Detecting ancient co-dispersals and host shifts by double dating of host and parasite phylogenies: application in proctophyllodid feather mites associated with passerine birds

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Abstract

Inferring co-phylogeographic events requires matching the timing of these events on both host and symbiont (e.g., parasites) phylogenies because divergences of hosts and their symbionts may not temporally coincide, and host switches may occur. We investigate a large radiation of birds (Passeriformes) and their permanent symbionts, the proctophyllodid feather mites (117 species from 116 bird species; 6 genes, 11,468 nt aligned) using two time-calibration strategies for mites: fossils only and host phylogeography only. Out of 10 putative co-phylogeographic events 4 agree in timing for both symbiont and host events being synchronous co-origins or co-dispersals; 3 were based on host shifts, but agree in timing being very close to the origin of modern hosts; 2 disagree; and 1 large basal mite split was seemingly independent from host phylogeography. Among these events was an ancient (21-25.3 Mya), synchronous co-dispersal from the Old World leading to the origin and diversifications of New World emberizoid passerids and their mites, the *thraupis+quadratus* species groups of *Proctophyllodes*. Our framework offers a more robust detection of host and symbiont co-phylogeographic events (as compared to host-symbiont reconciliation analysis and using host phylogeography for time-calibration) and provides independent data for testing alternative hypotheses on timing of host diversification and dispersal.

Introduction

Both phylogeny and biogeography of permanent symbionts (e. g., parasites) are expected to mirror those of their hosts (Page 1993; Page 1994; Hafner and Page 1995; Paterson et al. 2000; Clayton et al. 2003; Dabert 2003; Johnson and Clayton 2003; Weckstein 2004; Banks et al. 2005; Dabert 2005; Hughes et al. 2007; Light and Hafner 2008; Light et al. 2010; Demastes et al. 2012), although discordance can be introduced by various events, such as host shifts, speciation within a host species (duplication), failure to speciate, and extinction (Ronquist 1995, 2003). Counterintuitively, these latter events can also generate concordant host and symbiont phylogenies, for instance by non-random host shifts (depending on host relatedness) (Charleston and Robertson 2002; Sorenson et al. 2004; de Vienne et al. 2007; Klimov et al. 2007; Herrera et al. 2016) or by non-random colonization of islands (depending on their proximity to the source area) (Percy et al. 2004). Thus, to demonstrate strict co-divergence or co-dispersal in these systems, both topological and temporal concordance in host and symbiont divergences or dispersals should be estimated (Page 1991; Paterson and Banks 2001; Page 2003; Percy et al. 2004; Sorenson et al. 2004; Lopez-Vaamonde et al.

2006; Werth et al. 2013). Incorporating the temporal aspect in co-phylogeographic inferences calls for distinguishing two basic macroevolutionary scenarios: a synchronous scenario (host and symbiont diverge and disperse synchronously) and an asynchronous scenario (host-symbiont divergences do not coincide, hosts acquire symbionts from unrelated hosts after dispersal). On the microevolutionary scale, differences in divergence times of hosts and their symbionts can be generated even without host shifts or horizontal transmissions, by unequal effective population sizes and generation times (Hafner et al. 1994; Rannala and Michalakis 2003; Stefka et al. 2011), or other factors, such as disproportional host and parasite dispersal/gene flows (Huyse et al. 2005; Levin and Parker 2013).

Here we elucidate a common biogeographic history of proctophyllodid feather mites associated with passeriform birds (co-phylogeography) on the macroevolutionary scale. This is an interesting system because gene flow in both hosts and symbionts is expected to be linked since the majority of feather mites are very common, single-host symbionts, which are usually transmitted vertically (from parent to offspring) or rarely during host copulation or roosting (Gaud and Atyeo 1996; Dabert and Mironov 1999; Proctor 2003; OConnor 2009). In the evolutionary history of their hosts, certain historical, intercontinental dispersals were apparently nearly singular events, with a single bird lineage colonizing a continent or large landmass, followed by extensive radiation in the new area (Cibois et al. 2001; Ericson et al. 2002; Barker et al. 2004; Jonsson et al. 2011; Fritz et al. 2012; Barker et al. 2013; Fjeldsa 2013; Ericson et al. 2014; McGuire et al. 2014; Barker et al. 2015). Yet, for their symbionts, various synchronous and asynchronous co-phylogeographic scenarios are possible: 1) the dependent organisms can stochastically "miss the boat" during the bird dispersal; 2) they may go extinct as a result of competitive exclusion or random events; 3) hosts may acquire new symbionts from local hosts; or 4) local hosts may acquire symbionts from newly arrived hosts. Identifying these complex scenarios involving host and symbiont dispersal requires their dated phylogenies.

Numerous studies on co-phylogenetic history and co-biogeography of avian hosts and their ectoparasitic arthropods are available (Paterson and Gray 1997; Ehrnsberger et al. 2001; Dabert 2003; Mironov 2005; Zhu et al. 2015), but only a few employ dated phylogenies. For time-calibration of parasite trees, these studies use either a combination of host fossils and host biogeographic events (Smith et al. 2011; Zhu et al. 2015) or only the latter (Light et al. 2010). Using only host information to time-calibrate symbiont trees may create circular evidence in time estimates for co-phylogenetic and biogeographic events, favoring synchronous scenarios (i. e., simultaneous codiveregence and codispersal of host and their symbionts) (Sorenson et al. 2004; de Vienne et al. 2007; de Vienne et al. 2013). Furthermore, the effect of combining host-derived calibration points and symbiont fossil-based calibration in a single calibration scheme is unknown.

To explicitly account for the temporal component in inferring co-phylogeographic scenarios, we used proctophyllodid feather mites (family Proctophyllodidae) as model organisms.

Proctophyllodids (400 named species) are common symbionts of mostly passerine birds, with usually very high prevalence, for example, between 60 and 100% across different bird species (Behnke et al. 1995), or nearly 53% based on our unpublished database (5911 records total). As with lice, most of which are also associated with birds, feather mites are permanent symbionts, spending their entire life cycle on the host body. Permanent symbionts cannot survive away from their hosts and strongly depend on them for dispersal since they do not have a specialized dispersal stage. Transmission to unrelated host species is also possible but rarely occurs (e.g., through brood parasitism, prey to predator, sharing dust baths or nesting sites) (Dubinin 1951; Atyeo and Gaud 1983; Dabert and Mironov 1999). Proctophyllodids are primarily associated with passerine birds (Passeriformes), but the pterodectine tribe Rhamphocaulini (53 named species) is exclusively associated with hummingbirds (Apodiformes: Trochilidae). A few proctophyllodid species are known from other bird orders: Piciformes, Coraciiformes, Charadriiformes, Gruiformes, Trogoniformes and Musophagiformes (Gaud and Atyeo 1996; Mironov 2009; Hernandes and Valim 2014). However, all these latter proctophyllodids form small isolated clades within species-rich lineages associated with passerine birds, suggesting that these clades have resulted from recent host shifts from passerines.

We sequenced 6 genes (11,468 bp aligned, no missing data) from 133 individuals and 117 species of proctophyllodid feather mites, representing all major genera, and all major species groups of the largest genus *Proctophyllodes*, plus 40 outgroups. As in previous studies of ectoparasitic arthropods (Light et al. 2010; Smith et al. 2011; Zhu et al. 2015), we time-calibrated our symbiont phylogeny using both host divergence and biogeographic data (with the implied danger of introducing circular evidence). However, in contrast to the previous works, we then compared our results with time estimates inferred independently from fossil mite outgroups.

Material and Methods

Taxonomic sampling. Feather mites were collected from 2003–2014 by the authors in eight countries (Costa Rica, Kazakhstan, Mexico, Panama, Peru, Russia, Tanzania, USA), with all appropriate permits. Mites were mostly sampled from live birds; after sampling, avian hosts where photographed (to confirm identification) and released to the wild. We also examined some bird hosts that had been killed by falcons or cats and donated to the University of Michigan Museum of Zoology. We also examined a few specimens of ground dwelling birds that were inadvertently caught in snap-traps during a survey of small mammals in Peru. Those bird specimens are now housed in the Museum of the National University of San Marcos in Lima, Peru. Under a dissecting microscope, mites were removed from the plumage of an open wing with a needle or fine forceps, placed in 0.2-1.5 □L plastic tubes with 96% ethanol, and kept in a household refrigerator, on ice (in the field) or in an ultracold (-80°C) freezer (in the lab). After the procedure of DNA extraction (see below), mite exoskeletons

(vouchers) were mounted in Hoyer's medium; several additional mite individuals from the same series (co-vouchers) were also mounted to confirm identification. All vouchers and co-vouchers were deposited in the University of Michigan, Museum of Zoology (UMMZ); accession numbers are listed in Table S1.

Six families and 40 species of feather mites were used as distant outgroups. Ingroup sampling (Table S1, Fig. 2) included all major generic groupings of Proctophyllodinae (108 individuals, 92 species, 5 genera) and Pterodectinae (25 species/individuals, 11 genera). For the genus *Proctophyllodes* (*s. lat.*), the most species-rich genus of the family, we sequenced representatives of all major recognized species-groups (Atyeo and Braasch 1966; Mironov and Kopij 1996) (82 species, 98 individuals). Samples suitable for DNA extraction from Eurilaimides (Old World suboscine passerines) were not available. Eurilaimides is relatively small, monophyletic bird lineage (52 species) that originated around 70.2 Mya (Moyle et al., 2006) and forming the sister group to Tyrannides (New World suboscines). Like Tyrannides, the ancestor of Eurilaimides probably had a southern origin but was transported to Asia via the Deccan Plate (Greater India) (Moyle et al., 2006). Current distribution of Eurilaimides (Africa, Asia, Australia) can be explained by overwater dispersal rather than plate tectonics (Moyle et al., 2006). The single Neotropical species, *Sapayoa aenigma*, is probably a result of an ancient dispersal from the Old World via the North Atlantic route nearly 52 Mya (Moyle et al., 2006). Despite extensive sampling efforts by J. Gaud and W. T. Atyeo in the 1970's, Eurilaimides are only known to harbor two proctophyllodid species, *Philepittalges rotundus* and *Proctophyllodes pittae*. Based on morphology, only *Philepittalges rotundus* (host *Philepitta castanea*, Madagascar) may represent a mite lineage that coevolved with Eurilaimides since their origin (it has some apomorphies with the *Nycteridocaulus* generic group associated with Tyrannides, and we have seen an undescribed species from *Neodrepanis*, a genus related to *Philepitta*). *Proctophyllodes pittae* (Old World) shows some similarities to the *detruncatus* species group (hosts: oscine birds), and therefore, it is likely to have had a secondary origin resulting from a host shift from some Indo-Malayan oscine passerines. Given these arguments, we believe that the lack of sampling from Eurilaimides will not affect results of our analyses because Eurilaimides represents a monophyletic lineage that, except for *Sapayoa*, has never been in contact with Neotropical birds. Hypothetically, mites associated with the ancestor of *Sapayoa* could have given rise to the entire *Nycteridocaulus* genus group (associated with New World suboscines), albeit with a complete extinction of the primary mites in this genus group. This massive extinction scenario on Tyrannides is less parsimonious and, therefore, not likely. Other than the absence of mites from Eurilaimides, we believe that our taxonomic sampling is representative of the known proctophyllodid diversity.

For 173 taxa we sequenced 6 genes, 18S ribosomal RNA gene (18S), 28S ribosomal RNA gene (28S), elongation factor 1alpha100E Ef1alpha100E (EF1-α), signal recognition particle protein 54k Srp54k (SRP54), heat shock protein cognate 5 Hsc70-5 (HSP70), cytochrome c oxidase subunit I (COX1), using previously published amplification, sequencing, and DNA

extraction protocols (Klimov and OConnor 2008; Knowles and Klimov 2011; Klimov and OConnor 2013; Bochkov et al. 2014). Our aligned matrix had 11,468 sites and did not have missing data due to amplification/sequencing failures. From a total of 1038 sequences, 562 were generated as part of this study (GenBank accession numbers KU202752 - KU203313). GenBank accession numbers for all sequences are given in Table S1. Matrices and trees from this study are available from TreeBASE (http://www.treebase.org) accession number 18565. The host-symbiont network was visualized in *igraph* v1.0.1 (Csardi and Nepusz 2006).

Time-calibration using host events. A time-calibrated tree was inferred in *BEAST v.2.3.1* (Bouckaert et al. 2014) with unlinked substitution and linked tree and clock models. The 'best' partitioning scheme (rDNA stem, rDNA loop, EF1-α, SRP54, HSP70, CO1) and substitution models (GTR+I+G for all) were found in *PartitionFinder v1.1.1* (Lanfear et al. 2012). The clock model was set to 'Relaxed Clock Log Normal', and the speciation model was set to the 'Birth Death Model' based on our *a priori* expectation that feather mites, along with their avian hosts, experienced many extinctions. A separate analysis using the Yule model inferred almost identical or very similar time estimates (not reported). There are no fossil records for feather mites; however, it was possible to use two calibration points for three nodes based on bird divergence and biogeographic data (Fig. 2). The first calibration point was the dispersal of emberizoid Passerida (Emberizoidea sensu Barker et al. 2013) into the New World around 20-22 Mya (point 16, Table 2 of Barker et al. 2004). It matches the origin and diversification of two New World lineages of mites: the *thraupis+quadratus* clade (genus *Proctophyllodes*) and the *Amerodectes* clade (Figs 2, 3, S2, S3; Table 1 #4, 7). Representatives of these two phylogenetically independent lineages often co-occur on the same bird hosts, and apparently their evolutionary histories independently mirrored this biogeographic event in the evolution of their hosts. For this event, a normal prior with the mean of 21 Mya and σ=2.85 was used in the *BEAST* analyses. The mean was averaged among the two time estimates (NPRS and PL) for this host divergence and biogeographic event (Barker et al. 2004), while for estimating the sigma (σ), the extreme range values (Barker et al. 2004) were conservatively chosen. The normal prior was used because the bird dispersal event was estimated from bird phylogeny. The second calibration point was the split into suboscine and oscine passeriform birds (76-77 Mya) (Fig. 2, Table 1 #2). This split matches the feather mite split: *Proctophyllodes* vs. *Nycteridocaus* clades (Figs 2, S2, S3; Table 1 #2). For this calibration point, the mean (76.5) and sigma (3.0) were calculated as before.

A total of 18 independent *BEAST* analyses were run with a sampling frequency of 5000. Of these, 10 converged on a similar solution with a substantially higher mean posterior (e.g., -186225 vs -186300) and likelihood (e.g., -186300 vs -185525). Therefore, these 10 analyses were allowed to run for a larger number of generations, while the eight suboptimal runs were stopped. For the 10 well-behaved analyses, convergence and adequacy of the posterior sample size of mcmc runs was further assessed in *Tracer* v1.6 (Rambaut and Drummond 2009); ESSs for all parameters substantially exceeded 200. A total of 84,650 postburnin trees

were combined and summarized to obtain a maximum credibility tree (with the node heights calculated as median heights) in *TreeAnnotator* v. 2.3.1 (Rambaut and Drummond 2009). This time-calibrated phylogeny was visualized in *FigTree* v1.4.2 (Rambaut 2009) (Fig. 1). For comparison, an additional analysis using the same time calibration scheme was run in *TreePL* (Fig. S6).

Time-calibration using mite fossils. We validated our *BEAST* time calibration with independent time estimates, using a large, 315-taxon published phylogeny of sarcoptiform mites (Klimov and OConnor 2013) and several fossil-based calibration points (the maximum age was estimated): *Alicorhagia* – 410-456.5 Mya (fossil: *Pseudoprotacarus scoticus*, 410 Mya) (Hirst 1923; Dubinin 1962); Enarthronota (7 taxa on tree) – 326.7-421.8 Mya (fossil: *Palaeohypochthonius jerami*, 326–330 Mya) (Norton et al. 1988; Subias and Arillo 2002); *Anachipteria* – 145-382.5 Mya (fossil: *Achipteria obscura*, 153-145 Mya) (Krivolutsky and Krasilov 1977). Known fossils of Astigmata were not included because they either could not be confidently placed among modern lineages (*Glaesacarus,* 44 Mya) (Sidorchuk and Klimov 2011) or sequences of modern taxa were lacking (*Amphicalvolia*, 16 Mya) (Türk 1963). This phylogeny was based on five nuclear genes, of which three protein-coding genes were translated to amino acids prior to analysis (Klimov and OConnor 2013), and included 44 proctophyllodid terminals (40.7% of our ingroup sampling). Diversification times were estimated in the program *TreePL* (Smith and O'Meara 2012) since *BEAST* failed to achieve convergence after several trials with or without parameter tuning. This result is consistent with previous observations reporting difficulties in convergence and prohibitively low speed when analyzing large time-calibrated datasets in *BEAST* (Tamura et al. 2012). We conducted two *TreePL* analyses: (1) the maximum likelihood sarcoptiform tree (Klimov and OConnor 2013) was time-calibrated with the three mite fossils (1000 replicates) (Fig. S2); (ii) 18,000 stationary Bayesian trees (Klimov and OConnor 2013) were thinned to 1000 trees; each of these 1000 trees was time-calibrated with the mite fossils in *TreePL* and then the results were summarized in *TreeAnnotator* to obtain a maximum clade credibility tree (Fig. S3). This time calibration generally provides reasonable time estimates. For example, our estimate of the age of the crown group Chaetodactylidae (mites exclusively associated with bees), 119.9 Mya, is nearly the same as a recent estimate for the crown group of bees, 123 Mya (Cardinal and Danforth 2013). These two analyses were also repeated for the hybrid (mite fossil+host phylogeographic events) calibration scheme (Fig. S4, Fig. S5).

Co-phylogenetic analyses. We compared the degree of congruence between host and parasite phylogenies in PACo (Balbuena et al. 2013). This approach converts host and parasite trees to patristic distance matrices; the parasite matrix is then rotated and scaled to fit the host matrix using Procrustean superimposition. The significance of the global fit is tested by a permutation procedure where hosts are randomly assigned to symbionts. Finally, to assess the contribution of individual host-parasite associations to the global fit, a goodness-of-fit statistic is calculated (the smaller the value the better the contribution is). We used PACo as a primary test over other similar distance-based tests because scaling of the parasite matrix to

the host matrix produce sensible results when symbionts experience host shifts to host lineages that originated earlier than symbionts. In contrast, ParaFit (Legendre et al. 2002) tends to infer these links as significant. For co-phylogenetic tests, we used 200 random stationary Bayesian time-calibrated trees downloaded from the site "A global phylogeny of birds" (http://birdtree.org). These trees are based on Ericson constraints to represent the relationships among major lineages (Jetz et al. 2012) and up-to-date bird fossil calibrations ("Stage2 MayrAll Ericson"). For each host tree, a separate analysis was done and then results were summarized using a custom R script. For the mite tree, we used the *BEAST* chronogram (see above) (Fig. 2).

Furthermore, we conducted an exploratory event-based reconciliation analysis in *Jane 4* (Conow et al. 2010). This program, like other currently available event-based programs, cannot analyze chronograms directly. Instead, it removes branch lengths (which are expressed in time units in chronograms) and then offers an option to set "time zones" manually (a nearly impossible task for large trees). A *Jane* run with the default settings yielded a set of maximum-parsimony solutions with a cost of 258 (co-divergences=52, duplications=4, duplication & host switches=116, losses=22, failures to diverge=0). As expected, the overall solution was time-incompatible. For example, mites originated much later than an important host node, Muscicapoidea+Passeroidea (see below, point 3). We do not report this analysis further.

Biogeographic analysis. Biogeographic reconstruction was done in *BioGeoBEARS* (Matzke 2013). Given a phylogeny and geographic distribution of modern taxa, this approach reconstructs ancestral areas and estimates several biogeographically relevant parameters including: range expansion (D parameter), range contraction (E), and the founder-event speciation parameter (J). The latter parameter accounts for the case where, at cladogenesis, a daughter lineage disperses to a new range outside the range of the ancestor. In other words, this parameter can appropriately handle intercontinental dispersals followed by diversification in the new area. For this analysis, we used the *BEAST* chronogram (see above) (Fig. 2). Geographic ranges were coded for two categories (New and Old Worlds), omitting unnatural bird/mite dispersals due to human activities. The maximum number of areas was set to two.

Results

Comparison of methods of time-calibration. For the proctophyllodid dataset, we compared divergence time estimates obtained by two approaches, penalized likelihood (*TreePL*) and Bayesian time estimation with prior distribution densities set on the calibrated nodes (*BEAST*). Excluding the estimates for the nodes directly used for calibration, *TreePL* time estimates (Fig. S6) overall were very similar (events 5, 6, 8) or older (events 1, 3, 9, 10) than those inferred by *BEAST*; this pattern was similar to *TreePL* analyses conducted with fossil-

only calibration points. Hence, we expect that in comparison between *TreePL* and *BEAST* analyses (see the following section), the maximum likelihood estimates could be similar or older than Bayesian estimates.

Biogeography. Our reconstruction (BAYAREALIKE+J, dAICc=-6.27 with the next best-fitting model, DEC+J) was nearly unambiguous for all but one of the key nodes discussed further (Fig. S8, Table 1). The exception was the *Amerodectes* genus group, a lineage distributed entirely in the New World (Fig. S8 #7). Its sister group, *Pterodectes rutilis*, is associated with the widely distributed, migratory swallows. Hence, the reconstruction was equivocal in this portion of the tree.

Timing host-symbiont phylogeographic events. Our proctophyllodid (173 taxa) tree time-calibrated with host events was nearly identical to the relevant portion of the sarcoptiform tree (315 taxa) time-calibrated with fossils (Figs S2, S3). Ten important points in the proctophyllodid evolutionary history were recovered in these topologies (Figs 2, S2, S3, Table 1), which will be discussed further in the paper. Our topologies were largely congruent to both morphological (focusing on Pterodectinae), or molecular (focusing on the *Proctophyllodes pinnatus* group) trees published previously (Mironov 2009; Knowles and Klimov 2011). Within the genus *Proctophyllodes,* the largest and most challenging from a morphological perspective, we recovered most previously recognized species-groups (Atyeo and Braasch 1966; Mironov and Kopij 1996): *anthi*, *caulifer, detruncatus*, *weigoldi,* and *quadratus* species groups, plus the "genera" *Monojoubertia* and *Joubertophyllodes* (Fig. 2). In contrast, representatives of the two other groups, *musicus* and *stylifer*, appeared to be mixed in one clade. Furthermore, a clade containing the core of the *thraupis* group also included a number of species previously referred by taxonomists to the *glandarinus* and *weigoldi* groups (Fig. 2). These results make morphological sense if the phylogenetic value of the extremely long male aedeagus (used to define the *glandarinus* group) is diminished and alternative character states are used to define species groups in *Proctophyllodes*. Our phylogenetic analysis inferred three new lineages, all supported by morphological apomorphies: the *ceratophyllus*, *vassilevi*, and *markovetsi* groups (Fig. 2). Morphological analysis for these findings will be presented elsewhere.

Given our topology, two independent monophyletic lineages of proctophyllodid mites currently associated with emberizoid Passerida invaded the New World: (i) the ancestor of the *Proctophyllodes thraupis+quadratus* clade and (ii) the ancestor of the *Amerodectes* clade (Figs 2, S8, S9). The origin of the *thraupis+quadratus* clade (23.8 Mya) nearly coincides with independent time estimates based on fossils for the common ancestor of this clade plus its sister-group (25.7-26.9 Mya based on the fossil-calibrated phylogeny vs. 24.5 Mya for the compatible node on the host biogeography-calibrated phylogeny) (Table 1 #4). These time estimates for the origin of the *thraupis+quadratus* clade are close to the timing of the dispersal of emberizoid Passerida, the modern hosts of this mite clade, into the New World (20-22 Mya). In contrast, the *Amerodectes* clade shows substantial discordance in timing of

dispersal to the New World (S8 #7): mites 44.3-44.8 (fossil-calibrated) or 32.0 Mya (host biogeography-calibrated) vs. birds 21 Mya (Table 1 #7).

The origin of the *Nycteridocaulus* clade was inferred to be younger than the corresponding event in the evolutionary history of their hosts (split of oscines vs. suboscines): 45.1-49.3 (fossil-calibrated) or 69.9 (host biogeography-calibrated) for mites vs. 76.5 Mya for birds (Table 1 #2).

Proctophyllodid mites associated with hummingbirds were inferred as a monophyletic lineage (Rhamphocaulini), which is consistent with a recent morphological hypothesis (Mironov 2009), but not with earlier hypotheses emphasizing autapomorphies (Park and Atyeo 1971b, a). The origin of this clade is dated from 61.6-71.7 Mya (fossil-based calibration) or 57.2 Mya (host biogeography calibration) (Table 1 #10, Fig. S9).

Discussion

We calibrated three nodes of the proctophyllodid tree using two time-calibration points based on host biogeographic events (intercontinental dispersals) (Fig. 2, Table 1). This approach can introduce biases toward synchronous co-biogeographic scenarios but is a common practice in studies of host-parasite, or more generally, host-symbiont coevolution (Light et al. 2010; Smith et al. 2011; Zhu et al. 2015). Therefore, we also obtained divergence time estimates using mite fossil outgroups (Table 1), an approach that was found to be the best strategy in the absence of ingroup fossils and which may not have a drastic influence on age estimates across the tree (Sauquet et al. 2012). Summarily, these two approaches, and another "hybrid" approach (see comparison of time-calibration schemes below), allowed more precise time estimates for major biogeographic, co-phylogenetic, and diversification events in proctophyllodid feather mite evolution. Although multiple studies agree on the pattern of phylogenetic relationships of passerine birds, there are disparate time estimates (Cracraft 2001; Ericson et al. 2002; Barker et al. 2004; Irestedt and Ohlson 2008; Cracraft and Barker 2009; Ericson et al. 2014; Prum et al. 2015). For this reason, below we compare our findings with two major hypotheses, suggesting either older (Barker et al. 2004) or more recent (Prum et al. 2015) timing of divergence and dispersal in passerine lineages.

Comparison of schemes for time-calibration of symbiont phylogenies. Nodes calibrated by biogeographic or host information are usually secondary calibrations derived from previous studies and with the normal prior distribution set on the calibrated nodes (Drummond et al. 2006; Ho and Phillips 2009). Hence these secondary estimates may be inferred to be more similar to their original primary time estimates in comparison to fossil-based calibration. Because fossils only provide evidence for the minimum age of a clade, there is much more uncertainty associated with setting the priors on the node ages (Rutschmann et al. 2007; Sanders and Lee 2007; Lukoschek et al. 2012; Sauquet et al. 2012). Everything else being

equal, the accuracy of host/biogeographic event calibration strongly depends on the accuracy of the primary calibration, while the accuracy of fossil-based calibration strongly depends on the uncertainty in estimating the minimum age of the fossils (Forest 2009). As a result, either method can be either more or less accurate in comparison to each other, depending on a particular dataset. When no suitable fossils are available to calibrate the group of interest, sampling more outgroup taxa to include external fossil age constraints is a better option than relying on secondary calibration (Sauquet et al. 2012). In our system, secondary time estimates on symbiont trees were indeed more similar to their primary estimates derived from the host/biogeographic data (Table 1 #2, 4, 7, compare values in two columns "Bird phylogeny" vs two columns "Mite phylogeny: Host phylogeography"). This was also true for nodes of the symbiont tree that were not directly used as calibration points (Table 1 #5, 6). In contrast, trees calibrated with mite fossils gave more dissimilar time estimates (Table 1 #2, 4, 5, 6, 7, compare values in two columns "Bird phylogeny" vs two columns "Mite phylogeny: Mite fossil"), except for event 3. We also note that divergence time estimates based on the secondary calibrations are usually younger (Table 1, except for events 2 and 6), an observation consistent with that reported in another study (Sauquet et al. 2012). A hybrid calibration scheme, where both mite fossil and host geographic events were used as calibration points (Table 1, two columns "Mite phylogeny: fossil+host)" resulted in much higher time estimates for events 3 and 5 as compared to both fossils only or host-event-only calibration schemes, or intermediate estimates (event 6), or matching those of the fossil calibration scheme (event 10) (Table 1). Based on our data, the hybrid approach, therefore, is a less preferable strategy as compared to fossil-only calibration.

To detect potentially erroneous calibration points, cross-validation of both biogeographic/hosts and fossil time calibrations is necessary (Near et al. 2005). In our case, this point could be the origin of hummingbirds and associated mites (Table 1, #10). Some recent estimates from bird phylogenies suggested a recent origin of hummingbirds, which is in conflict with the mite time estimates (see below). Different time-calibration schemes inferred a substantially older age of the mites then their present hosts (Table 1, #10). Calibration points like this should be excluded from time calibration analyses, validated with independent lines of evidence.

Early evolution. Proctophyllodids probably originated on the ancestors of passerines, with the first split into the subfamilies Proctophylodinae and Pterodectinae 85.4 Mya (or 142.6-166.4 Mya, fossil-calibration) (Table 1 #1), which probably took place in Gondwana, before the splitting of passerines into major lineages (Ericson et al. 2002) (Figs 2, 4). The old split between the two mite subfamilies is supported by the fact that both mite subfamilies occur on most extant families of passerines and usually coexist on the same host, although occupying different microhabitats (Mironov 2009). Representatives of Pterodectinae were recently found on the oldest passerine lineage, the family Acanthisittidae (Mironov and OConnor 2017), which originated in New Zealand after its break-up from Gondwana nearly 82 Mya (Barker et al. 2004). This is consistent with the hypothesis of Gondwanan origins of the two

mite lineages and their early independent evolution and dispersal, mirroring the early dispersal pattern of their avian hosts (Fig. 4). In contrast, our data show little agreement with recent a recent study (Prum et al. 2015) that inferred the origin of Acanthosittidae as much later, 50 Mya (i.e., after the separation of New Zealand from Gondwana).

The basal divergence of proctophyllodine mites into the *Proctophyllodes* clade (oscine birds) and the *Nycteridocaulus* clade (suboscine birds) was dated at 69.9 Mya (or 45.1-49.3 Mya, fossil-calibration) (Table 1 #2). Based on the mite topology (i. e., *Platyacarus* and *Nycteridocaulus* do not form a monophyletic clade) and host distribution, this mite split probably corresponds to the split of passerines into oscines and suboscines dated by various studies as 76-77 Mya (Barker et al. 2004), 62–79 Mya (Ericson et al. 2002) or 58–84 Mya (Ericson et al. 2014). The *Platyacarus* lineage split earlier (74.1 Mya, or 54.8-91.12 Mya fossil-calibration) and, as is the case with the *Nycteridocaulus* lineage, does not occur on oscine passerines. This lineage, currently restricted to the New World, either went extinct or 'missed the boat' during the bird dispersal through Africa and Australia (Fig. 4).

Proctophyllodes – extensive diversification in the Old World. The clade comprising the genus *Proctophyllodes* was formed and subsequently evolved on oscine passerines, which underwent their basal radiation 62-65 Mya (Barker et al. 2004). The expansion of various oscine lineages throughout the Old World from their ancestral areas, Australia and New Guinea, started in the Middle Eocene (e.g., 47 Mya for Picatarthidae) (Barker et al. 2004; Jonsson et al. 2011), and up to the Early Oligocene 34 Mya, they successfully colonized Africa and Eurasia (Fjeldsa 2013). The major clade that originated after the basal mite split (*detruncatus+caulifer+vassilevi,* and *weigoldi*) 36.6 Mya shows a mosaic distribution on the two major lineages of oscine passerines (Passerida and Corvida) and forms associations with the largest number of host families and suprafamilial taxa when normalized by the number of mite species (Figs 3, S9, Table S7). This pattern is indicative of relatively frequent host shifts having occurred in the early period of evolution on this lineage. The origin of the *musicus/stylifer + ceratophyllus* lineage and its sister clade including the *anthi* and four other species groups, is dated 34.3 Mya (39.3-42.4 Mya fossil-calibration) (Table 1 #3; Fig. 2). Based on known diversity and host ranges, it is likely that the origin of these two major clades is related to the origin and diversification of the superfamilies Muscicapoidea and Passeroidea, which originated in the Old World 38.2–40.2 Mya (Cracraft and Barker 2009).

Co-dispersal of Proctophyllodes *to the New World*. The origin and diversification of the *thraupis+quadratus* lineage, as inferred in our study, coincided with a corresponding event in their avian hosts: the dispersal of emberizoid Passerida into the New World, following their extensive diversification (Klicka et al. 2000; Ericson et al. 2002; Yuri and Mindell 2002; Carson and Spicer 2003; Lovette et al. 2010; Klicka et al. 2014; Powell et al. 2014). The timing for these dispersal events was inferred at 23.8 Mya (biogeographic data) or 25.3-26.9 Mya (fossil data) (Table 1 #4; Fig. 2) for mites and 20-22 Mya (Barker et al. 2004) or 32–15 Mya (Ericson et al. 2014) for birds, indicating that the two dispersals probably coincided in

time, and the mites co-dispersed with their hosts into the New World. In contrast, our results strongly disagree with the recent time estimate dating the origin of New World emberizoids only as 12.0 Mya (Prum et al. 2015).

The sister of the *thraupis+quadratus* group, the *pinnatus+Joubertophyllodes* group, probably originated in the same time period on finches (Fringillidae), a diverse Old World lineage of Passeroidea that originated 18.0–21.0 Mya (Cracraft and Barker 2009). Representatives of various generic lineages of the fringillid subfamily Carduelinae (e.g., *Carduelis*, *Haemorhous*) appeared in the New World at a much later time, within the period 3.0-14.6 Mya (Arnaiz-Villena et al. 1998; Smith et al. 2013). Fringillids are the most likely ancestral hosts of the *pinnatus+Joubertophyllodes* group because these birds harbor its greatest diversity (Fig. 3). Subsequently, this species-group colonized other hosts in Muscicapoidea, Sylvioidea, and Certhioidea, which now harbor a much lower diversity of these mites (Fig. S9). *Joubertophyllodes*, which evolved from the core of the *pinnatus* clade and is a young (11.6 Mya, 4.4-5.3 Mya fossil-calibrated; Table 1 #3; Figs 2, S9) and morphologically highly derived lineage, apparently evolved on birds of the genus *Emberiza* (Emberizidae), which originated 12 Mya (Barker et al. 2013).

Co-dispersal of Amerodectes *to the New World: Double co-migration event?* The above section documented an intercontinental co-dispersal of the proctophyllodine *thraupis+quadratus* group corroborated by independent time estimates of both mites and hosts. It is likely that at the time of this event, the avian hosts also harbored pterodectine mites (see above). Hence, it is reasonable to assume that the two mite groups simultaneously co-dispersed with their hosts, emberizoid Passerida, into the New World. Although our time estimates for the *thraupis+quadratus* group nearly coincide with those of their hosts, they do not perfectly match those for the *Amerodectes* clade (a derived lineage of New World pterodectines) and are substantially older that those for the *thraupis+quadratus* group (32.1 [44.3-44.8 fossil-calibration] Mya vs. 23.8 Mya) (Table 1 #7). Nevertheless, the confidence interval inferred for the *Amerodectes* clade (27.9-36.2 Mya, or 32.8-63.9 fossil-calibration) (Table 1 #7) overlaps or nearly overlaps the confidence intervals for the bird dispersal to the New World 32–15 Mya (Ericson et al. 2014). At this point simultaneous co-dispersal of the *Amerodectes* clade and the *thraupis+quadratus* group is possible, but other scenarios cannot be ruled out. For example, the *Amerodectes* clade could have formed on the ancestors of Passeroidea or even Passerida in the Old World, followed by subsequent extinction. It would not be possible to propose the latter scenario based on the commonly used methodology relying on reconciliation analysis of host and symbiont topologies, without considering the timing of host and symbiont phylogeographic events.

Host shifts and extinctions in New World Proctophyllodes. Because both host shifts and extinctions of symbionts may be temporally separated from host divergence or dispersal events, using only host biogeography or divergence to time-calibrate symbiont phylogeny may result in failure to correctly identify these non-synchronous scenarios. Using our dated

phylogeny, we can explain time mismatches in host and symbiont events by co-phylogeographic scenarios involving a sequence of extinctions and host shifts. Below we discuss two such scenarios that resulted in different outcomes, with recent avian migrants either receiving symbiotic mites from local birds or spreading their own mites to local birds upon arrival.

The ancestor of the *Euphonia* lineage (Fringillidae: Euphoniinae) dispersed from Eurasia to the New World, although probably at a much later time as compared to the similar migration of the ancestors of emberizoid Passerida (Zuccon et al. 2012). The ancestor of euphonias (Fig. 2, event 8, Fig. S9) would be expected to harbor mites of the *pinnatus* or *glandarinus* groups (Fig. 2), common on its presumed sister-clades, Fringillinae and Carduelinae, all belonging to the same family, Fringillidae (Fig. 3) and having the greatest diversity in the Old World (Fig. S9). However, modern euphonias lack members of either the *pinnatus* or *glandarinus* groups, but have several *Proctophyllodes* species that are very close to *P. thraupis* and *P. megathraupis* associated with tanagers, which belong to a different bird lineage (family Thraupidae) (Fig. 3, S9). This suggests that the original euphonias' mites were replaced by mites that recently shifted from tanagers, an exclusively New World bird lineage. According to our estimates, this host shift could have occurred 8.7 Mya (Table 1 #8), which is much later than the origin of the main subfamilial lineages of Fringillidae in the Old World, about 20 Mya (Cracraft and Barker 2009; Zuccon et al. 2012; Smith et al. 2013).

While species of the *thraupis* group shifted from native birds to recently arrived birds, with replacement of the original mite fauna, host shifts also occurred in a different direction, from recent migrants to native birds. *Proctophyllodes empidonicis* (*musicus*/*stylifer* group) is associated with suboscine fluvicoline tyrant flycatchers (Tyrannidae), despite New World suboscines usually harboring the *Platyacarus* and *Nycteridocaulus* mite lineages (Atyeo 1966; Atyeo and Gaud 1968; Kudon 1982) (Fig. 3, S9). The only possible explanation of this host association is that the ancestor of *Pr. empidonicis* shifted from an oscine passerine belonging to the Mimidae, Turdidae or Troglodytidae, which are the typical hosts of the *musicus/stylifer* group in the New World (Fig. 3). Our time estimate of this shift is around 14.3 Mya (Table 1 #9), which is very close to the time inferred for the origin of fluvicoline tyrant flycatchers, 14 Mya (Ohlson et al. 2008), and much younger than the origin of the oscine passerines, 71–67 Mya (Barker et al. 2004). These data suggest that there was a host switch from recent migrants to native birds in this system.

Are hummingbirds older than previously thought? - Evidence from mite associations. The mite tribe Rhamphocaulini (Proctophyllodidae: Pterodectinae) is exclusively associated with hummingbirds (Apodiformes: Trochilidae), while its sister lineage, the tribe Pterodectini, is primarily associated with passerines (Figs 2, 3, S9). Because hummingbirds are phylogenetically quite distant from passerines (Livezey and Zusi 2007; Prum et al. 2015), and their sister-group, swifts (Apodidae), lack any proctophyllodids (Gaud and Atyeo 1996; Proctor and Owens 2000), it has been hypothesized that pterodectines appeared on

hummingbirds as the result of an ancient host switch (Mironov 2009). Hence, the rhamphocaulin mites should be more recent than their hummingbird hosts or have nearly the same age (if the shifts nearly coincided with the origin of hummingbirds).

Unfortunately, there is strong disagreement in timing of the origin of hummingbirds: the earliest fossils of true hummingbirds from the Old World are dated 30-34 Mya (Mayr 2004); a study based on multigene phylogeny of 400+ hummingbird species dated the origin of the true hummingbirds at 42 Mya (36.9–47.4 Mya) (McGuire et al. 2014); a study based on ordinal phylogenomic data, where hummingbirds were represented by a few terminals, at 54 Mya (51-57 Mya) (Prum et al. 2015); 65.4 Mya based on mitogenomic phylogeny (Pacheco et al. 2011), or an earlier study even at 70 Mya (van Tuinen and Hedges 2001). The latter three time estimates are closer to our dating of the origin of Rhamphocaulini, 57.2 Mya (host biogeography with no hummingbird-related calibration points) or 67.6-71.7 Mya (mite fossils) (Table 1 #10). Thus, given our mite data, the time estimate for the early origin of hummingbirds (McGuire et al. 2014) should be reconsidered, and an older origin for this group (van Tuinen and Hedges 2001; Pacheco et al. 2011; Prum et al. 2015) is likely. We, therefore, interpret the origin of rhamphocaulin mites to an ancient host shift from passerines to hummingbirds that occurred nearly simultaneously with the origin of hummingbirds. Lice, with confirmed fossil records, offer another system to study co-phylogeographic events, and potentially can provide additional lines of evidence for or against this hypothesis. Unfortunately, hummingbird lice have not been included in available dated phylogenies so far (Smith et al. 2011).

In conclusion, we show that feather mites can be useful models for studying co-phylogeographic events. Based on our independently dated phylogeny, we discuss important radiations and biogeographic events in the evolutionary history of proctophyllodid feather mites and compare them with events in the evolution of their hosts. Despite bird and mite phylogenies being incongruent to some extent, most historical intercontinental dispersals of mites and their hosts that were followed by extensive radiations in the new areas coincided in time as estimated independently for both birds and mites (e. g. the *Proctophyllodes thraupis+quadratus* lineage and emberizoid Passerida) (Table 1 #4). This strongly supports a synchronous intercontinental co-dispersal of mites with their hosts from the Old World to the New World. There were other events where timing for both bird and mite events coincided (Table 1 #3, 5). Two other events coincided with host-calibrated data (Table 1 #6, 9), but either could be validated only by Bayesian mite fossil time calibration (*Joubertophyllodes,* the mite subgroup associated with *Emberiza*; Table 1 #6) or could not be independently validated because a particular node was absent from the mite fossil-calibrated tree (*Proctophyllodes empidonicis* associated with fluvicoline flycatchers, Table 1 #9). Some other phylogeographic events (Table 1 #2, 10), most importantly, the origin of hummingbird mites (Table 1 #10), were inferred to have been much earlier than that of their hosts (many,

but not all time estimates). Thus, our results and future studies utilizing host-independent time-calibration of symbiont phylogenies may have predictive value in comparing alternative hypotheses in divergence times of their hosts.

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Table 1. Phylogeographic events and their estimated dates (Mya) in the evolution of proctophyllodid mites and their avian hosts. Time estimates are given as means and ranges unless otherwise indicated.

		Result		Bird phylogeny		Mite phylogeny						Interpretation
#	Event	Bird lineage	Mite lineage	(Barker et al. 2004)	(Prum et al. 2015)	Mite fossil (ML)[i]	Mite fossil (Bayesian)[k]	Host phylogeography (BEAST)[l]	Host phylogeography (TreePL)[l]	fossils+host (ML)[i]	fossils+host (Bayesian)[k]	
1	Mite basal divergence	none	Proctophyllodinae/Pterodectinae split	-	-	142.65 (117.42-152.77)	166.42 (132.31-178.52)	85.43 (75.37-96.66)	107.37(99.94-115.6)	99.59 (96.58-103.72)	101.78(93.78-109.14)	Mite split independent from host phylogeography
2	Split Suboscines/Oscines	Suboscines and Oscines	*Nycteridocaulus* generic clade	76.5 (76-77)[a]	47(39.0-54.0)	45.1(35.59-48.92)	49.27 (35.99-97.25)	69.9(63.97-75.78)	76.0(76.0-76.0)	76.0(76.0-76.26)	76.0(76.0-76.31)	Co-divergence
3	Diversification of Oscine birds in OW	Origin of Muscicapoidea and Passeroid	*Pr. ceratophyllus-pinnatus* clade (8 species groups)	38.2–40.2[b]	24 (15.0-33.0)	39.28(31.23-42.63)	42.42(31.83-88.13)	34.31(28.76-40.38)	47.32(43.0-52.26)	54.58(51.17-60.63)	55.99(47.92-64.68)	Co-origin followed by extensive diversificati

		ea			[h]							on
4	Dispersal from OW to NW	NW emberizoid Passerida	*Pr. thraupis+quadratus* clade	21(20-22)[c]	12(2.5-21.5)	25.3(19.79-29.00)	26.87(17.69-59.34)	23.8(20.26-27.55)	22.0(22.0-22.0)	32.02(29.97-34.23)	32.87(27.33-38.0)	Co-dispersal
5	Origin of finches	finches (Fringillidae)	*Pr. pinnatus+Joubertophyllodes* clade	18.0-21.0[b]	-	25.3(19.79-29.00)	26.87(17.69-59.34)	23.8(20.26-27.55)	22.0(22.0-22.0)	32.02(29.97-34.23)	32.87(27.33-38.0)	Co-origin followed by extensive diversification
6	Origin of *Emberiza*	*Emberiza*	*Joubertophyllodes* subgroup	10.0[d]	-	4.4 (3.41-5.17)	5.34 (2.55-28.18)	11.61(9.26-14.39)	11.85(10.63-13.17)	6.86(5.74-7.93)	7.91(4.7-11.55)	Origin after shift of the ancestor from OW fringillids followed by diversification
7	Dispersal from OW to NW	NW emberizoid Passerida	*Amerodectes* generic clade	21(20-22) [c]	12(2.5-21.5)	44.33 (35.65-47.61)	44.79 (32.79-63.87)	32.06 (27.91-36.28)	22.0(22.0-22.0)	34.21(32.88-35.27)	33.61(29.3138.48)	Time mismatch. Most likely, mites originated earlier than birds, on the emberizoid's ancestors in OW
8	Dispersal of ancestor of *Euphonia* from Eurasia to NW	*Euphonia*	*Pr.* sp. n. (*thraupis* species complex)	<<21(20-22)[e]	-	[j]	[j]	8.73 (5.61-12.22)	8.5(7.43-9.44)	j	j	Extinction/ missing the boat of original mites (*Pr. pinnatus* or *glandarinus* groups) followed by host shift from NW tanagers
9	In-place (NW) origin and diversification of fluvicolines tyrant flycatchers	Fluvicolines (Tyrannidae)	*Pr. empidonicis*	14[f]	-	[j]	[j]	14.28(11.46-17.38)	22.3(18.77-25.61)	j	j	Host shift from an oscine passerine (Mimidae, Turdidae or Troglodytidae) recently arrived from OW to NW, with replacement of original mites (*Platyacarus* or *Nycteridocaulus* clades)
1	Split Apodidae/Tro	Apodidae and Trochilid	Rhamphocaulini	42.1(36.9-	53.5 (50.5 -	67.61(52.46-	71.65(53.45-	57.25(47.	68.25(61.	65.74(60.75-	68.87(59.6	Time mismatch. Ancient

0	chilidae	ae		47.4)[g]	58.0)	76.57)	106.87)	6-67.8)	87-76.01)	71.83)	8-78.88)	host shift of the ancestor from passerines

a = calibration point 2 for the mite tree (Fig. 2); b = after this reference (Cracraft and Barker 2009); c = calibration point 1 for the mite tree (Fig. 2); d = after this reference (Barker et al. 2015); e = "much later than NW emberizoid Passerida" (Zuccon et al. 2012) ; f = after this reference (Ohlson et al. 2008); g = after this ref (McGuire et al. 2014); h = see node 46, Fig.1 in this reference (Prum et al. 2015); i = median (95% HPD interval from 1000 replicates); j = absent from phylogeny; k = median (95% HPD interval from 1000 stationary Bayesian trees); l = median (95% HPD interval);

Figure legends

Fig. 1. Feather mites, *Proctophyllodes ampelidis* (right) on the underside of wing feathers (inset) of the cedar waxwing, *Bombycilla cedrorum* (left). Bird photo: Glenn Bartley (VIREO).

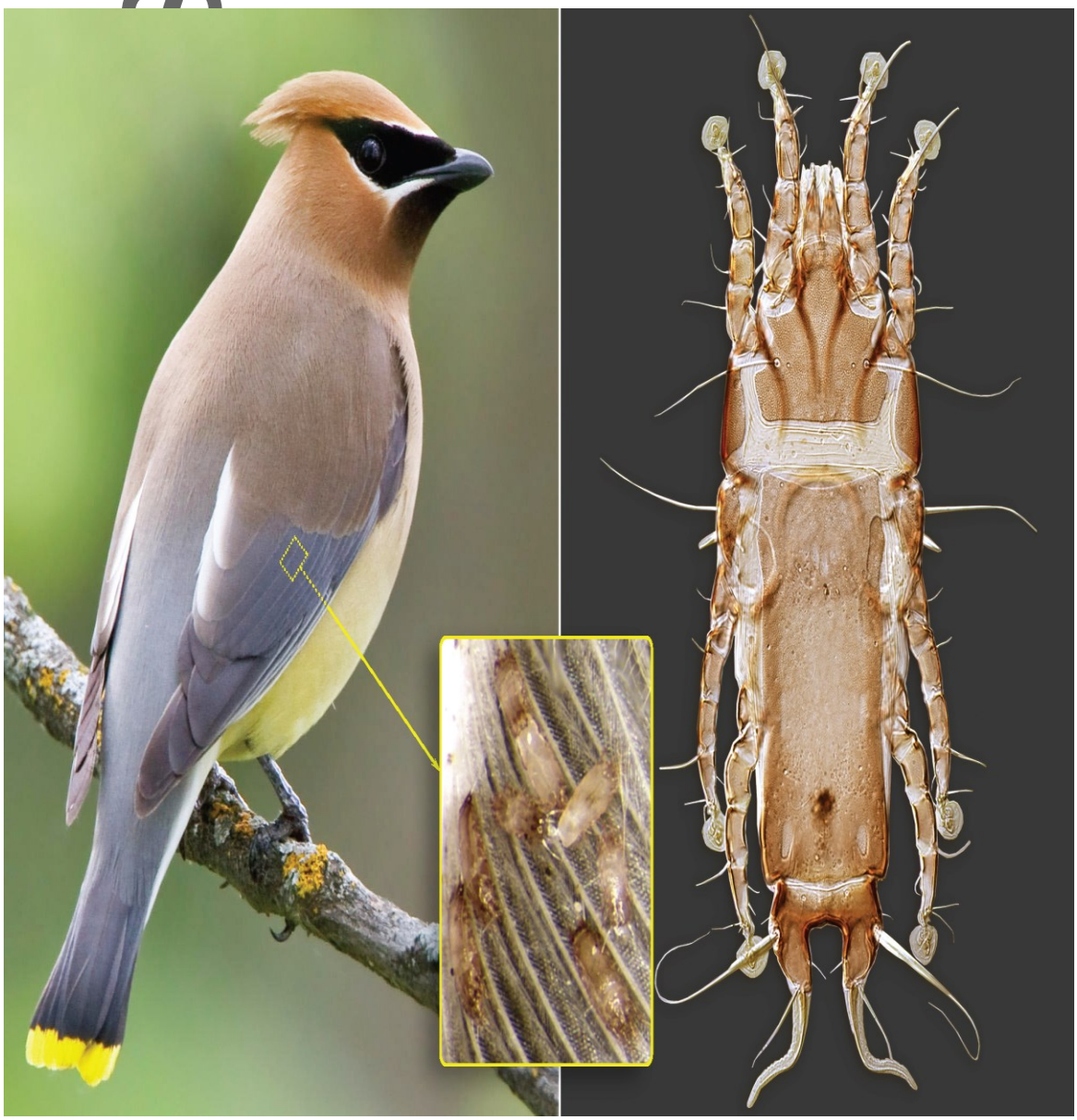

Fig. 2. Chronogram (maximum credibility tree) of the feather mite family Proctophyllodidae inferred in BEAST v.2.3.1. For each node, medians of time estimates and vertical bars representing 95% Highest Posterior Density (HPD) of these estimates are given. Out of 40 outgroups used in this analysis (Table S1), only *Steatacarus bifiditibia* (Trouessartiidae) is shown. Numbered nodes in blue circles refer to phylogeographic events 1-10 in Table 1. Nodes 2, 4, and 7, are time calibration points based on host biogeographic events, which were validated by a separate molecular clock analysis using fossil mite calibration points. Different lineages are identified by different colors and their taxonomic placement is indicated above the tree.

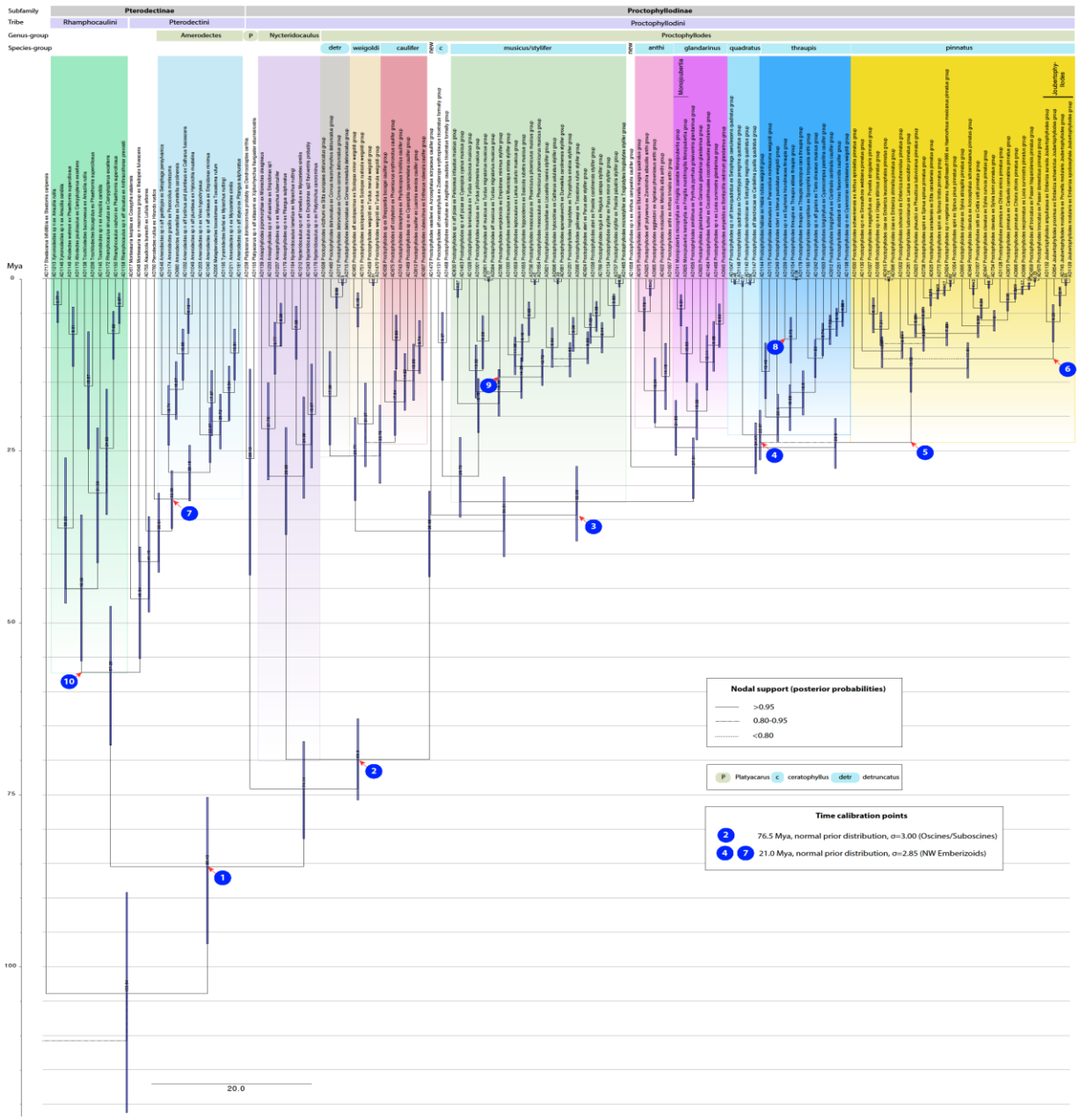

Fig. 3. Host-parasite associations of *Proctophyllodes* species groups (black front) and families of their avian hosts (blue font). Species groups are color-coded to match those on Fig. 2. The thickness of the connecting lines represents the strength of association (e. g., the number of mite species on a particular bird family). For summary statistics see Table S7.

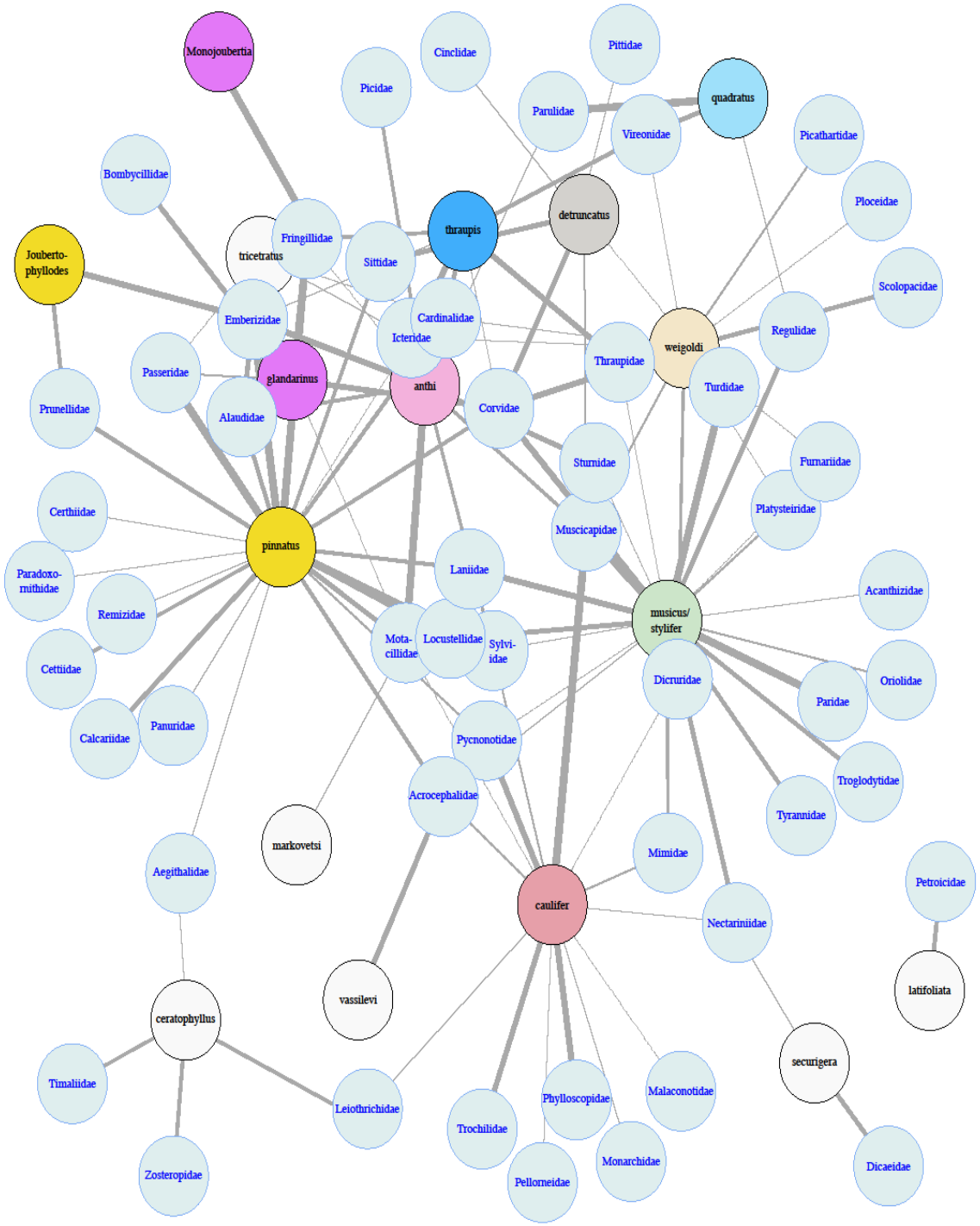

Fig. 4. Biogeographic history of feather mites subfamily Proctophyllodinae superimposed on that of their hosts, passerine birds (simplified from Ericson et al. 2002). Main biogeographic events of birds and mites are shown. Dotted lines inside arrows indicate situations where historical dispersal or diversification pattern of birds is obscured in mites, presumably because of extensive host shifts. Outlines of continents are given at approximate time of the basal divergence of proctophyllodine mites (90 Mya); image credit: Colorado Plateau Geosystems, Inc. http://cpgeosystems.com/rect_globe.html; under license CC BY-SA 4.0.