

Does evolution of plumage patterns and of migratory behaviour in Apodini swifts (Aves: Apodiformes) follow distributional range shifts?

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The Apodini swifts in the Old World serve as an example for a recent radiation on an intercontinental scale on the one hand. On the other hand they provide a model for the interplay of trait and distributional range evolution with speciation, extinction and trait transition rates on a low taxonomic level (23 extant taxa). Swifts are well adapted to a life mostly in the air and to long-distance movements. Their overall colouration is dull, but lighter feather patches of chin and rump stand out as visual signals. Only few Apodini taxa breed outside the tropics; they are the only species in the study group that migrate long distances to wintering grounds in the tropics and subtropics. We reconstructed a dated molecular phylogeny including all species, numerous outgroups and fossil constraints. Several methods were used for historical biogeography and two models for the study of trait evolution. We finally correlated trait expression with geographic status. The differentiation of the Apodini took place in less than 9 Ma. Their ancestral range most likely comprised large parts of the Old-World tropics, although the majority of extant taxa breed in the Afrotropic and the closest relatives occur in the Indomalayan. The expression of all three investigated traits increased speciation rates and the traits were more likely lost than gained. Chin patches are found in almost all species, so that no association with phylogeny or range could be found. Rump patches showed a phylogenetic signal and were correlated with Indomalayan distribution. Apodini swifts performed long-distance migration whenever they expanded their range to temperate latitudes during warm periods, repeatedly in the Pleistocene.

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10 **Introduction**

11 Adaptive radiations coincide with an accelerated speciation rate combined with an accelerated
12 differentiation of traits that are adapted to the requirements of a new environment (Schluter, 2000;
13 Price, 2008). Most examples of adaptive radiations have been extensively studied on oceanic islands of
14 mostly volcanic origin (Darwin finches on Galápagos (Rands et al., 2013); honeycreepers on Hawaii
15 (Lerner et al., 2011)). They mostly concern species of low dispersal ability: One accidental founding
16 event through passive displacement was followed by the differentiation of a single ancestor into several
17 descendant species with quite different adaptive traits in a relatively short time without further
18 invasions of closely related species. Neither has the colonising species been outcompeted by species of
19 a similar niche nor were the niches of the resulting species filled on the respective islands because the
20 oceanic islands are often young and harbour few endemics.

21 On larger islands or continents, the situation is different, since most potential niches have been
22 occupied over time so that dispersers rarely get the chance to establish (Price, 2010). And if in the case
23 of harsher climate regimes (at higher latitudes or elevations) niche space in general is restricted, no
24 further congener could disperse into the same area.

25 If a species instead was pre-adapted to dispersal rather than to the actual habitat or food requirements
26 of the newly colonized area, a full competition on these resources could be avoided. Laube et al. (2013)
27 found that migratory behaviour has an indirect positive effect on range size via better dispersal ability.
28 Since dispersal ability is positively correlated with migratory behaviour, dispersal to less suitable areas
29 should coincide with the evolution of long-distance migration (LDM). Winker (2000) considered
30 migration a key innovation that occasionally enables lineages to radiate in new environments. So,
31 LDM can accelerate speciation of that lineage. Despite initial comparative approaches (reviewed by
32 Joseph, 2005) the “adaptive reasons for interspecific variation in migratory behaviour” (Bennett &
33 Owens, 2002) have not yet been found.

34 Swifts (Apodidae) represent a prominent avian example of high dispersal ability and LDM. These birds
35 feed on airborne arthropods and are highly specialised for aerial life and particularly during migration
36 they are capable of staying entirely airborne across large distances and over long time periods.

37 Migratory Common Swifts (*Apus apus*) combine almost permanent flying with foraging, thereby reach
38 higher speeds and cover longer distances per day than any similar-sized bird species (Åkesson et al.,
39 2012) and Alpine Swifts (*Tachymarptis melba*) were recently shown to perform non-stop flights of a
40 proven maximum of 200 days (Liechti et al., 2013). The optimal body shape for such a life style is
41 based on long pointed wings, which are generally associated with high dispersal ability and LDM

42 (Winkler & Leisler, 1992; Marchetti, Price & Richman, 1995; Dawideit et al., 2009; Baldwin et al.,
43 2010; Förschler & Bairlein, 2011; Claramunt et al., 2012).

44 We chose the apodiform tribe of typical swifts (Apodini) with 23 extant taxa for a study of trait
45 evolution with potential impact on speciation rates in birds on a low taxonomic level. In a previous
46 publication we (Päckert et al., 2012) presented a taxon-complete molecular phylogeny at the species
47 level of this lineage comprising the genera *Apus*, *Cypsiurus* and *Tachymarptis*. However, the
48 delimitation of the Apodini has still not been fully understood. Monophyly was uncertain for some
49 species: Some species appeared paraphyletic and lineage sorting among some sister species was found
50 to be incomplete. A rapid diversification of the study group within the narrow morphological limits due
51 to the highly specialised life style seemed to be responsible for that. The molecular phylogeny needed
52 to be dated to quantify the speciation rates and to study evolutionary changes such as distribution and
53 the expression of morphological traits and migratory behaviour, the latter perhaps being interrelated
54 with dispersal/diversification.

55 Based on their pre-adaptation, swifts should exhibit an accelerated speciation, since they could occupy
56 new breeding grounds as soon as they become available and eventually become reproductively isolated
57 from populations that remain *in situ* or discover other new grounds. Although related swift lineages are
58 exclusively Indomalayan or even partially Australasian, we expected the Apodini swifts to have
59 originated from the Afrotropic, where most of the extant species breed (Figure 1). Because of the fast
60 aerial life of swifts, only one of the two plumage patterns should be of importance: the rump patch
61 should – beside acoustic signals – be relevant for species recognition whereas the chin patch can hardly
62 be seen. Either way these plumage patterns should evolve stochastically along the phylogeny instead of
63 being under sexual selection or adapted to the breeding range. Migratory behaviour – like behaviour in

64 general – should be a more labile trait because climate conditions have seen dramatic changes
65 especially during the Pleistocene when the northern hemisphere went through series of cold and warm
66 periods. If the ancestral-state reconstruction for LDM is nevertheless possible, it should mirror the
67 extant situation of LDM being performed by species breeding in temperate regions.

68 **Materials & Methods**

69 **Tree reconstruction**

70 We (Päckert et al., 2012) had previously presented a molecular phylogeny of swifts of the genera *Apus*,
71 *Cypsiurus* and *Tachymarpis*, with a complete taxon sampling at the species level. Phylogenetic
72 reconstructions were based on two mitochondrial (cytochrome *b*, 12S rDNA) and three nuclear
73 markers (intron 7 of fibrinogen, GAPDH, anonymous marker 12884). In order to compile a robust
74 taxonomic sampling for fossil molecular dating, we added sequences of further representatives of
75 *Aerodramus*, *Hirundapus*, *Hemiprocne* and *Streptoprocne* to the original data set of our previous study
76 (for origin of samples and GenBank accession numbers see Supplementary Table S1).

77 The sequences for each gene were aligned by ClustalW using MEGA v5.1 (Tamura et al., 2011) and
78 slightly adjusted by eye. The best-fit model for each locus was identified with the Akaike Information
79 Criterion (AIC) implemented in MRMODELTEST v2.3 (Nylander, 2004) in conjunction with PAUP*
80 v4.0b10 (Swofford, 2003).

81 Phylogenetic relationships were reconstructed using Bayesian inference through BEAST v1.4.8
82 (Drummond & Rambaut, 2007). In BEAST, we used the following settings: All five genes were treated
83 as separate partitions with unlinked substitution and clock models. According to MRMODELTEST
84 estimates, the HKY+I+ Γ model was assigned to the *cytb* partition, the HKY+ Γ model was assigned to

85 partitions Fib7, GAPDH and nuclear 12884 and the GTR+I+ Γ model was assigned to the 12S rRNA
86 partition (Table 1). Furthermore, cytochrome *b* was partitioned into three codon positions after clipping
87 of the stop codons and all parameters were unlinked. A relaxed uncorrelated log-normal clock was
88 used with no rate specified and a Yule process (speciation) assumed as a tree prior. The reconstruction
89 was for 30,000,000 generations. The log files were checked with TRACER v1.5 (Rambaut et al., 2013)
90 in order to set the burn-in value. The BEAST trees were summarised with TREEANNOTATOR v1.4.8 using
91 a burn-in value of 9,000 and median node heights and the final tree visualised in FIGTREE v1.2.2.

92 Molecular dating of the multilocus tree was done in a fossil approach applying three fossil age
93 constraints to fixed nodes of the Apodidae phylogeny. Because fossils are generally considered
94 representatives of minimum split ages, we applied fossil constraints as time intervals using a lognormal
95 t_{MRCA} prior distribution according to the standards given in Benton, Donoghue & Asher (2009, figure 2).
96 We chose three fossils for calibration and set the fossil age as hard minimum age constraint (zero offset
97 of lognormal t_{MRCA} prior in BEAST). The probability density (lognormal distribution range) was then
98 codified by manually adjusting lognormal means and standard deviations to soft maximum constraints
99 in order to match the distribution in real space.

100 The root (Figure 2, node 1) was calibrated using two of the oldest known apodiform fossils
101 from the middle Eocene *Argornis caucasicus* (Karhu, 1999; Mayr, 2003a) and a further *Argornis*-like
102 bird that was described from the Messel pit (Germany), *Parargornis messelensis* (Mayr, 2003b).
103 According to cladistic analyses of skeletal anatomy both taxa resulted as the oldest splits in an
104 unresolved trichotomy of the Trochilidae clade, thus as the oldest representatives of modern
105 hummingbirds (Mayr, 2005; Mayr, 2010, figure 1; but compare Ksepka et al., 2013). For calibration of
106 node 1 we applied a zero offset of 47 Ma according to the older of the two fossil ages (*Parargornis* 47–

107 49 Ma (Mayr, 2003a; Mayr, 2003b; Mayr, 2005)) and set the lognormal range to a soft maximum of 56
108 Ma thus spanning the entire early Eocene epoch (logNormalPrior mean="2.0" stdev="0.5").

109 Node 2 (Figure 2) was calibrated using the oldest known fossils of early swifts first described
110 from the Eocene Røsnæs Clay of Denmark, *Scaniacypselus wardi* Harrison, 1984), however this genus
111 was also represented by another fossil taxon in the Messel fauna, *S. szarskii* (Peters, 1985). Again we
112 adjusted the lognormal prior distribution range to the early Eocene period and applied a zero offset of
113 48.6 Ma according to the slightly older Røsnæs Clay fossil (Ypresian: ~48.6–55.8 Ma; cf. Lindow &
114 Dyke, 2006) and set the lognormal prior distribution according to the early Eocene interval, as for node
115 1 (settings see above).

116 Node 3 (Figure 2) was calibrated using the oldest known modern swift fossil from the
117 Riversleigh formation, Australia, *Collocalia buday* (Boles, 2001). The formation is considered an
118 Awamoan to Lillburinian age of roughly 19–16 Ma and we adjusted the logprior distribution
119 accordingly (logNormalPrior mean="0.25" stdev="0.5" offset="16.0").

120 We performed an independent dating approach based on the extended cytochrome-*b* data set
121 alone using the same three fossil ages for calibration and assigned a fourth fossil age to an ingroup
122 node of the *Aerodramus* clade. The fossil taxon *Collocalia manuoi* was described from the early
123 Holocene Ana Manuku rockshelter (~7000–2000 years ago) on Mangaia, Cook Islands, and was
124 considered a close relative of extant *Ae. sawtelli* (Steadman, 2002). We therefore assigned the fossil
125 age to the node uniting the sister species *Ae. sawtelli* and *Ae. bartschi* using a zero offset of 0.007 Ma
126 and adjusted the lognormal prior distribution to the beginning of the Holocene (logNormalPrior
127 mean="0.005" stdev="0.5").

128 **Ancestral-area reconstruction**

129 The total breeding range of *Apus* and *Tachymarptis* swifts (Figure 1) was subdivided into five discrete
130 areas (Table 2). Taxon-specific distributional data (Table 3) were compiled based on the maps in the
131 Handbook of the Birds of the World (Chantler, 1999) and in Chantler & Driessen (2000),
132 supplemented by range descriptions in Dickinson (2003) and corrected for our taxon delimitation.

133 Two parsimony-based and one likelihood-based approach were applied to compensate for the
134 disadvantages of single reconstruction methods: Weighted Ancestral Area Analysis (WAAA;
135 Hausdorf, 1998), RASP v2.1 beta for a Statistical DIspersal-Vicariance Analysis (S-DIVA; Yu, Harris
136 & He, 2013), and Likelihood Analysis of Geographic RANGe Evolution (Lagrange; Ree & Smith,
137 2008) in its C++ version of 17 January 2011. A random subset of 1,000 trees was chosen from the last
138 10,000 trees for replication in S-DIVA. In Lagrange, a step matrix defined dispersal rates for each pair
139 of areas: 1 for 1 area transition, 0.5 for 2, 0.25 for 3 and so forth. For each area, the areas considered its
140 neighbours are listed in Table 2. See Tietze & Borthakur (2012) for further details. An Indomalayan
141 outgroup was assumed.

142 The potential interplay between speciation and extinction of lineages and the occupation of two regions
143 was investigated with the help of the Geographic State Speciation and Extinction (GeoSSE; Goldberg,
144 Lancaster & Ree, 2011) model implemented in the R package DIVERSITREE v0.9-3 (FitzJohn, 2012).

145 The five areas were summarized under the following three scenarios: temperate (BCD) vs. tropical
146 (AE), non-African (BCDE) vs. African (A), non-Indomalayan (ABCD) vs. Indomalayan (E).

147 Probabilities for either region were reconstructed for all nodes including the root for the ingroup,
148 neglecting the possibility that both regions were inhabited.

149 **Trait evolution**

150 We tested the traits chin patch, rump patch and LDM for phylogenetic signal, using Pagel's λ
151 (fitDiscrete in R package GEIGER (Harmon et al., 2009) and Blomberg's K (phylosignal in R package
152 PICANTE (Blomberg, Garland & Ives, 2003; Kembel et al., 2010)). Markov models of discrete character
153 evolution to trace characters across the phylogeny (make.mk2, find.mle, asr.marginal in R package
154 DIVERSITREE) and to test, if the model is improved by different parameters for gain and loss of the
155 character.

156 The potential interplay between the speciation and extinction of lineages and the expression of the
157 three traits was investigated with the help of the Binary State Speciation and Extinction (BiSSE) model
158 (Maddison, Midford & Otto, 2007) implemented in the R package DIVERSITREE v0.9-3 (FitzJohn,
159 2012). Probabilities for the presence of a trait were reconstructed for all nodes including the root for
160 the ingroup. Further tests determined whether the model is improved by different parameters for gain
161 and loss of the character and trait-specific speciation parameters. 10,000 generations of Markov Chain
162 Monte Carlo chains were run for each GeoSSE and BiSSE reconstruction.

163 Finally, we tested whether reconstructed geographic and character states were correlated across all
164 internal nodes. All analyses were performed in R v2.15.2 (R Core Team, 2012).

165 **Results**

166 **Time-dated phylogeny**

167 We successfully delimited Apodini (from *Aerodramus/Hydrochous*) and confirmed the sister
168 relationship between *Apus* and *Tachymarptis* and of the latter two with *Cypsiurus*, and gained good
169 support for three major lineages within *Apus* (clades 1–3 in Figure 3). Despite the rapid diversification,
170 our multi-locus phylogeny succeeded in almost completely resolving the phylogenetic relationships of
171 the Apodini. Some monophyletic taxa received additional strong support from large indels in the fib7
172 intron: all Apodini shared a 29-bp-long deletion and all Apodidae differed from the sister family
173 Hemiprocnidae and from the Trochilidae by a 96-bp-long deletion (Figure 2). Recognised genera were
174 of unexpectedly young age and 95% HPD intervals were relatively narrow (Table 4): 3.6 Ma crown
175 age for *Apus*, 3.8 Ma for *Tachymarptis*, and 5.3 Ma for *Cypsiurus*. The ingroup as a whole (Apodini)
176 appeared to be 8.5 Ma old.

177 A mere cytochrome-*b* phylogeny dated with fossils gained a mean rate of 0.5% (without codon
178 partitioning) and 0.6% (with codon partitioning) changes per site and lineage and million years.

179 **Historical biogeography**

180 We reconstructed ancestral areas along the dated phylogeny and obtained Afrotropic-Indomalayan
181 origin for the ingroup (Apodini; Figure 4a, Table 4). Outgroup swift genera *Aerodramus* and
182 *Collocalia* were of Indomalayan origin. Ingroup genera *Apus*, *Cypsiurus* and *Tachymarptis* were all of
183 different origin: *Cypsiurus* was unequivocally of Afrotropic-Indomalayan and *Tachymarptis* of
184 Afrotropical origin, *Apus* also had Afrotropical origin according to parsimony methods, but Afrotropic-

185 Indomalayan origin according to Lagrange. *Apus* clade 1 was of eastern Palaearctic-Indomalayan
186 origin, but clades 2 and 3 were Afrotropic.

187 When testing for tropical origin under the GeoSSE model, *Apus* received 42%, *Tachymarptis* 62%,
188 *Cypsiurus* 64% and the ingroup 55% probability (Figure 4a). When testing for African origin, *Apus*
189 received 33%, *Tachymarptis* 58%, *Cypsiurus* 40% and the ingroup 42% probability (Figure 4b). When
190 testing for Indomalayan origin, *Apus* received 41%, *Tachymarptis* 31%, *Cypsiurus* 42% and the
191 ingroup 40% probability (Figure 4c).

192 Likelihoods were not significantly different for geographic scenarios with the same speciation or
193 dispersal rate in the two regions, respectively, from area-specific rates (Table 5). Nevertheless,
194 speciation rate was higher in the tropics than outside, higher in the Afrotropic than outside and higher
195 in the Indomalaya than outside, but in the latter two scenarios speciation rate was much higher when a
196 lineage was reconstructed to occur in the respective region *and* outside than in only one of them.

197 Extinction rates were also higher in the tropics, the Afrotropic and the Indomalaya than outside the
198 respective region. In contrast, dispersal rates were higher outside than inside these three regions.

199 **Evolution of morphological features and long-distance migration**

200 We found a phylogenetic signal for a white rump patch, but neither for a chin patch nor LDM (Table
201 5). Under a Markov model, the ingroup root state was clearly rump patch, but undecided for chin patch
202 and LDM. Under a BiSSE model, chin patch received 71%, rump patch 52% and LDM 59%
203 probability as the root state (Table 5, Figure 5).

204 Likelihoods were not significantly different for traits with the same speciation or transition rate for the
205 two character states, respectively, from state-specific rates (Table 5). Nevertheless, speciation rate was

206 higher, if the trait was expressed, for all three traits, but the ratio was least for rump patch and highest
207 for chin patch. Accordingly, extinction rates were higher if the trait was *not* expressed. Rates for losing
208 the trait were higher than for gaining it, also for all three investigated traits, whereby the ratio was
209 highest for rump patch and clearly lowest for LDM.

210 Likelihoods for Markov models were (nearly) significantly lower for unconstrained than for models
211 with identical speciation and transition rates (Table 5). In contrast, likelihoods for constrained and
212 unconstrained BiSSE models were not significantly different from each other.

213 A light rump patch was correlated with Indomalayan distribution across the internal nodes (Table 6,
214 Figure 6a). LDM was correlated with temperate distribution across the internal nodes (Table 6, Figure
215 6b).

216 **Discussion**

217 **Fast radiation**

218 Due to their high dispersal ability based on their pointed wings, swifts should have quickly reached
219 new inhabitable areas and consequently differentiated from conspecifics elsewhere. Our dated
220 molecular phylogeny confirms the expectation of numerous speciation events within a relatively short
221 term, most recently driven by rapid changes of warm and cold periods in the northern hemisphere
222 during the Pleistocene. Timely dimensions of our split age estimates deviate from previous dating
223 approaches (across different avian families with only a few representatives of Apodiformes included)
224 in a younger root age and a slightly older age estimate for node 2 (review in Brown & Mindell, 2009).
225 For the latter node Mayr (2010) already argued against a late Eocene split age estimate among

226 Hemiprocnidae and Apodidae (34 Ma, as estimated by Brown & Mindell, 2009) based on the
227 considerably older fossil age of the stem group of Apodidae (*Scaniacypselus*; fixed node age 2 in our
228 calibration).

229 The ages of the genera investigated here are much younger than that of other genera of small birds: in a
230 comparative study of East Asian passerines, Päckert et al. (2012) dated eight genera to 5–21 Ma.

231 Among our study genera, *Apus* swifts in particular are one of the few examples of avian “great
232 speciators” that underwent explosive Quaternary radiations including accelerated speciation rates in a
233 single genus. As in swifts these processes included long-distance transcontinental colonisation like that
234 in *Turdus* thrushes (Nylander et al., 2008) and typically island radiations like those in white-eyes
235 (*Zosteropidae* (Moyle et al., 2009) or in the Red-bellied Pitta complex (*Erythropitta erythrogaster*
236 (Irestedt et al., 2013)). While in the latter two examples these island radiations were restricted to a
237 single event including stepping-stone colonisation on the Indomalayan archipelago, the *Apus* radiation
238 involved at least two separate colonisation events on Madagascar and Macaronesia (clade 3). These
239 two events occurred independently at the fringes of a predominantly continental African swift radiation
240 with a terminal colonisation of the Palaearctic. Some driving factors for the diversification rate increase
241 in *Zosterops* white-eyes do not apply to swifts, e.g. rapid morphological evolution (see below); others
242 do, such as sociality and group dispersal as a precondition for successful colonisation (Moyle et al.,
243 2009).

244 We are less sure about “generalist ecology” (Moyle et al., 2009) as another driving factor: Chantler &
245 Driessens (2000) comment on the Common Swift that “it has a greater variety of prey items than any
246 similarly well studied bird, with over 500 prey species recorded in Europe”. On the other hand, some
247 species quite selectively feed on hymenopterans; and apparently there is some ecological segregation

248 among Common and Pallid Swifts with respect to prey choice and foraging behaviour as well.
249 Nevertheless, there is one ecological factor that might have a key role in rapid adaptation of swifts to
250 short-term and long-term climatic changes (see below): availability of aerial plankton. As a
251 consequence, swifts are highly sensitive to even short-term climate-induced shifts of aerial insect
252 abundance and even perform seasonal moves to avoid stormy depressions (Udvardy, 1954; Cucco &
253 Malacarne, 1996). Because reproductive success of swift species is highly dependent on these factors
254 (Cucco et al., 1992; Rajchard, Procházka & Kindlmann, 2006), long-term climate changes might have
255 caused repeated range shifts (colonisation events) from suboptimal towards optimal breeding grounds.
256 In contrast to higher speciation rates, we found substitution rates in *cyt-b* that were about half the
257 general rule of thumb (1.05% substitutions per site and lineage and million years). Weir & Schluter
258 (2008) listed a clearly lower 0.86% for the Apodiformes based on a single calibration for
259 hummingbirds only; their estimate tends towards our 0.5–0.6% substitutions/site/lineage/Ma.

260 **Geographic whereabouts**

261 The onset of basal lineage separation among Apodini clades was dated to the Miocene-Pliocene
262 boundary and gave rise to three major clades of Afrotropical-Indomalayan origin, against our
263 expectation of mere Afrotropical origin based on extant species numbers. The fact that extant members
264 of the sister clade (*Aerodramus*) also breed in various parts of the Old-World tropics (Chantler, 1999),
265 supports this reconstruction. Later in the Pliocene, the Afrotropic was the diversification centre of most
266 Apodini lineages until the late Pleistocene except for *Apus* clade 1 (East Asian diversification centre).
267 For terrestrial birds, Voelker, Outlaw & Bowie (2010) suggested an impact of Pliocene climate change
268 as a driver of speciation in African forest robins, and the assumption of African montane centres of

269 Pliocene-Pleistocene speciation processes was corroborated for African greenbuls (Pycnonotidae:
270 *Andropadus*), too (Roy, 1997). Though the predominantly aerial swift species do not directly depend
271 on forest or other land ecosystems, Pliocene climate changes might have had a similar impact on aerial
272 plankton communities and thus on swift prey availability. Despite the strong airbound life style of all
273 swifts, distribution of many species is also waterbound; this is particularly evident for those species
274 that penetrate continental arid regions where they are locally restricted to river valleys, oases and
275 swamps (Chantler, 1999). Therefore, Pliocene desertification processes on the African continent
276 (Micheels, Eronen & Mosbrugger, 2009; Senut, Pickford & Ségalen, 2009) might have induced range
277 shifts, exodus and colonisation waves and even local extinctions in Afrotropical Apodini swifts (cf.
278 scattered distributional areas today).

279 Accordingly, within-clade differentiation in Apodini was dated back to the Pleistocene with strongest
280 diversification in *Apus* clade 3: four allopatric African species, one on Madagascar, two in
281 Macaronesia and two in Eurasia and the Mediterranean. Strikingly, a similar diversification pattern in
282 space and time was reconstructed for the Common Kestrel (*Falco tinnunculus*) and allies (figure 3 in
283 Groombridge et al., 2002) and for *Falco biarmicus* and allied hierofalcons (Nittinger et al., 2005). Like
284 Apodidae swifts, these falcon species are highly mobile and able to perform long-distance overseas and
285 transcontinental dispersal of founder populations towards new breeding grounds.

286 Warm and cold period changes took place around every 100,000 years during the Pleistocene which
287 probably influenced speciation in some swifts. As a terminal late- or even post-Pleistocene event,
288 colonisation of the Palaearctic occurred four times independently in *Apus* and *Tachymarptis*.

289 Considering suboptimal climatic conditions throughout Eurasia at least around the Last Glacial
290 Maximum, ancestors of all extant Palaearctic species might have survived glacial periods at the

291 southern margins of the Palaearctic (Mediterranean refuges: *A. apus*, *A. pallidus*, *T. melba*; East Asian
292 refuges: *A. pacificus*) and rapidly dispersed northward after Holocene glacial retreat. Apart from
293 incomplete lineage sorting among the very young Western Palaearctic sister species *A. apus* and *A.*
294 *pallidus* (Päckert et al., 2012), other factors might have enhanced repeated genetic admixture among
295 their ancestral populations: i) past hybridisation due to partial overlap of their Mediterranean refuges,
296 ii) “repeated colonisation of genetically similar individuals from the same source populations” (Baker,
297 2008). Similar processes during very recent speciation events might have enhanced past genetic
298 admixture among avian close relatives in Mediterranean refuges, too (hierofalcons (Nittinger et al.,
299 2005), gulls (Liebers, de Knijf & Helbig, 2004; Sternkopf et al., 2010)).

300 Current trans-Atlantic vagrancy in both directions in swifts (Chantler, 1999) proves their ability to
301 randomly reach far distant potential breeding grounds.

302 **Evolutionary (plumage) patterns**

303 In contrast to frequent speciation events, morphology evolved negligibly. The almost permanent aerial
304 life style of swifts puts constraints on body proportions and physiology. This left little room for any
305 kind of ecological speciation. Swifts thus followed the more common pattern of non-ecological
306 speciation, differentiated in allopatry and regained sympatry after reproductive isolation (Rundell &
307 Price, 2009). Overall size varies to allow for niche partitioning among sympatric species (Chantler &
308 Driessens, 2000); e.g. gape size and wing length corresponding to prey size and foraging behaviour
309 (Salomonsen, 1976; Salomonsen, 1983). A parapatric ecological speciation process can be observed in
310 a later stage among *A. apus* and *A. pallidus*, which are hardly separable by phylogenetic markers
311 (Päckert et al., 2012): body size differs negligibly, but foraging occurs at different altitudes (aerial

312 stratification in mixed flocks) and the range of food items differs accordingly (Cucco & Malacarne,
313 1987; Cucco, Bryant & Malacarne, 1993).

314 Due to the fast aerial life style of swifts, plumage colouration should not be driven by either sexual
315 selection or distribution, but might rather evolve randomly under phylogenetic constraint. Findings
316 were different for the two investigated plumage patterns: the facial character was neither bound to
317 phylogeny nor explained by one of the geographic scenarios. It remains obscure why this trait was lost
318 in only one species per *Apus* clade and one *Cypsiurus* species.

319 The conspicuous rump patch on the other hand showed a phylogenetic signal, but nevertheless its
320 expression was correlated with Indomalayan distribution. Both findings can be explained by the fact
321 that the feature occurs only in species of *Apus* clades 1 and 2, which are most likely sister to each
322 other. (Only one species per clade actually lacks a rump patch.) The only four terminal taxa in *Apus*
323 that breed in the Indomalaya belong to clades 1 and 2 (two taxa each).

324 Both markers (insignificantly) increased speciation and extinction rates, but both traits were more
325 likely to have been lost during the diversification of the Apodini swifts than to be gained. Hugall &
326 Stuart-Fox (2012) investigated polymorphic plumage in several larger groups of birds (family to
327 order). In their larger data sets, polymorphism was a rarely expressed trait that significantly increased
328 speciation rates, and rates of losing polymorphism were significantly higher than rates of gaining it. So
329 maybe these findings are significant in contrast to ours due to the larger and thus older clades
330 investigated. We consider it more likely that the two plumage traits we investigated have been
331 irrelevant under natural and sexual selection and consequently evolved under a Brownian motion
332 model or got fixed after being expressed for the first time.

333 FitzJohn, Maddison & Otto (2009) contrasted sexual monomorphism with dimorphism within the
334 Charadriiformes (shorebirds) and found that diversification rates and character transition rates differed
335 between sexually monomorphic and dimorphic species. However, the threshold level of sexual
336 dimorphism used to classify species as monomorphic and dimorphic can vary; their evidence for a
337 correlation between sexual dimorphism and diversification rates is thus equivocal. They also confirmed
338 that the rarer a state the more likely its diversification rate would be underestimated.

339 If this holds true, in our relatively common traits diversification rates for the expressed traits should not
340 have been underestimated and consequently should actually significantly differ from the rates for not-
341 expressed traits. At least for the more widespread trait chin patch the λ_1/λ_0 ratio is much higher than
342 for the other two traits.

343 **Switching on and off long-distance migration**

344 Swifts should only migrate between breeding grounds and winter quarters if they breed in high-latitude
345 areas, which cannot provide enough small aerial insects to feed the swifts in the cold season. This holds
346 true for the extant species, but could also be confirmed for their ancestors, even though tropical
347 distribution and migratory behaviour were reconstructed independently. Thus older approaches to
348 studying LDM evolution in a phylogenetic context (in passerines only) could be confirmed in that
349 LDM evolved several times independently in a genus (Joseph, Lessa & Christidis, 1999; Joseph, Wilke
350 & Alpers, 2003; Helbig, 2003; Outlaw et al., 2003). LDM was the most labile trait in our study, as
351 expected for a behavioural trait (Blomberg, Garland & Ives, 2003). That suggested that the expression
352 of this trait did not depend on common ancestry. Migrating Apodini swifts were more likely to speciate
353 (significant only under the Markov model) and to become extinct; it was slightly more likely for a
354 migratory species to become sedentary than for a sedentary species to switch to LDM. Consequently,

355 LDM is a rarely expressed trait in the Apodini, but this behaviour has not only opened up new areas for
356 reproduction and foraging for these swifts, it has also accelerated diversification within the clade.
357 Newton (2008) summarised why natural selection should favour LDM: birds can i) better survive the
358 winter, if there is more food available in the winter quarters, ii) more productively breed, if there is
359 seasonally more food available in the summer quarters. Additionally, competition is avoided without
360 major adaptation, if the season of reproduction, which is most critical in respect to food resources, is
361 spent in different areas. LDM also imposes quite some cost and risk, but they are apparently relatively
362 low in swifts due to their perfect adaptation to aerial life.

363 Previous work often found the ancestors of their study groups to be sedentary and breed in the tropics
364 (but see Voelker, Bowie & Klicka, 2013). From the combined analysis of geographic ancestry and trait
365 evolution we may also conclude that the MRCA of the Apodini swifts bred in the tropics and was
366 sedentary (ignoring the tendency of the BiSSE and GeoSSE models to reconstruct equivocal root
367 states). The Markov model remained also undecided about the MRCA being migratory or not. This is
368 consistent with the fact that migration behaviour proved to be a labile trait in the swifts, too, and the
369 knowledge that migratory behaviour can be intensified or lost within small birds in only a few
370 generations (Berthold et al., 1992). The nearly perfect adaptation to dispersal and other long-distance
371 movements in swifts supports Pulido's (2007) suggestion that migratory behaviour might be immanent
372 in sedentary populations and "switched on" or selected for, if altered climatic conditions make
373 surviving during the winter unlikely (Bruderer & Salewski, 2008). Surprisingly, Winger, Lovette &
374 Winkler (2012) found a strong phylogenetic signal for LDM in the American passerine family of the
375 Parulidae (Blomberg's K between 0.79 and 0.90) and could even predict the migratory distance of their
376 study species through the phylogeny.

377 In contrast to our results from trait evolution analysis, Helbig (2003) – based on incomplete data for
378 few passerine genera – argued that highly migratory species show less tendency to speciate than more
379 sedentary species; this referred to descriptive facts regarding extant species. Second, Helbig (2003)
380 expected less differentiation along the migratory axis (north-south) than along the west-east axis. This
381 is certainly true, because tropical ecosystems are older than temperate ones and have more reliably
382 provided prey to swifts throughout a year over geological times. We confirmed his third hypothesis
383 that LDM evolved several times independently, but found that this was not due to a lower speciation
384 rate in migrants but a higher rate of transition to sedentary behaviour. Although often assumed that
385 lineages with higher dispersal ability experienced lower speciation rates (Claramunt et al., 2012), we
386 found a four times higher speciation rate in migratory species, i.e. species with apparently higher
387 dispersal ability, in contrast to sedentary species across the phylogeny (Table 5).

388 This is not the first study that combined a phylogenetic and biogeographic approach to the evolution of
389 migration (even with diversitree tools): Winger, Lovette & Winkler (2012) found for their Parulidae
390 that losses of LDM were only “at least as prevalent as” gains and that the speciation rate for migrants
391 was slightly lower than for sedentary birds, whereas in the Apodini migratoriness clearly increased the
392 speciation rate and was much more likely to be lost than gained (Table 5).

393 So far we considered long-distance migration as an intercontinental movement (Europe to Sub-Saharan
394 Africa; East Asia to Australia). This is fundamentally different from seasonal movements inside a
395 continent as described for several African *Apus* species. In some of these species these seasonal
396 movements in the tropics depend on the availability of aerial prey and change of weather conditions
397 (also observable in *A. apus* during the breeding season in Europe), in others they depend on the change
398 between wet and dry season (*A. niansae*) and some mountain populations perform seasonal altitudinal

399 movements. There are also some seasonal southward coastal movements in *A. berliozii* and nomadic
400 behaviour of *A. bradfieldi* outside the breeding season. All these rather short-distance movements show
401 the general aptitude for “migration”. This pre-adaptation can be extended to LDM if required. However,
402 such short-distance movements are not known from among the Indomalayan islands.

403 **Conclusions**

404 Apodini swifts radiated into 20 currently recognised species within less than 8.5 Ma. Originally
405 distributed across the Old-World tropics, several lineages expanded their ranges into the Palaearctic
406 independently both from the East and the West. Because of their already highly specialised life style
407 and connected physical adaptations, only subtle adaptations are observable. Obvious plumage patches
408 are not among them: A light chin patch is generally present and has been lost in four species
409 independently. A white rump patch in contrast is the synapomorphy of a monophylum of half the *Apus*
410 species, in which two species lost the feature, giving this whole trait a phylogenetic signal as well as
411 apparent dependency on Indomalayan distribution. LDM turned out to be the only trait of three
412 investigated traits that might be an adaptation to the requirements of the new environment of the high
413 latitudes. The trait was expressed several times independently whenever a swift lineage expanded to
414 the Palaearctic. Area- and trait-specific speciation and transition rates did not differ from general ones,
415 so that the GeoSSE and BiSSE models were actually too complicated on this low taxonomic level. We
416 would suggest further comparative studies of this model system including continuous traits such as
417 body dimensions and life-history traits (cf. Pienaar et al., 2013). Furthermore, it would be interesting to
418 work out the impact of microevolutionary processes (cf. incomplete speciation e.g. in *A. apus/A.*
419 *pallidus*) on the interspecific trait evolution (Simpson, 2013). But also many interesting questions
420 related to the comparative evolutionary patterns across the whole family remain to be answered.

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617 **Figure Legends**

618 **Figure 1. Breeding distribution of swift (tribe Apodini) species** according to BirdLife International
619 & NatureServe (2011) subdivided into five areas (A–E), with number of swift species per area and
620 connectivity among areas (Table 3).

621 **Figure 2. Dated phylogeny of Apodiformes** based on the same reconstruction as in Figure 3; fixed
622 fossil ages assigned to nodes 1–4, † = fossil taxon used for calibration; shared indels of monophyletic
623 groups indicated by grey bars: A = 96-bp deletion, B = 29-bp deletion; size of triangles does not
624 correspond to number of species in the respective clade.

625 **Figure 3. Molecular phylogeny of swifts (tribe Apodini)** and swift outgroup based on a 3601-bp
626 alignment of five genes (cyt-b, 12S rRNA, fib7, GAPDH and nuclear marker 12884) reconstructed in
627 BEAST (genes and codon positions partitioned, GTR/HKY models, 30,000,000 generations, for node
628 age constraints see Materials and Methods section). At the nodes are posterior probabilities, unless they
629 gained full support, indicated by an asterisk; outgroups Hemiprocnidae and Trochilidae not shown
630 (compare Figure 2); tree rooted with *Amazilia tzacatl*, a hummingbird.

631 **Figure 4. Reconstructed ancestral areas for swifts (Apodini).** a) Area(combination)s for extant
632 species and ancestral nodes according to Weighted Ancestral Area Analysis (WAAA), Statistical
633 DIspersal-Vicariance Analysis (S-DIVA), and Likelihood Analysis of Geographic RANGe Evolution
634 (Lagrange; in this order, if different; for area coding see Figure 1); a–c) reconstructed ancestral region
635 under a Geographic State Speciation and Extinction (GeoSSE) model with probabilities (in %) of a)
636 tropical origin, b) African origin, c) Indomalayan origin (taxa in the region of origin in green, in the
637 other region in red, in both in black).

638 **Figure 5. Evolution of plumage patterns and long-distance migration (LDM) in swifts (Apodini).**

639 a) chin patch, b) rump patch, c) LDM. Red indicates the presence of a character. Thermometers and
640 node labels (in %) show the probability of the expression of a character under a Markov or a Binary
641 State Speciation and Extinction (BiSSE) model, respectively.

642 **Figure 6. Significant correlations of probability of a character state with probability of a regional**
643 **origin across the internal nodes.** a) rump patch against Indomalayan origin, b) long-distance
644 migration against tropical origin. For parameters see Table 6.

645 **Tables**

646 **Table 1. Model settings** as estimated with MRMODELTEST for the different gene regions analysed.

647 **Table 2. Areas inhabited by swifts (tribe Apodini)** with adjacent areas and number of species
648 breeding therein.

649 **Table 3. Taxa treated in this study** with inhabited areas (for area codes see Figure 1 or Table 2) and
650 character states (0 = character absent, 1 = character present).

651 **Table 4. Important nodes in the ingroup phylogeny** with age (and 95% highest-probability density)
652 and reconstructed areas; Age 1: tree prior = Yule process, all model priors estimated by BEAST; Age
653 2: tree prior = birth-death process, all model priors estimated by BEAST; Age 3: tree prior = birth-
654 death process, model priors set according to best-fit model for each partition.

655 **Table 5. Characteristics of trait evolution** including phylogenetic signal (Pagel's λ , Blomberg's K),
656 root states, rates of speciation (λ , s), extinction (μ , x), trait state transition (q) and dispersal (d), ratios

657 of speciation rates under expressed over not-expressed trait and transition rate for loss over gain, *P*
658 values of ANOVAs comparing constrained/unconstrained Markov models and speciation/transition
659 rates, respectively.

660 **Table 6. Correlation coefficients *r* and *P*-values** for correlations between the three traits and the
661 three geographic scenarios across the internal nodes. **P* < 0.001.

662 **Supplemental Information**

663 **Supplementary Table S1. Samples for each taxon** with GenBank accession numbers and sampling
664 location.

665 **File S1. Apodini phylogeny** as NEXUS file.

Table 1 (on next page)

Model settings

Model settings as estimated with MRMODELTEST for the different gene regions analysed.

Partition	cytb	cytb1	cytb2	cytb3	12S rRNA	GAPDH	Fib7	12884
Model	HKY+I+ Γ	GTR+I+ Γ	GTR+ Γ	GTR+ Γ	GTR+I+ Γ	HKY+ Γ	HKY+ Γ	HKY+ Γ
R(a) [A-C]	-	22.9236	2.3088	0.0435	3.7802	-	-	-
R(b) [A-G]	-	41.7812	0.0000	6.7175	40.6859	-	-	-
R(c) [A-T]	-	12.2952	1.2674	0.2491	4.6645	-	-	-
R(d) [C-G]	-	6.8762	1.4906	0.3697	1.6670	-	-	-
R(a) [C-T]	-	103.9030	5.1977	2.6417	69.2465	-	-	-
alpha	1.1381	0.5771	0.2915	2.7189	0.6707	1.3598	0.5474	0.3806
p-inv	0.5360	0.4429	0.0000	0.0000	0.5366	0.0000	0.0000	0.0000

Table 2 (on next page)

Areas inhabited by swifts (tribe Apodini)

Areas inhabited by swifts (tribe Apodini) with adjacent areas and number of species breeding therein.

Code	Name	Adjacency	Apodidae	Apodini
A	Afrotropic	BCE	12	12
B	Macaronesia	AC	4	4
C	Western Palearctic	ABDE	5	5
D	Eastern Palearctic	CE	3	3
E	Indomalayan	ACD	14	6

Table 3 (on next page)

Taxa treated in this study

Taxa treated in this study with inhabited areas (for area codes see Figure 1 or Table 2) and character states (0 = character absent, 1 = character present).

Taxon	Areas	Region	Chin	Rump	Migration
<i>Apus acuticauda</i>	E	tropical	0	0	0
<i>Apus affinis</i> Asia	E	tropical	1	1	1
<i>Apus affinis</i> Palaearctic	AC	both	1	1	0
<i>Apus alexandri</i>	B	temperate	1	0	0
<i>Apus apus</i>	BCD	temperate	1	0	1
<i>Apus balstoni</i>	A	tropical	1	0	0
<i>Apus barbatus</i>	A	tropical	1	0	0
<i>Apus batesi</i>	A	tropical	0	0	0
<i>Apus berliozi</i>	A	tropical	1	0	0
<i>Apus bradfieldi</i>	A	tropical	1	0	0
<i>Apus caffer</i>	AC	both	1	1	0
<i>Apus horus</i>	A	tropical	1	1	0
<i>Apus niansae</i>	A	tropical	1	0	0
<i>Apus nipalensis</i>	DE	both	1	1	0
<i>Apus pacificus cooki</i>	E	tropical	1	1	0

<i>Apus pacificus pacificus</i>	D	temperate	1	1	1
<i>Apus pallidus</i>	BC	temperate	1	0	1
<i>Apus unicolor</i>	B	temperate	0	0	0
<i>Cypsiurus balasiensis</i>	E	tropical	1	0	0
<i>Cypsiurus parvus</i>	A	tropical	0	0	0
<i>Tachymarptis aequatorialis</i>	A	tropical	1	0	0
<i>Tachymarptis melba marjoriae</i>	A	tropical	1	0	0
<i>Tachymarptis melba melba</i>	CE	both	1	0	1
<i>Aerodramus brevirostris</i>	E	tropical			
<i>Aerodramus fuciphagus</i>	E	tropical			
<i>Aerodramus maximus</i>	E	tropical			
<i>Aerodramus salangana</i>	E	tropical			
<i>Aerodramus vulcanorum</i>	E	tropical			
<i>Collocalia esculenta</i>	E	tropical			
<i>Collocalia linchi</i>	E	tropical			

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<i>Hydrochous gigas</i>	E	tropical			
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Table 4(on next page)

Important nodes in the ingroup phylogeny

Important nodes in the ingroup phylogeny with age (and 95% highest-probability density) and reconstructed areas; Age 1: tree prior = Yule process, all model priors estimated by BEAST; Age 2: tree prior = birth-death process, all model priors estimated by BEAST; Age 3: tree prior = birth-death process, model priors set according to best-fit model for each partition.

Clade	Age 1 (Ma)	Age 2 (Ma)	Age 3 (Ma)	WAAA	S-DIVA	Lagrange	Areas
<i>Collocalia</i>	5.30 [4.47–6.16]	5.13 [4.32–6.01]	5.29 [4.50–6.11]	E	E	E	Indomalaya
<i>Aerodramus</i>	5.98 [5.26–6.68]	5.93 [5.07–6.72]	6.07 [5.38–6.79]	E	E	E	Indomalaya
Apodini	8.48 [7.56–9.43]	8.70 [7.43–9.89]	8.88 [7.94–9.89]	A(E)	A(E)	AE	Afrotropic/Indomalaya
<i>Cypsiurus</i>	5.27 [4.35–6.19]	5.54 [4.47–6.59]	5.39 [4.49–6.35]	AE	AE	AE	Afrotropic/Indomalaya
<i>Apus/Tachymarptis</i>	4.85 [4.35–5.37]	4.90 [3.15–5.78]	4.82 [4.35–5.30]	A	A	AE	Afrotropic(/Indomalaya)
<i>Tachymarptis</i>	3.83 [3.26–4.42]	3.91 [3.29–4.56]	3.92 [3.36–4.46]	A	A	A	Afrotropic
<i>Apus</i>	3.56 [3.20–3.92]	3.55 [3.15–3.95]	3.62 [3.27–3.98]	A	A	AE	Afrotropic(/Indomalaya)
<i>Apus</i> Clade 1	2.16 [1.80–2.57]	2.00 [1.68–2.32]	2.16 [1.84–2.49]	DE	DE	DE	E Palearctic-Indomalaya
<i>Apus</i> Clade 2	2.93 [2.60–3.26]	2.93 [2.54–3.29]	3.19 [2.61–3.25]	A	A	A	Afrotropic
<i>Apus</i> Clade 3	1.98 [1.69–2.28]	2.26 [1.80–2.72]	2.18 [1.82–2.52]	A	A	A	Afrotropic

Table 5(on next page)

Characteristics of trait evolution

Characteristics of trait evolution including phylogenetic signal (Pagel's λ , Blomberg's K), root states, rates of speciation (λ , s), extinction (μ , x), trait state transition (q) and dispersal (d), ratios of speciation rates under expressed over not-expressed trait and transition rate for loss over gain, P values of ANOVAs comparing constrained/unconstrained Markov models and speciation/transition rates, respectively.

Trait	Pagel's λ	Blomberg's K	Root state (Markov)	Root state (BiSSE)	λ_0	λ_1		μ_0	μ_1	q01	q10	λ_1/λ_0	q10/q01	P (Markov constrained)	λ constrained	q constrained
Chin patch	0.00	0.31	0.50	0.71	0.0 0	0.4 4	n/a	0.7 2	0.0 0	0.0 0	0.2 0	4288655.2 1	40714.70	0.06	0.21	0.63
Rump patch	1.00	0.67	1.00	0.52	0.3 6	0.4 3	n/a	0.1 4	0.0 0	0.0 0	0.2 6	1.18	2044234.8 6	0.06	0.76	0.10
Long-distance migration	0.00	0.22	0.50	0.59	0.2 2	0.7 7	n/a	0.0 4	0.0 0	0.3 9	1.6 6	3.45	4.30	0.03	0.26	0.17
Geographic scenario				Root state (GeoSSE)	sA	sB	sA B	xA	xB	dA	dB				s constrained	d constrained
Tropics	n/a	n/a	n/a	0.55	0.5 4	0.3 5	0.0 0	0.8 8	0.0 8	0.0 0	0.3 8	n/a	n/a	n/a	0.70	0.40
Afrotropic	n/a	n/a	n/a	0.42	0.3 6	0.2 5	0.7 6	0.2 3	0.0 0	0.0 5	0.2 4	n/a	n/a	n/a	0.91	0.70
Indomalaya	n/a	n/a	n/a	0.40	0.3 3	0.0 8	1.2 2	0.0 0	0.0 0	0.0 9	0.2 1	n/a	n/a	n/a	0.37	0.68

Table 6 (on next page)

Correlation coefficients and P-values

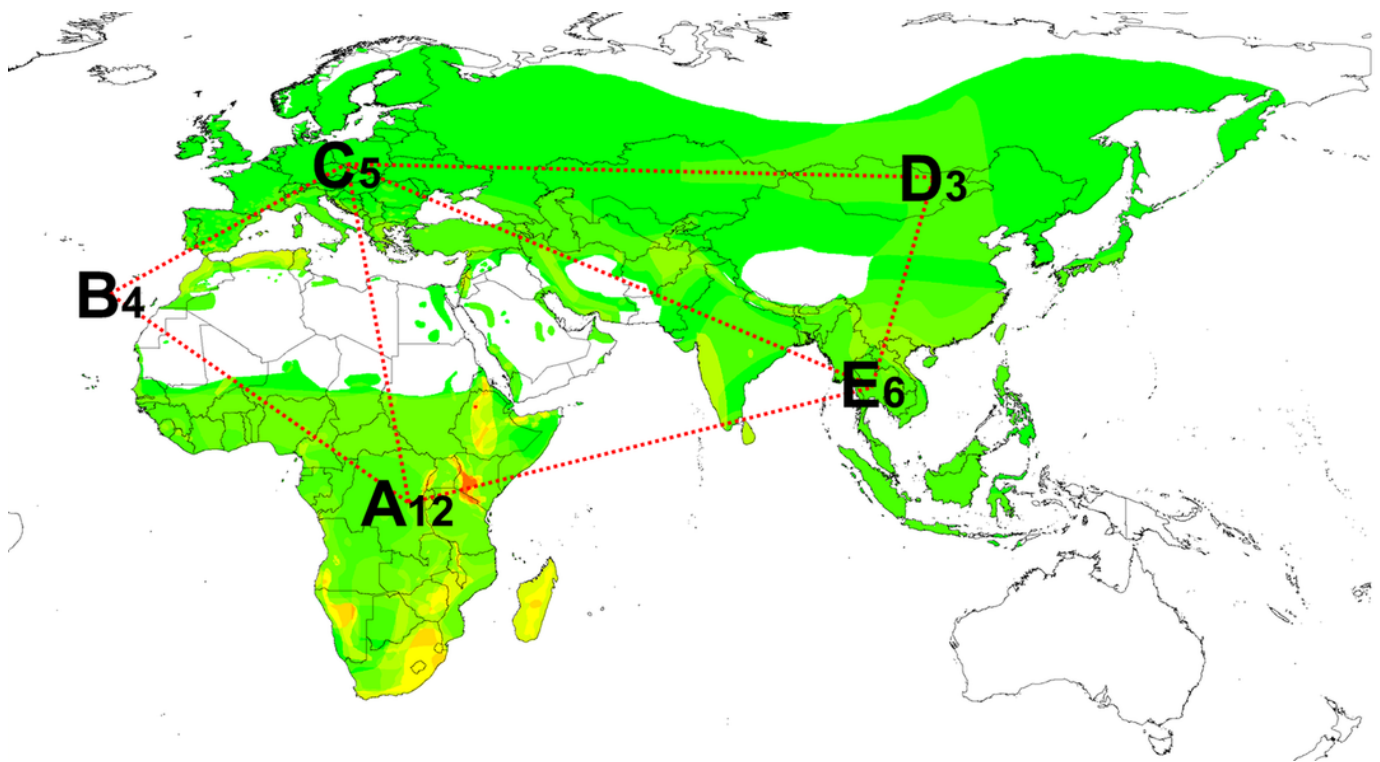
Correlation coefficients r and P-values for correlations between the three traits and the three geographic scenarios across the internal nodes. * $P < 0.001$.

Trait	Geographic scenario	r	P
Chin patch	Tropics	-0.16	0.47
	Afrotropic	0.01	0.95
	Indomalaya	-0.26	0.24
Rump patch	Tropics	0.24	0.28
	Afrotropic	-0.33	0.13
	Indomalaya	0.79	*
Long-distance migration	Tropics	-0.71	*
	Afrotropic	-0.38	0.08
	Indomalaya	-0.31	0.17

1

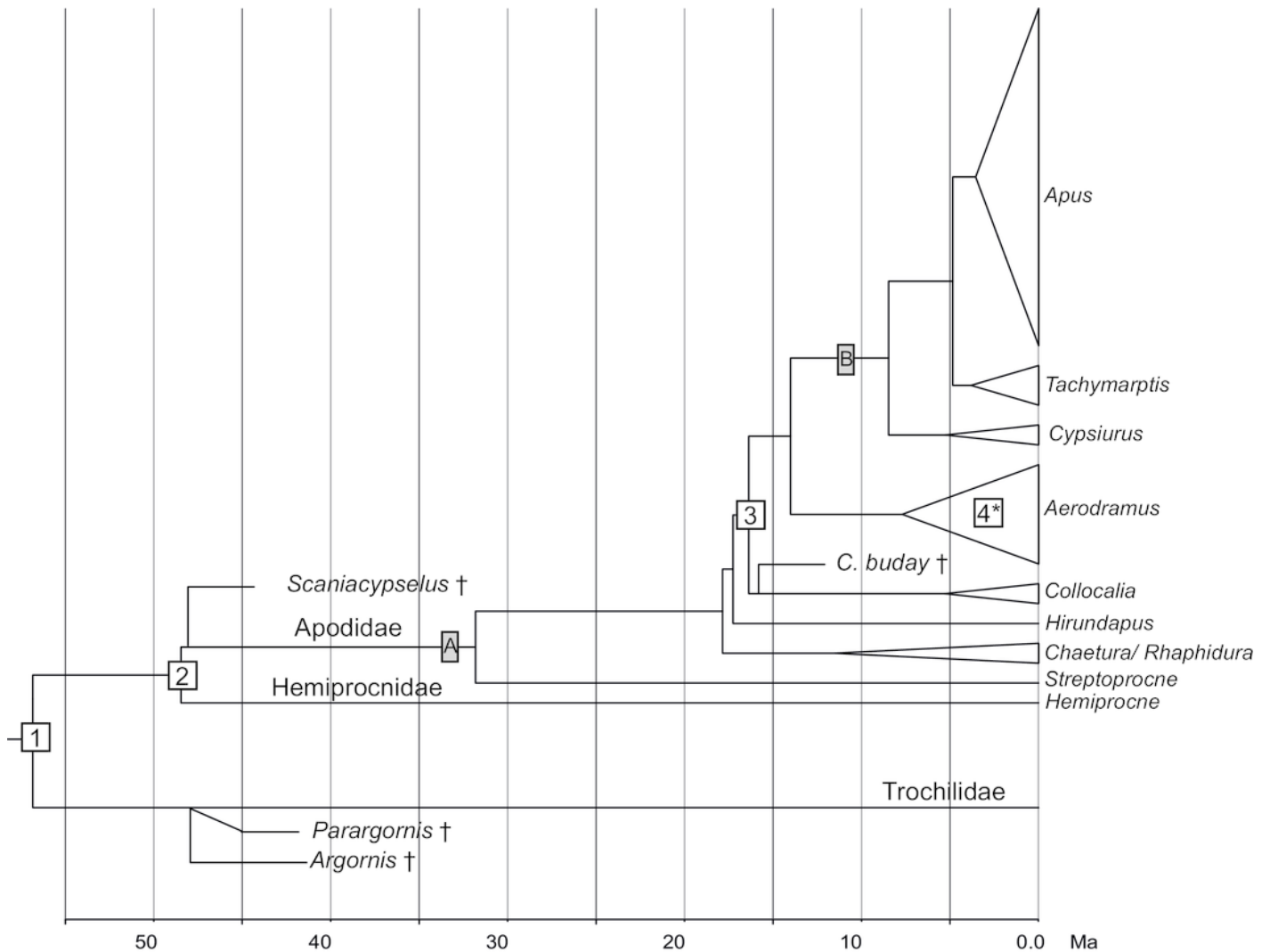
Breeding distribution of Apodini species

Breeding distribution of swift (tribe Apodini) species according to BirdLife International & NatureServe (2011) subdivided into five areas (A-E), with number of swift species per area and connectivity among areas (Table 3).



Dated phylogeny of Apodiformes

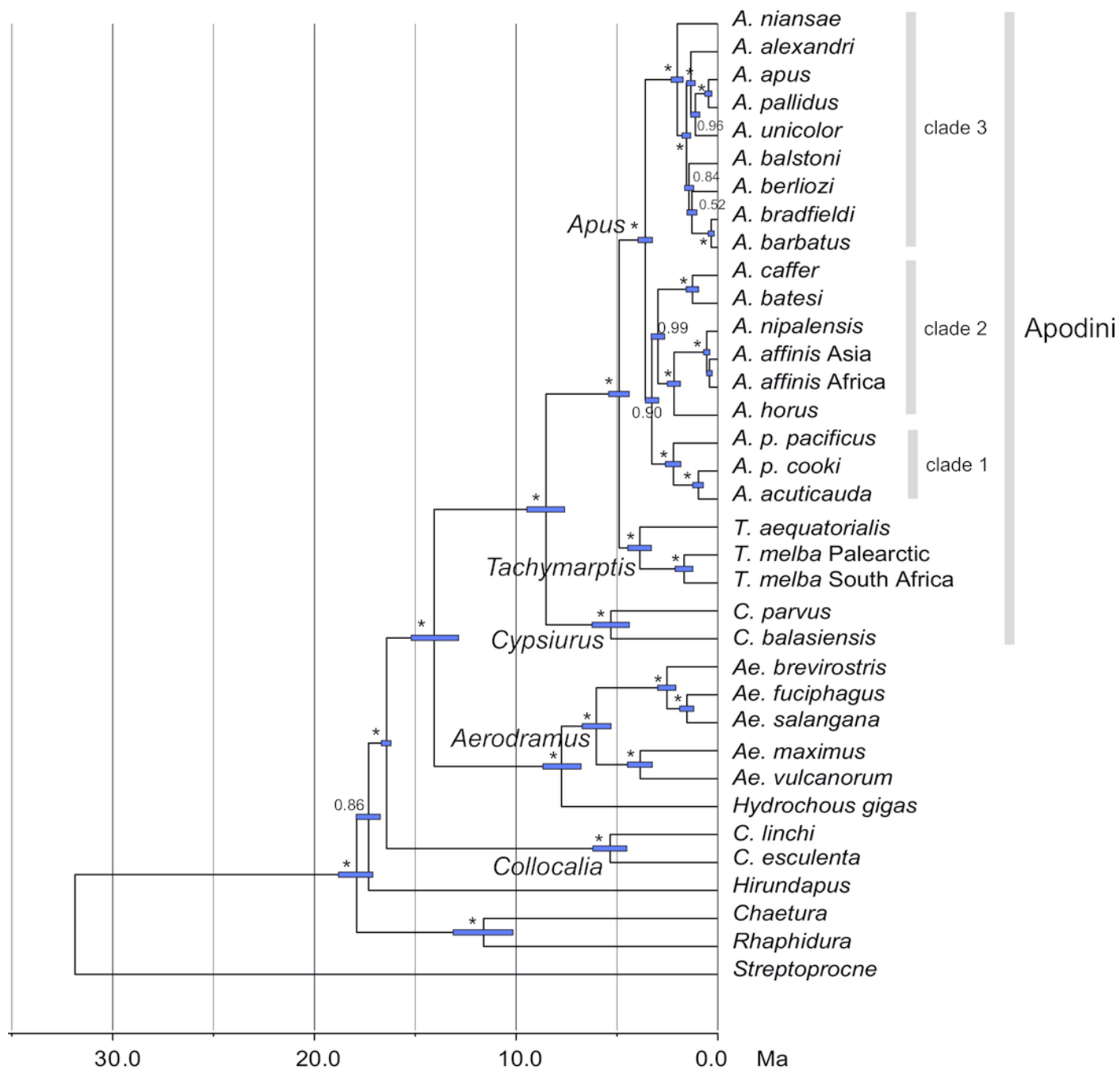
Dated phylogeny of Apodiformes based on the same reconstruction as in Figure 3; fixed fossil ages assigned to nodes 1-4, † = fossil taxon used for calibration; shared indels of monophyletic groups indicated by grey bars: A = 96-bp deletion, B = 29-bp deletion; size of triangles does not correspond to number of species in the respective clade.



3

Molecular phylogeny of Apodini swifts

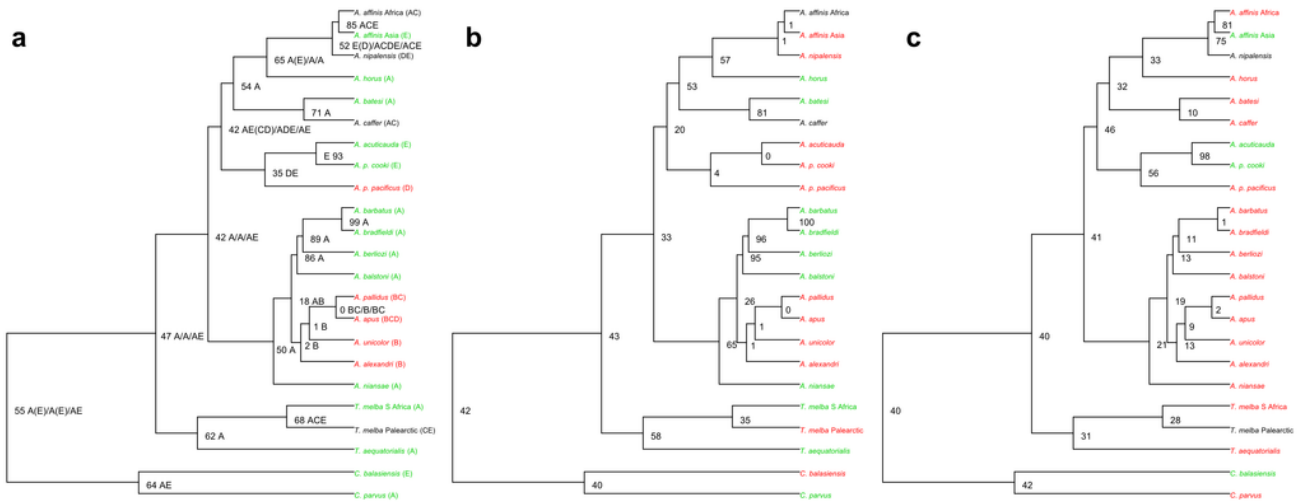
Molecular phylogeny of swifts (tribe Apodini) and swift outgroup based on a 3601-bp alignment of five genes (cyt-b, 12S rRNA, fib7, GAPDH and nuclear marker 12884) reconstructed in BEAST (genes and codon positions partitioned, GTR/HKY models, 30,000,000 generations, for node age constraints see Materials and Methods section). At the nodes are posterior probabilities, unless they gained full support, indicated by an asterisk; outgroups Hemiprocnidae and Trochilidae not shown (compare Figure 2); tree rooted with *Amazilia tzacatl*, a hummingbird.



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Reconstructed ancestral areas for swifts (Apodini)

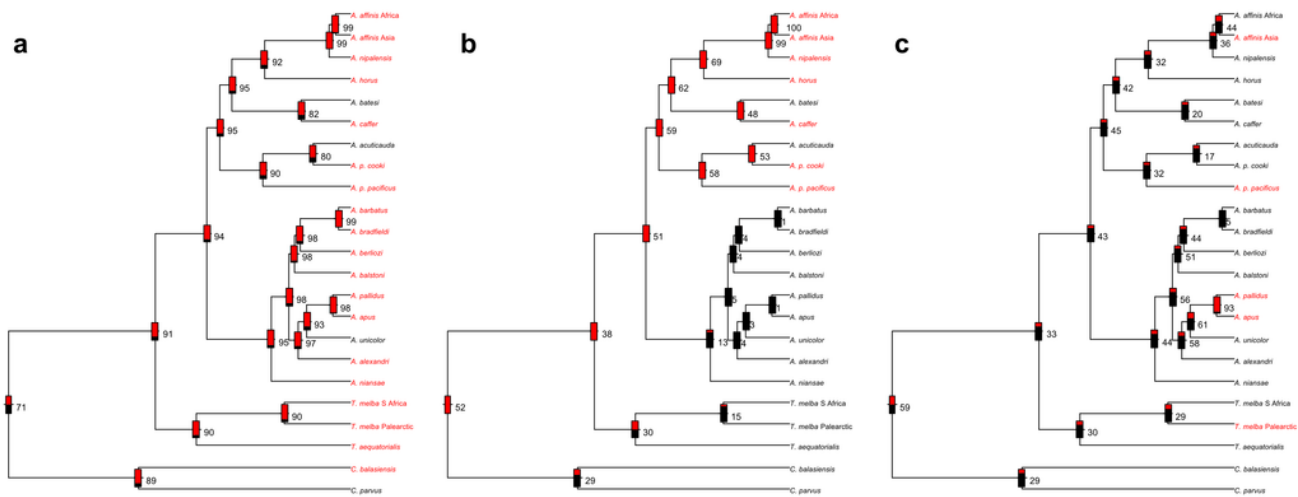
a) Area(combination)s for extant species and ancestral nodes according to Weighted Ancestral Area Analysis (WAAA), Statistical Dispersal-Vicariance Analysis (S-DIVA), and Likelihood Analysis of Geographic RANGE Evolution (Lagrange; in this order, if different; for area coding see Figure 1); a-c) reconstructed ancestral region under a Geographic State Speciation and Extinction (GeoSSE) model with probabilities (in %) of a) tropical origin, b) African origin, c) Indomalayan origin (taxa in the region of origin in green, in the other region in red, in both in black).



Evolution of plumage patterns and long-distance migration (LDM) in swifts (Apodini)

a) chin patch, b) rump patch, c) LDM. Red indicates the presence of a character.

Thermometers and node labels (in %) show the probability of the expression of a character under a Markov or a Binary State Speciation and Extinction (BiSSE) model, respectively.



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Significant correlations of probability of a character state with probability of a regional origin across the internal nodes

a) rump patch against Indomalayan origin, b) long-distance migration against tropical origin.

For parameters see Table 6.

