five parameter model, assuming unequal speciation rates and character states transition rates but equal extinction rates had the lowest AIC values in all three chronogram analyses. The difference, after simulations (1000 birth–death trees), in likelihood scores (both fossils: ΔAIC = 4.7, *Pedohierax* only ΔAIC = 4.2, *Thegornis* only ΔAIC = 4.3) between the best fit model and a model that assumes no link between being migratory and speciation rates (four parameters, equal speciation and extinction rates but asymmetric transition rates) was significant after simulations ($p = 0.026–0.04$). This result, which is not dependent on the chronogram used for the analyses, suggests that migratory species have higher speciation rates than non-migratory species.

For diet, the three parameter model, assuming equal speciation rates, extinction rates and character transition rates had the lowest AIC in two of the three chronograms (both fossils, *Thegornis* only). The five parameter model with unequal speciation and character state transition rates was only marginally better that the simplest model in the last chronogram (*Pedohierax* only: ΔAIC = 0.3). The improvement in AIC score was not significant after simulations ($p = 0.44$). Hence, this result suggests that diet had no impact on the diversification of falcons.

For habitat, the five parameter model assuming unequal speciation rates and transition rates and equal extinction rates had the lowest AIC in all three chronograms. The second lowest AIC was a model assuming equal character state transition but unequal speciation and extinction. The difference, after simulations (1000 birth–death trees), in likelihood scores (both fossils: ΔAIC = 11.5, *Pedohierax* only ΔAIC = 11.2, *Thegornis* only ΔAIC = 11.2) between the best fit model and a model that assumes unequal character state transitions (four parameters, equal speciation and extinction rates and unequal character change rates) was highly significant after simulations ($p = 0.01$). This result suggests that lineages found in open habitats tend to have higher speciation rates than lineages found in forest and dense woodlands.

4. Discussion

4.1. Phylogeny and systematics of the Falconinae

The phylogeny we provide here is congruent with previous hypotheses (Griffiths, 1999; Griffiths et al., 2004; Fuchs et al., 2011a,b, 2012), especially for the higher-level taxonomic partitions (e.g., monophyly and sister relationships among subfamilies). We recovered the same species level relationships within two of the

subfamilies, Herpetotherinae and Polyborinae as previously described (Fuchs et al., 2011a, 2012). Here, we focus on the phylogenetic relationships within Falconinae, where all species have been sampled for the first time and included within a single molecular phylogenetic study.

We found two primary clades within Falconinae: *Polihierax semitorquatus*/*Microhierax* and *Polihierax insignis*/*Falco*, both with maximum nodal support in the concatenated analyses. We found a distant relationship between the two species (*semitorquatus* and *insignis*) currently assigned to the genus *Polihierax*. Their non-sister relationship has also been suggested based on morphology (syrinx, biometrics), and several authors considered *insignis* sufficiently distinct to be retained as a separate genus (Wolters, 1975–1982; Kemp and Crowe, 1994; Griffiths, 1999). Hence, both morphology and DNA support the recognition of *Neohierax* for the species *insignis*.

Microhierax (five species) was monophyletic in all analyses and the taxonomic status of each species was well supported (e.g., White et al., 1994), with the Philippine falconet (*M. erythrogenys*) diverging first within the genus, followed by two clades of two species each, *M. caerulescens*/*M. melanoleucos* and *M. fringillarius*/*M. latifrons*.

Monophyly of the genus *Falco* has never been in doubt, but the phylogenetic relationships among *Falco* species and the taxonomic status of some (e.g., *F. peregrinus*) have long puzzled systematists (Cade and Digby, 1982). Our exhaustive sampling at the species level, with several individuals per species in most cases, allowed us to address some of those unresolved questions. Previous phylogenetic studies have failed to resolve most relationships among *Falco* species, suggesting that the genus may have diversified in a short period of time. Our results also suggest a recent (within the last 8 myrs) and rapid radiation for *Falco*. The concatenated analyses, however, did identify nine well supported species groups (Old World kestrels; *F. sparverius*; *F. amurensis*/*F. vespertinus*; *F. ardosiaceus*/*F. dickinsoni*; *F aesalon*/*F. columbarius*; *F. berigora*; *F. femoralis*/*F. novaezeelandiae*; hobbies; Hierofalcons/*F. chicquera*), but relationships among them remain unclear. Some individuals, often from the same species group (e.g., *F. rufigularis*/*F. subbuteo* in the hobbies group) shared identical autosomal alleles. The latter pattern could be either due to stochastic lineage sorting of ancestral polymorphism (e.g., Hudson and Coyne, 2002; Rosenberg, 2003) or hybridization. Ancestral polymorphism is more likely given the fact that in most cases, alleles were shared among species that have allopatric distributions (e.g., *F. cenchroides*/*F. vespertinus*, *F. rufigularis*/*F. subbuteo*) and for which hybridization has not been recorded (McCarthy, 2006). Hence, the presence of shared alleles for non-sister lineages that span the base of the *Falco* tree support the suggestion that the diversification of the primary *Falco* lineage occurred during a short period of time.

One of the highly supported groups consists of the typical Old World kestrels (ten Old World species with a reddish-brown or chestnut back and wing coverts) and the atypical banded kestrel (*F. zoniventris*) from Madagascar. The Old World kestrel lineage stems from the earliest divergence within *Falco* (Fig. 3). The American kestrel had been considered to be closely related to the Old World kestrels in a superspecies with *F. tinnunculus*, *F. rupicolus*, *F. cenchroides*, *F. araea*, *F. moluccensis* and *F. newtoni* (referred to as the *F. tinnunculus* superspecies; Wolters, 1975–1982; Cade and Digby, 1982; Sibley and Monroe, 1990), whereas the banded kestrel has been associated with the gray and Dickinson kestrels in the 'atypical kestrels' clade (subgenus *Dissodectes*), mostly due to their gray plumage (Cade and Digby, 1982; White et al., 1994). This traditional hypothesis is not supported by our data as (1) the banded kestrel is not directly related to the gray and Dickinson kestrel and (2) the American kestrel is more closely related to other falcons than to Old World kestrels. The relationship between the American kestrel and all other *Falco* species but the Old World kestrels is also supported by a unique insertion of one nucleotide in the $tRNA_{Met}$ (Fig. 1). The fact that *F. sparverius* may not be closely associated to other kestrels was also suggested by DNA/DNA hybridization work of Sibley and Ahlquist (1990) and Groombridge et al. (2002).

Whereas many relationships in the kestrel assemblage were expected (e.g., close relationships between the Madagascar, Seychelles and Mauritius kestrels; Groombridge et al., 2002), some unexpected relationships based on traditional hypotheses, were identified using more data and individuals than previous studies. First, the fox kestrel (*F. alopex*), restricted to the Sudanian bioregion *sensu* Linder et al. (2012), is not the sister species of the greater kestrel (*F. rupicoloides*), found in the Ethiopian and South African region *sensu* Linder et al. (2012). Rather, they form a paraphyletic assemblage with the greater kestrel being sister to all other kestrels from the *F. tinnunculus* group (Fig. 3). This pattern is at odds with a conventional view for species of the African savannah belt, in which species distributed in the Sudanian/Ethiopian and Zambezian/South African bioregions are sister-species (e.g., Lorenzen et al., 2012; Fuchs et al., 2011b). Second, the common kestrel *F. tinnunculus* (sensu White et al., 1994; Dickinson, 2003), is paraphyletic with the South African taxon (*F. t. rupicolus*) being sister to the clade formed by the Palearctic common kestrel (*F. tinnunculus sensu stricto*), Moluccan kestrel (*F. moluccensis*), Australian kestrel (*F. cenchroides*) and the three Indian Ocean species (*F. araea*, *F. newtoni* and *F. punctatus*), a result also suggested by Groombridge et al. (2002). Third, mtDNA genetic distances among species were very low, and although each species appears monophyletic based on mtDNA, in many cases nuclear alleles were still shared among closely related species (e.g., between *F. moluccensis*, *F. tinnunculus* and *F. cenchroides*), indicating incomplete lineage sorting for many nuclear alleles and recent divergence.

Another lineage whose relationships within *Falco* are poorly resolved is the red-footed falcon species pair *F. amurensis* and *F. vespertinus*. These two parapatric migratory species are often considered a superspecies closely related to the Old World hobbies (Cade and Digby, 1982; White et al., 1994). The two taxa possess distinct and divergent mtDNA haplotypes and do share a few nuclear intron alleles. Given that their mtDNA divergence is higher than that among well recognized species (e.g., *F. cenchroides* and *F. tinnunculus*), and that they show striking differences in female plumage and distribution (parapatric in both breeding and wintering areas), it is very likely that the two taxa are distinct species and that the shared nuclear alleles are due to incomplete lineage sorting of ancestral polymorphism.

Another pair of closely related species was formed by the merlin lineages, which have been considered a single species until recently (White et al., 1994; Dickinson, 2003), when mitochondrial COI barcoding analyses identified two genetic clusters correlated with geography (Johnsen et al., 2010). This molecular divergence, confirmed by our study, is coupled with plumages differences; based on this pattern we consider the Old World and New World merlin groups as different species (*F. aesalon* and *F. columbarius*, respectively) in the present study. Mitochondrial data suggest that the two species' ranges are separated by the Bering Strait and the Atlantic Ocean (Johnsen et al., 2010) but further sampling of subspecies is clearly needed to define the extent of possible gene flow. The two merlin lineages grouped in a weakly supported clade that also included two African atypical kestrels, the gray and Dickinson's, that were sister species in all analyses. The latter two species were often included in the subgenus *Dissodectes*, with the phylogenetically unrelated banded kestrel (e.g., Wolters, 1975–1982). The gray and Dickinson's kestrels are parapatrically distributed and when compared to most falcon species, they likely represent a relatively old species pair.

The brown falcon (*F. berigora*), with its relatively long legs, represents one of the most morphologically distinctive *Falco* species, owing to its more *Accipiter* or hawk-like shape. This distinctiveness in shape has led some authors to retain it in a separate genus or subgenus *Hieracidea* (e.g., Wolters, 1975–1982), at the base of the *Falco* tree (Cade and Digby, 1982). The brown falcon was nested within *Falco* in all our analyses, suggesting that a generic distinction for this species is not supported.

The New Zealand *F. novaezeelandiae* has been variously associated with the brown falcon, or related to the hobbies, or even placed in its own genus or subgenus, *Nesierax* (Wolters, 1975–1982). Our analyses revealed a new hypothesis with the New Zealand falcon being sister to the aplomado falcon (*F. femoralis*) in what constitutes the seventh primary *Falco* lineage. This well supported relationship is surprising not only because of the large gap in geographic distribution between the two species but also because of the overall plumage similarity between the aplomado falcon and two other South American species, the bat (*F. rufigularis*) and orange-breasted (*F. deiroleucus*) falcons (White et al., 1994). The three later species were considered closely related based on morphology (Cade and Digby, 1982). Our finding suggests a potential role for convergence in phenotypic traits among these taxa.

The bat (*F. rufigularis*) and orange-breasted (*F. deiroleucus*) falcons were sister species in all our analyses. These two species are sister to a clade of six closely related aerial hunting species known as the Old World hobbies. The monophyly of the Old World hobby clade was strongly supported in all analyses but the relationships within this clade differ from traditional hypotheses. First, the Australian hobby (*F. longipennis*) appears to be the first lineage to diverge in this group, followed by the Oriental hobby (*F. severus*). Whereas these two species have been considered to form a superspecies (White et al., 1994), our analyses did not recover them as sister species. A similar case involves the patchily distributed eleonorae (*F. eleonorae*) and sooty (*F. concolor*) falcons. The sooty falcon is in fact more closely related to the species pair formed by Eurasian (*F. subbuteo*) and African (*F. cuvieri*) hobbies. Our analyses favor a hypothesis of the African hobby being actually nested within the Eurasian hobby.

A major clade (*F. chicquera*/Hierofalcons *sensu* Cade and Digby, 1982) includes eleven species, including the charismatic peregrine (*F. peregrinus*), saker (*F. cherrug*) and gyrfalcon (*F. rusticolus*). The clade is characterized by the early sequential divergence of three species that are usually considered to have uncertain affinities, the red-necked (*F. chicquera*), prairie (*F. mexicanus*) and gray (*F. hypoleucos*) falcons. The next divergence is between clades for the three species of peregrine-like species (*F. peregrinus*, *F. fasciinucha*, *F. pelegrinoides*) and the Hierofalcons, the largest five species (*Hierofalco sensu stricto*): lanner (*F. biarmicus*), laggar (*F. jugger*), saker (*F cherrug*), gyr (*F. rusticolus*) and black (*F. subniger*) falcons. Genetic divergence among these species was low. Although low divergence was expected between the barbary (*F. pelegrinoides*) and peregrine (*F. peregrinus*) falcons, often considered conspecific (e.g., White et al., 1994), the close association of the rare and patchily distributed taita falcon (*F. fasciinucha*) with the barbary/peregrine clade was not expected based on traditional hypotheses (Cade and Digby, 1982), although some early authors have suggested a possible relationship among these three species (Wolters, 1975–1982). Indeed, the taita's small size and plumage led some authors to consider that it could be related to the Oriental hobby (Cade and Digby, 1982; White et al., 1994). Recently, mitochondrial data even suggested that the taita falcon could be nested within the barbary/peregrine complex (White et al., 2013; Bell et al., 2014); this pattern was also recovered in our analyses of the mitochondrial data set. Yet, our nuclear data suggested that allele sharing between the barbary/peregrine and taita falcons was only found in one locus (PEPCK). In most loci, there were indications for the taita falcon to be sister to the barbary/peregrine lineage instead of being nested within it. This pattern of shared mitochondrial haplotypes and nuclear alleles could be due to incomplete lineage sorting of ancestral polymorphism or recent gene flow with capture of the barbary/peregrine mitochondrion in the taita falcon lineage. Determining which process best explains this pattern clearly requires more data and the use of coalescent methods.

The peregrine falcon is one of six species of birds that have a cosmopolitan distribution and up to 16 peregrine subspecies are currently recognized (Dickinson, 2003). We found very low divergence among the peregrine individuals we analyzed, despite having sampled a significant portion of the geographic distribution (South America, North America, Western Palearctic, Africa and Australia). A pattern of low differentiation among subspecies has been reported previously (Brown et al., 2007; Johnson et al., 2010; Talbot et al., 2011; White et al., 2013; Bell et al., 2014); for example a peregrine mitochondrial control region haplotype was shared between individuals sampled in Alaska and the Fiji Islands.

The Hierofalcon clade also presents a puzzling case for taxonomy, as three (*F. biarmicus*, *F. cherrug*, *F. rusticolus*) of the five species were not monophyletic in our analyses, a pattern that has been highlighted previously (Nittinger et al., 2005, 2007; Johnson et al., 2007). We also found the black falcon to be associated with the Hierofalcons; though its relationship was previously considered uncertain (White et al., 1994). Interestingly, the adult plumage of the black falcon is very similar to the juvenile plumage of its apparent sister species, the laggar falcon. The black falcon was the only species in the Hierofalcon clade that appeared monophyletic based on mtDNA analyses (using three individuals), though only one individual of the laggar falcon was sampled. The pattern we found of non-monophyly based on both mitochondrial and nuclear genomes could be explained as incomplete lineage sorting of ancestral polymorphism and/or recent hybridization (Nittinger et al., 2005, 2007; Johnson et al., 2007).

4.2. Timing of diversification and biogeography: a Late Miocene/Pliocene radiation

Our discussion here will focus on the diversification and biogeography of the family as a whole or on the Falconinae, as biogeographic histories of the two New World endemic subfamilies, the Herpetotherinae and Polyborinae have been addressed previously (Fuchs et al., 2011a, 2012).

The ancestral area for the Falconidae was either the Neotropics or a combination of all seven biogeographic areas. A Neotropical origin for the Falconidae is supported by the fact (1) that the two basal lineages (Herpetotherinae and Polyborinae) are endemic and/or highly diversified there, (2) that the oldest fossils that could be assigned to the crown clade Falconidae (*Pedohierax* and *Thegornis*) are Neotropical, (3) that the Falconidae is part of a clade (Falconidae, Psittaciformes, Passeriformes and Cariamidae) that appears to be of Austral origin (Ericson et al., 2006; Hackett et al., 2008). Tambussi and Acosta Hospitaleche (2007) assigned a distal tarsometatarsus from the middle Eocene La Meseta Formation of Seymour Island (Antarctica) to the Falconidae. The relationships of this fossil are uncertain as the trochlea for the second toe does not reach as far distally as in extant Falconidae (Mayr, 2009), and thus could potentially constitute a stem Falconidae. Assuming our divergence time analyses are correct, this fossil would be too ancient, as our oldest estimate for the first Falconidae split is 34.2 mya, to be assigned to the crown group.

The Falconinae started to diversify between 12.6 (95% HPD: 10.6–14.7) and 19.3 mya (95% HPD: 14.4–24.6), at about the same time as the Mid-Miocene Climatic Optimum (Zachos et al., 2001; Jacobs, 2004). The divergence between the Ethiopian

P. semitorquatus and the Oriental *Microhierax* occurred between 9.3 mya (95% HPD: 7.2–11.3) and 14.3 mya (95% HPD: 10.0–18.6), at the same time as the divergence between the Oriental *P. insignis* and the cosmopolitan genus *Falco*, about 10.1 mya (95% HPD: 8.0–12.2) and 15.3 mya (95% HPD: 10.9–20.1). Subsequent increasing aridity after the Mid-Miocene Climatic Optimum favored the spread of savannahs (Cerling et al., 1997; Jacobs, 2004) and may have triggered the divergence among these lineages.

The species-rich genus *Falco* started to diversify in the Late Miocene, between 5.0 mya (95% HPD: 4.0–6.1) and 7.7 mya (95% HPD: 5.6–9.8). This period corresponds to the spread of open savannahs dominated by plants for which the first product of carbon fixation is a 4-carbon molecule (C_4), advantageous over C_3 and CAM carbon fixation in hot and dry environments, especially in Africa (Cerling et al., 1997; Osborne and Beerling, 2006; Edwards et al., 2010). An association between increasing grassland habitats and *Falco* diversification had been suggested by Cade and Digby (1982). The Late Miocene was also a time of major turnover in mammalian communities, including the explosive radiation of Ethiopian rodents (Lecompte et al., 2008), a group that several Ethiopian falcons feed on (e.g., *F. alopex*, *F. rupicolus*), as well as felids (Johnson et al., 2006b), mustelids (Koepfli et al., 2008), bears (Krause et al., 2008), and most large grazer/browser lineages (Hassanin et al., 2012). Diversification of *Gyps* vultures (Johnson et al., 2006a) also dates to this time period. Our estimates for the timing of diversification in *Falco* (Late Miocene/Early Pliocene) are in very good agreement with paleontological data, as several *Falco* palaeospecies have been described from that period (e.g., Boev, 2011). For example, a new palaeospecies of stem Old World kestrel was recently described from the Late Miocene deposits of Linxia Basin in northwestern China (Li et al., 2014). The age of this fossil (Late Miocene) corresponds well with the basal divergence for the genus *Falco* and thus the first appearance of Old World kestrels. Umanskajaa (1981, *fide* Becker, 1987) described a fossil species (*Falco medius*) from the Late Miocene that appears to be closely related to *F. tinnunculus*, *F. naumanni* and *F. vespertinus* (Becker, 1987), which represent the most basal splits in the *Falco* phylogeny. The same reasoning applies for *?Falco*, from the Late Miocene of Idaho, which, is similar in size to another ancient lineage in the *Falco* phylogeny, the merlins (Becker, 1987).

In contrast, fossils that can unambiguously be attributed to derived lineages (e.g., *F. subbuteo*, *F. cherrug*, *F. rusticolus*, *F. peregrinus*) are only present in the Early to Middle Pleistocene, about 2.6–0.126 myrs (Mlíkovský, 2002). Based on full genome data (Zhan et al., 2013), the split between the saker and peregrine falcon has been estimated to have occurred about 2.1 mya (95% CI: 0.9–4.2), an estimate that is very similar to our estimates for the same split (between 1.2 mya, 95% HPD: 0.8–1.6 and 1.8 mya: 95%HPD: 1.2–2.5). Hence there is strong congruence between divergence time estimates obtained from independent molecular data and the fossil record for the genus *Falco*.

From a biogeographic point of view, one of our most striking results is the position of *Polihierax insignis* as sister to the genus *Falco*. This pattern is very similar in time and space to the pattern observed in the Picinae, a subfamily of woodpeckers, in which the Oriental genus *Hemicircus*, with only two species, is sister-group to all other Picinae (176 species) (Dickinson, 2003; Fuchs et al., 2007). Hence it appears that the Oriental biome is not only distinctive because it holds a large number of endemic species and genera but also because it holds lineages of low diversity that are sister to widely distributed clades with much higher species diversity (see also Johnson et al., 2006b for the origin of Felidae). This result highlights the importance that this biome had in the evolution of the modern avifauna and the need to promote conservation efforts in this heavily exploited region (Sodhi et al., 2004, 2006).

The Oriental genus *Microhierax* diversified during the Early Pliocene (3.4 mya, 95% HPD: 2.4–4.5; 5.1 mya, 95% HPD: 3.4–7.1). The inferred pattern and timing of diversification includes a first divergence for taxa from the Philippines (*M. erythrogenys*), then islands of the Greater Sunda archipelago (*M. fringillarius* and *M. latifrons*) from the mainland (between 2.0 mya, 95% HPD: 1.3–2.7 mya and 3.0 mya, 95% HPD: 2.0–4.3 mya), followed by the divergence of continental taxa (*M. melanoleucos* and *M. caerulescens*) (1.4 mya, 95% HPD: 0.8–1.9; 2.0 mya, 95% HPD: 1.1–3.0). The two species from the Greater Sunda diverged about 1.2–1.8 mya (95% HPD: 0.6–1.8 mya; 95% HPD: 0.8–2.8 mya). This pattern of early divergence for Philippine taxa followed by sequential divergence of taxa from the Greater Sunda Islands and then mainland taxa is commonly observed for vertebrates in this geographic region (e.g., Sheldon et al., 2009).

The biogeographic analyses indicate that the current disjunct distributions observed between the mostly Neotropical aplomado and New Zealand falcons is not necessarily due to long over-water dispersal, as extinction of taxa from intervening biogeographic regions (Oriental, Palearctic) was favored (but see Waters et al., 2013). Similar disjoint distribution patterns between New Zealand and the Neotropics have also been reported for *Nothofagus* beeches (Knapp et al., 2005), and for tinamous and moas (Haddrath and Baker, 2012). Divergences for the latter are not younger than the early Oligocene and contrast with the estimate we obtained for the aplomado/New Zealand falcons split (between 2.0 mya 95% HPD: 1.4–2.8 mya and 3.2 mya 95% HPD: 2.1–4.4). To our knowledge, the situation encountered in *Falco* is the only documented recent sister-group relationship for terrestrial birds between New Zealand and the New World.

For *Falco*, relatively little diversification occurred within a bioregion, unlike the situation for Herpetotherinae, Polyborinae and *Microhierax*. As an extreme example, none of the seven Australasian species has its closest relative in the same biome. Such a pattern was noted earlier by Cade and Digby (1982), although White et al. (1994) suggested that *F. berigora* and *F. novaezeelandiae* might be closely related. Leaving the New Zealand falcon aside, the divergences between Australasian species and their closest relative or subspecies cluster around three dates. In the analyses using both fossils as calibration points, the divergence times clustered around 4.9 mya (95% HPD: 3.6–6.2; *F. berigora*), 2.0–2.1 mya (95% HPD: 1.4–2.8; *F. longipennis*; 95% HPD: 1.4–2.8; *F. hypoleucos*), and 0.12–0.70 mya (95% HPD: 0.08–0.3; *F. peregrinus*; 95% HPD: 0.1–0.50; *F. subniger*; 95% HPD: 0.3–1.0; *F. cenchroides*). Palearctic falcons (e.g., *F. cherrug*/*F. rusticolus*, *F. subbuteo*/*F. concolor*/*F. eleonorae*, *F. amurensis*/*F. vespertinus*), however, are an exception to this pattern of low diversification within a bioregion.

4.3. A shift in diversification rates in a clade of birds

Our diversification rate analyses revealed the existence of a shift in net diversification rate in the Falconidae which was based on both a twofold increase in speciation rate and a drop in extinction rate, at the base of the genus *Falco* using Turbo-Medusa, a pattern that was not recovered using Laser. The primary difference between the two methods is that the algorithm in Laser scans for a shift in diversification rate that would have affected the whole tree at a particular time whereas Turbo-Medusa scanned for a shift at a particular node and its descendants (i.e., that rates are inherited). Thus, the fact that Laser could not statistically detect the shift may be due to the constant diversification rates observed for the Herpetotherinae, Polyborinae, and the falconets.

Recently, shifts in diversification rates have been detected in various lineages of vertebrates (birds: Jetz et al., 2012, mammals: Meredith et al., 2011; Stadler, 2011; ray-finned fishes: Rabosky et al., 2013) with the development of more powerful algorithms (Rabosky, 2006a; Harmon et al., 2008). Using the MEDUSA algorithm, Jetz et al. (2012) detected several shift for birds, mostly concerning relatively recent lineages (e.g., white eyes, woodpeckers and gulls), but the falcons were not among the groups for which a shift was detected. Although all bird species were included in Jetz et al. (2012), genetic data were lacking for a substantial number of species (about 30%). The fact that falcons were not detected by Jetz et al. (2012) as having encompassed a shift in diversification rates could be due to missing genetic data for this particular clade, and consequently inaccurate divergence times, and suggests that missing data may have impacts on the findings for other avian taxa as well.

4.4. An association between diversification rates and habitat/migration: support for an early adaptive radiation?

The BISSE analyses indicated that habitat and migration, two of the three eco-ethological characters tested, had a strong correlation with diversification rates. Indeed, lineages found primarily in open habitat (grasslands, semi deserts, tundra, open savannah) and exhibiting migratory behavior, had higher speciation rates compared to lineages found in more densely vegetated habitats (woodlands and forests) and to species that are mostly sedentary. Most migratory or open habitat species are members of genus *Falco* (although some *Falco* are also found in more forested habitat; e.g., *F. deiroleucus*/*F. rufigularis*). Most Herpetotherinae and Polyborinae species (excluding *Milvago* and some *Phalcoboenus*, *Polihierax*, *Microhierax*) are found in woodlands and forest. Current diets did not show any significant relationship with diversification rates.

Hence, it seems that the triggers for the diversification of the genus *Falco* were the opening of the habitat that occurred at the Miocene/Pliocene transition when the C_4 grasslands expanded (Cerling et al., 1997; Fortelius et al., 2006) and the evolution of migration in some falcons over the last 5 myrs. This result is in accord with a recent study that showed that migratory species have a higher diversification rate (Rolland et al., 2014). The adaptation to more open and arid habitats deserves further analysis using larger genomic data sets, with the potential to show greater variation among close relatives. For example, the copy numbers of some genes vary between the saker and peregrine (Zhan et al., 2013). Genomic data for typical woodland/forest species (e.g., *Polihierax*, *Neohierax* or *Micrastur*) that are outside of the *Falco* radiation would be necessary to confirm that these genomic changes may have allowed adaptations to new habitats.

4.5. Falconidae classification

In seeking to keep classification consistent with phylogeny, our best estimate for Falconidae phylogeny (Fig. 3) supports three recommended changes to traditional taxonomy. One is changing *Polihierax insignis* to *Neohierax insignis* to maintain monophyly for genera as used by Swann (1922). A second is to recognize *Falco columbarius aesalon*, the Old World merlin, as a distinct species, *F. aesalon*, based on its reciprocal monophyly with *F. columbarius*, the New World merlin, and its genetic distinctiveness being similar or greater to that found between other distinct *Falco* species. The third recommendation is expanding genus *Daptrius* to also include all species currently in *Milvago*, *Phalcoboenus* and *Ibycter*. This provides greater similarity in age for the genera of Falconidae. Systematists have long discussed ideal classifications in which the categorical ranks of named taxa corresponded to their relative ages, or recency of common ancestry (Bigelow, 1956; Sibley and Monroe, 1990; Avise and Mitchell, 2007). This would enable meaningful comparisons of taxa of similar age in the study of biological features like diversification rate as conducted here for Falconidae. The traditional falconid taxonomy, with the minor changes noted above, does yield subfamilies and other genera of similar age, roughly Late Miocene/Early Pliocene (Fig. 3).

5. New Falconidae classification

Falconidae
- **Subfamily Herpetotherinae**
  - **Genus** *Herpetotheres* Vieillot, 1817
    - *Herpetotheres cachinnans* (Linnaeus, 1758)
  - **Genus** *Micrastur* G.R. Gray, 1841
    - *Micrastur buckleyi* Swann, 1919
    - *Micrastur mirandollei* (Schlegel, 1862)
    - *Micrastur semitorquatus* (Vieillot, 1817)
    - *Micrastur gilvicollis* (Vieillot, 1817)
    - *Micrastur ruficollis* (Vieillot, 1817)
    - *Micrastur mintoni* Whittaker, 2002
- **Subfamily Polyborinae**
  - **Genus** *Spiziapteryx* Kaup, 1852
    - *Spiziapteryx circumcincta* (Kaup, 1852)
  - **Genus** Caracara Merrem, 1826
    - *Caracara plancus* (J.F. Miller, 1777)
    - *Caracara cheriway* (Jacquin, 1784)
  - **Genus** *Daptrius* Vieillot, 1816
    - *Daptrius americanus* (Boddaert, 1783)
    - *Daptrius chimango* (Vieillot, 1816)
    - *Daptrius ater* Vieillot, 1816
    - *Daptrius chimachima* (Vieillot, 1816)
    - *Daptrius australis* (J.F. Gmelin, 1788)
    - *Daptrius carunculatus* (Des Murs, 1853)
    - *Daptrius megalopterus* (Meyen, 1834)
    - *Daptrius albogularis* (Gould, 1837)
- **Subfamily Falconinae**
  - **Genus** *Microhierax* Sharpe, 1874
    - *Microhierax erythrogenys* (Vigors, 1831)
    - *Microhierax fringillarius* (Drapiez, 1824)
    - *Microhierax latifrons* Sharpe, 1879
    - *Microhierax caerulescens* Linnaeus, 1758
    - *Microhierax melanoleucos* (Blyth, 1843)
  - **Genus** *Polihierax* Kaup, 1847
    - *Polihierax semitorquatus* (Smith, 1836)
  - **Genus** *Neohierax* Swann, 1922
    - *Neohierax insignis* (Walden, 1872)
  - **Genus** *Falco* Linnaeus, 1758
    - *Falco zoniventris* W.K.H. Peters, 1854
    - *Falco naumanni* Fleischer, 1818
    - *Falco alopex* (Heuglin, 1861)
    - *Falco rupicoloides* A. Smith, 1829
    - *Falco rupicolus* Daudin, 1800
    - *Falco tinnunculus* Linnaeus, 1758
    - *Falco moluccensis* (Bonaparte, 1850)
    - *Falco cenchroides* Vigors & Horsfield, 1827
    - *Falco araea* (Oberholser, 1917)
    - *Falco newtoni* (J.H. Gurney, 1863)
    - *Falco punctatus* Temminck, 1821
    - *Falco sparverius* Linnaeus, 1758
    - *Falco aesalon* Tunstall, 1771

(*continued on next page*)

Falco columbarius Linnaeus, 1758
Falco dickinsoni P.L. Sclater, 1864
Falco ardosiaceus (Vieillot, 1823)
Falco vespertinus Linnaeus, 1766
Falco amurensis Radde, 1863
Falco berigora Vigors & Horsfield, 1827
Falco novaezeelandiae J.F. Gmelin, 1788
Falco femoralis Temminck, 1822
Falco deiroleucus Temminck, 1825
Falco rufigularis Daudin, 1800
Falco longipennis Swainson, 1837
Falco severus Horsfield, 1821
Falco concolor Temminck, 1825
Falco eleonorae Géné, 1839
Falco subbuteo Linnaeus, 1758
Falco cuvieri A. Smith, 1830
Falco chicquera Daudin, 1800
Falco mexicanus Schlegel, 1851
Falco hypoleucos Gould, 1841
Falco peregrinus Tunstall, 1771
Falco pelegrinoides Temminck, 1829
Falco fasciinucha Reichenow & Neumann, 1895
Falco biarmicus Temminck, 1825
Falco subniger G.R. Gray, 1843
Falco jugger J.E. Gray, 1834
Falco rusticolus Linnaeus, 1758
Falco cherrug J.E. Gray, 1834

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2014.08.010.

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