

# Historical biogeography of tits (Aves: Paridae, Remizidae)

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**Abstract** Tits (Aves: Paroidea) are distributed all over the northern hemisphere and tropical Africa, with highest species numbers in China and the Afrotropic. In order to find out if these areas are also the centers of origin, ancestral areas were reconstructed based on a molecular phylogeny. The Bayesian phylogenetic reconstruction was based on sequences for three mitochondrial genes and one nuclear gene. This phylogeny confirmed most of the results of previous studies, but also indicated that the Remizidae are not monophyletic and that, in particular, *Cephalopyrus flammiceps* is sister to the Paridae. Four approaches, parsimony- and likelihood-based ones, were applied to derive the areas occupied by ancestors of 75 % of the extant species for which sequence data were available. The common ancestor of the Paridae and the Remizidae inhabited tropical Africa and China. The Paridae, as well as most of its (sub)genera, originated in China, but *Baeolophus* originated in the Nearctic and *Cyanistes* in the Western Palearctic. Almost all biogeographic

reconstruction methods produced similar results, but those which consider the likelihood of the transition from one area to another should be preferred.

**Keywords** Lagrange · S-DIVA · Weighted ancestral area analysis · Mesquite ancestral states reconstruction package · Passeriformes

## Introduction

How to determine where a given taxon originated has long been a problem. Darwin (1859) and his followers (e.g., Matthew 1915) considered the center of origin to simultaneously be the diversity hotspot and had the concept of mere dispersal of species out of this area—even if long distances had to be covered. Croizat et al. (1974) questioned that and emphasized vicariance as the driver in historical biogeography. McCoy and Heck (1983) finally concluded that the concepts of dispersal and vicariance are not incompatible. Thus, they are both permissible in the most commonly applied method of ancestral-area reconstruction [Ronquist 1997; but see Kodandaramaiah (2010) for critical points of dispersal-vicariance analysis]. Consequently, the center of origin is understood here as ancestral area sensu Bremer (1992), i.e. the area occupied by the most recent common ancestor (MRCA) of a clade. In the absence of fossils, this is estimated with the help of molecular phylogenies. The danger lies in disentangling the center of origin (cradle of diversity), the center of accumulation and the museum of diversity (Gaston and Blackburn 1996), all of which could make up today's diversity hotspot, but for different reasons: high speciation rates (Ekman 1953, Ricklefs and Schluter 1993), high immigration rates (Ladd 1960) and low extinction rates respectively (Goldberg et al. 2005).

Here, tits serve as a model of comparing current approaches in reconstructing the geographic origin of a clade. Tits are a

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mostly Holarctic monophyletic songbird clade with expansions to the African and Southeast Asian tropics, comprising the families Paridae and Remizidae. They are sister groups and are often considered a superfamily Paroidea after exclusion from the Sylvioidea (Alström et al. 2006; Barker et al. 2004; Beresford et al. 2005; Sheldon and Gill 1996). Tits are generally found all over the forested parts of the northern hemisphere. Their affinity to trees does not only extend their area into Southeast Asian tropics, but also to sub-Saharan Africa. They are completely absent from Antarctica, Australia and South America. Their exclusion from the Neotropic may be due to the fact that suboscine birds had filled their niche before the Isthmus of Panama closed (Weir et al. 2009). Highest species numbers are found in tropical Africa and China (Fig. 1, Table 1), but there is a tendency for vertical segregation in China [McCallum et al. 2001; low plateau with mid-elevational peak sensu McCain (2009) in the breeding season] and in the Himalayas (Martens and Eck 1995; Price et al. 2011: mid-elevational peak). Such vertical segregation could mean that co-occurrence of species was successively established during the mountain uplift and does not refer to geographic origin in that particular area (Päckert et al. 2012).

Tits are very common and amongst the most intelligent songbirds (del Hoyo et al. 2007, 2008) and, thus, amongst the best-investigated birds. Nevertheless, no one has ever presented a complete phylogeny on this widespread group. Gill et al. (1989, 1993, 2005), Kvist et al. (1996), Sheldon and Gill (1996), and Slikas et al. (1996) undertook the major attempts so far to shed light on the interspecific relationships in tits. Gill et al.'s (2005) cytochrome-*b* (cytb) phylogeny comprised 42 out of the 65 species recognized in this article. Recent work focused instead on widespread Palearctic species (assemblages), such as *Parus major* (Päckert et al. 2005) or *Parus ater* (Tietze et al. 2011), evaluated the molecular clock along parid lineages (Päckert et al. 2007) or compared biogeographic patterns in East Asia amongst various passerine clades, including the *Periparus* tits (Päckert et al. 2012).

GenBank sequences from previous work (mostly data produced in laboratories where D.T.T. worked) were supplemented by own sequences from a community phylogeny for the Himalayas (Price et al. 2011) in order to undertake first

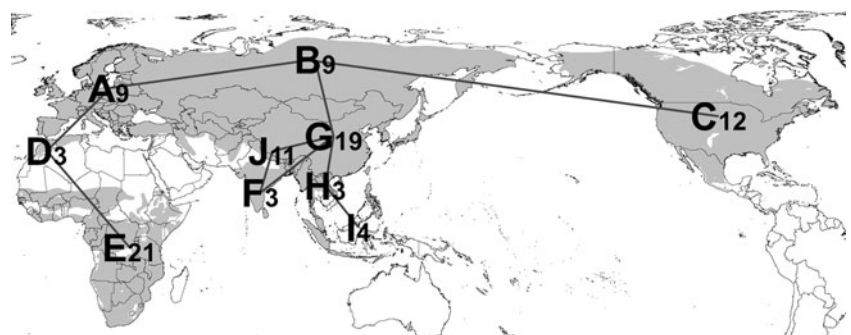
historical biogeographic analyses on a global scale applying different methods of ancestral-area reconstruction for all 49 species with sequence data available. By combining traditional parsimony-based methods with more recent Bayesian and likelihood approaches better support for estimates at given nodes should be gained and an initial comparative study of these methods for such a large passerine clade be provided. The assumption that the ancestral area was where we find highest diversity today (center of origin as cradle of diversity; see earlier) served as a starting point. As all Afrotropical parid species belong to the same lineage (*Parus sensu stricto*), whereas almost all lineages are represented in China, the latter was more likely to be the region where tits, in the narrower sense (*Parus sensu lato*, as well as Paridae), originated. For the MRCA of true (Paridae) and penduline tits (Remizidae), the Afrotropic might also have been part of the range, as many remizid tits occur there, too. Therefore, the purpose of the present article is to test these assumptions about the center of origin of tits.

## Material and methods

### Study group

Taxonomy and nomenclature follow the Handbook of the Birds of the World (del Hoyo et al. 2007, 2008) with the following exceptions (see also Päckert and Martens 2008; full list of accepted species in Table 2): *Parus sensu lato* refers to the former genus *Parus* (Dickinson 2003), including *Pseudopodoces* [according to Gill et al. (2005) and James et al. (2003)]; *Parus s.s.* refers to all the former *Parus* species not placed in any (other) former subgenus in the Handbook. *Parus (Poecile) hyrcanus* (Zarudny & Loudon, 1905) is a split from *P. lugubris* within the Western Palearctic for behavioral reasons to be doubted according to Eck (2006) and is thus ignored. *Parus hypermelaenus* is considered a species separate from *P. palustris* despite weak evidence (Eck and Martens 2006), but *Parus (Poecile) songarus* Severtsov, 1873 is included in *P. montanus* (Kvist et al. 2001; Martens and Eck 1995; Martens et al. 1995; contra Harrap and Quinn 1995)

**Fig. 1** Breeding distribution of extant parid and remizid tit species according to BirdLife International and NatureServe (2011) subdivided into ten areas (A–J) with number of Paroidea species per area and connectivity among areas (Table 1)



**Table 1** Areas inhabited by tits with number of species recognized in this study and breeding there, and percentage of species included in this study

Code	Area	Neighbors	Paroidea			Paridae		
			Species	In this study	%	Species	In this study	%
A	Western Palearctic without North Africa (Europe, Middle East)	BD	9	9	100 %	8	8	100 %
B	Siberia	ACG	9	8	89 %	6	6	100 %
C	North America	B	12	12	100 %	11	11	100 %
D	North Africa, including the Canary Islands	AE	3	3	100 %	3	3	100 %
E	Tropical Africa	D	21	9	43 %	14	6	43 %
F	India south of the Himalayas	GJ	3	2	67 %	3	2	67 %
G	China	BFHJ	19	18	95 %	18	16	89 %
H	Southeast Asia (mainland)	GI	3	3	100 %	3	3	100 %
I	Southeast Asia (islands)	H	4	3	75 %	4	3	75 %
J	Himalayas	FG	11	11	100 %	10	10	100 %
			65	49	75 %	53	42	79 %

from which rather *P. (Poecile) weigoldicus* O. Kleinschmidt, 1921 should be split off (Salzburger et al. 2002a). *Parus (Periparus) melanolophus* Vigors, 1831 is nested in *P. ater* (Gill et al. 2005; Martens et al. 2006; Tietze et al. 2011) and thus included therein. The polyphyly of *P. elegans* with respect to *P. amabilis* and *P. venustus* (Martens et al. 2006) is ignored, as this does not affect the distribution of the whole clade whose phylogeny/phylogeography needs a more thorough investigation. *Parus (Baeolophus) atricristatus* Cassin, 1850 is a recent split from *P. bicolor* within North America and thus ignored (Grubb and Pravosudov 1994). *Parus (Parus) guineensis* Shelley, 1900 is a split from *P. leucomelas* based on eye color within the Afrotropic and thus ignored following Dickinson (2003). *Parus (Parus) bokharensis* M.H.K. Lichtenstein, 1823 is nested in *P. major* (Kvist et al. 2003; Päckert et al. 2005) and thus included therein. North African subspecies of *P. caeruleus* belong to *P. teneriffae* (Dietzen et al. 2008; Illera et al. 2011; Kvist et al. 2005; Päckert et al. 2007; Salzburger et al. 2002b). *Parus (Cyanistes) flavipectus* Severtsov, 1873 is a recent split from *P. cyanus* within Central Asia (Salzburger et al. 2002b) and thus ignored. *Parus cyanus* itself is retained despite the low genetic distance to *P. caeruleus*, as they are almost completely acoustically isolated from each other in spite of similar song syntax between *flavipectus* and *caeruleus* (Martens and Schottler 1991). Finally, *Remiz macronyx* (Severtsov, 1873) is considered conspecific with *R. pendulinus* (Eck and Martens 2006).

## Material

Three mitochondrial and one nuclear gene, i.e. 410 cytb sequences (47 species), 371 sequences of the NADH dehydrogenase subunit 2 (ND2; 18 species), 31 sequences of the cytochrome c oxidase subunit I [COI; 13 species; mainly

from Dai et al. (2010)] and 32 sequences of intron 7 of the fibrinogen gene (Fib7; 11 species; from Illera et al. (2011) and Tietze et al. (2011)], were aligned from GenBank in MEGA v5 (Tamura et al. 2011). If necessary, species names were corrected to those in Table 2. For each gene and species the longest available sequence was chosen regardless of geographic origin in order to maximize the amount of sequence data for the analysis, thus concatenated sequences per species often do not originate from the same individual (Table 2).

## Phylogenetic reconstruction

Phylogenetic relationships were reconstructed in BEAST v1.6.2 (Drummond and Rambaut 2007) with the following settings: all four genes were treated as separate partitions with unlinked substitution and clock models; GTR (HKY for Fib7) was set as substitution model according to MrModelTest (Nylander 2004); empirical base frequencies were used; and  $\Gamma$  and invariant sites were chosen as the site heterogeneity model (except for Fib7; see Table S1 for all model parameters). Furthermore, cytb and ND2 were partitioned into three codon positions after clipping of the stop codons; all parameters were unlinked. A relaxed, uncorrelated log-normal clock was used and a birth-death process assumed as a tree prior; the reconstruction was for 100,000,000 generations. The log files were checked with Tracer v1.5 (Rambaut and Drummond 2007) in order to set the burn-in value. The BEAST trees were summarized with TreeAnnotator v1.6.2 using a burn-in value of 50 % and median node heights, and the final tree visualized in FigTree v1.3.1 (Rambaut 2009).

## Ancestral-area reconstructions

The total range of tits (Fig. 1) was subdivided into ten discrete areas (Table 1). As species diversity is higher in eastern

**Table 2** Species recognized in this study with GenBank accession numbers (if available) and inhabited areas (for area codes see Table 1)

Species	Cytb	ND2	COI	Fib7	Distribution
<i>Anthoscopus minutus</i> (Shaw & Nodder, 1812)	AF347970				E
<i>Anthoscopus musculus</i> (Hartlaub, 1882)		AY136585			E
<i>Anthoscopus caroli</i> (Sharpe, 1871)					E
<i>Anthoscopus flavifrons</i> (Cassin, 1855)					E
<i>Anthoscopus parvulus</i> (Heuglin, 1864)					E
<i>Anthoscopus punctifrons</i> (Sundevall, 1850)					E
<i>Auriparus flaviceps</i> (Sundevall, 1850)	AF347969		DQ433342		C
<i>Cephalopyrus flammiceps</i> (E. Burton, 1836)	JX221705	JX221706	JX221707		GJ
<i>Melanochlora sultanea</i> (Hodgson, 1837)	JX221708	JX221713			GHJ
<i>Parus (Baeolophus) bicolor</i> Linnaeus, 1766	AF347957	AY825995	DQ434341	AY827402	C
<i>Parus (Baeolophus) inornatus</i> Gambel, 1845	X60944		DQ432762		C
<i>Parus (Baeolophus) ridgwayi</i> Richmond, 1902	AY607688		DQ433346		C
<i>Parus (Baeolophus) wollweberi</i> (Bonaparte, 1850)	AF347956		DQ432765		C
<i>Parus (Cyanistes) caeruleus</i> Linnaeus, 1758	AF347961		GU571359		A
<i>Parus (Cyanistes) cyanus</i> Pallas, 1770	AF347966		HM185327	JN392863	B
<i>Parus (Cyanistes) teneriffae</i> Lesson, 1831	DQ473999			HQ417153	D
<i>Parus (Lophophanes) cristatus</i> Linnaeus, 1758	AF347954		HM185312		A
<i>Parus (Lophophanes) dichrous</i> Blyth, 1844	JX221709	JX221714	HM185314		GJ
<i>Parus (Parus) afer</i> J.F. Gmelin, 1789					E
<i>Parus (Parus) albiventris</i> Shelley, 1881	AF347965				E
<i>Parus (Parus) carpi</i> Macdonald & B.P. Hall, 1957					E
<i>Parus (Parus) cinerascens</i> Vieillot, 1818					E
<i>Parus (Parus) fasciiventer</i> Reichenow, 1893	AY308728				E
<i>Parus (Parus) fringillinus</i> G.A. Fischer & Reichenow, 1884					E
<i>Parus (Parus) funereus</i> (J. & É. Verreaux, 1885)	AY308732				E
<i>Parus (Parus) griseiventris</i> Reichenow, 1882					E
<i>Parus (Parus) holsti</i> Seebohm, 1894	AY308724				G
<i>Parus (Parus) leucomelas</i> Rüppell, 1840					E
<i>Parus (Parus) leuconotus</i> Guérin-Ménéville, 1843					E
<i>Parus (Parus) major</i> Linnaeus, 1758	EU167009	AY732696	HM185334	AY494590	ABDFGIJ
<i>Parus (Parus) monticolus</i> Vigors, 1831	JX221710	JX221715	HM185330		GJ
<i>Parus (Parus) niger</i> Vieillot, 1818	AF347967				E
<i>Parus (Parus) nuchalis</i> Jerdon, 1845					F
<i>Parus (Parus) pallidiventris</i> Reichenow, 1885	AY308723				E
<i>Parus (Parus) rufiventris</i> Barboza du Bocage, 1877					E
<i>Parus (Parus) semilarvatus</i> (Salvadori, 1865)					I
<i>Parus (Parus) spilonotus</i> Bonaparte, 1850	JX221711	JX221716	HM185328		GHJ
<i>Parus (Parus) thruppi</i> Shelley, 1885	AY308731				E
<i>Parus (Parus) xanthogenys</i> Vigors, 1831	AY308734	JX221717			FJ
<i>Parus (Periparus) amabilis</i> Sharpe, 1877	AY308730				I
<i>Parus (Periparus) ater</i> Linnaeus, 1758	AF347959	JX221718	HM185324	HQ417146	ABDGJ
<i>Parus (Periparus) elegans</i> Lesson, 1831	AF347964				I
<i>Parus (Periparus) rubidiventris</i> Blyth, 1847	JX221712	JX221719		HQ417145	GJ
<i>Parus (Periparus) rufonuchalis</i> Blyth, 1849	AY308729	JX221720		HQ417144	J
<i>Parus (Periparus) venustus</i> Swinhoe, 1870	HM185353		HM185326	HQ417141	G
<i>Parus (Poecile) atricapillus</i> Linnaeus, 1766	AF284066		HM033704	HQ417160	C
<i>Parus (Poecile) carolinensis</i> Audubon, 1834	AF347941		HM033705		C
<i>Parus (Poecile) cinctus</i> Boddaert, 1783	AF347950		GU571587		ABC
<i>Parus (Poecile) davidi</i> (Berezowski & Bianchi, 1891)	AF347953				G

**Table 2** (continued)

Species	Cytb	ND2	COI	Fib7	Distribution
<i>Parus (Poecile) gambeli</i> Ridgway, 1886	AF347939	AY329433	DQ433973		C
<i>Parus (Poecile) hudsonicus</i> J.R. Forster, 1772	AF347949		DQ433980		C
<i>Parus (Poecile) hypermelaenus</i> (Berezowski & Bianchi, 1891)					G
<i>Parus (Poecile) lugubris</i> Temminck, 1820	AF347951				A
<i>Parus (Poecile) montanus</i> Conrad von Baldenstein, 1827	DQ792792	AY733007	HM185317		ABG
<i>Parus (Poecile) palustris</i> Linnaeus, 1758	DQ792789	AY734248	HM185319		ABG
<i>Parus (Poecile) rufescens</i> J.K. Townsend, 1837	EU075501		HM033710		C
<i>Parus (Poecile) sclateri</i> O. Kleinschmidt, 1897	AF347947		DQ433135		C
<i>Parus (Poecile) superciliosus</i> (Przewalski, 1876)	AF347952				G
<i>Parus (Poecile) varius</i> Temminck & Schlegel, 1848	AB239510				G
<i>Parus (Pseudopodoces) humilis</i> (Zarudny & Loudon, 1902)	AF377281		HM185309		G
<i>Pholidornis russiae</i> (Cassin, 1855)		AY136586			E
<i>Remiz consobrinus</i> (Swinhoe, 1870)	HM185374		HM185298		BG
<i>Remiz pendulinus</i> (Linnaeus, 1758)	AF347968		GU572079	GU433987	AB
<i>Remiz coronatus</i> (Severtsov, 1873)					B
<i>Sylviparus modestus</i> E. Burton, 1836	AY308733	JX221721	HM185311		GHJ

Eurasia than in tropical Africa, the Western Palearctic or North America, a finer subdivision in eastern Eurasia was applied. Species-specific distributional data (Table 2) were compiled based on the maps in the Handbook of the Birds of the World (del Hoyo et al. 2007, 2008), supplemented by range descriptions in Dickinson (2003) and corrected for our species delimitation (see above).

Under the general assumption that the tits did not change their preferred habitat within the timeframe under consideration, ancestral areas in Siberia are highly unlikely, as the area was repeatedly treeless through the ice ages (Hewitt 1996) apart from some forest relicts where pure Siberian species might have survived glaciations (Frenzel 1968). Thus, if Siberia is part of an area combination for older nodes, it has to be subsumed either under the Western Palearctic and/or the Eastern Palearctic/China, as would be the case for extant species accounting for the last glaciation [Pavlova et al. (2006): W Palearctic for *P. major*, *P. montanus*, Tietze et al. (2011): E Palearctic/N China for *P. ater*]. Nevertheless, Siberia is treated as a separate area, as it covers a considerable part of (forested) Eurasia, harbors 14 % of all tit species and has repeatedly connected Europe, China and North America throughout tit phylogenesis.

Several parsimony-based and one likelihood-based approach were applied to compensate for the disadvantages of single reconstruction methods.

A parsimony-reconstruction method was performed on the summarized tree under a user-defined step-matrix model in Mesquite v2.75 (Maddison and Maddison 2011; Ancestral States Reconstruction Package). The step matrix defines the costs for the transition from one area to the other, which

accounts for the assumption that dispersal to a neighboring region is more likely than to a more remote one. For each area the areas considered to be its neighbors are listed in Table 1. Values in the step matrix are the smallest numbers of neighboring areas a species would have to disperse to in order to reach the column area from the row area. This approach was repeated after collapsing all nodes with posterior probability support lower than 0.95.

Dispersal-Vicariance Analysis (Ronquist 1997) as a parsimony method (minimizing of dispersal and extinction events to explain the distribution of extant species) has become the standard approach for ancestral-area reconstruction. But, because it neglects phylogenetic uncertainty, Nylander et al. (2008) introduced a Bayesian approach which applies DIVA to many trees arising from the Bayesian phylogenetic reconstruction, and then integrates node support and uncertainty in biogeographic reconstruction. Yu et al. (2010) took this approach further by statistically evaluating the alternative ancestral ranges at each node in a tree accounting for phylogenetic uncertainty and uncertainty in DIVA optimization (S-DIVA). As incorrect constraints set on the maximum number of areas and analyzing a clade without a sister group may also affect the outcome of any DIVA approach (Kodandaramaiah 2010), the maximum number of areas for a given node was set to seven (maximum number of areas inhabited by any extant species) and the Remizidae considered as the sister group for reliable results for, and within, the Paridae. In RASP v2.0 beta, the current implementation of S-DIVA, the last 1,000 trees from the BEAST run were used, and the hold and bound parameters left at 32,767. The percentages for area combinations

were reasonably summarized in ambiguous cases for major nodes.

Weighted Ancestral Area Analysis (WAAA; Hausdorf 1998) is another cladistic approach which circumvents the trend in DIVA towards fewer ancestral than extant areas. It combines reversible parsimony with a weighting scheme that weights earlier gains and losses higher than later ones. The sum of all such weighted gains is divided by all according losses for each area and these ratios are compared with each other in order to decide whether a single area was—definitely or potentially—part of the ancestor's range at the analyzed node. D.T.T. implemented this method in R 2.13.2 (R Development Core Team 2011) using the R package APE (Paradis et al. 2004). This approach was applied to the summarized tree, setting the threshold for integrating (additional) areas as 2/3 (1/3) of the maximum ratio value.

Ree and Smith (2008) presented a maximum-likelihood approach, Likelihood Analysis of Geographic RANGE Evolution (Lagrange), which assumes vicariance as one mode of speciation along with dispersal and local extinction rates. Lagrange considers more parameters than do parsimony-based methods: divergence time is evaluated through branch lengths and (combinations of) areas and dispersal events can be constrained. The C++ version of 2011-01-17 was used and all area combinations allowed, but a step matrix of dispersal rates was required (1 for 1 area transition, 0.5 for 2, 0.25 for 3 and so forth).

## Results

### Phylogeny of extant tits

The Paridae, *Parus s.l.*, and subgenera *Baeolophus*, *Cyanistes*, *Lophophanes*, *Periparus* and *Poecile* gained full node support (Fig. 2). Inside these subgenera almost all nodes supported in Gill et al. (2005) could be recovered with high support values. The sister relationship of *Baeolophus* and *Lophophanes* failed to gain support of at least 0.95 in our reconstruction, as is the case for *Parus s.s.* and its two daughter lineages.

*Melanochlora* has good support as the sister to *Parus s.l.* and *Sylviparus* is sister to that clade. *Baeolophus*, *Lophophanes*, *Periparus* and *Poecile* together form a fully supported crown group within *Parus s.l.* Sister to this is a fully supported clade comprising *Cyanistes* and *Parus s.s./Pseudopodoces*.

Remizid *Cephalopyrus flammiceps* is sister to the Paridae with good support. All other nodes connecting the remizid species with each other and the Paridae are not supported: *Anthoscopus minutus/Remiz* appears to be sister to *Cephalopyrus/Paridae* and this clade would then be sister to (*Anthoscopus musculus/Auriparus*)/*Pholidornis*. Thus, this phylogenetic reconstruction destroys not only

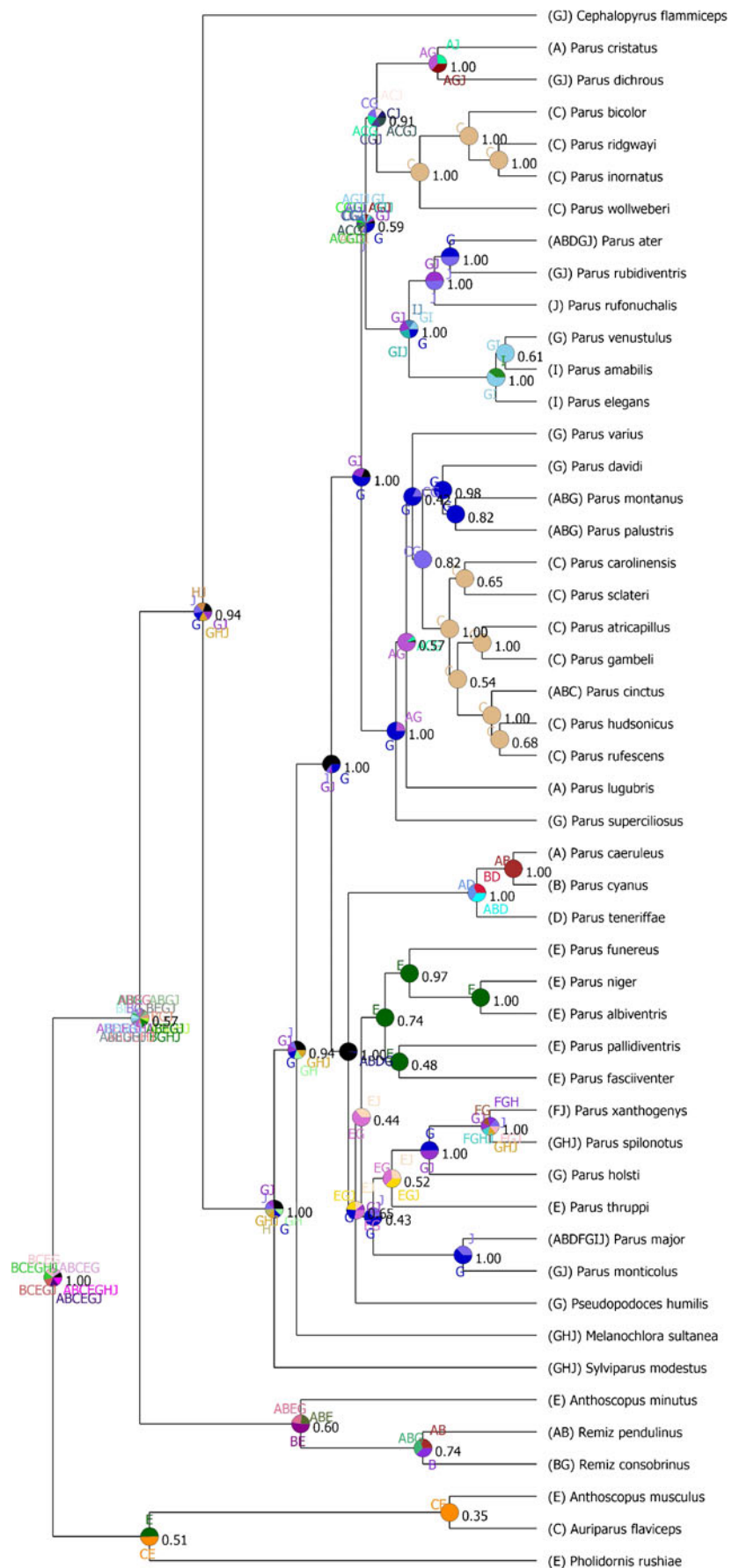
the monophyly of the Remizidae, but also renders *Anthoscopus* polyphyletic.

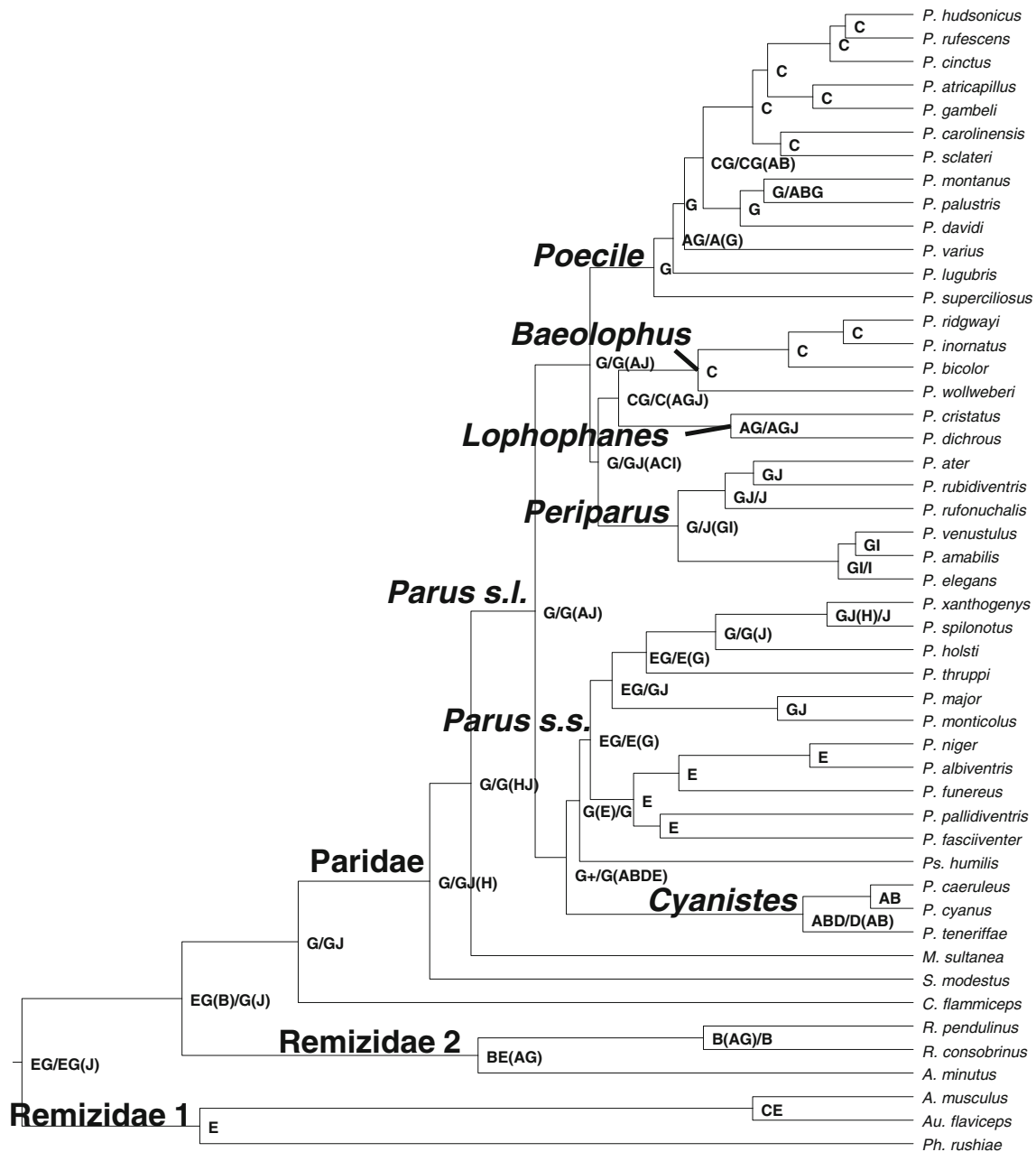
### Historical biogeography

Following the Lagrange approach (but strikingly different results in other approaches) the geographic history of Paroidea reads as follows (Fig. 3): the MRCA of all Paroidea split into two lineages occurring in the Afrotropic and China (and presumably further areas in between); the basal remizid lineage diversified in the Afrotropic from where *Auriparus* emigrated recently to the Nearctic; all other Remizidae except for *Cephalopyrus flammiceps* diversified independently in the Afrotropic, from where the *Remiz* lineage spread throughout the Palearctic via North Africa; vicariantly, *Cephalopyrus flammiceps* was separated from Paridae in China, where *Sylviparus modestus* was split off the remaining larger-sized parids towards Southeast Asia; then, the large-bodied, also Southeast Asian *Melanochlora sultanea* diverged from the species-rich *Parus s.l.* of medium size—the latter radiated within China. While the MRCA of the crown group also diversified in China the basal lineage split in China and (collapsed Mesquite: or) other Old World areas. Within the latter, *Cyanistes* is the youngest radiation, taking place in the Western Palearctic; the lineage of only Tibetan *Pseudopodoces* and the MRCA of *Parus s.s.* split off early in China and the Afrotropic (no connecting areas reconstructed by any method). Within the Afrotropic, one daughter lineage radiated into almost all the Afrotropical parid species. Its sister lineage diversified in China and the Afrotropic, leaving only *P. thruppi* (and potentially further unsequenced African species) in tropical Africa, otherwise diversifying in the Sino-Himalayas and, in one case (*P. major*), occupying Eurasia almost completely. The crown group radiated into the remaining (sub)genera in China. *Poecile* diversified also within China from where three species made it to Europe and one lineage emigrated to the Nearctic where it gave rise to several species, one of which (*P. cinctus*) expanded back to the Old World throughout the boreal forest in the Pleistocene. The Chinese (WAAA: Himalayan) MRCA of *Periparus* tits split into a quite recently diversified Southeast Asian and a Sino-Himalayan lineage, the latter of which split off *P. ater*, which diversified almost all over Eurasia. A second emigration to the Nearctic took place, successively splitting off a total of four extant species in *Baeolophus*. In *Lophophanes*, the trans-Palearctic ancestor split into a Sino-Himalayan and a European species.

The results from S-DIVA are presented in Fig. 2, those from WAAA with those from Lagrange are presented in Fig. 3, and those for major nodes in the phylogeny only are compared with the ones from other approaches in Table 3. Results from Mesquite (especially the ones with nodes with low support

**Fig. 2** Molecular phylogeny of Paroidea (tits and penduline tits) based on up to 2035 bp in a 4404-bp alignment of up to four genes (for details see Table S1) reconstructed in BEAST (genes and codon positions partitioned, GTR/HKY models, 100,000,000 generations). At the tips are all extant species recognized in this study for which any sequence was available on GenBank, preceded by distributional areas (see Table 1) in parentheses; at the nodes are posterior probabilities and ancestral-area reconstructions from S-DIVA (maxarea=7) as pie charts (color does not refer to a certain area, but to percentage of area combinations in decreasing order)





**Fig. 3** Molecular phylogeny of Paroidea (tits and penduline tits) as in Fig. 2, but with ancestral-area reconstructions according to Lagrange and WAAA (in this order if different) indicated at the nodes

collapsed) differ most strikingly from the others, but results for younger nodes—if present—are mostly consistent. Ancestral-area reconstructions for younger nodes were, in general, more consistent among approaches than were those for older nodes (Figs 1, 2 and Table 3). The number of areas in an area combination for a given node varies among approaches. WAAA, for instance, failed to restrict the range of the *Periparus* ancestor to China—the unequivocal outcome of all other approaches.

## Discussion

### Phylogeny and taxonomic interpretation

Our phylogenetic approach failed to resolve older nodes in the Paridae (posterior probabilities below 0.95; Fig. 2). This may be a result of an incomplete taxon sampling (especially for the Remizidae), relatively low number of (nuclear) markers and the quite mosaic concatenated alignment



**Table 3** Major nodes in the tit phylogeny (Fig. 2) with ancestral-area reconstruction according to the different approaches and concluded area sets (for area codes see Table 1)

Taxon	Mesquite	Collapsed	WAAA	S-DIVA	Lagrange	Ancestral area(s)
Paroidea	ABDE	B	EG(J)	BCEG(AJ)	EG	Afrotropic and China
Remizidae ( <i>Auriparus</i> clade)	ABDE	n.d.	E	E(C)	E	Afrotropic
Remizidae ( <i>Remiz</i> clade)	ABDE	n.d.	BE(AG)	BE	BE(AG)	Afrotropic
Paridae	G	G	G(HJ)	G(HJ)	G	China
<i>Parus s.l.</i>	G	G	G(AJ)	G(J)	G	China
Basal clade	G	AD	G(ABDE)	G(ABD)	G(...)	China
<i>Cyanistes</i>	AB	AD	D(AB)	D(AB)	ABD	North Africa (and further W Pal.)
<i>Parus s.s.</i>	G	n.d.	E(G)	EG	EG	Afrotropic and China
<i>Parus</i> (Africa)	E	n.d.	E	E	E	Afrotropic
<i>Parus</i> (rest)	G	n.d.	GJ	G	EG	China
Crown group	G	G	G(AJ)	G	G	China
<i>Baeolophus</i>	C	C	C	C	C	Nearctic
<i>Lophophanes</i>	BG	G	AGJ	AGJ	AG	China and Europe
<i>Periparus</i>	G	G	J(GI)	G(IJ)	G	China
<i>Poecile</i>	G	G	G	G	G	China

n.d. no area reconstruction, as node collapsed

(Table 2). One exception is the clade of *Baeolophus*, *Lophophanes*, *Periparus* and *Poecile*. This crown group also has behavioral autapomorphies: hole-digging and food-caching behavior is not observed in any other parid species (del Hoyo et al. 2007; Štorchová et al. 2010). *Cyanistes* is part of *Parus s.l.* with full support, as opposed to reported in Gill et al. (2005).

We recommend not to up-rank all monophyletic species groups in *Parus s.l.* to separate genera, as suggested by Gill et al. (2005; cf. Dai et al. 2010). Generic upgrade of the subgenera in the crown group, as performed in the Handbook, would be justified because of node support and (almost) complete taxon sampling. Conversely, node uncertainties and highly incomplete taxon sampling render conclusions within the basal species set (subgenera *Cyanistes*, *Parus*, *Pseudopodoces*) premature, especially as the positioning of *Pseudopodoces humilis* is not constant over different approaches [sister to *Parus s.s.* in this article, to *Parus s.s.* or to all *Parus s.l.* except *Cyanistes* (Gill et al. 2005) or to *P. spilonotus* (Dai et al. 2010)].

*Cephalopyrus flammiceps* has mostly been considered a remizid. Wolters (1980) placed it in a separate family close to the Paridae. *Cephalopyrus flammiceps*, unlike other remizids, builds cup-shaped nests in cavities in tree trunks (Bocheński 1998; Löhrl 1967; Martens, pers. comm.), but shares other behavioral traits with remizid species (Löhrl 1967, 1981). Although the position close to the Paridae is quite well supported here, we refrain from including it in that family. More data (taxa and markers) are needed for the Remizidae to clarify the relationships among them and with the Paridae. At least, node uncertainty and depth support the

species split between *R. consobrinus* and *R. pendulinus*, as suggested by Harrap and Quinn (1995).

Obviously, there is urgent need for a fully resolved multi-gene phylogeny incorporating all recognized species in Paroidea to shed more light on the systematics of remizid species and the delimitation of (sub)genera in *Parus s.l.*

#### Historical biogeography

Our hypotheses about the centers of origin of tits were confirmed. The hotspots of tit diversity were the centers of origin and thus the Afrotropic (for Paroidea, remizid lineages, and African *Parus s.s.*) and China (for most other major nodes) served as ‘cradles of diversity’ from where other areas were (repeatedly) colonized. Päckert et al. (2012) reconstructed the eastern Himalayas and southeast China as ancestral area of *Periparus* tits whereas the same (and most other) approaches in this study restrict it to China (Table 3); the decisive reason for this deviation lies in the fact that Päckert et al. (2012) did not include the actual sister lineage into their outgroup.

We confirmed the findings of Gill et al. (2005) that North American tits are two independent offshoots of an Old World family. For a more detailed discussion of intra-American diversification see Gill et al. (2005). However, we want to emphasize here that in tits—relatively small passerines in contrast to thrushes of the genus *Turdus*, which also occur in the New World as well as in Eurasia and Africa (Voelker et al. 2009)—there is no evidence for repeated trans-Atlantic dispersal, as both North American radiations are nested in the East Asian context with only a single

species (*P. cinctus*) returning to (Northern) Eurasia, presumably most recently. Thus, tit radiations, if connected with dispersal, rely on land bridges (but see *Auriparus*), particularly as there is no indication that any ancestor of modern Paroidea was more suitable for long-distance migration/dispersal and less specialized on arboreal life.

Both dispersals to North America in the Paridae (MRCA of *Baeolophus* species and ancestor of *P. sclateri* in Figs. 2 and 3) must have occurred before the Bering Strait opened 5.5 Ma ago (Gladenkov et al. 2002). On the one hand, mitochondrial lineages of North African/Macaronesian and Eurasian blue tits (*Cyanistes*) certainly diverged after the Messinian salinity crisis, i.e. when the Strait of Gibraltar was flooded again less than 5.33 Ma ago (Krijgsman et al. 1999) separating Europe from North Africa in a dynamic process with multiple phases of colonization (Illera et al. 2011). On the other hand *Cyanistes* tits managed to disperse to the Canary Islands, after they had become inhabitable 4.0 Ma ago (Ancochea et al. 1990), a distance of at least 100 km off the North African coast. Extant North African *Cyanistes* tits are the result of a back colonization from the Canary Islands (Illera et al. 2011). Ancestors of Taiwanese tits (endemic *P. holsti* and other parids) covered even more than 160 km. We consider this a rare event, as the maximum dispersal distance reported for the common and relatively large *P. major* on Continental Europe is only 120 km and most individuals breed where they hatched or bred in the previous year. or close to that area (Glutz von Blotzheim 1993; Greenwood et al. 1979; Paradis et al. 1998). Maybe on islands rare immigration events were more effective when niches were unoccupied, whereas on a continental scale a larger founding population was needed for a tit species to establish. Sister species have to be old and must have diverged ecologically to become sympatric (Price 2010). Consequently, we also explain repeated interchange between Africa and Asia/North America in Paroidea rather with vicariance than over-sea dispersal across the Indian Ocean, as Voelker and Outlaw (2008) postulate for *Geokichla* thrushes.

## Conclusions

We would suggest that for ancestral-area reconstructions in taxa that depend on land bridges for their dispersal methods taking connectivity between areas into account should be preferred to those which treat all areas as equally likely to be reached through a single dispersal step from any other area. In this study, consequences of including a step matrix (Mesquite, Lagrange) are that the number of areas occupied by ancestors decreases by exclusion of improbable combinations and that intermediate areas (North Africa, Europe, and Siberia between Afrotropic and China) become less often part of the (most likely) ancestral area set.

The example of the tits also confirms that besides dispersal, vicariance plays a major role (e.g., *Cyanistes versus*

*Parus s.s.*, the two *Periparus* lineages). Thus, it is reasonable that modern methods for ancestral-area reconstruction consider both ways of area transitions. We recommend the application of different approaches in ancestral-area reconstructions and modeling the connectivity of areas via the likelihood of transitions between two given areas and allowing for different scenarios in different periods in the past in Lagrange (where appropriate).

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## References

- Alström, P., Ericson, P. G. P., Olsson, U., et al. (2006). Phylogeny and classification of the avian superfamily Sylvioidea. *Molecular Phylogenetics and Evolution*, 38, 381–397.
- Ancochea, E., Fuster, J. M., Ibarrola, E., et al. (1990). Volcanic evolution of the island of Tenerife (Canary Islands) in the light of new K-Ar data. *Journal of Volcanology and Geothermal Research*, 44, 231–249.
- Barker, F. K., Cibois, A., Schikler, P., et al. (2004). Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 11040–11045.
- Beresford, P., Barker, F. K., Ryan, P. G., et al. (2005). African endemics span the tree of songbirds (Passeri): molecular systematics of several evolutionary ‘enigmas’. *Proceedings of the Royal Society of London B*, 272, 849–858.
- BirdLife International and NatureServe (2011). *Bird species distribution maps of the world*. Cambridge: BirdLife International and NatureServe.
- Bocheński, Z. (1998). Systematyczne implikacje oparte na budowie gniazd remizów [the nest building of penduline tits and its systematic implications]. *Notatki Ornitologiczne*, 39, 231–241.
- Bremer, K. (1992). Ancestral areas: a cladistic reinterpretation of the center of origin concept. *Systematic Biology*, 41, 436–445.
- Croizat, L., Nelson, G., & Rosen, D. E. (1974). Centers of origin and related concepts. *Systematic Zoology*, 23, 265–287.
- Dai, C., Chen, K., Zhang, R., et al. (2010). Molecular phylogenetic analysis among species of Paridae, Remizidae and Aegithalidae based on mtDNA sequences of *COI* and *cyt b*. *Chinese Birds*, 1, 112–123.
- Darwin, C. (1859). *On the origin of species by means of natural selection*. London: John Murray.
- del Hoyo, J., Elliot, A., & Christie, D. (Eds.). (2007). *Handbook of the birds of the world. Volume 12. Picathartes to tits and chickadees*. Barcelona: Lynx Edicions.
- del Hoyo, J., Elliot, A., & Christie, D. (Eds.). (2008). *Handbook of the birds of the world. Volume 13: Penduline tits to shrikes*. Barcelona: Lynx Edicions.

- Dickinson, E. C. (Ed.). (2003). *The Howard & Moore complete checklist of the birds of the world* (3rd ed.). London: Christopher Helm.
- Dietzen, C., Garcia-del-Rey, E., Delgado Castro, G., et al. (2008). Phylogeography of the blue tit (*Parus teneriffae*-group) on the Canary Islands based on mitochondrial DNA sequence data and morphometrics. *Journal of Ornithology*, *149*, 1–12.
- Drummond, A. J., & Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, *7*, 214.
- Eck, S. (2006). The Palaearctic titmouse species (Aves: Paridae: *Parus sensu lato*) – a current survey. *Zootaxa*, *1325*, 7–54.
- Eck, S., & Martens, J. (2006). Systematic notes on Asian birds. 49. A preliminary review of the Aegithalidae, Remizidae and Paridae. *Zoologische Mededelingen (Leiden)*, *80–5*, 1–63.
- Ekman, S. (1953). *Zoogeography of the Sea*. London: Sidgwick and Jackson.
- Frenzel, B. (1968). The pleistocene vegetation of Northern Eurasia. *Science*, *161*, 637–649.
- Gaston, K. J., & Blackburn, T. M. (1996). The tropics as a museum of biological diversity: an analysis of the New World avifauna. *Proceedings of the Royal Society of London B*, *263*, 63–68.
- Gill, F. B., Funk, D. H., & Silverin, B. (1989). Protein relationships among titmice (*Parus*). *Wilson Bulletin*, *101*, 182–197.
- Gill, F. B., Mostrom, A., & Mack, A. L. (1993). Speciation in North American chickadees: I. Patterns of mtDNA genetic divergence. *Evolution*, *47*, 195–212.
- Gill, F. B., Slikas, B., & Sheldon, F. H. (2005). Phylogeny of titmice (Paridae): II. Species relationships based on sequences of the mitochondrial cytochrome-*b* gene. *The Auk*, *122*, 121–143.
- Gladenkov, A. Y., Oleinik, A. E., Marincovich, L., Jr., et al. (2002). A refined age for the earliest opening of Bering Strait. *Palaogeography, Palaeoecology, Palaeoecology*, *183*, 321–328.
- Glutz von Blotzheim, U. N. (Ed.) (1993). *Handbuch der Vögel Mitteleuropas. Band 13/I. Passeriformes (4. Teil). Muscicapidae – Paridae*. Wiesbaden: Aula.
- Goldberg, E. E., Roy, K., Lande, R., et al. (2005). Diversity, endemism, and age distributions in macroevolutionary sources and sinks. *The American Naturalist*, *165*, 623–633.
- Greenwood, P. J., Harvey, P. H., & Perrins, C. M. (1979). The role of dispersal in the great tit (*Parus major*): the causes, consequences and heritability of natal dispersal. *The Journal of Animal Ecology*, *48*, 123–142.
- Grubb, T. C., & Pravosudov, V. V. (1994). Tufted titmouse (*Parus bicolor*). In A. Poole & F. Gill (Eds.), *The birds of North America*. No. 86. Washington, DC: AOU.
- Harrap, S., & Quinn, D. (1995). *Chickadees, tits, nuthatches & tree-creepers*. Princeton, NJ: Princeton University Press.
- Hausdorf, B. (1998). Weighted ancestral area analysis and a solution of the redundant distribution problem. *Systematic Biology*, *47*, 445–456.
- Hewitt, G. M. (1996). Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*, *58*, 247–276.
- Illera, J. C., Koivula, K., Broggi, J., et al. (2011). A multi-gene approach reveals a complex evolutionary history in the *Cyanistes* species group. *Molecular Ecology*, *20*, 4123–4139.
- James, H. F., Ericson, P. G. P., Slikas, B., et al. (2003). *Pseudopodoces humilis*, a misclassified terrestrial tit (Paridae) of the Tibetan Plateau: evolutionary consequences of shifting adaptive zones. *Ibis*, *145*, 185–202.
- Kodandaramaiah, U. (2010). Use of dispersal-vicariance analysis in biogeography – a critique. *Journal of Biogeography*, *37*, 3–11.
- Krijgsman, W., Hilgen, F. J., Raffi, I., et al. (1999). Chronology, causes and progression of the Messinian salinity crisis. *Nature*, *400*, 652–655.
- Kvist, L., Ruokonen, M., Orell, M., et al. (1996). Evolutionary patterns and phylogeny of tits and chickadees (genus *Parus*) based on the sequence of the mitochondrial cytochrome *b* gene. *Ornis Fennica*, *73*, 145–156.
- Kvist, L., Martens, J., Ahola, A., et al. (2001). Phylogeography of a Palaearctic sedentary passerine, the willow tit (*Parus montanus*). *Journal of Evolutionary Biology*, *14*, 930–941.
- Kvist, L., Martens, J., Higuchi, H., et al. (2003). Evolution and genetic structure of the great tit (*Parus major*) complex. *Proceedings of the Royal Society of London B*, *270*, 1447–1454.
- Kvist, L., Broggi, J., Illera, J. C., et al. (2005). Colonisation and diversification of the blue tits (*Parus caeruleus teneriffae*-group) in the Canary Islands. *Molecular Phylogenetics and Evolution*, *34*, 501–511.
- Ladd, H. S. (1960). Origin of the Pacific island molluscan fauna. *American Journal of Science*, *258-A*, 137–150.
- Löhr, H. (1967). Zur verwandtschaftlichen Stellung von *Cephalopyrus flammiceps* auf Grund des Verhaltens. *Bonner zoologische Beiträge*, *18*, 127–138.
- Löhr, H. (1981). Verhaltensmerkmale der Familie Remizidae. *Journal für Ornithologie*, *122*, 307–309.
- Maddison, W. P., & Maddison, D. R. (2011). Mesquite: a modular system for evolutionary analysis. Version 2.75. <http://mesquiteproject.org>.
- Martens, J., & Eck, S. (1995). Towards an ornithology of the Himalayas. Systematics, ecology and vocalizations of Nepal birds. *Bonner zoologische Monographien*, *38*, 247–251.
- Martens, J., & Schottler, B. (1991). Akustische Barrieren zwischen Blaumeise (*Parus caeruleus*) und Lasurmeise (*Parus cyanus*)? *Journal für Ornithologie*, *132*, 61–80.
- Martens, J., Ernst, S., & Petri, B. (1995). Reviergesänge ostasiatischer Weidenmeisen *Parus montanus* und ihre mikroevolutionäre Ableitung. *Journal für Ornithologie*, *136*, 367–388.
- Martens, J., Tietze, D. T., & Sun, Y.-H. (2006). Molecular phylogeny of *Parus (Periparus)*, a Eurasian radiation of tits (Aves: Passeriformes: Paridae). *Zoologische Abhandlungen (Dresden)*, *55*, 103–120.
- Matthew, W. D. (1915). Climate and evolution. *Annals of the New York Academy of Sciences*, *24*, 171–318.
- McCain, C. M. (2009). Global analysis of bird elevational diversity. *Global Ecology and Biogeography*, *18*, 346–360.
- McCallum, D. A., Gill, F. B., & Gaunt, S. L. L. (2001). Community assembly patterns of parids along an elevational gradient in western China. *Wilson Bulletin*, *113*, 53–64.
- McCoy, E. D., & Heck, K. L., Jr. (1983). Centers of origin revisited. *Paleobiology*, *9*, 17–19.
- Nylander, J. A. A. (2004). MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.
- Nylander, J. A., Olsson, U., Alström, P., et al. (2008). Accounting for phylogenetic uncertainty in biogeography: a Bayesian approach to dispersal-vicariance analysis of the thrushes (Aves: *Turdus*). *Systematic Biology*, *57*, 257–268.
- Päckert, M., & Martens, J. (2008). Taxonomic pitfalls in tits – comments on the Paridae chapter of the Handbook of the Birds of the World. *Ibis*, *150*, 829–831.
- Päckert, M., Martens, J., Nazarenko, A. A., et al. (2005). *Parus major* – a misclassified ring species. *Biological Journal of the Linnean Society*, *86*, 153–174.
- Päckert, M., Martens, J., Tietze, D. T., et al. (2007). Calibration of a molecular clock in tits (Paridae) – do nucleotide substitution rates of mitochondrial genes deviate from the 2% rule? *Molecular Phylogenetics and Evolution*, *44*, 1–14.
- Päckert, M., Martens, J., Sun, Y.-H., et al. (2012). Horizontal and elevational phylogeographic patterns of Himalayan and Southeast Asian forest passerines (Aves: Passeriformes). *Journal of Biogeography*, *39*, 556–573.
- Paradis, E., Baillie, S. R., Sutherland, W. J., & Gregory, R. D. (1998). Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology*, *67*, 518–536.
- Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, *20*, 289–290.

- Pavlova, A., Rohwer, S., Drovetski, S. V., et al. (2006). Different post-pleistocene histories of Eurasian parids. *The Journal of Heredity*, *97*, 389–402.
- Price, T. D. (2010). The roles of time and ecology in the continental radiation of the Old World leaf warblers (*Phylloscopus* and *Seiurus*). *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 1749–1762.
- Price, T. D., Mohan, D., Tietze, D. T., et al. (2011). Determinants of northerly range limits along the avian Himalayan diversity gradient. *The American Naturalist*, *178*, S97–S108.
- R Development Core Team (2011). R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. <http://www.r-project.org>.
- Rambaut, A. (2009). FigTree v1.3.1. <http://tree.bio.ed.ac.uk/software/figtree>.
- Rambaut, A., & Drummond, A. J. (2007). Tracer v1.5. <http://beast.bio.ed.ac.uk/Tracer>.
- Ree, R. H., & Smith, S. A. (2008). Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, *57*, 4–14.
- Ricklefs, R. E., & Schluter, D. (1993). *Species diversity in ecological communities. Historical and geographical perspectives*. Chicago: University of Chicago Press.
- Ronquist, F. (1997). Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology*, *46*, 195–203.
- Salzburger, W., Martens, J., Nazarenko, A. A., et al. (2002a). Phylogeography of the Eurasian Willow Tit (*Parus montanus*) based on DNA sequences of the mitochondrial cytochrome *b* gene. *Molecular Phylogenetics and Evolution*, *24*, 26–34.
- Salzburger, W., Martens, J., & Sturmbauer, C. (2002b). Paraphyly of the Blue Tit (*Parus caeruleus*) suggested from cytochrome *b* sequences. *Molecular Phylogenetics and Evolution*, *24*, 19–25.
- Sheldon, F. H., & Gill, F. B. (1996). A reconsideration of songbird phylogeny, with emphasis on the evolution of titmice and their sylvioid relatives. *Systematic Biology*, *45*, 473–495.
- Slikas, B., Sheldon, F. H., & Gill, F. B. (1996). Phylogeny of titmice (Paridae): I. Estimate of relationships among subgenera based on DNA-DNA hybridization. *Journal of Avian Biology*, *27*, 70–82.
- Štorchová, Z., Landová, E., & Frynta, D. (2010). Why some tits store food and others do not: evaluation of ecological factors. *Journal of Ethology*, *28*, 207–219.
- Tamura, K., Peterson, D., Peterson, N., et al. (2011). MEGA5: Molecular Evolutionary Genetics Analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution*, *28*, 2731–2739.
- Tietze, D. T., Martens, J., Sun, Y.-H., et al. (2011). Song evolution in the Coal Tit (*Parus ater*). *Journal of Avian Biology*, *42*, 214–230.
- Voelker, G., & Outlaw, R. K. (2008). Establishing a perimeter position: speciation around the Indian Ocean Basin. *Journal of Evolutionary Biology*, *21*, 1779–1788.
- Voelker, G., Rohwer, S., Outlaw, D. C., et al. (2009). Repeated trans-Atlantic dispersal catalysed a global songbird radiation. *Global Ecology and Biogeography*, *18*, 41–49.
- Weir, J. T., Bermingham, E., & Schluter, D. (2009). The Great American Biotic Interchange in birds. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 21737–21742.
- Wolters, H. E. (1980). *Die Vogelarten der Erde. Eine systematische Liste mit Verbreitungsangaben sowie deutschen und englischen Namen*. Pt. 5. Hamburg and Berlin: Parey.
- Yu, Y., Harris, A. J., & He, X. J. (2010). S-DIVA (Statistical Dispersal-Vicariance Analysis): a tool for inferring biogeographic histories. *Molecular Phylogenetics and Evolution*, *56*, 848–850.