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A Paleogene origin for crown passerines and the diversification of the Oscines in the New World

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ABSTRACT

In this study, we present a detailed family-level phylogenetic hypothesis for the largest avian order (Aves: Passeriformes) and an unmatched multi-calibrated, relaxed clock inference for the diversification of crown passerines. Extended taxon sampling allowed the recovery of many challenging clades and elucidated their position in the tree. Acanthisittia appear to have diverged from all other passerines at the early Paleogene, which is considerably later than previously suggested. Thus, Passeriformes may be younger and represent an even more intense adaptive radiation compared to the remaining avian orders. Based on our divergence time estimates, a novel hypothesis for the diversification of modern Suboscines is proposed. According to this hypothesis, the first split between New and Old World lineages would be related to the severing of the Africa–South America biotic connection during the mid–late Eocene, implying an African origin for modern Eurylaimides. The monophyletic status of groups not recovered by any subsequent study since their circumscription, viz. Sylvioidea including Paridae, Remizidae, Hyliotidae, and Stenostiridae; and Muscicapoidea including the waxwing assemblage (Bombycilloidea) were notable topological findings. We also propose possible ecological interactions that may have shaped the distinct Oscine distribution patterns in the New World. The insectivorous endemic Oscines of the Americas, Vireonidae (Corvoidea), Mimidae, and Troglodytidae (Muscicapoidea), probably interfered with autochthonous Suboscines through direct competition. Thus, the Early Miocene arrival of these lineages before any other Oscines may have occupied the few available niches left by Tyrannides, constraining the diversification of insectivorous Oscines that arrived in the Americas later. The predominantly frugivorous–nectarivorous members of Passeroidea, which account for most of the diversity of New World-endemic Oscines, may not have been subjected to competition with Tyrannides. In fact, the vast availability of frugivory niches combined with weak competition with the autochthonous passerine fauna may have been crucial for passeroids to thrive in the New World.

1. Introduction

The diversity of life is not homogeneously distributed among taxonomic groups. In many taxa, such as rodents in mammals and beetles in insects, a single clade contains most of the diversity (Raikow and Bledsoe, 2000). Among birds, the order Passeriformes includes more than five thousand species that represent 60% of the extant diversity of the class (Ericson et al., 2003; Sibley and Monroe, 1990).

The remarkably diverse passerines provide an interesting model for biogeographic analyses. Their putative feeble-winged ancestors would allow the emergence of historical patterns by minimizing the masking effects of avian flight (see Ericson et al., 2003, for discussion). Several paleontological and molecular studies have agreed on a Gondwanan origin for the passerines (Barker et al., 2004; Edwards and Boles, 2002; Ericson et al., 2002). Therefore, the early history of these birds might be associated with the major events in the breakup of this southern megacontinent (Ericson et al., 2002; Mayr, 2013).

The main rupture of the Gondwanan continent would have caused the core split of the Eupasseres, which were divided into two very large groups: the Suboscines (suborder Tyranni) in Western Gondwana and the Oscines (suborder Passeri) in Eastern Gondwana (Ericson et al., 2003). The third passerine suborder includes the peculiar Acanthisittia wrens, a small group endemic

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to New Zealand (Ericson et al., 2002). After holding a controversial position within the phylogeny for decades (Ericson et al., 2003, 2002), the Acanthisittia has finally been established by molecular phylogenetic analyses as the sister lineage of the large Eupasseres clade (Barker et al., 2004, 2002; Ericson et al., 2002).

The consistent phylogenetic position of the Acanthisittia, and their endemism to New Zealand, further supports a close association between Gondwana and the passerines, as New Zealand was the first area to break away in the East (Cooper and Millener, 1993). Hence, the calibration of long-anticipated passerine timescales was finally possible (Barker et al., 2004; Ericson et al., 2002, 2014; Aggerbeck et al., 2014) using a Cretaceous estimate (around 80 million years [Ma]) for this continental breakup (Cooper and Millener, 1993).

Nevertheless, geologic data cast doubts on the reliability of the Cretaceous calibration. A more detailed survey has indicated that the northern portions of New Zealand and Australia most likely remained connected until the Early Cenozoic (Gaina et al., 1998). According to gravity field records, the final rupture between these landmasses took place only when seafloor spreading led to the formation of the Cato Trough during the middle Paleocene, before ceasing in the early Eocene (Gaina et al., 1998; Schellart et al., 2006; Worthy et al., 2010).

Additionally, a Cretaceous origin of the crown group of passerines seems questionable when their fossil record is juxtaposed with the relatively recent fossil record for modern birds (Neornithes) (Mayr, 2013). The passerines are deeply nested within Neornithes (Hackett et al., 2008; Jetz et al., 2012) and the oldest known neornithine fossil dates to the Cretaceous–Paleogene boundary (ca. 66 Ma; Clarke et al., 2005). Thus, if modern passerines originated at 80 Ma, their neoavian ancestor would most likely date to the early Cretaceous which seems unlikely due the dearth of neoavian fossil records at this stratum (Feduccia, 2003; Mayr, 2013).

Two new molecular time-scales for birds reported a recent Paleocene date for the earliest passerine divergence (Haddrath and Baker, 2012; Jarvis et al., 2014). However, these studies had a very poor taxon sampling for passerines and no more than two internal calibrations were used in spite of the large number of potential passerine priors available. Because internal calibrations are deemed critical for obtaining accurate estimates (Yang and Rannala, 2006; Yang and Yoder, 2003), reliable divergence times for the major passerine lineages have yet to be estimated.

Limited taxon sampling has also been a concern in previous studies on passerines (Barker et al., 2004, 2002; Irestedt and Ohlson, 2008). Thus, we decided to assemble a large dataset using molecular sequences for 1119 genera of Passeriformes (approximately 86% of passerine generic diversity; Gill and Donsker, 2014). The dataset was used in monophyly tests for 127 families (98% of familial diversity) and more inclusive passerine groups.

In this study, we present a comprehensive family-level phylogenetic hypothesis for passerines. We generated an unmatched relaxed Bayesian clock time-tree for Passeriformes using 15 internal fossil calibrations to accurately date the first node in the passerines (the Acanthisittia–Eupasseres split) and to identify the pivotal factors that allowed their impressive radiation. In particular, we focus on the peculiar colonization patterns by the different passerine lineages in the New World, which have received less attention than their Old World counterparts (Alstrom et al., 2006; Barker et al., 2004; Cibois and Cracraft, 2004; Fregin et al., 2012).

2. Material and methods

2.1. Taxon sampling and geographical distribution

In our analysis, we assumed the monophyly of passerine genera by concatenating sequences for different species into a single (mosaic) genus sequence to construct a comprehensive molecular phylogeny for this group. The use of all recognized passerine species (roughly 5700 species) would significantly increase the proportion of missing data in our matrix. In addition, the computational time required for such a dataset would inevitably make the tree search algorithm suboptimal (Stamatakis, 2006a).

The genera and family classifications follow the International Ornithological Committee (*IOC* 4.4) nomenclature (Gill and Donsker, 2014). Higher ranks follow Sibley and Ahlquist's (1990) proposal and other major passerine studies (Ericson et al., 2003; Ohlson et al., 2013). Five non-passerine genera (*Amazona*, *Nestor*, *Cuculus*, *Falco*, and *Grus*) were selected as outgroups based on phylogenetic results obtained for this purpose (Suh et al., 2011; Wang et al., 2012). The distribution and geographic data follow the *Handbook of Birds of the World* (del Hoyo et al., 1992–2011). For each genus, the distribution was determined by the sum of individual species distributions. Finally, we restricted our biogeographical perceptions using the two geographical regions that are deeply connected to passerine history: the New World and the Old World.

2.2. Sequence alignments

Our dataset was assembled using the PhyLoTA browser release 1.5 (Sanderson et al., 2008). A total of five mitochondrial (cytochrome b – *cytb*, cytochrome oxidase I – *coxI*, NADH dehydrogenase subunit 2 – *nd2*, and ribosomal 12S and 16S) and four nuclear (myoglobin exons 2 and 3 – *myo*, ornithine decarboxylase exons 6 through 8 – *odc*, and the recombination-activating protein genes 1 and 2 – *rag1*, *rag2*) genes were selected. These markers include sequences available for a wide range of passerine families and fall within the scope of the present study.

For each marker, a single representative sequence was chosen for each passerine genus based on the length and quality of the sequences available. Each gene was individually aligned using the MUSCLE algorithm (Edgar, 2004) in SeaView 4 (Gouy et al., 2010) and adjusted by eye, preserving the correct reading frame for all protein coding sequences before concatenation. The ribosomal genes showed a sharp similarity after the algorithmic alignment, discarding additional secondary structure prediction procedures. Our primary dataset comprised an alignment of 12,575 nucleotides for 1119 passerine genera (see Table S1 for complete list of genera). Alignments are available upon request from the authors.

2.3. Phylogenetic analyses and sampling strategies

The phylogeny reconstruction of the primary dataset followed a maximum likelihood (ML) approach (Felsenstein, 1981) implemented in RaxML-HPC 7.3.2 (randomized accelerated maximum likelihood for high performance computing), which is widely recognized as suitable for very large phylogenetic datasets (Izquierdo-Carrasco et al., 2011; Lartillot and Philippe, 2008; Philippe et al., 2012; Stamatakis, 2006b). All phylogenetic analyses were conducted using the CIPRES Science Gateway (Portal 2) online server (Miller et al., 2012).

To identify putative partition schemes (Minin et al., 2003), we analyzed the dataset using PartitionFinder 1.0.1 (Lanfear et al., 2012). For this purpose, we adopted the Bayesian Information Criterion (BIC) because it accommodates uncertainty in parameter estimation (Sullivan and Joyce, 2005) and avoids over-parameterization (Rannala, 2002) by penalizing over-fitting (Minin et al., 2003; Sullivan and Joyce, 2005). Due to the large dataset size, we ran this program using a pruned dataset (329 genera, see details below) testing two partitions between three mitochondrial and three nuclear markers. A single partition under the general time reversible (GTR) model (Lanave et al., 1984) with a gamma-distributed rate variation (Yang, 1994) was indicated as the best scheme under the BIC criterion. Since we were unable to evaluate our original dataset in the Partition Finder, we estimated a RaxML tree on a 12-partition scheme equivalent to each gene and compared the likelihood values with the 'n' function in RaxML 7.3. The likelihood values of the 12-partitioned tree were smaller than the one obtained from the single-partitioned dataset, and thus we adopted the single-partitioned as our default.

Nevertheless, tree searches do not perform well in large datasets under the GAMMA model (Stamatakis, 2006a) due to restrictions on the number of rate categories. In such cases, the CAT approximation of rate heterogeneity with more rate categories is recommended (Izquierdo-Carrasco et al., 2011). In this study, we applied the ML search algorithm using both the CAT approximation with 40 rate categories and the GAMMA model with the default four-rate categories in RaxML. After the tree search, the likelihood values of the trees were compared using the –z function in RaxML (Izquierdo-Carrasco et al., 2011). The comparison showed that the CAT tree was the best; therefore, it was chosen as the tree on which we based the subsequent analyses. For large datasets, a rapid bootstrap combined with a fast ML search is known to perform best when using a large number of bootstrap pseudo replicates (Stamatakis et al., 2008). In our case, branch support values for the primary ML tree were estimated using 2000 bootstrap pseudo replicates (Stamatakis et al., 2008).

Additionally, we excluded *rogue* taxa from our primary dataset to improve the phylogenetic resolution of our tree. Rogues are defined as taxa with insufficient or ambiguous phylogenetic signals that dramatically reduce the resolution of the entire phylogenetic tree (Aberer et al., 2013; Aberer and Stamatakis, 2011). For this analysis, we used the RogueNaRok algorithm (available at http://exelixis-lab.org/roguenarok.html). The statistical threshold for identifying rogues depends on user input (Aberer, personal communication). Thus, we only removed rogues that dramatically decreased the support values (0.5 threshold) so that genera diversity would be maintained for our phylogenetic purposes. A total of 58 rogues were identified and pruned from our primary alignment, resulting in a final dataset of 1061 genera.

A ML tree search algorithm was implemented a second time using the final (rogue-excluded) dataset under the same conditions described above for the primary dataset. This search resulted in a topology (Fig. S1) that was virtually identical to the primary ML tree with 1119 genera (not shown). Because there was a notable increase in support values throughout the tree, we adopted the rogue-excluded tree as our final phylogenetic tree (collapsed Fig. 1, non-collapsed Fig. S1).

2.4. Topological consistency tests

Tests involving phylogenies constructed using different taxon sampling schemes attest to the robustness of our result (Chesser and Have, 2007). The ML topologies for the primary (1119 genera), final (1061 genera), and pruned (329 genera – see next section for pruning strategy) datasets were strikingly similar. We then performed two additional topological tests to verify the robustness of the data.

The first test consisted of removing mutually non-overlapping sequences to allow a full comparison between all taxa, resulting in an 816-genera dataset. The second test consisted of a super-tree analysis using the PhySIC-IST program that unveils topological conflict between individual marker trees (Scornavacca et al., 2008). For this analysis, we used a subset (87 genera; Table S1) and the molecular markers that were available for all major passerine lineages (*nd2*, *cytb*, *cox1*, *rag1*, *rag2*, *odc*, and *myo*). The final topological result was a super-tree (Fig. S2) that was virtually identical to that retrieved using the concatenated dataset. Thus, the five topological tests (primary, final, pruned, overlapping, and super-tree) provided very similar results, which, along with the high bootstrap support values for the clades, strongly attest to the robustness of the final topology.

2.5. Divergence time analysis

We performed two separate analyses to estimate divergence times. The dating analyses were first tested in the primary (1119 genera) and final (1061 genera) datasets using BEAST (Drummond et al., 2012) and MCMCtree (Yang, 2007) but they failed to stabilize. Thus, a pruned dataset was built for the time inference analyses (this dataset was also used for the partition testing analyses; see above).

The pruning strategy was performed as follows. For each monophyletic family (see Fig. S1), up to three genera were selected according to sequence length. In the case of non-monophyletic families, we maintained this strategy for the core-family clade but also included the outlier genera. Furthermore, because we were particularly interested in studying the New World colonization by Oscines, we kept the first branching-off of all New World-endemic clades to estimate the time of these key divergences. The pruned dataset comprised 329 taxa and all 127 families from the original dataset (Fig. S3). The dataset was submitted to an ML phylogenetic analysis in RaxML using the same procedure described above.

For time inferences, the pruned topology from RaxML was input to BEAST v. 1.8 software (Drummond et al., 2012) and to MCMCTree software (PAML v. 4.3 package; Yang, 2007) for uncorrelated relaxed-clock analyses using the CIPRES Science Gateway (Miller et al., 2012). In BEAST, independent runs failed to converge when topology was allowed to vary, and thus the topology was fixed for the molecular dating analyses. For fossil calibration points, the use of lognormal distributions is recommended as they better represent a hard minimum (using the age of the fossil) and soft maximum constraints (Benton et al., 2009; Forest, 2009; Parham et al., 2012; see also Ho and Phillips, 2009). Nevertheless, the program again failed to run using lognormal priors with the RaxML tree, therefore we performed a rough divergence times estimate to generate an ultrametric topology for this analysis. The ultrametric tree was estimated using normal distributions for all priors. In this case, the dates on the ultrametric tree served only as starting points for the final divergence time inferences that used lognormal distributions for all internal priors as recommended (see next section for details). In some cases, time estimates for this ultrametric topology slightly violated our original time bounds and this information was used to extend time bounds for the final dating analyses (Table 1).

In the BEAST analysis, the divergence times were estimated under the GTR + gamma model (GTR + Γ, five rate categories) using the lognormal uncorrelated relaxed clock model (Drummond et al., 2006). The tree prior was set as a Yule speciation process birth rate to estimate node heights (Gernhard, 2008). The priors of all remaining parameters, such as the base frequencies, gamma shape parameter, and root height of the tree, were kept at default values. Five independent Markov Chain Monte Carlo (MCMC) chains were run to check the convergence of the results. The stability of the combined MCMC chains and the Effective Sample Size values for most nodes were greater than 500 performed with Tracer 1.5 (Drummond and Rambaut, 2007). The only node that failed to reach such robust stability was the root for which an effective sample size of 152 was recovered which is considered acceptable (Drummond and Rambaut, 2007). A total of 124×10^6 generations were run using sampling intervals at every 1000th generation and a *burn-in* of 12×10^6 generations was discarded.

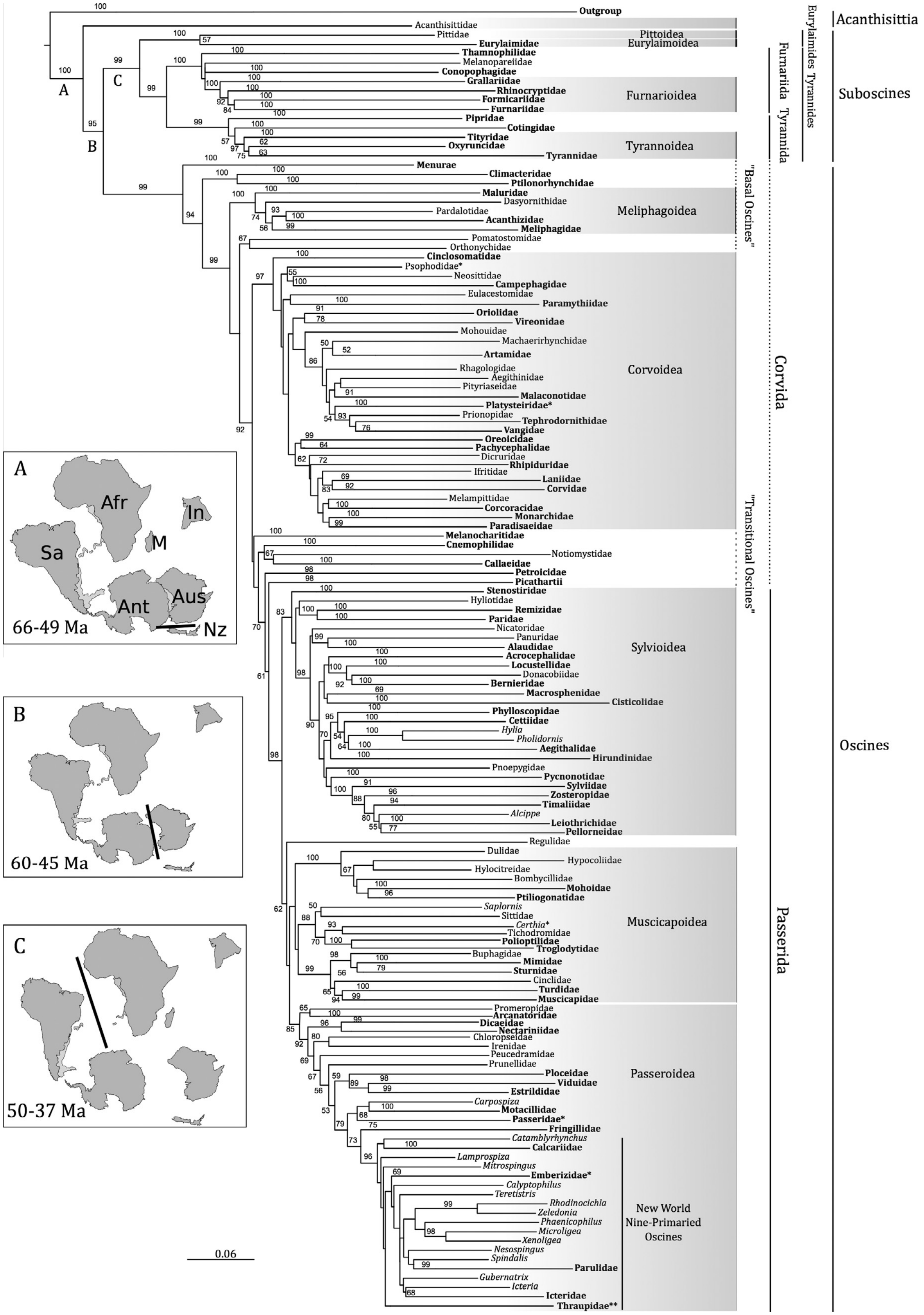

Fig. 1. Passerine phylogenetic relationships. Final maximum likelihood tree using 1061 genera (and 127 passerine families) and nine markers (five mitochondrial and four nuclear genes). Monophyletic families are shown as single lineages and bold family names indicate more than one genus was included. Asterisks indicate paraphyletic families; double asterisks in Thraupidae signal the insertion of the Cardinalidae and Coerebidae. Bootstrap values greater than 50 are shown. Capital letters represent the main Gondwana breakup events: (A) Acanthisittia–Eupasseres divergence and the rupture of Neozelandic plate; (B) Oscine isolation in the Australian plate and (C) Tyrannides–Eurylaimides divergence and the rupture of the insular connection between Africa and South America. Maps show the continental arrangement for the respective nodes. South America (Sa); Africa (Afr); India (In); Madagascar (M); Antarctic (Ant); Australia (Aus) and New Zealand (Nz).

Table 1
Details on the sixteen calibration points (the root and 15 internal) used as time priors for the divergence time analyses. Times are given for the upper and lower bounds (in millions of years) imposed using the 97.5% confidence interval of the lognormal distribution for BEAST and the uniform prior in MCMCTree. The asterisk (*) indicates the fossils that were described based on explicit apomorphic characters.

Divergence	Clade	Prior ranges (Ma) and prior distributions		Fossil specimen/geological evidence	Museum numbers	Type locality	References
		BEAST	MCMCTree (uniform priors with soft bounds)				
Neornithes	Modern birds (Root)	65–120 Normal	Hard bound on 100 Ma	*Vegavis iaai*, disarticulated partial postcranial skeleton	MLP 93-I-3-1	Vega Island – Antarctica	Clarke et al. (2005)
Passeriformes	Crown passerines	45–82 Lognormal	82–52	Passeriformes gen. sp. Indet carpometacarpus and tibiotarsus/Cato Trough formation and de facto separation of New Zealand from Gondwana	QM F20688, QM F24685	Murgon – Queensland – Australia	Boles (1995a, 1997), Mayr (2013), and Worthy et al. (2010)
Eurylaimidae-Pittidae*	Old World Suboscines	16–82 Lognormal	20–16.9	Eurylaimidae gen. sp. Indet tarsometatarsus, humerus and ulna	Wi-We II (1937) 18189, 18188, 18191	Wintershof (West) – Bavaria	Ballmann (1969)
Atrichornis-Menura*	Menurae (Basal Oscines)	16–82 Lognormal	23–16	*Menura tyawanoides*, metacarpus	QM F.20887 (AR 11466)	Riversleigh – Queensland – Australia	Boles (1995b)
Meliphagidae*	Meliphagoidea (Basal Oscines)	7–82 Lognormal	16–7	Meliphagidae gen. sp. Indet, tarsometatarsus	QM F24684	Riversleigh – Queensland – Australia	Boles (2005)
Galerida-Alauda	Alaudidae (Sylvioidea)	7–82 Lognormal	23–15.97	*Galerida cserhatensis* tibiotarsus, ulna	Litke 2, P 2010.5/1	North Hungary	Jenõ and János (2012)
Anthus-Macronyx	Motacillidae (Passeroidea)	5–80 Lognormal	15.97–11.63	*Anthus antecedens*, phalanga alae	Felsőtárkány, P 2006.352/1	North Hungary	Jenõ and János (2012)
Cinclus-Turdidae + Muscicapidae	Muscicapoidea	16–82 Lognormal	23–15.97	*Cinclus major*, carpometacarpus	Litke 2, P 2010.6	North Hungary	Jenõ and János (2012)
Erithacus-Alethe	Muscicapidae (Muscicapoidea)	11–82 Lognormal	15.97–11.63	*Erithacus horusitzkyi*, ulna	Mátraszőlős 1, P 2008.335/1	North Hungary	Jenõ and János (2012)
Luscinia-Brachypteryx	Muscicapidae (Muscicapoidea)	10–80 Lognormal	23–15.97	*Luscinia praeluscinia*, coracoid	Litke 2, P 2010.8.	North Hungary	Jenõ and János (2012)
Certhia-Tichodroma	Certhioidea (Muscicapoidea)	5–80 Lognormal	11.63–5.33	*Certhia janossyi*, coracoid	Rudabánya 2, MÁFI V.11,130.1; V. 29205	North Hungary	Jenõ and János (2012)
Phylloscopus-Seicercus	Phylloscopidae (Sylvioidea)	11–82 Lognormal	15.97–11.63	*Phylloscopus miocaenicus*, phalanga alae	Felsőtárkány, P 2006.352.2	North Hungary	Jenõ and János (2012)
Lanius-Corvinella	Laniidae (Crown Corvoidea)	4–80 Lognormal	15.97–11.63	*Lanius schreteri*, scapula	Felsőtárkány–Felnémet, P 2010.30	North Hungary	Jenõ and János (2012)
Bombycilla	Bombycilloidea (Muscicapoidea)	16–82 Lognormal	23–15.97	*Bombycilla hamori*, tibiotarsus	Litke 2, P 2010.9/1	North Hungary	Jenõ and János (2012)
Sturnus-Lamprotornis	Sturnidae (Muscicapoidea)	5–80 Lognormal	11.63–5.33	*Sturnus kretzoii*, carpometacarpus	Rudabánya 2, MÁFI V. 11.131.1; V. 29206	North Hungary	Jenõ and János (2012)
Emberiza-Miliaria	Emberizidae (Passeroidea)	8–83 Lognormal	23–15.97	*Emberiza bartkoi*, humerus	Litke 2, P 2010.11/1	North Hungary	Jenõ and János (2012)

For the MCMCTree program, the input tree was the original RaxML pruned topology but no branch length information was required. In this analysis, time priors have a uniform distribution by default; thus, equal probabilities are assigned for any data within the soft-bound limits. This analysis was conducted with the HKY substitution model with five gamma categories. The number of samples was 200,000, sampling frequency was 10, and burn-in was 1000. The stability of the run was verified in Tracer and the analysis was run twice to check for convergence.

2.6. Fossil calibrations

Time-trees were calibrated with independent time priors for one or more nodes in the phylogeny (Rambaut and Bromham, 1998; Sanderson, 1997; Yang and Rannala, 2006). In this study, the calibrations included the root, the Acanthisittia–Eupasseres split and 14 internal passerine nodes (Table 1). For the root, the time priors were set to accommodate the Cretaceous (Barker et al., 2004) and the Cenozoic (Mayr, 2013) hypotheses for the origin of passerines. Hence, time bounds in BEAST and MCMCTree ranged from 50 to 120 Ma for this node (Brown et al., 2008; Ho and Phillips, 2009).

In our final BEAST analysis, all time priors for internal nodes followed a lognormal distribution, which is recommended due to their direct fossil calibration (Benton et al., 2009; Forest, 2009; Parham et al., 2012; see also Ho and Phillips, 2009). For the root, however, we used a normal distribution, as it is considered best when no direct fossil record is available for the node. This situation was the case for our analysis, as we used the date of the fossil duck *Vegavis* (oldest Neornithes ~66 Ma) to establish a minimum date for our root at the Passeriformes–Psittaciformes split (Ho and Phillips, 2009; Suh et al., 2011).

Table 2
Time estimates for the Acanthisittia–Eupasseres split using different time prior schemes in BEAST. Final estimates discussed in text are those using all time priors.

Number of internal calibrations (lognormal)	Acanthisittia–Eupasseres calibration (lognormal)	Acanthisittia–Eupasseres node date (median)	95% HPD
14	Present	56.7	48.9–66.1
	Absent	59.2	50.4–69.8
3	Present	49.7	45–64.2
	Absent	58.1	36.7–83.1

The second calibration node was the Acanthisittia–Eupasseres split. The prior for this node was allowed to vary between 45 and 82 Ma in the lognormal density in BEAST. Also, for the MCMCTree program, this node was calibrated using the default flat prior (95% of confidence) between 52 Ma and 82 Ma and soft bounds (5% remaining). Again, in both programs, the time prior range for this node included time estimates to accommodate the two competing hypotheses regarding the origin of passerines (Table 1).

The remaining 14 internal passerine calibrations were based on reliably dated and identified fossil specimens of Eupasseres, which represented main lineages of the group. Three of these 14 fossil calibrations follow the standards of a recent study as they were based on distinct apomorphic characters (Parham et al., 2012) namely the eurylaimid Suboscines (Ballmann, 1969); the Basal Oscines Menurae (Boles, 1995b) and Meliphagidae (Boles, 2005). On the other hand, the remaining 11 fossils were only recently identified from the Miocene of Hungary [Corvoidea, Sylvioidea, Muscicapoidea, and Passeroidea] (Jenõ and János, 2012), but they lack explicit apomorphy-based taxonomic assignments and do not satisfy the ideal requirements for calibrations (Parham et al., 2012).

Thus, to verify the consistency of our calibration points, alternative calibration schemes were performed on the original BEAST set (Table 2). First, we removed the Acanthisittia–Eupasseres calibration, allowing this node to be estimated without any prior information. Our second calibration scheme included a reduced set with the three fossils that satisfy the requirements for ideal fossil based calibrations (see Parham et al., 2012), plus the *Vegavis* time prior at the root. The third calibration scheme added the Acanthisittia–Eupasseres calibration to the second scheme. A final test was performed as the shape of the log-normal induces most of the points of the distribution to the minimum (time) bound. In BEAST, this would produce a bias in favor of the Paleogene hypothesis for the origin of passerines. Thus, we have also performed a final test using the normal distribution for all 16 priors. Even though time results between all calibration schemes were extremely close, it would be interesting to perform a formal phylogenetic analysis for all passerine fossils to verify whether our divergence times remain consistent.

For these calibrations, the lognormal priors were configured with the age of the fossil as the minimum date and the maximum was extended to 80–82 Ma, the maximum date for the Acanthisittia–Eupasseres prior. For the MCMCTree program, time priors included the range of the geologic period from which the fossil was recovered (Table 1; Geologic Time Scale 2012, Gradstein et al., 2012).

3. Results and discussion

Due to the magnitude of the final dataset, a summarized version of the final ML passerine tree (1061 genera and 127 families) is shown in Fig. 1 depicting monophyletic families as individual lineages. Of the 127 families sampled, 38 were monogeneric, and only the family Pomatostomidae was sampled for a single genus. Our topology shows that only 7 families out of the 88 formally tested were not recovered as monophyletic clades. In all those cases, only a single genus or a small number of genera deviated from the family core. These non-monophyletic families are depicted in our tree with an asterisk (Fig. 1). All 7 paraphyletic families were members of the suborder Oscines and were evenly distributed among the large superfamily clades Corvoidea (2), Muscicapoidea (1), and Passeroidea (4). This result indicates that current taxonomic assignments for passerine families are largely unequivocal.

It should be noted that most of the phylogenetic relationships in our topology are strongly supported despite the magnitude of the passerine radiation and our unparalleled taxon sampling effort. Due to space limitations passerine groups that were monophyletic in the tree (Fig. 1) are indicated by the number of genera and a bootstrap support along this section. The time inferences were based on a pruned alignment representing all major passerine lineages (329 genera and 127 families; Fig. S3; see Material and Methods for details). Topological differences between final and pruned trees are discussed in the text.

The distributional patterns in Passeriformes demonstrate a well-known distinction between clades endemic to the New World and those restricted to the Old World (Barker et al., 2012; Moyle et al., 2006; Robinson et al., 2010). Hence, we plotted the entire final topology against those geographic distributions (Fig. 2) to unveil the details of passerine history in the New World.

In our tree, the order Passeriformes (1061 genera, 100 Bootstrap Probability [BP]) was divided into three lineages that properly represent the three currently recognized passerine suborders. The suborder Acanthisittia (one genus) was sister to the Eupasseres (1060 genera, 95 BP), which contains the other two suborders: the Suboscines (suborder Tyranni; 284 genera, 99 BP) and the Oscines (suborder Passeres; 776 genera, 99 BP). As mentioned, this first passerine split between the Acanthisittia and the Eupasseres is most likely associated with the breakup of Gondwana, as the former are endemic to New Zealand (Barker et al., 2004; Ericson et al., 2002; Fig. 1a).

3.1. Acanthisittia

Our time estimate for the Acanthisittia–Eupasseres split, between the late Paleocene and early Eocene (56 Ma; Tables 2 and 3; and Fig. 1a), strongly contrasts with previous passerine calibrations (Barker et al., 2004; Ericson et al., 2002, 2014; Aggerbeck et al., 2014), which assumed that Acanthisittia separated from Eupasseres during the initial breakup of New Zealand in the Cretaceous at around 80 Ma (Cooper and Millener, 1993). Our results suggest that the Neozelandic passerine ancestors were able to maintain gene flow across the continental Gondwana until the Paleocene when the Cato Trough formed. Seafloor spreading created this vault in the Tasman Sea, which was responsible for the complete isolation of these landmasses in the Paleocene (Gaina et al., 1998; Schellart et al., 2006). This finding indicates that previous passerine divergence estimates were biased by nearly 30 Ma.

The oldest passerine fossil (Boles, 1995a, 1997), from the Paleocene, lacks derived osteological characters and is considered a member of the stem lineage of passerines (Mayr, 2013). Because passerines are deeply nested within modern birds (Neornithes), a Cretaceous origin for crown passerines would push the origin of Neornithes farther back to the early Cretaceous, which is unlikely given that avian fauna records from this period are very rare (Feduccia, 2003; Mayr, 2013). Hence, our Paleogene estimate for the origin of passerines is also more concordant with the fossil

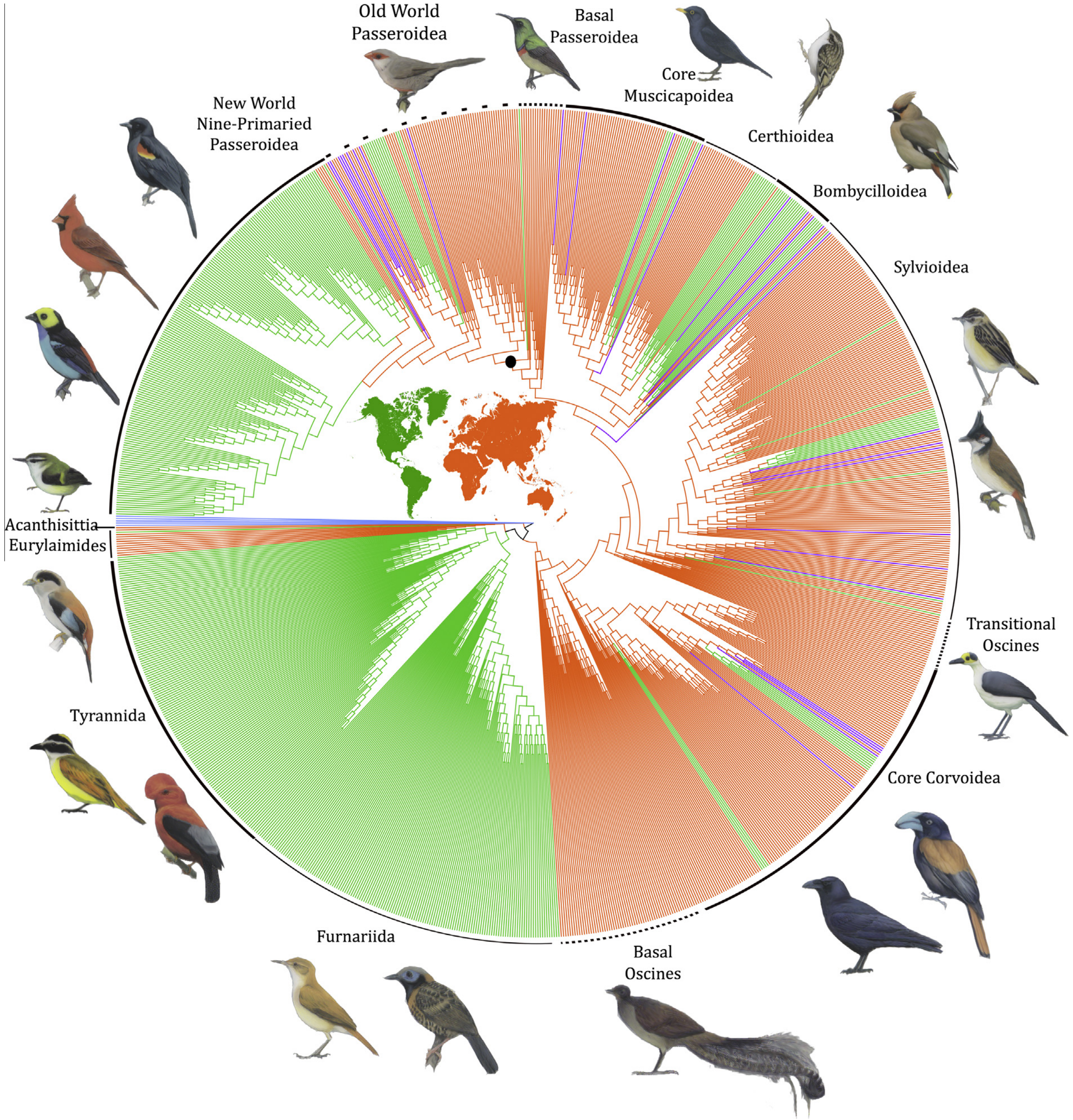

Fig. 2. Geographic distribution of passerine genera. The geographic distribution is based on a New World (green) and Old World (orange) division using the final Maximum Likelihood tree topology. Pink color indicates occurrence in both regions. The black circle indicates the shift from nectarivory to frugivorous-granivorous feeding habits, found almost without exception in Core Passeroidea, which could have been decisive to the extremely high diversity found in this group. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

record for Neornithes than previous estimates for the Acanthisittia split.

According to our time-scale, after the Acanthisittia split, the Eupasseres ancestor gave rise to the Suboscine and Oscine lineages at the early Eocene, between 52 and 45 Ma (Table 3). This estimate also supports the hypothesis that the vicariant events in the early passerines were closely connected to the subsequent rupture of Gondwana. In this case, the geological event that spurred the reproductive isolation between these major passerine suborders was the drifting of Australia from the Gondwana mainland (Haddrath and Baker, 2012; Woodburne and Case, 1996; Fig. 1b).

Antarctica and Australia started to drift apart in the latest Cretaceous (Li and Powell, 2001; Woodburne and Case, 1996). Nevertheless, overland dispersal was viable until the early Eocene (55–52 Ma) (Tambussi and Degrange, 2012; Woodburne and Case, 1996), when the formation of a shallow seaway between Eastern Antarctica and Australia might have critically reduced faunal interchange (Li and Powell, 2001; Woodburne and Case, 1996). Geological data indicate that faunal exchange was virtually impossible after the final rupture between the landmasses in the late Eocene (35 Ma) (Li and Powell, 2001).

This ancient seaway formation clearly agrees with our time estimate for the Suboscines–Oscines split (52 Ma; Table 3; and Fig. 1b) and is supported by different taxonomic groups that diverged around the same time. One such example is the divergence between the South American rheas and the Australian cassowaries in the middle Eocene (Härlid et al., 1998). In marsupial mammals, the split of the monotypic South American

Table 3
Divergence time estimates for main splits in Passeriformes using the BEAST and MCMCTree programs. The mean age estimate is shown with the high posterior density (HPD) of 95%. "Lineage" indicates the time estimate for the first split in the clade.

Node/divergence	BEAST Normal (root) and lognormal priors		MCMCTree Uniform priors with soft bounds	
	Node age	95% HPD	Node age	95% HPD
Acanthisittia/Eupasseres	56.7	49–66.2	52.4	49.2–55.7
Oscines/Suboscines	52.2	45.5–60.8	48.9	45.5–52
Eurylaimides/Tyrannides	43.4	37.7–50.5	40.5	36.4–44.1
Sapayoa/(*Eurylaimus*, *Philepitta*)	29.2	24–35.1	18.7	17.3–19.6
Furnariida/Tyrannida	38.9	33.4–44.9	36.3	32.7–39.4
Furnariida lineage	32.7	28.2–37.7	29.9	26.8–32.6
Tyrannida lineage	27.5	23.7–32.1	27.6	24.8–29.8
Oscines lineage	41.6	36.4–48.1	41	37.8–43.9
Corvoidea lineage	27.5	24–31.7	28.4	26 – 30.5
Passerida/Petroicidae	30.6	26.6–34.8	30.7	28.2–32.5
Sylvioidea lineage	28.1	24.8–32.2	28.3	26–30
Muscicapoidea lineage	27.4	24.2–31.4	27.5	25.4–29
Bombycilloidea lineage	21.6	18.8–25.1	22.2	19.8–24.4
Certhioidea lineage	24.5	21.2–28.3	24	21.2–26.2
Core Muscicapoidea lineage	22.8	19.9–26.1	23.3	21.9–24.3
Passeroidea lineage	27.1	23.8–31	27.6	25.4–29.2
Prunella/Core Passeroidea	22.8	20.1–26.2	24	22.1–25.5
Fringillidae/New World Nine Primaried Oscines	19	16.7–21.9	21	19.4–22.3

Microbiotheria from the Australian bandicoots and numbats was also estimated at the middle Eocene (45 Ma) (Nilsson et al., 2004). These studies corroborate the notion that the separation of Australian and South American faunas took place between the early and middle Eocene. Altogether, our results strongly suggest a major vicariance process for the Suboscines–Oscines divergence after the rupture of Australia and Eastern Antarctica. The Oscine isolation on the drifting Australian plate left the Suboscine ancestor dwelling in the Antarctic–South American remnants of Gondwana. The main passerine diversifications were about to start.

3.2. Suboscines

The suborder Suboscines is traditionally divided into two infraorders, which were recovered as clades in our study (Fig. 1). The Tyrannides (272 genera, 99 BP) are endemic to the New World and are mostly restricted to South America. The second Suboscine clade includes the Eurylaimides (12 genera, 100 BP), which are widely distributed in the Old World. These clades have diversified into very distinctive life histories since their common ancestor. According to our time results, the Suboscine ancestor originated the Eurylaimides (in the Old World) and Tyrannides (in the New World) lineages in the middle Eocene (Fig. 1c). In fact, the Tyrannides are usually considered autochthonous to the American continent (Ohlson et al., 2013) and thrived there since Gondwana broke apart.

3.2.1. Tyrannides (New World Suboscines)

Tyrannides are often called New World Suboscines, and their descendants have undergone an incredible radiation, with nearly 1200 living species (Moyle et al., 2009; Ohlson et al., 2013; Tello et al., 2009). However, despite the magnitude of their diversity, tyrannids are ecologically restricted and are mainly insectivorous birds that inhabit tropical forests of Central and South America (del Hoyo et al., 1992–2011). In fact, only six extant genera (four lineages in the family Tyrannidae) have extended their original distribution into North America (del Hoyo et al., 1992–2011). Moreover, the single paleontological evidence for the group, an unidentified specimen from early Miocene deposits of Patagonia, Argentina (Noriega and Chiappe, 1993), does not extend the geographic range of tyrannids.

The Tyrannides are divided into the parvorders Furnariida (131 genera, 100 BP) and Tyrannida (141 genera, 99 BP) (Ohlson et al., 2013), a division that agrees well with our clades (see Fig. 1). The Furnariida are traditionally separated into the superfamilies Thamnophiloidea (typical ant-birds) and Furnarioidea (ovenbirds and allies) (Ohlson et al., 2013), but our topology contradicts this interpretation. In our results, Thamnophiloidea was recovered as a paraphyletic collection that includes the Furnarioidea (86 genera, 100 BP), causing the family Thamnophilidae (42 genera, 100 BP) to be a sister group of all remaining Furnariida (89 genera, 22 BP) (Fig. 1). Similarly, previous studies have found contradictory results in Furnariida relationships. For instance, Ohlson and collaborators (Ohlson et al., 2013) sampled 94 genera and recovered the two superfamilies as monophyletic groups, whereas Moyle and collaborators (Moyle et al., 2009), with a larger generic sampling (124 genera), found a topological result similar to ours. These results illustrate how major groups are sensitive to poor taxon sampling, and show that more detailed topological assessments are revealed only with exhaustive taxon sampling (Wiens, 2003). However, it should be noted that bootstrap support is low for this particular branch of the Suboscine tree (Moyle et al., 2009; Ohlson et al., 2013; Fig. 1).

The parvorder Tyrannida comprised three major lineages in our final tree: Cotingidae (cotingas; 23 genera, 100 BP), Pipridae (manakins; 15 genera, 100 BP), and the superfamily Tyrannoidea (tyrant flycatchers; 103 genera, 97 BP) (Fig. 1). In the pruned tree, the Tyrannida were primarily divided into a Cotingidae plus Pipridae cluster (97 BP), with Tyrannoidea as a sister group. Conversely, in the final tree, Pipridae was the sister group to the clade that includes Cotingidae and Tyrannoidea (57 BP). This result also reinforces the importance of large taxon sampling to resolve higher-group relationships, as shown by the Cotingidae plus Pipridae clade, which had a very high support value that was broken by increased taxon sampling.

Our time results indicate that the earlier Furnariida diversification in the early Oligocene did not prevent the subsequent New World radiation of their cousins, the Tyrannida, in the late Oligocene (see Table 3). Although the geographic distributions of Furnariida and Tyrannida greatly overlap (del Hoyo et al., 1992–2011), distinct niches may have made their diversification equally successful. The majority of Furnariida lineages inhabit wet forests (del Hoyo et al., 1992–2011; Willis, 1976), whereas most of the Tyrannida dwell in open areas, such as savannahs and forest edges (Willis, 1976).

It is well documented that the entomological fauna experienced a severe decline during cold temperature epochs (Sinclair et al., 2003; Willis, 1976). The glaciation period in the early Oligocene (Zachos et al., 2001) may have confined the strictly insectivorous Furnariida (Willis, 1976) to warmer environments such as tropical forests, where insect abundance may have remained high. This would have allowed furnariids to diversify despite the colder climate during the early to middle Oligocene. Subsequently, the Andean uplift in the second half of Oligocene (Hoorn et al., 2010) contributed to the rise in temperature in the Neotropics (Zachos et al., 2001) and intensified the desertification process (Hoorn et al., 2010), resulting in the expansion of the savannah habitats occupied by Tyrannida (Ohlson et al., 2008; Willis, 1976). The higher temperatures would have also driven the radiation of fruit-bearing plants and insects into the savannah areas, opening up more niches for the more generalist feeding Tyrannida to thrive in. This scenario fits well our time-estimates for the diversification of the Tyrannides.

3.2.2. Eurylaimides (Old World Suboscines)

The sister group of the New World tyrannids, the Eurylaimides, underwent a sharply distinct diversification process in the Old World. The Eurylaimides are currently less diverse than their New World counterparts but are well distributed in Africa, Madagascar, and Southeast Asia (Ericson et al., 2003; Moyle et al., 2006). In addition, paleontological records from the Miocene stratum of Bavaria (Germany) (Ballmann, 1969) and the Oligocene stratum of France (Mayr and Manegold, 2006) suggest an even greater geographic range throughout central Europe (Manegold et al., 2004; Mourer-Chauviré, 1995). Given their extensive distribution, it is not surprising that hypotheses for the diversification of Eurylaimides remain highly controversial (Irestedt et al., 2006; Moyle et al., 2006; Prum, 1993).

The ancestral region of the Old World Suboscines is difficult to pinpoint based on the current distribution of any of the first three splits of Eurylaimides (Moyle et al., 2006; Irestedt et al., 2006; Fig. S1). At the same time, a biogeographic analysis of Eurylaimides from a genus-level perspective is tentative, as the first split is between the pittas (Pittidae) and broadbills (Eurylaimidae), which present wide and overlapping distributions in the Old World.

The leading hypothesis for the diversification of Eurylaimides begins with a long overwater dispersal of their ancestors from East Gondwana to isolated India in the late Cretaceous (70 Ma; Moyle et al., 2006), requiring that a considerable extent of sea be covered (>2000 km; Ali and Aitchison, 2008; Chatterjee et al., 2012). Under this hypothesis, the main diversification begun when India collided with Southeast Asia in the Paleocene, subsequently spreading Eurylaimides ancestors into Africa (Moyle et al., 2006). However, these time frames were proposed based on the Cretaceous calibration for the Acanthisittia–Eupasseres split (Barker et al., 2004; Ericson et al., 2002), which is shown to be unreliable in this study. Our results indicate that eurylaimids split from the tyrannid stock much later, in the middle Eocene (around 40 Ma; Table 3). At that time, the Tyrannides had been long isolated in the South-American plate, and the Indian plate had been in contact with continental Asia since 50 Ma (Chatterjee et al., 2012), making an Antarctica–India dispersion virtually impossible. Hence, based on our time estimates, an alternative hypothesis for the divergence of the New and Old World Suboscines must be proposed.

As previously mentioned, it is clear that the ancient distribution of the Suboscines involves the Gondwana remnants (Ericson et al., 2003). Thus, another possible origin for the Eurylaimides would be Asia, having dispersed from an Antarctic or an Australian stock. Nevertheless, according to our time estimate for the main Suboscine split, Antarctica had already begun the cooling process that most likely reduced or virtually impeded trans-continental dispersions with South America (Woodburne and Case, 1996). Furthermore, since the early Eocene the Australian plate had long since severed from Antarctica (Woodburne and Case, 1996), also demanding a long over-water dispersal to Australia and then Continental Asia.

A distinct possibility would be migration through North America that was, at the time, still isolated from South America. However, this route would also require two long water dispersals, one from South America to North America and a second from North America to Europe or Northeast Asia, as no insular connections are reported until the middle Miocene (Blakey, 2014). This situation would make a South American distribution for the Suboscines ancestor more likely.

The sister group of the Eurylaimides is a clade endemic to the Americas, and sister group relationships between African and South American clades have been previously identified (Oliveira et al., 2009; Poux et al., 2006; Schrago and Russo, 2003; Ezcurra and Agnolin, 2012). Geological data on the continental separation of these landmasses indicate a Cretaceous (~100 Ma) isolation (Ali and Krause, 2011; Oliveira et al., 2009) that conflicts with our recent Eocene estimate for the Tyrannides–Eurylamides split (Table 3). However, our molecular-based estimate coincides nicely with several other divergence dates of hypothesized trans-Atlantic disjunct taxa, such as platyrrhini monkeys (35–40 Ma; Schrago and Russo, 2003), caviomorph rodents (45 Ma; Poux et al., 2006), and amphisbaenian lepidosaurs (40 Ma; Müller et al., 2011; Vidal et al., 2008).

Geological data have recently been used to model the connection between Africa and South America in the Cenozoic based on horizontal plate motion, sea level fluctuations, and thermal subsidence of the oceanic lithosphere (Oliveira et al., 2009). That study considered any continuous land connection between the continents after 100 Ma to be unlikely, but indicated the presence of a chain of oceanic islands that might have lasted until the Eocene (Oliveira et al., 2009). Indeed, at approximately 50 Ma, a series of islands stretching from the African shore might have formed that were connected to the emergent Rio Grande Rise in southern Brazil, consolidating a long terrestrial strip between the two continents (Oliveira et al., 2009). However, this island chain started to be disrupted at 40 Ma and by 30 Ma no longer existed (Oliveira et al., 2009). These geological estimates agree well with our divergence times (Table 3 and Fig. 1c), which would be compatible with an African origin for Eurylaimides. In this sense, assuming a South America as the ancestral area of the Suboscines, this group would have diversified into a pan-tropical lineage dispersing into Africa before the severance of the Rio Grande Rise insular chain. The hypothesis of an African origin for Eurylaimides was first proposed by R. Prum based on a phylogenetic study of morphological characteristics (Prum, 1993). Nevertheless, these results were based on different taxon sampling and, thus, topological results are not directly comparable to those presented here.

The Eurylaimides are a peculiar lineage among passerines for which, in contrast to other lineages of the group, mass extinctions and past dispersion events may have played a key role during the Neogene. Our African origin hypothesis seems to be the best-fit model for our novel passerine time-scale as other scenarios would have required long overwater dispersal events between continents, which are unlikely to have happened at that point in time. A species-level biogeographical analysis with a large taxon sampling could possibly lead to a more detailed picture of the historical events that shaped their diversification.

3.2.3. The enigmatic Sapayoa

The only exception to the Old World–New World geographical consistency in Suboscine distribution is the puzzling *Sapayoa aenigma*. This monotypic genus was nested within the Old World eurylaimid clade (42 BP). Unsurprisingly, *Sapayoa* was originally placed in Tyrannides for geographical reasons but is now largely accepted in Eurylaimides, as it lacks all synapomorphies of the New World group (Fjeldsa et al., 2003). However, details of the New World colonization by *Sapayoa* remain unclear.

The eurylaimid affinity for the genus *Sapayoa* was originally explained as the result of a secondary Suboscine lineage sprung from the Gondwana passerine stock (Fjeldsa et al., 2003). However, according to our African-first scenario, a direct invasion into South America from Gondwana (Fjeldsa et al., 2003) would be unlikely as our time results indicate a 29–18 Ma divergence for *Sapayoa* and the remaining Eurylaimides (Table 3). No land communication between Africa and South America is likely to have occurred after 30 Ma (Oliveira et al., 2009) and a Laurasian origin of this lineage seems more consistent with phylogenetic, geographic, and fossil data (see also Moyle et al., 2006) that includes a Bavarian and a French fossil records (Ballmann, 1969; Mayr and Manegold, 2006).

Indeed, the existence of European fossil records for taxa that are now restricted to the Americas, such as hummingbirds (Trochilidae) and todies (Todidae) (Louchart et al., 2008; Mayr, 2005; Mayr and Micklich, 2010), does support a connection between Europe and the New World via the North Atlantic Ocean. In any case, the insectivorous *Sapayoa* would have entered the New World well after the main diversification of the tyrannids, preventing the diversification of the eurylaimid lineage in the Americas.

3.3. Oscines

The Oscines, or true songbirds (776 genera; 99 BP; Fig. 1), are the sister clade to the Suboscines and include nearly 80% of all passerine diversity. The study by Sibley and Ahlquist (1990) represented a landmark in songbird relationships. For instance, their results disclosed two large and geographically distinct parvorders in the group: Corvida, centered in the Australo-Papua region, and Passerida, centered in Eurasia. More recently, molecular phylogenies revealed the paraphyletic status of Corvida with the monophyletic Passerida nested within (Barker et al., 2004, 2002; Ericson et al., 2002). This new proposal switched the synchronous diversification scenario of Passerida in the Northern hemisphere and Corvida in the Southern hemisphere, proposed by Sibley and Ahlquist (1990), to rooting the entire Oscine diversity in Australia as previously mentioned.

3.3.1. The paraphyletic Corvida

Our topological results agree with an Australian origin for the Oscines, as Corvida is paraphyletic and Menurae, sister to the remaining Oscines, is confined to the eastern Australian coast. According to our time-scale, these early Oscines may have drifted northward on the isolated Australian plate during early–mid Eocene (Table 3). In our tree, Corvida is represented by three large assemblages: the paraphyletic Basal Oscines, the monophyletic Corvoidea, and the paraphyletic Transitional Oscines, which include the sister group to the entire Passerida parvorder (Fig. 1; see also Aggerbeck et al., 2014; Jonsson et al., 2011).

The Basal Oscines are, in our topology, divided into four clades with a rather modest diversification, which is more or less confined to the Australian–Oceanian realms (*sensu* del Hoyo et al., 1992–2011; Holt et al., 2013). After the Australian Menurae split, the second clade (i.e., the Climacteridae and Ptilonorhynchidae clade; five genera, 100 BP) is endemic to the Australian continent and to New Guinea (del Hoyo et al., 1992–2011), which are geologically connected areas. Sometime between the late Eocene and the early Oligocene (35–30 Ma), the island of New Guinea emerged from the deep seafloor with the collision of the Australian and Pacific plates (Charles, 1991; Hall, 2002; van Ufford and Cloos, 2005). This tectonic event, combined with another drastic decline in sea level (Ali and Aitchison, 2008; Hall, 2002), caused the aerial exposure of several large ophiolite plateaus, including New Guinea (Charles, 1991; Hall, 2002, 1998; van Ufford and Cloos, 2005).

The continuous collision between the Australo-Papuan and Pacific plates also exposed aerial portions of the Melanesian Arc system in the late Oligocene (Hall, 2002). Many endemic Australian lineages of passerines were then able to expand their geographical distribution into the emerging ophiolites. These events, modeled from present-day seismicity data and geological evidence (Hall, 2002), fit well with our early Oligocene estimates for the initial diversification of the Oscines (Climacteridae and Ptilonorhynchidae) out of Australia. For instance, this diversification agrees with the first exposure of aerial plateaus in New Guinea that connected this region to the newly emerged Melanesian ophiolites (Hall, 2002, 1998).

The exposure of the Melanesian Arc system also triggered the diversification of the third lineage of the Basal Oscines, the Meliphagoidea (53 genera, 100 BP) (Fig. 1). This superfamily inhabits a larger geographical area, including Australia, New Guinea, and most of the Pacific Archipelagos (del Hoyo et al., 1992–2011; Gardner et al., 2010). In our time-tree, early meliphagoids split from the remaining Oscine core at the early Oligocene (35 Ma) and radiated later, during the second half of the Oligocene (27 Ma), when most of the western portion of the Australasian archipelago was still under water (Hall, 2002). The western and eastern areas of the Australasian Archipelago are curbed by the classical Wallace's line, an imaginary line that separates the geographic distribution of many species of birds and mammals (Holt et al., 2013). Again, this scenario agrees with the time estimates for the early Oscine diversification, which explains the absence of meliphagoids in the western archipelago.

The western part of the Australasian archipelago was formed only later, in the Miocene, when New Guinea collided with the Sulawesi plates and the East Philippines Arc system (Charles, 1991; Hall, 2002, 1998; van Ufford and Cloos, 2005). This latest collision formed a continental shelf region joined by a shallow sea known as the Sunda Shelf in the Indo-Malayan geographic region (Holt et al., 2013). Therefore, by the end of the Oligocene the geological configuration of the entire Australasian region would have linked the greater Australo-Papuan region, the Melanesia region (to the East), and the Indo-Malayan region (to the West). The drastic drop in sea level at the Oligocene–Miocene transition (Miller, 2005) would have facilitated the expansion of several oscine lineages into the continental Old World.

After the Meliphagoidea radiation, the fourth Basal Oscine lineage (Pomatostomidae and Orthonichidae) became sister to the crown Oscine clade (*sensu* Barker et al., 2004) (see Fig. 1). The crown Oscines are divided into two very large groups (Fig. 1). One group in our topology is largely equivalent to the original proposal for the Corvoidea (127 genera, 97 BP) (Sibley and Ahlquist, 1990) with high support but differs slightly from the core Corvoidea from more recent studies (Aggerbeck et al., 2014; Barker et al., 2004, 2002; Norman et al., 2009). The Corvoidea diversification marks the first great Oscine expansion out of Australasia, with lineages reaching Eurasia, Africa, and even the New World (Fig. 2). Our time estimates agree with current geological models (Hall, 2002), as the main radiation of Corvoidea occurred toward the Oligocene–Miocene transition (Table 3 and Fig. S3), after the formation of the Sunda Shelf, which enabled the Australasia and continental Asia connection (see also Aggerbeck et al., 2014; Jonsson et al., 2011).

In our Corvoidea, two lineages (12 genera in total) were found to be endemic to the New World: the blue jays (seven taxa, 89 BP; one lineage in the cosmopolitan Corvidae) and vireos (Vireonidae) (six taxa, 78 BP) (Figs. 1 and 2). Vireos are the sole non-Passerida Oscine family endemic to the Americas (del Hoyo et al., 1992–2011; Jonsson et al., 2008) (but see also Reddy and Cracraft, 2007), and they appear to have reached the Americas at the Oligocene–Miocene transition (22 Ma), considerably earlier than the jays, which only arrived in the middle Miocene (12 Ma) (Table 4).

The second group of the crown Oscines includes the paraphyletic Transitional Oscines (see also Jonsson et al., 2011) and the sister lineage to the monophyletic parvorder Passerida (Sibley and Ahlquist, 1990) (563 genera, 98 BP) (Fig. 1). The Transitional Oscines were originally allocated in the Corvoidea (*sensu* Sibley and Ahlquist, 1990), but in recent studies they have shown a closer affinity with Passerida (587 genera, 13 BP; Beresford et al., 2005; Jonsson et al., 2011, 2007) and also in our results (Fig. 1). The restricted distribution of this group in the Australo-Papuan and Melanesian regions is also compatible with our time results, indicating that this radiation took place prior to the formation of the Sunda Shelf.

3.3.2. Passerida

The sister group to the very large Passerida clade remains a controversial issue (Barker, 2011; Johansson et al., 2008; Jonsson et al., 2007) with two conflicting hypotheses. One hypothesis proposes a sister group relationship between Passerida and the Australasian robins (Petroicidae). This first hypothesis assumes an Asia-first entrance of Passerida through the Sunda Shelf, spreading afterward into Africa and the New World (Barker et al., 2004; Johansson et al., 2008). The competing biogeographic hypothesis indicates a closer relationship to Picathartii. The Picathartii are an odd clade with three monogeneric families with a remarkably disjunct geographic distribution in northwestern Africa, southern Africa, and the Malay Peninsula in southeastern Asia (Beresford et al., 2005; del Hoyo et al., 1992–2011; Ericson et al., 2003). This second relationship would favor an African origin for Passerida (Jonsson and Fjeldsa, 2006). Unfortunately, our results did not consistently pinpoint the sister group of Passerida. In our final tree, Picathartii shares an exclusive ancestor with Passerida (61 BP), but in the pruned tree it was Petroicidae that occupied that position (five genera, 79 BP).

Although our topological results did not reveal the geographical origin of the Passerida ancestor, our time estimate (25–30 Ma) for the origin of Passerida makes an African origin less likely. Indeed, at that time the Indian plate was well attached to Asia (Ali and Aitchison, 2008), making crossings from northwestern Australia to Africa unlikely (Ali and Aitchison, 2008). Hence, our time results tend to point to the Asia-first hypothesis.

According to this picture, an extremely rapid diversification among Transitional Oscines would have given rise to Passerida, which expanded into the Old World almost concomitantly with the exposure of the Sunda Shelf (Barker et al., 2004; Hall, 2002). Additionally, Barker (2011) recently argued that the Asia-first hypothesis is reconcilable with the Picathartii being the sister group of Passerida (as in our final topology) and further demonstrated that the evidence for the Africa-first hypothesis is tenuous at best.

Our topology indicates that the Passerida ancestor split into the superfamilies Sylvioidea (172 genera, 83 BP), Muscicapoidea (123 genera, 33 BP), and Passeroidea (267 genera, 85 BP), with minor adjustments from their original delimitations (Sibley and Ahlquist, 1990). In the case of Passeroidea, previous phylogenetic studies have found topological results similar to Sibley and Ahlquist's (1990) study, but Sylvioidea and, to a lesser degree, Musicapoidea have been considered problematic since their circumscription (Alstrom et al., 2006; Ericson and Johansson, 2003; Fregin et al., 2012; Johansson et al., 2008; Sheldon and Gill, 1996; Spellman et al., 2008).

In fact, the clustering of the original Sylvioidea with high support stands out as one important result in our study (Fig. 1). The clade encompasses all (except *Regulus*) genera that were originally placed in the group (Sibley and Ahlquist, 1990), and was only recovered very recently by Alström et al., 2014. Even with additional genes and taxa in our study, the monophyly of Sylvioidea remained, including all the lineages responsible for previous paraphyly results of the superfamily, such as the titmice–penduline tits, hyliotas, and fairy flycatchers (Alstrom et al., 2006; Ericson et al., 2003; Ericson and Johansson, 2003; Fregin et al., 2012; Johansson et al., 2008; Fig. 1). Members of this superfamily are widespread in most of the Old World, mainly in Africa and Eurasia, and a few lineages reached North America with one monospecific family (Donacobiidae) in South America (del Hoyo et al., 1992–2011). We found that the main Sylvioidea clades diversified somewhat earlier than the other two Passerida superfamilies, establishing the main lineages across the Old World around the late Oligocene (25–30 Ma) (Fig. S3).

We also recovered a clade close to the original Muscicapoidea in our topology, although with modest support (Fig. 1), encompassing more original lineages than any previous study (Fig. 1; Cibois and Cracraft, 2004). We recovered the position of waxwings back in Muscicapoidea, although with low support (33), and despite much evidence to the contrary (Ericson and Johansson, 2003; Spellman

Table 4

Divergence time estimates for main lineages of New World Oscines using the BEAST and MCMCTree programs. The mean age estimate is shown with the high posterior density (HPD) of 95%.

Endemic Oscine lineages in the New World	BEAST		MCMCTree		Clade	Approximate epoch
	Mean	95% HPD	Mean	95% HPD		
Vireonidae/Oriolidae	22.2	19–25.7	23.2	20.6–25.4	Corvoidea	Early Mio
New World jays	12.8	10.4–15.2	14.8	12.8–16.9		Mid Mio
Auriparus/*Remiz*	19.5	16.3–23.3	19.8	16.7–22.7	Sylvioidea	Early Mio
Baeolophus/*Parus*	9.8	7.5–12.5	11.9	10–14.5		Late Mio
Psaltriparus/*Aegithalos*	12.5	10.2–15.2	12.9	10.7–15.4		Mid Mio
New World swallows/Cosmopolitan swallows	14.1	11.7–16.9	15.3	13.2–17.6		Mid Mio
Donacobius/Bernieridae	18.1	15.3–21.2	18.7	16.5–20.8		Early Mio
Chamaea/*Chrysomma*	12	9.3–14.6	12.6	10.5–15.1		Late Mio
Dulus/other bombycilloids	21.6	18.8–25.1	22.2	19.8–24.4	Muscicapoidea	Early Mio
(Ptilogonatidae, Mohoidae)/Bombycillidae	19.1	16.7–22.2	19.7	17.5–21.9		Early Mio
Troglodytidae/(*Certhia*, Tichodromidae)	22.8	19.6–26.4	21.5	18.4–24.1		Early Mio
Mimidae/Sturnidae	17.7	15.3–20.9	17.8	15.8–19.6		Early Mio
Sialia/(*Myadestes*, *Necossyphus*)	16.9	14.4–19.7	17.6	15.7–19.1		Early Mio
Myadestes/*Necossyphus*	14.4	11.9–17.2	14.7	12.4–16.7		Mid Mio
Ixoreus clade/*Turdus* clade	13.6	11.5–16	14.8	13–16.6		Mid Mio
Cichlherminia clade/*Turdus*	5.8	4.6–7.3	6.7	5.2–8.4		Late Mio
Peucedramus/(*Prunella*, Core Passeroidea)	23.9	21.1–27.6	24.8	22.8–26.3	Passeroidea	Oligo–Mio
(*Chlorophonia*, *Euphonia*)/Other Old World finches	15.4	13.1–17.9	17.7	15.9–19.2		Mid Mio
New World Fringillidae clade/(*Carduelis*, *Loxia*)	11.4	9.3–13.6	13.4	11.2–15.5		Late Mio
Lamprospiza/Other Nine-Primaried Oscines	16.2	14.3–18.8	19	17.6–20.2		Mid Mio
New World Emberizidae clade/Old World Emberizidae	13.8	12–15.9	17.2	15.8–18.3		Mid Mio
(Parulidae, Icteridae)/Emberizidae	15.1	13.3–17.4	18	16.6–19.1		Mid Mio
(Thraupidae + Cardinal clade)/(Icteridae, Parulidae, Emberizidae)	16	14–18.4	18.7	17.3–19.8		Mid Mio

et al., 2008). Three minor groups are apparent in our Musicapoidea clade: Core Muscicapoidea (Buphagidae, Mimidae, Sturnidae, Turdidae, Muscicapidae, and Cinclidae; 96 taxa, 99 BP; *sensu* Barker et al., 2002), Certhioidea (Johansson et al., 2008; 18 taxa, 88 BP), and Bombycilloidea (waxwing assemblage) (Spellman et al., 2008; nine taxa, 100 BP).

The last Passerida superfamily, Passeroidea, includes a few lineages endemic to the Old World in places such as Africa and Eurasia and an astounding diversification in the New World. Remarkably, the group had the lowest number of invasions in the American continent compared to the other superfamilies of Passerida (Fig. 2). Similarly to our estimates for the superfamilies Sylvioidea and Muscicapoidea, the passeroid lineages split from the core Passerida in the late Oligocene.

The bulk of the New World passeroid diversity includes a clade traditionally named the New World Nine-Primaried Oscines assemblage (hereafter Nine-Primaried; 177 genera, 96 BP) (Figs. 1 and 2) (Edwards et al., 2005; Klicka et al., 2000; Sick, 1997). Although massively endemic to the Americas, there is a minute paraphyletic assemblage of six genera, all from a single family, Emberizidae, endemic to the Old World (Fig. 2). The Nine-Primaried Oscines are traditionally divided into five families: Emberizidae, Icteridae, Parulidae, Thraupidae, and Cardinalidae (Barker et al., 2012). In our tree, the Nine-Primaried Oscines had a paraphyletic grade with four lineages containing genera mostly assigned to Thraupidae and two large clades, one with Emberizidae (26 taxa, 69 BP), Icteridae (27 taxa, 68 BP), and Parulidae (19 taxa, 99 BP) and another with the Cardinalidae nesting within most of the Thraupidae diversity (89 taxa, 10 BP) (Fig. 1). The first clade is consistent with recent studies with large sample sizes that focused on Nine-Primaried Oscine relationships (e.g., Barker et al., 2012), but we could not recover either a monophyletic Thraupidae or Cardinalidae (Fig. 1).

3.3.3. Oscines in the New World

Our molecular dating results for the initial diversification of all three Passerida superfamilies indicate a rapid radiation between the late Oligocene and Early Miocene (26–20 Ma; Fig. S3). Our estimated time of diversification suggests that the Passerida ancestor did not face much competition from the low-diversity Eurylaimides in the Old World.

In the Old World, Sylvioidea had been diversifying (see Fig. 2) since the late Oligocene according to our time-tree (see Table 3 and Fig. S3). Today, Sylvioidea includes more Old World-endemic genera than both the Muscicapoids and Passeroids (Fig. 2). The generalist–insectivorous habits largely found in the Sylvioidea and Muscicapoidea (Alstrom et al., 2006; Cibois and Cracraft, 2004; Ericson et al., 2003) may have generated direct competition between these lineages in the Old World. Therefore, the earlier timing of Sylvioidea diversification (Table 3 and Fig. S3) would have granted them a head-start, constraining the radiation of Muscicapoids in the Old World. This competition in the Old World may have prompted the several notable entrances by Muscicapoids into the Americas, which may explain why this group includes the largest number of New World distinct lineages, even though they have the lowest genera diversity (see Fig. 2).

In fact, our time-scale also identified Muscicapoid families (Troglodytidae and Mimidae) along with Vireonidae (Corvoid) as the first Oscines to thrive in the New World during the first half of the Miocene (Table 4). This early oscine arrival, combined with the more generalist–insectivorous habit of these lineages (Beecher, 1953; Cibois and Cracraft, 2004; Ericson et al., 2003), may have been responsible for their limited success, as the insectivorous Tyrannides were already fully radiated in the Americas (Sick, 1997; Willis, 1976). Nevertheless, after this Musicapoid radiation the generalist–insectivorous niches were most likely saturated, restricting the insectivorous sylvioid newcomers (mid-late Miocene) to the Nearctic (Alstrom et al., 2006; Fregin et al., 2012; Table 4; and Fig. 2).

An important shift in foraging habits possibly occurred only when the Passeroidea ancestor showed a nectarivory inclination as opposed to its insectivorous counterparts (del Hoyo et al., 1992–2011; Johansson et al., 2008). The first passeroid branches recovered in our tree are almost exclusively nectarivorous, and the position of slender-billed accentors (Prunellidae) as sister group to the Core Passeroidea (Fig. 1) further corroborates this hypothesis (Johansson et al., 2008). However, the major foraging shift would be observed only later in the finch-like bills of Core Passeroidea, which were more in tune with frugivorous or granivorous habits (Fig. 2, black circle) (Edwards et al., 2005; Johansson et al., 2008), fueling new waves of passerine speciation in the New World (250 taxa, 53 BP). The superb success achieved by the Passeroidea, and more specifically the Nine-Primaried Oscines during the middle Miocene, makes this group the largest passerine radiation in the Neotropics, behind only the autochthonous Tyrannides (Fig. 2).

Overall, our results indicate that the tapestry proposed by Sibley and Ahlquist yielded remarkably consistent results for the main passerine branches. This is somewhat surprising considering that these authors used DNA–DNA hybridization, which is a much criticized technique. Our topological results show that taxon sampling is crucial for refining phylogenetic hypotheses for an extremely diverse taxon such as passerines. Remarkable advances in passerine phylogeny have been made in the last decade, and it is our expectation that larger (species-level) datasets will provide further assistance in assembling the passerine tree of life.

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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.2015.03.018.

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