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Parallel Evolution of Bower-Building Behavior in Two Groups of Bowerbirds Suggested by Phylogenomics

PER G. P. ERICSON[1,*], MARTIN IRESTEDT[1], JOHAN A. A. NYLANDER[1], LES CHRISTIDIS[2,3], LEO JOSEPH[4], AND YANHUA QU[1,5,*]

[1]*Department of Bioinformatics and Genetics, Swedish Museum of Natural History, PO Box 50007, SE-104 05 Stockholm, Sweden;* [2]*School of Environment, Science and Engineering, Southern Cross University, Coffs Harbour, NSW, Australia;* [3]*School of BioSciences, University of Melbourne, Parkville, VIC, Australia;* [4]*Australian National Wildlife Collection, CSIRO National Research Collections Australia, Canberra, ACT 2601, Australia; and* [5]*Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing, 100101, China*

**Correspondence to be sent to: Department of Bioinformatics and Genetics, Swedish Museum of Natural History, PO Box 50007, SE-104 05, Stockholm, Sweden; Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing, 100101, China*
E-mail: per.ericson@nrm.se; quyh@ioz.ac.cn

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Abstract.—The bowerbirds in New Guinea and Australia include species that build the largest and perhaps most elaborately decorated constructions outside of humans. The males use these courtship bowers, along with their displays, to attract females. In these species, the mating system is polygynous and the females alone incubate and feed the nestlings. The bowerbirds also include 10 species of the socially monogamous catbirds in which the male participates in most aspects of raising the young. How the bower-building behavior evolved has remained poorly understood, as no comprehensive phylogeny exists for the family. It has been assumed that the monogamous catbird clade is sister to all polygynous species. We here test this hypothesis using a newly developed pipeline for obtaining homologous alignments of thousands of exonic and intronic regions from genomic data to build a phylogeny. Our well-supported species tree shows that the polygynous, bower-building species are not monophyletic. The result suggests either that bower-building behavior is an ancestral condition in the family that was secondarily lost in the catbirds, or that it has arisen in parallel in two lineages of bowerbirds. We favor the latter hypothesis based on an ancestral character reconstruction showing that polygyny but not bower-building is ancestral in bowerbirds, and on the observation that *Scenopoeetes dentirostris*, the sister species to one of the bower-building clades, does not build a proper bower but constructs a court for male display. This species is also sexually monomorphic in plumage despite having a polygynous mating system. We argue that the relatively stable tropical and subtropical forest environment in combination with low predator pressure and rich food access (mostly fruit) facilitated the evolution of these unique life-history traits. [Adaptive radiation; bowerbirds; mating system, sexual selection; whole genome sequencing.]

The bowerbirds (Ptilonorhynchidae) of New Guinea and Australia predominantly occupy rainforest habitats, although a few species have adapted to the considerably drier savannah habitats in monsoonal and arid Australia. Bowerbirds are traditionally divided into two categories based on their mating systems, the monogamous catbirds (*Ailuroedus*), which construct no bowers or display courts, and the polygynous, bower-building species (remaining genera). Among the latter, males spend considerable time and energy on constructing and decorating their bowers and courts with colorful objects and plant material, every species having its own preferred objects and color (Diamond 1986). Some bowers comprise large, complex stick towers built on the ground and which can be more than 2 m high, or hut-like structures having a diameter of up to 4 m (Borgia 1986; Frith and Frith 2004). In some species, the male clears a court of several square-meters for his elaborate display. The evolution of the elaborate breeding behavior of the polygynous bowerbirds is driven by female mate selection (Borgia 1986). Females visit and inspect several bowers and male displays before making their choice. The mating takes place in the bower but the female alone performs nest building and rearing of the young.

The bowers are of two general types, avenues and maypoles (cf. Gilliard 1969; Schodde 1976; Borgia 1995). The species building these different types have been shown to belong to different clades of bowerbirds (Kusmierski et al. 1993, 1997). Avenues are built by *Ptilonorhynchus*, *Sericulus*, and *Chlamydera* and they most often comprise two parallel walls made of vertically placed sticks and grass stems. Maypole bowers are built by *Prionodura* and *Amblyornis* and comprise sticks and other vegetation accumulated around young trees or larger twigs. An often circular court is built around the maypole where various decorations are placed. Two species of polygynous bowerbirds build no bower but do construct display courts. *Archboldia papuensis* prepares for display a massive mat of vegetation that differs in design from the typical maypoles, although it is still classified as such (Frith and Frith 2004). *Scenopoeetes dentirostris* meticulously clears a large display court on the rainforest floor around the trunk of a tree and decorates it with upturned leaves.

The evolution of bower building is largely unclear, although it has been assumed that the bowers function as a replacement or extension of male plumage ornaments. In five species of maypole-builders, Gilliard (1969) observed an inverse correlation between development of the male ornamental plumage and of the bowers. Some evolutionary benefits of this transfer would be to decouple the ornamentations from the constraints of the

bird's physiology and to reduce male conspicuousness to predators (Diamond 1986). Another hypothesis of the evolution of bower-building is that both maypoles and avenues provide protection to the females against unwanted mating (Borgia 1995). The male typically performs the display just outside the bower and the female observes it from inside the bower. This is also where the mating takes place if she accepts the male, but if the male tries approach the female without her wanting to mate she can easily escape before the male comes close. It has also been shown that females prefer to mate with males that build narrow rather than wider avenue bowers, presumably because the former gives her better protection (Katsuno et al. 2010).

The bowerbirds constitutes one of the earliest branches among the oscines, along with the Australian lyrebirds (Menuridae) and scrub-birds (Atrichornithidae), and Australo-Papuan treecreepers (Climacteridae) (Barker et al. 2002, 2004; Ericson et al. 2002). Until the era of molecular systematics, the bowerbirds were often associated with the birds-of-paradise (Paradisaeidae) and satinbirds (Cnemophilidae), with which they share both their New Guinean core-distributions and spectacular mating systems. Today, it is widely recognized that the three groups are not closely related, the birds-of-paradise and satinbirds being part of Corvides, a clade of crows and crow-like groups such as fantails (Rhipiduridae), drongos (Dicruridae), shrikes (Laniidae), and allies (Cracraft 2014). Of the traditionally recognized twenty bowerbird species, 10 occur in New Guinea, 8 in Australia, and 2 in both regions (Frith and Frith 2004). Many of these species are polytypic. Phylogenetic studies of the genera *Amblyornis* (Benz 2011) and *Ailuroedus* (Irestedt et al. 2016) have suggested that some subspecies are so morphologically and genetically distinct as to deserve recognition as full species. Indeed, Irestedt et al. (2016) argued that *Ailuroedus* consists of 10 species, compared to the three species previously recognized.

Although molecular studies have examined phylogenetic relationships within the family (Kusmierski et al. 1993, 1997; Christidis et al. 1996; Zwiers et al. 2008), only the cytochrome *b* study (Kusmierski et al. 1993, 1997) sampled enough taxa to allow comprehensive assessment of relationships of bowerbirds. In it, *Ailuroedus* catbirds form the sister group to all other bowerbirds, which is consistent with breeding behavior. The cytochrome *b* phylogeny supports a single origin of the polygynous mating system and male display in the family. Furthermore, it divides the remaining bowerbirds into two groups of which one includes all genera that build avenue bowers (*Sericulus, Ptilonorhynchus*, and *Chlamydera*) (Kusmierski et al. 1993, 1997). An earlier, protein allozyme study (Christidis and Schodde 1992) recovered the catbirds and *Amblyornis* in one clade and *Sericulus, Ptilonorhynchus*, and *Chlamydera* in a separate clade.

An unexpected and contentious result of the cytochrome *b* phylogeny is that the genera *Prionodura* and *Archboldia* are phylogenetically nested within the three species of *Amblyornis* that were included in the analysis. Given the relative phenotypic uniformity of *Amblyornis* and how morphologically divergent are *Prionodura* and *Archboldia*, Beehler and Pratt (2016) questioned this result and suggested it was an example of DNA producing erroneous results.

One taxon that has not been possible to confidently place in the cytochrome *b* phylogenies is *Scenopoeetes dentirostris*. This species is unique among bowerbirds in combining a sexually monomorphic plumage with a polygynous mating system, but does not build a bower. This species may thus hold a key to understanding various aspects of the evolution of sexual selection in bowerbirds, something that has been subject to considerable discussion (e.g., Endler et al. 2005; Borgia et al. 2007; Endler 2007).

Herein we reconstruct the evolutionary history of the bowerbirds using data from >12,000 aligned nuclear loci (in total >11 million bp) in order to better elucidate the origins of their complex mating systems. Furthermore, a good understanding of the evolutionary relationship of the family will provide a framework for future studies of the genetics and evolutionary adaptations in this family.

Material and Methods

Taxon Sampling

In the study, we include all traditionally recognized bowerbird species as well as representatives for each of the morphologically and genetically distinct populations of the genus *Ailuroedus* that recently were elevated from status as subspecies to full species (Irestedt et al. 2016). The number of *Ailuroedus* species thus increased from the traditionally recognized 3 species (*buccoides, crassirostris*, and *melanotis*; species epithets used for brevity when possible) to 10 (*buccoides, stonii, geislerorum, crassirostris, maculosus, melanocephalus, astigmaticus, arfakianus, jobiensis*, and *melanotis*). We used cryo-frozen tissue samples for most taxa, but for 12 individuals DNA was extracted from toe pad samples of museum study skins (Supplementary Table S1 available on Dryad at http://dx.doi.org.10.5061/dryad.6hdr7sqwp). We base our information on mating system, sexual plumage dimorphism, and building of courts and bowers on Gilliard (1969), Diamond (1986), Kusmierski et al. (1997), Frith and Frith (2004), and Frith et al. (2019).

Extraction, Library Preparation, and Sample Information

DNA from the frozen tissue samples was extracted using the KingFisher duo extraction robot and the KingFisher™Cell and Tissue DNA Kit according to the manufacturer's instructions, while museum toe pad samples were extracted using the Qiagen QIAamp DNA Mini Kit following the protocol described in Irestedt et al. (2006). The sequencing libraries for sequencing from fresh tissue samples were prepared

by National Genomics Infrastructure (NGI) using the Illumina TruSeq PCR-free (180/350 bp) kit. The libraries from museum specimens were prepared using the protocol published by Meyer and Kircher (2010). The samples were sequenced to a mean coverage of 19X (Supplementary Table S1 available on Dryad).

DNA extracted from an unsexed individual of *Amblyornis subalaris* (Museum of Victoria Z43620, voucher held as ANWC B26561) was used for *de novo* sequencing. Four DNA libraries, one short-insert-sized, paired-end (180 bp) and two mate-pair (3 and 5–8 kb) DNA libraries, were sequenced on an Illumina HiSeq X platform at the National Genomics Institute. We obtained 250 Gb sequencing data, which were assembled into a genome with length of 1.11 Gb and N50 scaffold length of 6.06 Mb. This assembly was used for downstream analyses.

Filtering of Raw Reads and Reference Mapping

The raw reads were processed using a custom-designed workflow available at https://github.com/mozesblom to remove adapter contamination, low-quality bases, and low-complexity reads. Raw reads from the sequencing of museum specimen were cleaned by same procedure except deleting 5 bp from both ends in order to avoid wrong sequences of the degraded DNA. We mapped these clean reads against the whole genome of *Amblyornis subalaris* using BWA mem v.0.7.12 (Li and Durbin 2009). A detailed description of the quality control is given in the Supplementary text available on Dryad.

Extracting and Aligning Homologous Exonic and Intronic Loci

We used profile hidden Markov models (HMM, Eddy 2011) to search sequence homologs of nuclear exonic and intronic loci across the whole genome using alignments generated by Jarvis et al. (2014). Profile HMMs use information from observed variation in multiple sequence alignments, to seek similarities in genome assemblies (Eddy 1998). For each HMM query and taxon, the location in the genome for the most significant hit was identified, and the coordinates were used to parse out the sequence. These steps were carried out using a custom-designed BirdScanner pipeline (available at github.com/Naturhistoriska/birdscanner). The extracted sequences were aligned and each alignment checked to remove nonhomologous sequences (indicated by an extreme proportion of variable positions in the alignment). We also removed alignments that contained no parsimony-informative sites. A detailed description of methods and pipeline used in this analysis can be found in the Supplementary text available on Dryad.

Mitochondrial Sequences

We assembled mitochondrial genomes from the resequenced data for each individual using MITObim 1.8 (Hahn et al. 2013), and used 11 of the 13 protein-coding genes to infer the phylogenetic tree. In most taxa, the NADH3 and NADH6 gene were only partially reconstructed by MITObim and we excluded these from the analyses. The aligned mitochondrial data set used in the analyses consists of 10,560 bp (3520 codons).

Phylogenetic Analyses

Individual trees were constructed for 5653 exonic and 7020 intronic loci using IQ-TREE (Nguyen et al. 2015) that automatically selects the best substitution model for each alignment. We used ASTRAL-III v.5.6.3 (Zhang et al. 2018; Rabiee et al. 2019) to construct species trees from the gene trees both for the exonic and intronic loci separately and for all loci combined. ASTRAL estimates a species tree given a set of unrooted gene trees and branch support is calculated using local posterior probabilities, LPP (Sayyari and Mirarab 2016). The phylogenetic analysis of the mitogenomic data set was performed with MEGA X (Kumar et al. 2018). We estimated the maximum-likelihood tree for the mitochondrial data using 100 bootstrap replicates to assess the reliability of the branches. The data set was analyzed both with all codon positions present and with the third codon positions excluded.

Ancestral Character Reconstruction

We estimated ancestral character states across the phylogenetic tree for discretely valued traits using the "ace" function in the "APE" package (Paradis et al. 2004). The maximum-likelihood method (Pagel 1994) was used to estimate parameters for an explicit model of discrete character evolution and probabilities for the character states at every node of the phylogeny. Finally, the reconstructed states were plotted as a maximum clade credibility tree using the "phytools" package (Revell 2012).

Estimating Time of Divergence

Divergence time estimates were obtained by implementing a Bayesian relaxed clock model in BEAST 2 (Bouckaert et al. 2014) based on 24,390 bp of nuclear intron data randomly selected from the concatenation of all intron loci. We ran Markov chain Monte Carlo chains for 80 million generations (sampling every 100 generations) using a relaxed lognormal distribution for the molecular clock model and assuming a birth–death speciation process for the tree prior. The gamma substitution model was applied. The tree was calibrated with two calibration points obtained from Oliveros et al. (2019: Figure 1): the split between Climacteridae and Ptilonorhynchidae was set to 31.6±5.5 Ma and the split

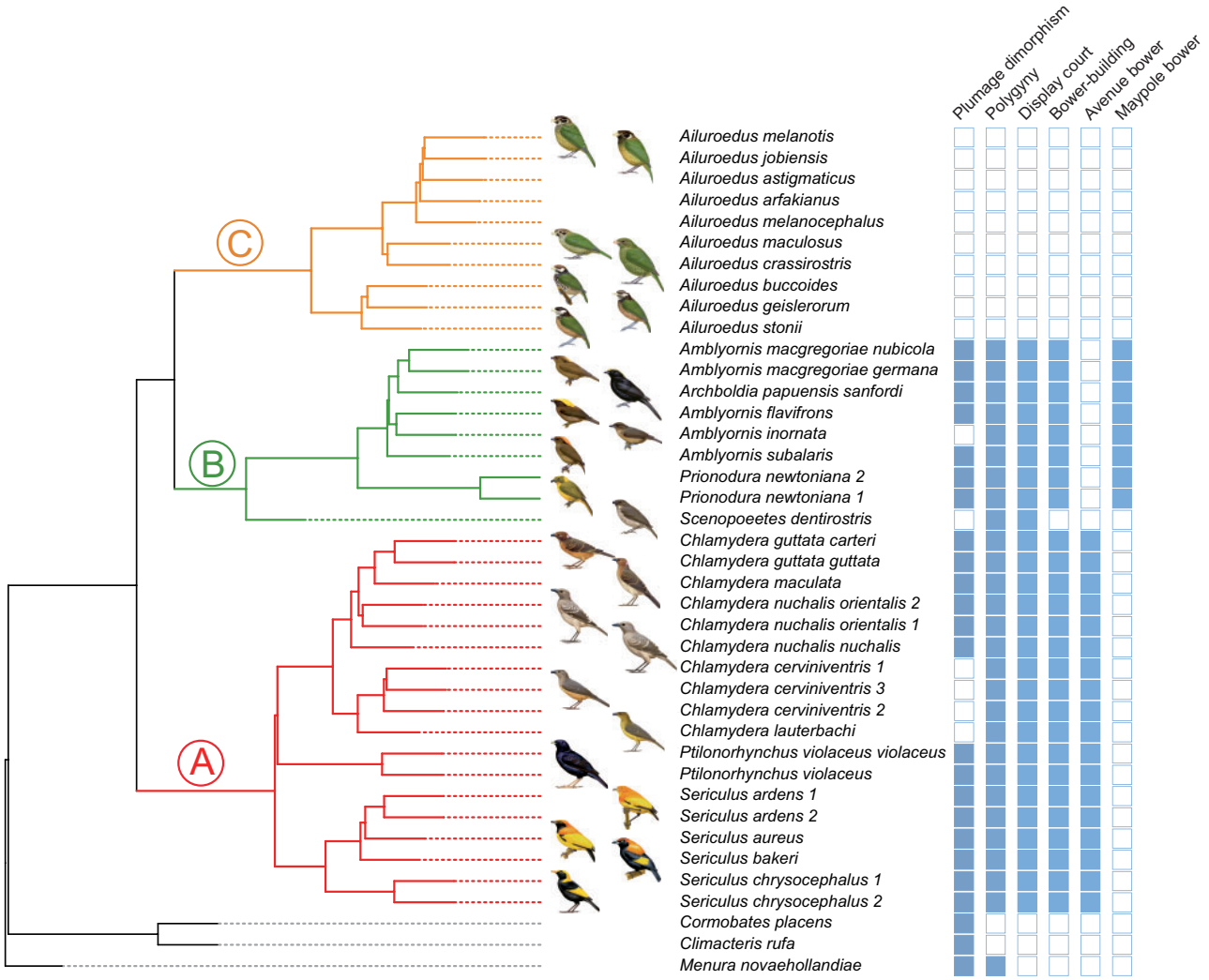

FIGURE 1. ASTRAL tree based on 12,628 individual trees (5653 exonic and 7020 intronic regions). All nodes in the tree received 100% LPP. For each species information on sexual plumage dimorphism, social mating system, display court, and bower construction are given in the right panel. The labels A, B and C refer to the clade names used in the text. The bird images are reproduced with permission from Lynx Edicions.

between the clade including *Ptilonorhynchus* and the clade with *Ailuroedus* to 15.0 ± 7.1 Ma. We checked for convergence between runs and analysis performance using Tracer v.1.5 and accepted the results if the values of the estimated sample size (ESS) were larger than 200, suggesting little autocorrelation between samples. The resulting trees were combined in TreeAnnotator v.1.7.5 and the consensus tree with the divergence dates was visualized in FigTree v.1.4.3.

RESULTS

Evolutionary Relationships

A total of 5653 exonic and 7020 intronic loci were extracted for the phylogenetic analyses. The maximum sequence divergence observed among the bowerbirds was 2.5% for exons, 4.2% for introns, and 19.0% for coding mitochondrial genes (Supplementary Table S2 available on Dryad). Phylogenetic analyses of the different data sets recovered almost the same pattern of relationships (Fig. 1, Supplementary Figs. S1–S3 available on Dryad). They suggest that all genera, except *Amblyornis*, are monophyletic. Monotypic *Archboldia* was nested within *Amblyornis*. Three distinct clades were recovered. Clade A comprised *Ptilonorhynchus, Chlamydera*, and *Sericulus*, Clade B comprised *Scenopoeetes, Prionodura, Amblyornis*, and *Archboldia*, while all *Ailuroedus* formed Clade C.

Within Clade A, *Ptilonorhynchus* and *Chlamydera* were sisters with 100% LPP in the analyses of both the intronic loci and the mitogenomes. The same topology was recovered also for the exonic loci but with a lower LPP (94%). Although *Chlamydera* was recovered as monophyletic by all analyses, the relationships among its species differ. *Sericulus* formed the sister group to the *Ptilonorhynchus-Chlamydera* clade in all analyses.

In Clade B, all analyses recovered monotypic *Scenopoeetes* as sister to the other species in the clade, and *Prionodura* as sister to *Amblyornis* and *Archboldia*. *Archboldia* was nested within *Amblyornis* in all analyses, but its relative position differed between data sets. In the analysis of the mitogenomic data set, it was sister to *Amblyornis inornata*, while the exonic and intronic data sets suggested it was sister to *Amblyornis macgregoriae*. Both the exonic and intronic data recovered a sister pair of *Amblyornis flavifrons* and *Amblyornis inornata*. In the analyses of the mitogenomes and the intronic loci, *Amblyornis subalaris* was sister to all other *Amblyornis* species and *Archboldia*. The exonic data instead showed 100% LPP for *Amblyornis subalaris* being sister to the *Amblyornis macgregoriae–Archboldia* clade. When combining all nuclear data *Amblyornis subalaris* was recovered as sister to *Archboldia* and the other *Amblyornis* species.

Within clade C all analyses recovered *Ailuroedus buccoides, A. geislerorum*, and *A. stonii* as sister to the other seven taxa. The combined nuclear data set strongly supported a sister group relationship between *A. crassirostris* and *A. maculosus*.

Although the phylogenetic analyses of all data sets recovered highly similar relationships among the bowerbirds they differed in the placement of the root. The analysis of the full mitogenomic data set (with all three codon positions included) rooted the tree between the *Ailuroedus* clade and all the other bowerbirds (Fig. 2a), whereas the exonic and intronic data robustly placed the root so that the *Ailuroedus* species instead formed a clade together with *Scenopoeetes, Prionodura*, and *Amblyornis*. After the exclusion of the third codon position in all mitochondrial coding genes, the rooting of the mitochondrial tree was identical with that for the two nuclear data sets (Fig. 2b). Although the bootstrap support for this topology was low (80%), it was equally low (82%) for the alternative topology recovered for the full mitogenomic data set.

The ancestral character analyses reconstructed the bowerbird ancestor as being sexually dimorphic in plumage, polygynous and most likely preparing a court for display (Fig. 3a–c, Supplementary Fig. S4 available on Dryad). However, the ancestral bowerbird was unlikely to have built a bower, as there was only a 25% support for bower-building being ancestral in the family, and 75% for it is not. All these characters were subsequently lost in the ancestor to the *Ailuroedus* clade. The ancestral character analysis also with high probabilities reconstructed the bower-building behavior to have evolved in parallel in the maypole and avenue clades, respectively (Fig. 3e, Supplementary Fig. S4 available on Dryad).

The time-tree based on the subsampled intron data set was calibrated to set the age of the most recent common ancestor (MRCA) of present-day bowerbirds to 15.0 million years ago (Ma). Our analysis resulted in an interval for the highest posterior density, HPD, of this node of 11.1–18.9 Ma (Supplementary Fig. S5 available on Dryad). During that time interval, the common ancestor of the maypole bowerbirds and the catbirds diverged from the ancestor of the avenue-builders. A few million years later the catbirds in turn split from the maypole bowerbirds (MRCA 12.8 Ma; HPD 9.3–16.5 Ma). The radiations within each of the two clades of polygynous species began in the late Miocene to earliest Pliocene but they were not simultaneous. The radiation within the maypole-builders began a few million years earlier (MRCA 8.7 Ma; HPD 6.0–12.0 Ma) than that of the avenue-builders (MRCA 5.4 Ma; HPD 3.7–7.6 Ma). The catbird radiation is Pliocene in age (MRCA 5.1 Ma; HPD 3.5–7.2 Ma).

Discussion

Our genome-wide data analyses, including more than 12,000 exonic and intronic gene regions, show that those bowerbirds having a polygynous mating system and bower-building behavior do not form a monophyletic group. Instead, the species that build the so-called maypole bowers, together with *Scenopoeetes*, are sister to the monogamous catbirds. Our findings raise the hypothesis that polygyny and bower-building behavior either are ancestral conditions in the family, secondarily lost in the catbirds, or have arisen in parallel. We outline a case below for favoring the latter hypothesis. Most likely, the relatively stable tropical and subtropical forest environment in combination with low predator pressure and rich food access (mostly fruit) are conditions that have facilitated the evolution of the extensive male displays and bower-building behavior (Diamond 1986). Another radiation of birds that probably evolved in response to the same factors is the New Guinean birds-of-paradise, which also have spectacular sexual display behavior. The analyses affirm an earlier contentious finding that the aberrant genus *Archboldia* is nested in *Amblyornis*, but could not corroborate the similarly contentious suggestion that this is also the case for *Prionodura* (see discussion in Supplementary Material).

Of utmost importance for our understanding of the evolution of the characteristic bower-building behavior and mating systems is how the phylogeny is rooted. Until now the most adequate molecular data on relationships among all bowerbirds stem from two analyses; one of the mitochondrial cytochrome *b* gene in fourteen species representing the three major groups recognized herein (Kusmierski et al. 1997), and a protein allozyme study (Christidis and Schodde 1992). By outgroup rooting using the lyrebird (*Menura novaehollandiae*), the root was placed between the catbirds and all other bowerbirds in both the parsimony and unweighted maximum-likelihood analyses of Kusmierski et al. (1997, Figure 1). This was in line with the expectation that the elaborate display behavior, including building and decorating bowers, sexual plumage dimorphism and a polygynous mating system, had evolved only once within the family, making the clade of the monogamous catbirds sister to that with the polygynous bower-building species (Frith and Frith 2004). The group of birds that is phylogenetically closest to the bowerbirds,

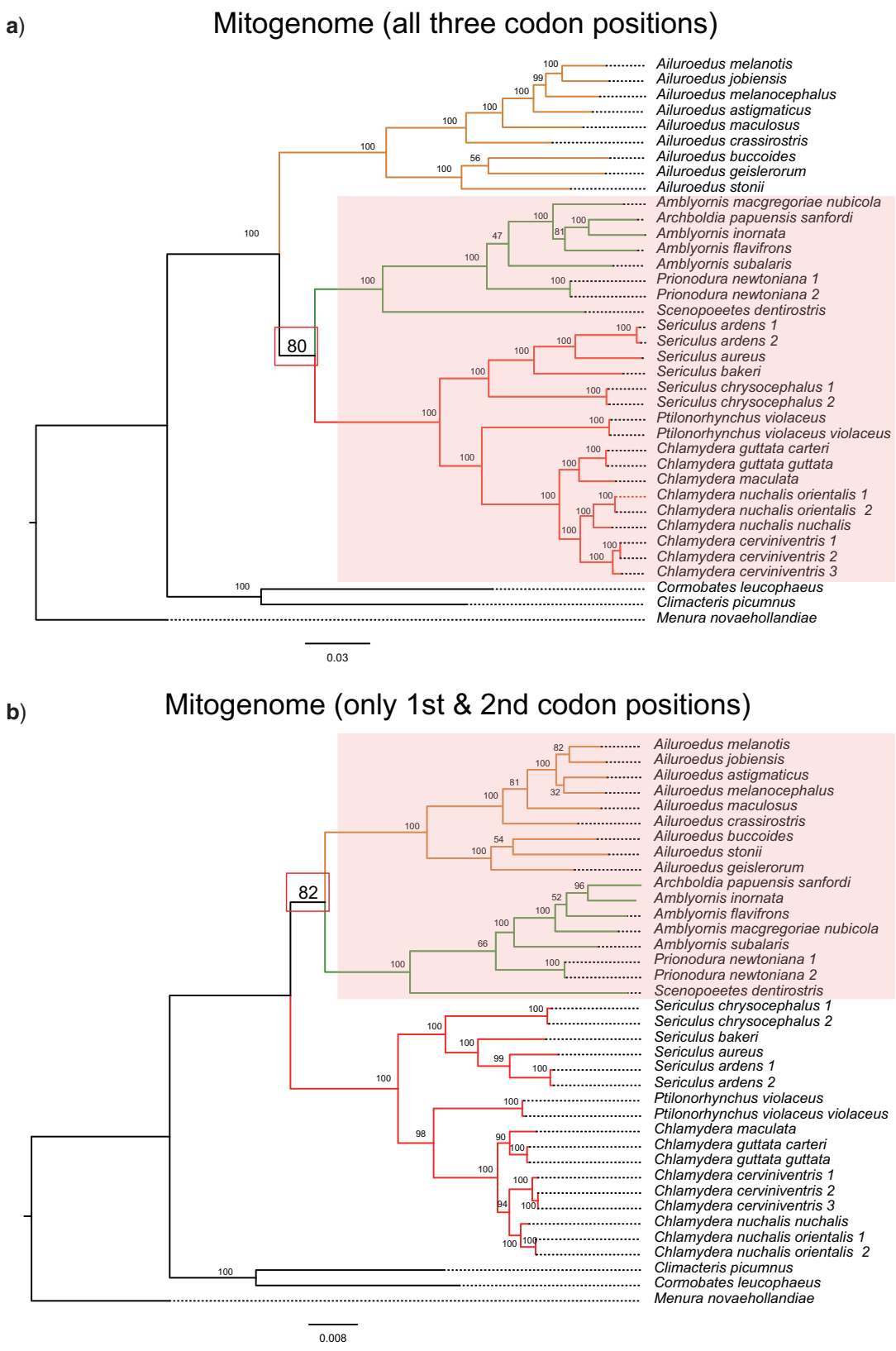

FIGURE 2. Mitogenomic trees based on maximum-likelihood analyses of 11 coding genes (3502 codons, 10,506 bp). a) All codon positions included in the analysis. All species with a polygynous mating system group together (marked with the reddish box). The position of the root of this tree differs from those based on nuclear data. b) Third codon positions excluded from the analysis. The overall phylogenetic structure of this tree closely resemble those based on nuclear data in suggesting non-monophyly of the species with polygynous mating system (marked with reddish boxes).

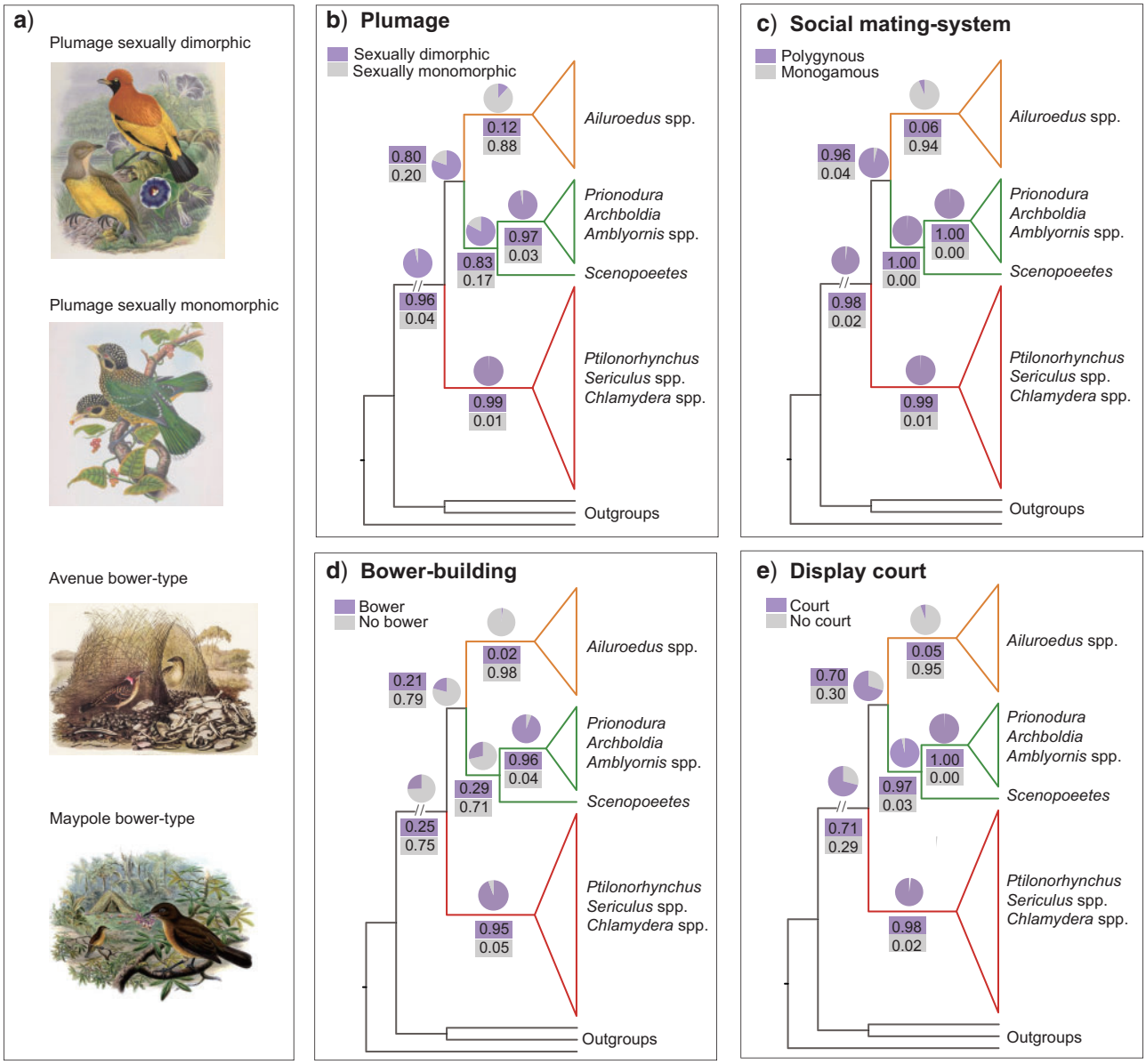

FIGURE 3. Ancestral state reconstructions for four characters related to sexual selection in bowerbirds. a) (From top to bottom) Examples of sexual plumage dimorphism in *Sericulus aureus*, sexual monomorphism in *Ailuroedus arfakianus*, avenue bower-type in *Chlamydera maculata*, and maypole bower-type in *Amblyornis inornata* (illustrations are from Sharpe 1898). The reconstructed probability for the ancestor of a major clade having a particular state is given for sexually dimorphic plumage (b), polygynous mating system (c), bower-building behavior (d), and clearing of a display court (e). Ancestral character state reconstructions in the entire phylogenetic tree are given in Supplementary Figure S4 available on Dryad.

the Australo-Papuan treecreepers (Climacteridae), has a monogamous mating system and only limited sexual dimorphism in plumage (Noske and Bonan 2019). In these features treecreepers resemble the *Ailuroedus* catbirds. This is consistent with the prevailing view that the monogamous mating system is ancestral in the family (Frith and Frith 2004). The formal ancestral character reconstruction presented herein does not support this however and instead suggests that polygyny is the ancestral mating system in bowerbirds. It should be noted that the present analysis of the total unweighted, mitogenomic data set analyzed herein recovered the same rooting as did the analysis of the cytochrome *b* gene alone, even after the addition of two species of Australo-Papuan treecreepers to the lyrebird outgroup.

However, neither the data set with 5653 exonic loci nor that with 7020 intronic loci recovered the monogamous *Ailuroedus* catbirds as sister to all other bowerbirds, as indicated by the mitochondrial data. To the contrary, both data sets provide strong support for the catbirds being sister to the polygynous, maypole- and court-building clade (*Scenopoeetes*, *Prionodura*, *Amblyornis*,

Archboldia). The mitochondrial data grouped the two bower-building clades together, but it should be stressed that the mitochondrial genome evolves faster on average than nuclear loci, which makes it less reliable for ancient divergences. The age of the basal divergences among the bowerbirds is estimated to ca 15 myr (Oliveros et al. 2019), an age at which the mitochondrial genome is assumed to have become affected by saturation and thus less useful for phylogenetic inference (Ho 2007; Barker 2014; Nguyen and Ho 2016). Indeed, if we instead analyze only the protein-coding genes of the mitogenomes (under the assumption that these are more conserved than the noncoding loci) and exclude the fast evolving third codon positions, the basal phylogeny becomes identical to that of the nuclear loci (Fig. 2b). This strengthens the assumption that saturation of the fastest evolving parts of the mitochondria explains the difference observed in the basal portions of the published mitochondrial tree and the nuclear trees. Another possible explanation to the nuclear-mitochondrial discordance may be a mitochondrial capture event early in the evolution of the family (cf. Ferreira et al. 2018), but the fact that the rooting depends on which codon positions are analyzed makes saturation more likely.

Two equally parsimonious hypotheses about the evolution of bower-building can be formulated based on the phylogenetic results. Either this behavior has evolved in parallel in the maypole- and avenue-building clades, or it is ancestral in the bowerbird family and was secondarily lost in the catbirds. The ancestral character reconstruction supports the first alternative as it suggests that there is only ca 25% probability that the bowerbird ancestor constructed bowers, despite 75% probability that it prepared a court for display (Fig. 3). Polygyny, however, is reconstructed with 98% probability as being the ancestral mating system in bowerbirds, suggesting it was lost in the now monogamous catbird clade.

Support for an independent origin of the bower-building behavior comes also from the observation that maypoles and avenues are different constructions. It has been suggested that the first bowers consisted of a sapling behind which the females could seek protection (Borgia 1995). The evolution from this initial stage to the present-day maypole bowers is then easy to envision under the assumption that bowers serve to protect females from unwarranted mating. Borgia (1995) also pointed out that a transition from a maypole bower to an avenue bower would require both the loss of using a sapling in the construction and the addition of a different barrier (op. cit. p. 547). Optimization of characters involved in the evolution of bower-building behavior onto the current phylogeny under the assumption that the bower building was present in the bowerbird ancestor, would thus require four steps in the tree: one loss of the sapling and one gain of another barrier in the ancestor to the avenue-building *Chlamydera* species, one loss of bower-building behavior in catbird ancestor, and one loss of bower-building behavior in the ancestor of *Scenopooetes*. Assuming independent origins requires only two steps, one gain of avenue-building behavior in the *Chlamydera* ancestor and one gain of maypole-building behavior in the *Amblyornis-Archboldia* ancestor. The hypothesis of independent origins is thus supported based on parsimony.

Interestingly, *Scenopoeetes*, the sister to the other species in the otherwise polygynous Clade B, is sexually monomorphic in plumage and it was also long believed to be monogamous (Frith et al. 2019). Indeed, it has at times been classified with the catbirds as the tooth-billed catbird *Ailuroedus dentirostris* (Sibley and Monroe 1990, 1993; Clements 2007). It clears a court around a tree for male display. It has also not been possible to unambiguously place *Scenopoeetes* based on cytochrome *b* data (Kusmierski et al. 1997; Endler et al. 2005). Various interpretations of the data have been used to support widely different hypotheses about the evolution of colorful display in bowerbirds (Endler et al. 2005; Borgia et al. 2007; Endler 2007). Doubtless, *Scenopoeetes* in many characters is indeed intermediate between the catbirds and the maypole-building *Prionodura* and *Amblyornis*.

Conclusions

Using a custom-designed pipeline for extracting large number of homologous loci from whole-genome sequence data we assembled a data set of more than 12,000 exonic and intronic loci (>11 million bp) from 37 bowerbirds in New Guinea and Australia, representing all recognized species and several subspecies. The reconstructed evolutionary phylogeny led to the unexpected observation that the eighteen polygynous species of bowerbirds are not monophyletic relative to the ten monogamous catbird species. We argue that polygyny is ancestral in bowerbirds and has been secondarily lost in catbirds and that bower-building has developed in parallel in two groups of bowerbirds. This is further indicated by the substantial differences in bower constructions in these clades. It is probable that the relatively stable tropical and subtropical forest environment, in combination with low predator pressure and rich access to food (mostly fruit), facilitated the evolution of the time-consuming behavior of males to build, decorate, and defend a bower to attract mating. We hypothesize that this evolved twice. Subsequently, members of the bowerbird family also colonized and diversified in arid parts of Australia.

Data Deposition

Raw Illumina sequences and the *Amblyornis subalaris* genome assembly are deposited in Sequence Reads Archive, National Center for Biotechnology Information, SRA accession PRJNA601961(https://www.ncbi.nlm.nih.gov/sra/PRJNA601961). Mitochondrial sequences have GenBank accession nos. MT249421-MT249794.

Supplementary Material

Data available from the Dryad Digital Repository: http://dx.doi.org.10.5061/dryad.6hdr7sqwp.

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