Deep global evolutionary radiation in birds: Diversification and trait evolution in the cosmopolitan bird family Rallidae

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ABSTRACT

Sufficient breadth of taxon sampling in major organisms groups is important to identify more realistic biological diversification processes that reveal the degree of historical biogeographic signal and net diversification retained in the current lineage distribution. We examine the mechanisms driving diversity in one of the major avian clades with an exceptional large-scale radiation, the family Rallidae, using the most complete species-level (∼70%) time calibrated hypothesis of evolutionary relationships produced to date. We find that Rallidae exhibit a pattern of diversification involving episodes of range expansion and regional speciation that results in most clades represented in all habitable continents. Our results suggest that several features may have played an important role on the diversification rates in Rallidae. Lineage accumulation is nearly constant and morphology (frontal shield and body size), innovate (flightlessness), habitat (forest) and distribution (insular) traits are possibly associated with increasing diversification rates along with spatial and ecological processes during the Miocene and Pliocene. Diversification and the global retention of lineage diversity have occurred in multiple lineages in Rallidae due to their dispersal ability and exploitation of ecological opportunities.

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1. Introduction

Unravelling the evolutionary ecology of birds requires extensive sampling of large phylogenetic groups comprising species that span several regions. Linking phylogenetics with analysis of speciation patterns and processes is hugely challenging, primarily because increasing phylogenetic time is accompanied by uncertainty about what taxa have existed and incomplete phylogenies are apt to give false or at least doubtful impressions of diversification rates (Crisp and Cook, 2009). Young and often abrupt species radiations provide compelling evidence of shallow ancestral traits. Island radiations routinely reveal decreased gene flow and exposure to an array of novel environmental conditions as drivers of diversification. Spatial isolation, environmental change and/or ability to colonize new habitats are all implicated in behavioural and physical adaptations (e.g. moa, Bunce et al., 2009; whistlers, Jønsson et al., 2010; vangas, Jønsson et al., 2012; honeycreepers, Lerner et al., 2011). Many empirical studies focus on radiations within archipelagos because of the opportunity to sample the majority of relevant extant species within well defined geographical boundaries (Jønsson et al., 2012; Moyle et al., 2009), and such systems provide fairly clear evidence about likely mechanisms influencing speciation. However, understanding of the mechanisms promoting diversification in older radiations across larger landscapes is generally less well informed (but see ovenbirds and woodcreepers, Derryberry et al., 2011; auks, Weir and Mursleen, 2013).

The evolutionary history of one of the most speciose clades of birds, the cosmopolitan family Rallidae, is not well known. This diverse family comprises between 135 and 148 recognized species, constituting approximately 1.3% of extant birds and 85% of Gruiform diversity, within 33–40 genera (Clements et al., 2012; Houde, 2009; Taylor, 1998), of these 39% are monotypic (Supplementary material – Fig. S1). Some members of this family possess a noted tendency to colonize oceanic islands and evolve insular and sometimes flightless species (Olson, 1973b; Ripley, 1977). At least 32 species are known to have this condition (Livezey, 2003; Taylor, 1998), providing a model system for studies in flightless evolution (Kirchman, 2009, 2012; Trewick, 1997a).

Because rails have encountered and adapted to similar environments across their geographic range, they have been subject to convergence that has hampered the understanding of their evolutionary origins, relationships, biogeography and diversification processes. This is reflected in the unstable taxonomy of the group. A large proportion of species have been placed in several different genera at one time or another as various morphological and ecological information is brought to bear on their systematics, whilst

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others have been abandoned in monotypic genera. Numerous rearrangements in the classification have been suggested in the last two centuries based on morphological characters (e.g. Berndt and Meise, 1960; Fisher and Peterson, 1964; Livezey, 1998; Olson, 1973a; Peters, 1934; Ripley, 1977; Sharpe, 1894), while subgroups of their diversity have received some attention with molecular data (e.g. Goodman et al., 2011; Groenenberg et al., 2008; Kirchman, 2009, 2012; Ruan et al., 2012; Sibley et al., 1993; Slikas et al., 2002; Tavares et al., 2010; Trewick, 1997a). However, no molecular study has had sufficient breadth of taxon sampling to resolve the core problems thoroughly. Previous studies have included no more than 20 rail species, about 14% of the diversity, only a single species per genus and/or too few relevant genera (e.g. Kirchman, 2012; Ruan et al., 2012; Slikas et al., 2002; Trewick, 1997a).

The available fossil record of the rails provides only scant information about the origins of the family despite detailed analysis of some species (Mayr, 2005, 2006, 2009; Mayr and Smith, 2001; Olson, 1985, 1977; Steadman, 1995, 2006). A recent fossil-calibrated analysis of entire mitochondrial genomes of rails and other birds has however estimated their origin in the Eocene around 40.5 (49–33) Million years ago – Mya (Garcia-R et al., in press). This has revealed considerable depth of both lineage origin and crown group diversification of ralloids and is at odds with the taxonomic instability that has plagued this group. Deep, phylogenetically distinct lineages would be expected to correlate with stable derived morphological traits.

The deep ancestry and large-scale radiations with high levels of sympatry found in Rallidae provide an opportunity to explore diversification patterns and understand the origin and evolution of biological diversity. We estimate phylogenetic relationships to support taxonomic rationalisation focusing on identification of major clades and species groups and timing of their formation. We establish a temporal phylogeny to provide insights into the underlying mechanisms driving evolution across global rail diversity. We integrate information on prominent morphological, ecological and biogeographical traits to expand hypotheses about character evolution that may be linked with the presence of rate shifts in diversification.

2. Materials and methods

2.1. Taxon sampling

Our dataset encompasses ∼50% of known extant or recent extinct rail diversity with 70 species in 22 of 33 extant genera. We included at least one representative of every genus comprising more than five described species. The sampling incorporates data from several flightless species including the extinct monotypic *Diaphorapteryx*. Our study included partial sequences of the mitochondrial genes cytochrome oxidase b (cyt*b*), cytochrome oxidase subunit I (COI) and 16S ribosomal RNA (16S) with a total of ∼2900 base pairs (bp). In addition, we sequenced ∼1900 bp from fragments of two nuclear genes beta-fibrinogen intron 7 (FGB-7) and Recombination Activating gene 1 (RAG-1) (Supporting material Table S1). Additional, complementary DNA sequences of the same gene fragments were downloaded from GenBank and DNA Barcode of Life (Table S2) to obtain a total of 94 rail species in this study. We mostly follow Taylor (1998) for the initial taxonomic assignment of the species used in this study.

2.2. Data collection

Genomic DNA was extracted from fresh tissues using either standard phenol–chloroform methods or the Qiagen QIAamp tissue kit. Preparations from old tissues (toe pads and bones) were carried out in a dedicated ancient DNA (aDNA) laboratory at Massey University (http://www.massey.ac.nz/~strewick/Text%20Files/DNA%20Toolkit.htm). DNA extractions from toe pad samples obtained from museum skins were performed using the Qiagen QIAmp DNA Minikit following standard procedures for aDNA (Rohland and Hofreiter, 2007a,b; Shepherd and Lambert, 2008), while DNA extractions from bones were carried out using phenol–chloroform after decalcification with EDTA and Proteinase K digestion in Tris–buffered saline. Mitochondrial and nuclear DNA fragments were PCR amplified using various combinations of primers (Table S3). Amplification from aDNA was focused on cyt*b* using a combination of primers designed in our lab (BR primers, Table S3). Each product was analysed on an ABI Prism 3730 automated DNA sequencer (Applied Biosystems) using the chemical reaction Big-Dye Terminator v3.1 reagents.

All sequences were edited and aligned using Geneious v6.0.5 (Drummond et al., 2012a). Reading frames in protein coding genes (cyt*b*, COI and RAG-1) were identified using amino acid translation in Geneious v6.0.5 (Drummond et al., 2012a). Ribosomal RNA 16S is a conserved mitochondrial marker but indel mutations are common in variable regions corresponding to loops in the ribosomal RNA structure. Gblocks 0.91b (Castresana, 2000) was used to remove ambiguously aligned regions of RNA 16S for all the analyses. The same approach was applied to FGB-7, which presented several indel mutations through the fragment amplified. GenBank accession numbers are found in Table S1.

2.3. Phylogenetic analyses

Prior to concatenated analyses, single gene, mitochondrial gene and nuclear gene datasets were inspected for evidence of significant incongruence by comparing preliminary Maximum Likelihood (ML) trees using RAxML and a general time reversible model with gamma distribution (GTR + Γ). The model was estimated in Model-Test v3.7 using the Akaike Information Criterion (Posada and Crandall, 1998). We observed no significant conflict among individual phylogenies, and found a similar level of support for clades. We performed all subsequent analyses with concatenated data. A 5-way partition by gene strategy was used for the concatenated analysis. We rooted our Rallidae phylogeny using an outgroup comprising *Heliornis fulica, Psophia crepitans, Aramus guarauna*, and *Grus americana* (Table S2). Maximum Likelihood analyses were implemented in RAxML using a GTR + Γ model with bootstrapping automatically stopped employing the majority rule criterion. Bayesian phylogenetic analyses (BA) were implemented in MrBayes using 3 million generations sampled every 4000th generation, a burn in of 10%, and GTR + Γ + I model of evolution. RAxML and MrBayes analyses were performed via the CIPRES portal (Miller et al., 2010). Trees were viewed using FigTree v1.3.1 (http://tree.bio.ed.ac.uk/software/figtree/) and SplitsTree v4.12.8 (Huson and Bryant, 2006).

2.4. Morphological phenogram

We constructed a Maximum Likelihood phenogram using available osteological, myological and integumentary characters (Livezey, 1998) for a range of extant and extinct rails. We identified a subset of available data corresponding to ingroup and outgroup species for which we had obtained molecular data. Maximum Likelihood (ML) was implemented in RAxML, which supports multistate morphological data (Stamatakis, 2014), via the CIPRES portal (Miller et al., 2010) and the resulting phenogram was visualized in FigTree v1.3.1 (http://tree.bio.ed.ac.uk/software/figtree/).

2.5. Molecular dating and diversification rate

Divergence times were estimated using a Lognormal relaxed Bayesian clock implemented in BEAST v1.7.5 (Drummond et al., 2012b). For calibration constraints we used the basal divergence estimation of Rallidae with Normal distribution of 33–49 Mya (95% range) and the basal split of Grues into Ralloidea (Rallidae and Heliornithidae) with Normal distribution of 59–75 Mya (95% range) based on the work of Garcia-R et al. (in press). These timing estimations were obtained using calibration constraints from a Galloanserae fossil (Benton and Donoghue, 2007; Benton et al., 2009) and the stem fossil of Sphenisciformes (Slack et al., 2006) with a dataset comprising mitochondrial genomes of representative Rallidae and other birds. We combined the results of three independent runs of 30 million generations each to ensure Effective Sample Sizes (ESS) above 200. Chains were sampled every 4000th generation and a burn-in of 10% (3 million generations) was used. The tree with the times of divergences and Highest Posterior Density (HPD) intervals was visualized using FigTree v1.3.1 (http://tree.bio.ed.ac.uk/software/figtree/).

Temporal shifts in diversification rates of the empirical phylogeny were visualized with logarithmic lineage-through-time (LTT) plots using the package Likelihood Analysis of Speciation and Extinction Rates (LASER v2.4, Rabosky, 2006a,b) from the R programming environment. We applied a null model of constant birth and death. Alternative diversification rates were compared to understand the effect of speciation and extinction using the R package TreeSim v1.9 (Ford et al., 2009). We incrementally adjusted the extinction rate of the birth–death process ($a = d/b$ from 0.5 to 0.95) in an attempt to obtain phylogenies with different shapes but similar root age ($\sim$40 Mya). The resulting empirical phylogeny of the ingroup was conditioned to the approximate diversity of the family Rallidae to infer mean LTT curves and explore departures from the constant-rate model. We simulated 100 phylogenies to 135 extant species while incorporating the effect of incomplete taxon sampling (i.e. $\sim$70% is the probability of sampling an extant species).

2.6. Trait mapping analysis

We used Mesquite v2.75 (Maddison and Maddison, 2011) to infer the ancestral state of frontal shield, body size, flightlessness, habitats and geographic distribution traits across the rail tree and estimate the number of times those characteristics have evolved in different species groups or clades. We based ancestral state reconstructions on the topology of the Maximum Likelihood tree from the RAxML analysis with the outgroup excluded to prevent biasing the reconstruction of the characters in the nodes of the tree. Traits were mapped onto the phylogeny using a Likelihood approach and restrictions of equal probability for all state changes with the Mk1 model. Trait data evaluated for the terminal taxa are listed in Tables S1 and S2 based on Taylor (1998). Ancestral character state reconstruction for the frontal shield (a) was coded as: 0 (absent = without frontal shield), 1 (small = not beyond the height of the eyes), 2 (large = notable and covering part of the head); body size (b): 0 (small = 12–19 cm.), 1 (medium = 18–40 cm.), 2 (large = 38–63 cm.); flightlessness (c): 0 (flightless), 1 (volant); ecology (d): 0 (forest), 1 (wetland), 2 (grassland/shrubland); and area distribution (e): 0 (insular), 1 (continent). Because characters cannot be treated as polymorphic for the Likelihood analysis, those species found in more than one habitat or area distribution category were treated as uncertain. However, analysis using Parsimony allowed polymorphic characters and this approach was used to compare the results of both analyses for these traits.

3. Results

3.1. Phylogeny of rails

Bayesian inference yielded a consensus tree that was topologically congruent with the ML tree, with ML bootstrap support and Bayesian posterior probabilities largely consistent among nodes (Fig. 1). However, sequence obtained from GenBank for *Micropygia schomburgkii* (JQ175375) was eliminated from all the analyses due to the conflicting phylogenetic signal shown by networks using SplitsTree v4.12.8 (Huson and Bryant, 2006) indicating that it was unreliable (result not shown). All analyses reconstructed the flufftail (*Sarothrura rufa*) and the members of *Canirallus* as a separate group from the rails (see also Fain et al., 2007; Hackett et al., 2008; Sibley and Ahlquist, 1990; Slikas et al., 2002) and sister to the sungrebe (*Heliornis fulica*). Separate analyses of the concatenated data using *Sarothrura rufa*, *Canirallus beankaensis* and *Canirallus kioloides* as the outgroup or with those species excluded (i.e. only the ingroup) showed similar support of the nodes and relationships among the ingroup (results not shown).

We identified numerous well-supported clades although deep phylogenetic structure was not fully resolved. Eight major clades based on the results of ML and BA were distinguished in our molecular analyses (Fig. 1). These included phylogenetically distinct groups that support several intergeneric and interspecific relationships not recognized by current taxonomy. A main well-supported split between the "*Rallus*" clade and all others was evident, with an indication of polytomy among those other groups (Fig. 1). "*Rallus*" is a large clade that includes several currently monotypic genera (*Dryolimnas, Aramidopsis, Eulabeornis, Habroptila* and *Diaphorapteryx*), the Australasian *Gallirallus, Nesoclopeus* and *Lewinia* and the widespread *Crex* and *Rallus*. Our "*Fulica*" clade comprises *Fulica* and species within *Gallinula* and *Porzana*. "*Aramides*" contains species of *Aramides, Amaurolimnas, Pardirallus, Neocrex erythrops* and *Porzana albicollis*. *Porphyrio* and *Rallina* are well resolved monophyletic clades as currently recognized. The core "*Porzana*" clade comprised most (but not all) of the *Porzana* species in our analysis plus *Amaurornis flavirostra* and *A. akool*. Species of *Laterallus* and *Coturnicops* along with *Porzana flaviventer, P. spiloptera* and *Anurolimnas viridis* form part of the "*Laterallus*" clade. An additional loose clade comprises the monotypic genera *Gallicrex, Megacrex* and *Himantornis* and two species of *Amaurornis* (*A. phoenicurus* and *A. moluccana*).

The morphological phenogram bears little resemblance to the molecular phylogenetic hypothesis and highlights the historic taxonomic problems (Fig. 2). These analyses were concordant only in clustering the species of the *Porphyrio* clade, the close affinity between *Fulica* and *Gallinula*. They clearly demonstrate the present *Porzana* to be polyphyletic. It is evident from the morphological phenogram the grouping of "long-billed" rails (*Rallus, Gallirallus, Dryolimnas* and *Pardirallus*), and the inclusion of *Sarothrura* and *Canirallus* within the core Rallidae contrary to molecular analyses.

3.2. Timing and rate of diversification

Our results suggest that major clades "*Laterallus*", "*Fulica*", "*Rallus*" and "*Gallicrex*" originated around the Oligocene/Miocene boundary (Fig. 3). However, most of the cladogenesis in "*Fulica*" and "*Rallus*" has been much more recent and with the currently recognized *Fulica* and *Gallirallus* groups. Around 13 (16–10) Mya marks the split between the coots (*Fulica*) from gallinules or moorhens (*Gallinula*). Diversification of the "*Rallus*" clade started in the Oligocene/Miocene boundary around 23 (29–19) Mya. The split of the *Gallirallus* group from other "*Rallus*" (*Dryolimnas, Crex, Aramidopsis, Lewinia* and *Gallirallus striatus*) occurred 21 (26–17) Mya. A
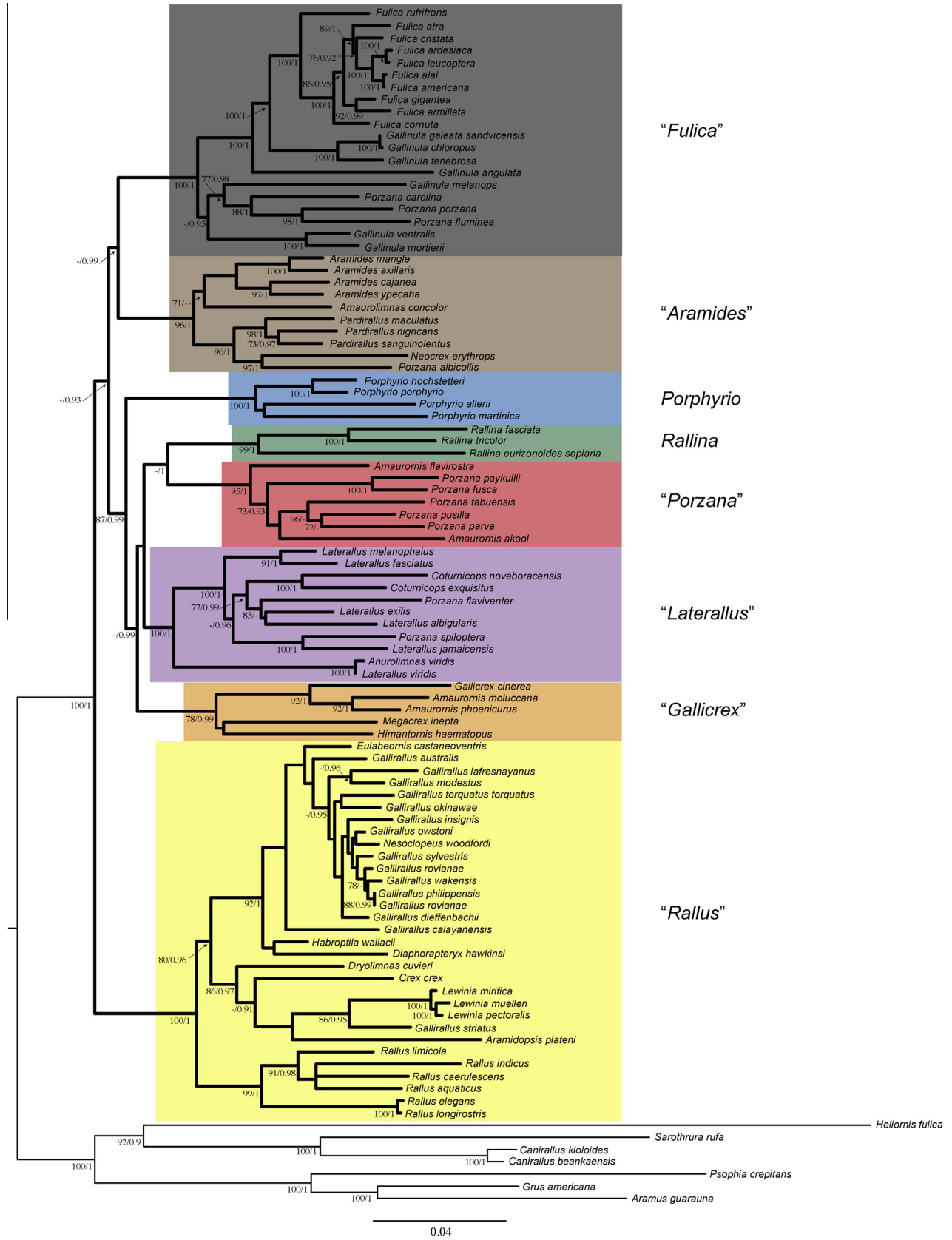
Fig. 1. Maximum Likelihood phylogeny based on a 5-gene concatenated analysis. Bootstrap supports (bs) over 70% and posterior probabilities (pp) over 0.90 are indicated in each branch.
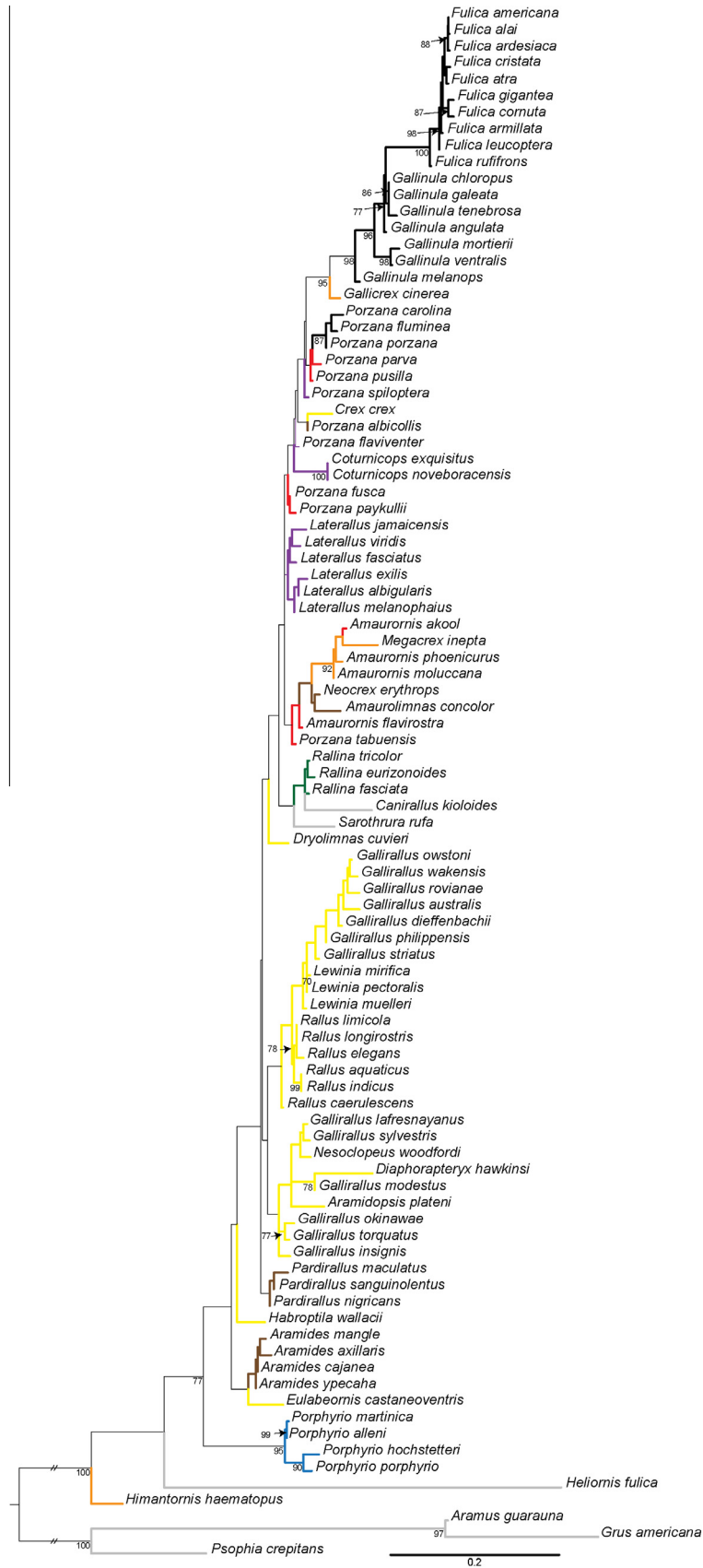
Fig. 2. Maximum Likelihood phenogram based on 570 osteological, myological and integumentary characters compiled by Livezey (1998) for species used in molecular analyses. Bootstrap supports over 70% are indicated in the nodes. Branch colours correspond to species in major clades based on our molecular results. Species in gray are of the outgroup.
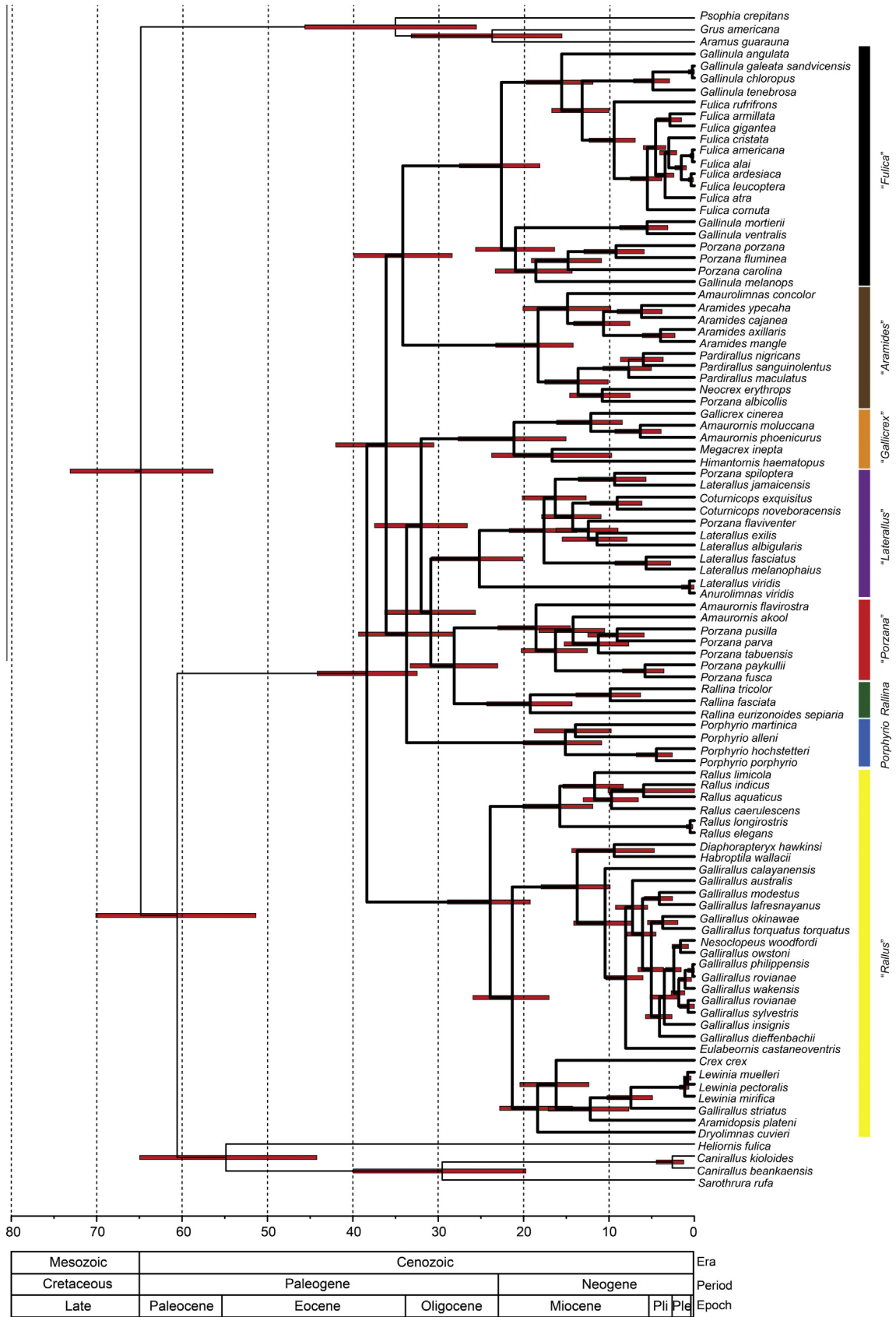
Fig. 3. Evolutionary time tree of the family Rallidae. Chronogram based on a relaxed-clock model calibrated with timing of split of Grues into Ralloidea (59–75 Mya) and crown Rallidae (33–49 Mya) estimated by Garcia-R et al. (in press). For each node the estimated time of divergence is indicated with a bar representing the 95% HPD intervals of node ages. The time scale is in millions of years ago (Mya) and geological eras, periods and epochs are indicated where Pli, Pliocene and Ple, Pleistocene.

first split in the *Gallirallus* group separates the small flightless Halmahera species *Habroptila wallacii*, and the giant flightless Chatham *Diaphorapteryx hawkinsi* from all other *Gallirallus* species around 14 (18–10) Mya. Lineage formation and diversification in "*Aramides*", "*Porzana*", *Rallina* and *Porphyrio* occurred in early and Mid-Miocene time. The origin of the *Rallina* clade is around 19 (24–14) Mya, "*Aramides*" and "*Porzana*" clades originated about 18 (22–14) Mya, and *Porphyrio* is the youngest about 15 (20–11) Mya.

The lineage accumulation analysis (Fig. 4) favoured a near constant rate of lineage increase in Rallidae, although a cluster of short internal nodes dated to between 40 and 30 Mya indicate a period of relatively abrupt diversification. Some acceleration is also apparent during the Early Miocene (~18 Mya) and further rallid diversification during the Pliocene (~6 Mya) is mainly associated with cladogenesis within *Gallirallus* and *Fulica*, as currently used (Fig. 4). The best combination of parameter values for the LTT plots of simulated phylogenies (Fig. S2), resulting in basal divergence close to the root age of Rallidae and producing an upturn in the number of lineages toward the present, was achieved with slow growth rate (0.4) and relative high *b/d* ratio (0.75).

3.3. Trait mapping

The frontal shield, which is a prominent feature of some species, appears to have evolved late in ralloid history (about 15 Mya), and independently in four main lineages within "*Fulica*", "*Gallicrex*" and *Porphyrio* clades (Fig. 5a). The two currently recognized genera with the largest frontal shields are *Porphyrio* and *Fulica* (within our current *Porphyrio* and "*Fulica*" clades, respectively). This trait represents independent evolution suggesting morphological convergence through similar selection. Our analysis showed that this trait might be plesiomorphic in *Porphyrio* clade. Present day lineages with small frontal shields are relatively younger (< 10 Mya) than those with large frontal shields. The ancestral character state in groups with small frontal shields is equivocal.

The parsimonious evolutionary scenario for body size suggests that small size has evolved twice and large size four times (Fig. 5b). Large species are found in volant and flightless lineages that otherwise also include medium size species, whilst small birds are mostly confined to "*Laterallus*" and "*Porzana*". The "*Fulica*" clade is inferred as having become larger from a medium size ancestor around 10 Mya and the *Gallirallus* lineage appears to have
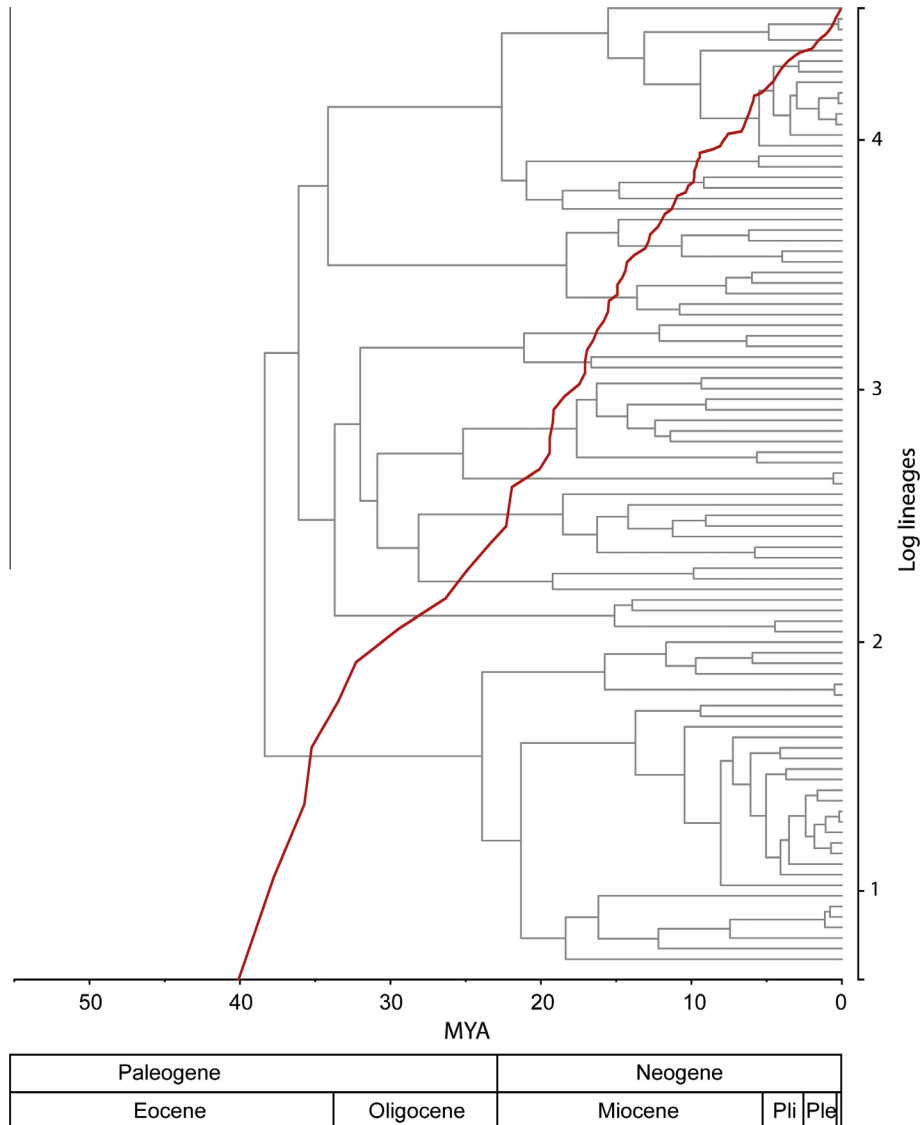

Fig. 4. Lineage through time plot representing the number of lineages (ln) in the Rallidae radiation under a constant-rate model of diversification. The red line represents the average of the number of lineages using the ML analysis of speciation in LASER. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

reverted around 6 Mya from a larger ancestral state to a medium size. Likely this is an artifact arising from extinction of relatively small ancestral flying species; an inference borne out by analysis of flight across the tree. Instances of flightless species are found through the phylogeny of rails, but the deepest node with an inferred flightless ancestral state in the present analysis is in the "*Rallus*" clade (Figs. 5c and 6a).

Likelihood and Parsimony analyses of ancestral habitat yielded no conflicts with the exception of the reconstruction for the group comprising *Lewinia, G. striatus, Aramidopsis, Crex* and *Dryolimnas* (Figs. 6b and S3). For the *Gallirallus* lineage the Likelihood approach reconstructed as ambiguous the three types of habitats with similar probability (36% for wetland, 36% for grassland and 28% for forest), while uncertainty in the parsimony analysis was among forest

and wetland (50% for both types of habitats). Other clades present wetland as plesimorphic (Fig. S3). Mapping the evolution of distribution types shows that islands could be construed as ancestral for the *Gallirallus* lineage and the allied group of species including *Lewinia, Gallirallus striatus, Aramidopsis, Crex* and *Dryolimnas* (Figs. 6c and S4).

4. Discussion

4.1. Phylogeny and trait evolution of rallids

Maximum Likelihood and Bayesian phylogenetic analyses of our multigene dataset produced congruent topologies with many well-resolved nodes that allow exploration of family wide-patterns of
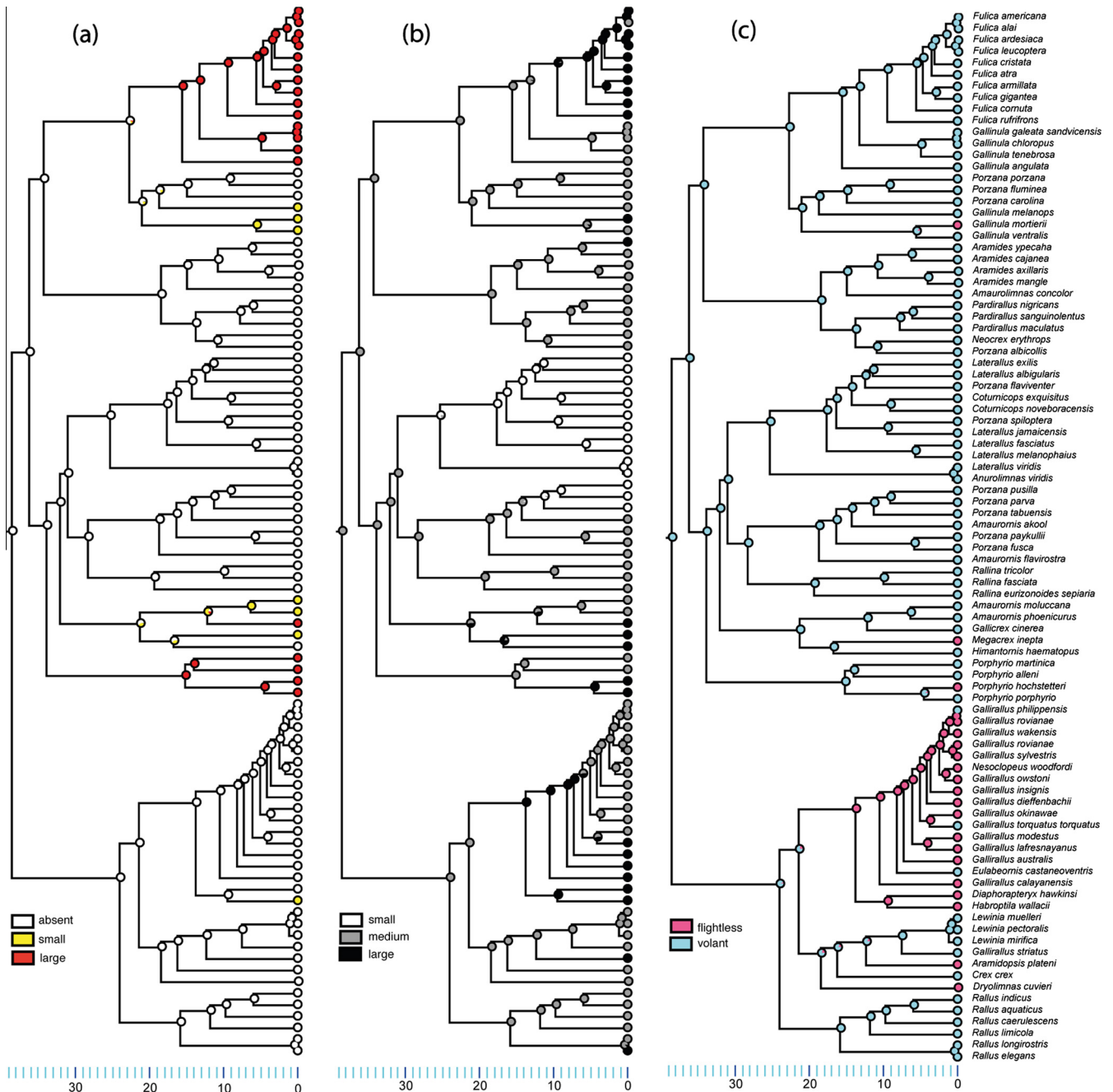

Fig. 5. Ancestral state reconstructions based on the Maximum Likelihood tree and using the likelihood model in Mesquite v.2.75 of: frontal shield (a); body size (b); and flighted condition (c). Coloured pie-charts represent proportions generated from the different assigned states of the character (see colour legends). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

phenotypic diversification. Our molecular analyses confirm that *Sarothrura* and *Canirallus*, which were previously placed in Rallidae have affinities outside the family, and are better treated as a distinct family Sarothruridae (Fain et al., 2007; Hackett et al., 2008; Slikas et al., 2002). Our phenetic analysis of morphology places these species among true rails, revealing the source of past misleading taxonomy (Fig. 2). Within the Rallidae we recognized eight major clades that help resolve taxonomic confusion arising from evolutionary convergence. Some of these clades render current genera as para- or polyphyletic. The molecular phylogenetic treatment of genera therefore reconciles a seemingly arbitrary taxonomic treatment (Table S4) that has developed since Linnaeus (1758), but is in many respects consistent with the simpler earliest proposals. Prominent in the morphological phenogram is the clustering of species that share the traits of flightlessness and large size (Fig. 2). Analysis of 570 osteological, myological and integumentary characters (Livezey, 1998) grouped, for example, flightless species of the *Gallirallus* group (*Gallirallus sylvestris, G. lafresnayanus* and *Nesoclopeus poecilopterus*) and *Porphyrio* (*Porphyrio hochstetteri, P. mantelli* and *P. kukwiedei*), with the exclusion of their respective flying relatives (Fig. 2, and see Fig. 3 in Livezey, 1998). Here homoplasy among flightless species obscures phylogenetic history (Olson, 1973b), and this also affects inferences of ancestral character reconstruction (see below). Similarly, representatives of *Porzana* (*Porzana pusilla, P. carolina, P. porzana* and *P. fluminea*) form a cluster (Fig. 4 in Livezey, 1998) that is explained by their shared gray underparts, olive and black dorsum streaked with white, and buffy juvenile plumage (Olson, 1973a). These species do not form a natural group in molecular analysis. We also found that traditional treatments of *Fulica* include only species with black plumage, large frontal shields and lobed toes, whereas other species with variable plumage, small frontal shield and straight toes (currently in *Gallinula*) also belong in the same clade.

Contrary to previous proposals (e.g. Olson, 1973a), forest is not supported as the ancestral habitat of the family, instead our results suggest that wetland is the most probable ancestral state for rallid habitat (Fig. S3). At the very least, wetland appears to be the predominant condition among extant taxa. Our reconstruction also shows that island distribution is a character that has evolved mainly in lineages within "*Rallus*", while continental distribution is the inferred ancestral state for all other groups in Rallidae. This finding mostly reflects the regional importance of *Gallirallus* in the "exploded continent" of Oceania and its recent diversification is mainly linked with isolation and adaptation to novel selective regimes that results in a tendency for enlarged, flightless forest-floor specialists.

The majority of flightlessness species of *Gallirallus* ("*Rallus*" clade) appear to have originated during the Late Miocene through the Pleistocene (Fig. 6a). Fitness advantages on oceanic islands that usually lack terrestrial mammal predators favours reversion to a terrestrial lifestyle in a trade-off between energy conservation and predator avoidance (McCall et al., 1998; McNab, 1994; McNab and Ellis, 2006; Olson, 1973b). The incidence of flightless species is so high that ancestral state analysis returns the ambiguous inference that flight has been re-evolved from flightless ancestors. Other evidence suggests this to be highly unlikely (Olson, 1973a; Trewick, 1997a). There are no authenticated examples of the re-emergence of flight in neoaves and this result is revealing about the sensitivity of ancestral state reconstructions to sampling of tip traits (Crisp and Cook, 2005; Crisp et al., 2011; Cunningham et al., 1998; Ekman et al., 2008; Omland, 1999). The apparent re-emergence of flight in this clade must reflect directional asymmetry in dispersal of birds of the banded rail *Gallirallus philippensis* lineage; *G. philippensis* is phylogenetically nested amongst flightless *Gallirallus* species. In fact, the flying lineage must have persisted through time and repeatedly established island populations each of which gave rise to insular flightless species that locally replaced their flying founder (Olson, 1973b; Trewick, 1997a). Likewise, the inference that large size is ancestral in *Gallirallus* is probably correlated with the evolutionary convergence of derived flightless species.

4.2. Lineage diversification and biogeography

Dispersal ability and novel ecological opportunities have allowed diversification and retention around the globe of lineage diversity in multiple clades within Rallidae (Olson, 1973a; Ripley, 1977). Bursts of lineage formation span archipelagos and continents. The result is a biogeographic pattern involving representation of most clades in all habitable continents rather than generic
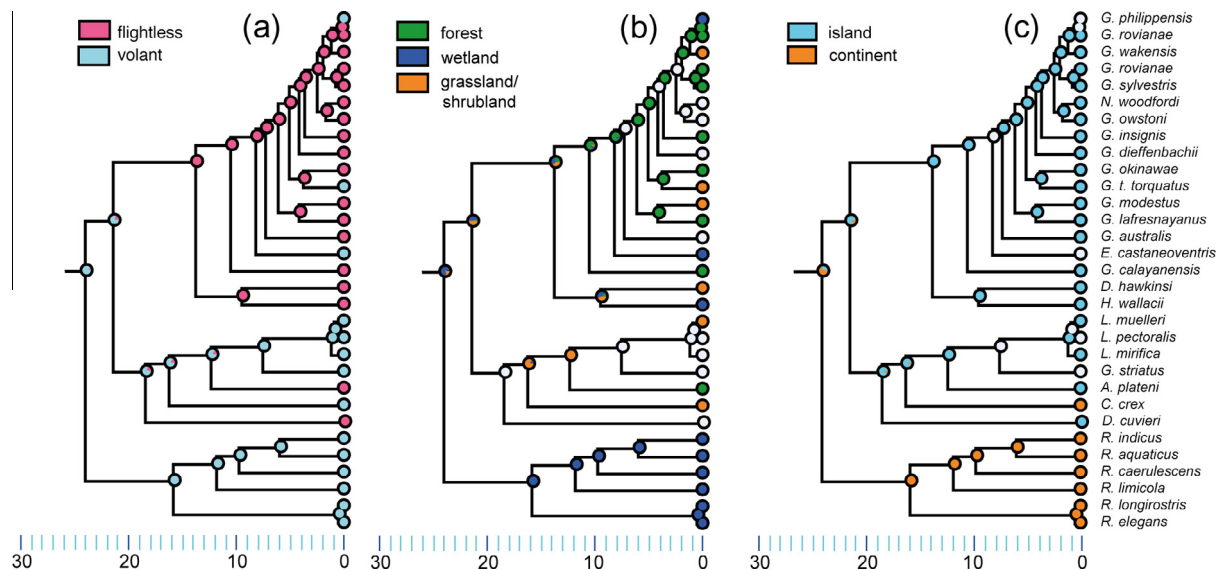

Fig. 6. Ancestral state reconstruction based on likelihood analysis of (a) flighted condition, (b) habitat, and (c) distribution for the "*Rallus*" clade. Terminals without coloured pie charts indicate species with polymorphic states of the character and are coded as uncertain in the data matrix. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

radiations being associated with particular geographic regions (Fig. S5). Rapid and shallow speciation is sometimes due to radiation on islands after colonisation (e.g. *Gallirallus*) and habitat patches in continental landscapes (e.g. *Fulica*), but other processes are also implicated. Our analysis tracks episodes of diversification over 30 Mya. Old clades are important for rail diversity and diversification may have been related to occupancy of novel habitats propelled by major climatic shifts in the past (Böhme, 2003; Kürschner et al., 2008; Tolley et al., 2008; Zachos et al., 2001). The curve of the LTT plot in the empirical phylogeny (Fig. 4) showed a pattern of high initial diversification followed by deceleration consistent with density-dependent cladogenesis after available ecological space was filled and constrained by resource limitation (Rabosky and Lovette, 2008). This pattern of lineage accumulation is characteristic of a near constant birth–death rate process with a low extinction rate. However, the relatively high b/d ratio from LTT plots of simulated phylogenies (Fig. S2) is consistent with the signature of extinction dynamics registered in different ralloid fossil clades (Olson, 1977; Steadman, 2006). Such levels of extinction may yield a highly stochastic birth–death process and more species-rich clades (Claramunt, 2010).

The molecular phylogeny suggests differing rates of diversification across the family. "*Rallus*", "*Fulica*" and "*Laterallus*" retain most species diversity within Rallidae compared to other clades, and contribute to the accumulation of diversity over time rather than a short-lived burst of speciation. Phenotypic differentiation associated principally with mate recognition (e.g. frontal shield) and morphological innovations (e.g. flightlessness) are also important in lineage diversification (Figs. 5, S3 and S4). Frontal shield evolved in four separate lineages within "*Gallicrex*", "*Fulica*" and *Porphyrio* clades around 15 Mya. In "*Fulica*" and *Porphyrio*, frontal shield is known to be associated with social interactions such as status, dominance, mate recognition and choice (Craig, 1977; Crowley and Magrath, 2004; Dey et al., 2014; Gordon, 1951) and this may be the case with other characters (e.g. plumage colour) in other clades that are involved in sexual selection and speciation. Together these features promote speciation of this cosmopolitan family and accumulation of diversity within rallid clades.

4.3. Distribution and ecological diversification of rails

Taking into account available information (Kirchman, 2012; Ruan et al., 2012; Slikas et al., 2002; Trewick, 1997a) and based on the present analyses, a reduced number of genera provides a clearer hypothesis of how diversity within Rallidae is distributed, where each clade may have originated, and possible directions of range expansion (Fig. S5). Many currently recognised genera are embedded within widespread clades that are less morphologically homogeneous. Several monotypic genera are strongly supported as belonging to larger widespread clades. In some cases, traits used in taxonomy agree with subclades inferred from molecular data but these are nested among species that share some of the supposedly diagnostic morphological features (e.g. *Fulica* within "*Fulica*"). In other cases, species that share morphological traits are clearly shown by molecular analysis to be non-monophyletic groups resulting from convergence (e.g. *Porzana*).

The large "*Rallus*" clade has a worldwide distribution but may have originated in the Americas. *Rallus* is traditionally applied to the subclade of northern hemisphere species, with *Gallirallus* used for species around Oceania. However, this has not always been the case and at one stage *Gallirallus* was applied to only some of the flightless island endemics of this group (Olson, 1973b). Other genera have in the past been erected to deal with supposedly aberrant island species including *Ocydromus* (= *Gallirallus australis*) in New Zealand and *Cabalus* (= *Gallirallus modestus*) on Chatham island. Even today some island species that fall within this clade are classified in additional genera (e.g. *Nesoclopeus* in Fiji). A second extinct species on the Chathams islands in the "*Rallus*" clade is currently placed in the monotypic *Diaphorapteryx*, and a third extinct Chatham "*Rallus*" species (*G. deiffenbachii*) has sometimes been considered to be a subspecies of the widespread volant *G. philippensis* despite significant size difference and little likelihood that it could fly (Ripley, 1977; Trewick, 1997b). In addition, the monotypic genera *Atlantisia* (Innaccessible island) and *Rougetius* (east of Africa) could be included within the "*Rallus*" clade (Olson, 1973a).

Gallirallus australis (weka) is at the tip of a long phylogenetic branch that might, parsimoniously, be inferred as implying existence of this flightless form in New Zealand since Miocene time. Alternatively, *G. australis* may be the remains of a subclade that included flying relatives that are now extinct. It is not possible to determine where on the long branch leading to *G. australis* flightlessness evolved, but the evolutionary convergence of morphologically similar endemic flightless species on other Pacific islands shows that it is not necessary to assume *G. australis* evolved a long time in the past. In contrast, *Eulabeornis castaneoventris* (chestnut rail) of north Australian mangrove also sits on a long phylogenetic branch in "*Rallus*" but has retained flight. The Eurasian landrail or corncrake *Crex crex* has long been treated as ecologically and thus taxonomically distinct but it falls within the "*Rallus*" clade and shares many plumage and morphological features with typical rails in this group. Indeed Linnaeus (1758) originally placed *Crex crex* in *Rallus*.

Black *Fulica* coots are readily recognised and this is one of the genera established by Linnaeus (1758). *Fulica* coots share the very distinctive trait of pale grey flatten toes that render them excellent swimmers. This is a synapomorphy that is demonstrated by the clustering of these species in molecular analysis but is of relatively recent origin. The emergence of *F. rufifrons* from the base of the *Fulica* lineage is consistent with the presence of distinctly narrower lateral membranes of the toes in this species compared to other coots (Olson, 1973a). Their normal habitats are lakes and slow moving rivers (Taylor, 1998) and the patchiness of these conditions demands that coots are strong fliers. Indeed the global distribution of this group of birds shows that ancestors must have moved among continents; one species is endemic to Hawaii (*F. alai*) but closed related to the North and Central American *F. americana*, while another (*F. cristata*) is centred in Africa. Four other species have sympatric ranges in South America but show marked differences in size and distinctive frontal shield colours and ornaments that likely aid mate recognition. One species (*F. atra*) occurs through Europe and Asia and appears to have extended its range in recent times into Australasia. Island colonisation resulted in the former existence of large endemic species including *F. newtonii* on the Mascerene Islands in the Indian Ocean, *F. prisca* in New Zealand and *F. chathamensis* on the Chatham Island.

Fulica is nested among species currently assigned to *Gallinula* rendering the latter paraphyletic. In fact *Gallinula* falls into two sister clades, one with *Fulica* and the other with species of *Porzana* (*P. carolina, P. fluminea* and *P. porzana*). Despite their current generic distinction, species in this subclade have broadly similar plumage and habits. Their chief distinction being that plumage is overall less dark than the coots and other *Gallinula* (e.g. the moorhen *G. chloropus* which Linnaeus (1758) originally placed in *Fulica*). On a relatively long branch from the base of the "*Fulica*" clade are the pair of relatively large, dark Australian gallinules, *G. ventralis* and the flightless Tasmanian *G. mortierii* (formerly *Tribonyx*). The frontal shield is variously developed in "*Fulica*" being large and red in *Gallinula galeata*, large and white in *Fulica atra*. In *F. cristata* the white shield is embellished with red knobs and in *F. cornuta* the shield is black and wattle-like. Most *Gallinula* and *Porzana* in this clade have much smaller, sometimes nondescript pale shields.

"*Porzana*" is widespread across Europe, Africa, Asia and Oceania, even when many of the species usually ascribed to this genus (*P. porzana, P. carolina, P. fluminea, P. albicollis, P. flaviventer* and *P. spiloptera*) are excluded for phylogenetic reasons. True "*Porzana*", which are typically inhabitants of swamps and reed beds, includes species in continental areas and some islands but we note some must be recent arrivals. For example, New Zealand, Australia and other Pacific islands share *P. tabuensis*. Several island endemics in this group (*P. palmeri* in Laysan island, *P. monasa* in Kosrae island, *P. atra* in Henderson island and *P. sandwichensis* in Hawaii) are descended from volant widespread species (Slikas et al., 2002).

"*Laterallus*" is largely confined to the Americas and includes the New World *Porzana* (*P. spiloptera* and *P. flaviventer*) as well as traditional *Laterallus, Anurolimnas* and *Coturnicops*. The latter includes *C. exquisitus* outside the Americas in Asia. The monotypic *Micropygia* is also endemic to the New World and probably belongs to the "*Laterallus*" clade (Howard and Moore, 1991). "*Aramides*" is another New World group that includes *Aramides, Pardirallus,* the monotypic *Amaurolimnas concolor* and the American *Porzana albicollis* and *Neocrex erythrops. Cyanolimnas* might also be embedded within "*Aramides*" sharing finely barred flanks, buffy crissum, drab olive–brown above and dark gray below, usually with light throats, bill shape (with a paint-like red spot at the base) and frontal plate (Olson, 1973a). We note that these two New World clades ("*Laterallus*" and "*Aramides*") are not phylogenetic sisters.

Rallina is found across Asia and Oceania and probably includes the three currently recognized species within *Gymnocrex* (Olson, 1973a) which are endemic to islands in Southeast Asia. The "*Gallicrex*" clade includes the Asian monotypic *Gallicrex cinerea,* two *Amaurornis* species from Asia and Oceania (*A. moluccana* and *A. phoenicurus*), and the monotypic African Nkulengu rail *Himantornis haematopus* that is allied to another aberrant species, the New Guinea flightless rail *Megacrex inepta. Himantornis haematopus* has been considered the most "primitive" rallid and consequently traditionally placed in its own subfamily, Himantornithinae (Livezey, 1998; Olson, 1973a; Ripley, 1977). Our results strongly indicate the placement of *H. haematopus* within core rails (i.e. discard subfamilies). Supposedly "primitive" characters in *H. haematopus* (Livezey, 1998; Olson, 1973a) are more parsimoniously inferred as uniquely derived, perhaps showing evolutionary response to habitat conditions. Species in this group inhabit a wide range of habitats including swamps and forests. An African origin might be ascribed to *Porphyrio* even though this requires long distance dispersal into the Americas and Europe, Asia and Oceania (Fig. S5). Like "*Rallus*" and "*Porzana*", *Porphyrio* includes many examples of island colonisation and instances of endemism involving evolution of flightlessness (e.g. *P. hochstetteri* in New Zealand).

Phylogenetic evidence suggests that diversification patterns within the Rallidae are structured ecologically and geographically. Widespread clades reflect the fact that long-distance dispersal has overcome potential ecological barriers including expanses of open water and land. We note, however, that representation of each clade around the world is often by one or few supertramp species such as purple swamphen (*Porphyrio porphyrio*) within *Porphyrio*, banded rail (*Gallirallus philippensis*) within "*Rallus*", common coot (*Fulica atra*) and common moorhen (*Gallinula chloropus*) within "*Fulica*", and Baillon's crake (*Porzana pusilla*) and spotless crake (*Porzana tabuensis*) within "*Porzana*". These species are widespread across several thousands of kilometres often with high numerical abundance in local populations (BirdLife International, 2014; Diamond, 1982; Mayr and Diamond, 2001; Sullivan et al., 2009). Dispersal behaviour as an important life-history trait in these species that has fueled a rapid radiation in archipelagos, particularly in the south west Pacific (Diamond, 1977; Mayr and Diamond, 2001; Trewick, 1996, 1997a; Trewick, 1997b). High dispersal ability, huge abundance and rapid adaptation of species (Kirchman, 2009;

Olson, 1973a,b; Ripley, 1977; Ripley and Beehler, 1985), has resulted in speciose and widespread genera (Darwin, 1859). The occurrence of species with remarkably different ecology and dispersal ability in the same clade likely indicates rapid shifts in these attributes over evolutionary time (Andersen et al., 2014).

Evolution in the Rallidae includes features that have been observed separately in other bird family radiations. The babblers (Moyle et al., 2012) appear to have a younger history than the rails and shows elements of dispersal and speciation around the world, but the majority of extant taxa are in Asia and the ancestral condition is inferred as Asian. Within the babblers, white-eyes (Moyle et al., 2009) show regional radiations but with spatial overlap of clades because one lineage has been more successful in spreading geographically. In contrast, New Zealand moa (Bunce et al., 2009), Hawaiian honeycreepers (Lerner et al., 2011), and Madagascan vangas (Jønsson et al., 2012) show rapid diversification, but only within geographically constrained island settings. In a more expanded geographical setting but more recently radiated in comparison to rails, passerine honeyeaters (Andersen et al., 2014; Driskell and Christidis, 2004), ovenbird-woodcreepers (Claramunt, 2010; Derryberry et al., 2011; Irestedt et al., 2009), whistlers (Jønsson et al., 2010), and non-passerine auks (Weir and Mursleen, 2013) show patterns of lineage accumulation involving specialisation of particular morphological characteristics (e.g. cranial kinesis, plumage, bill) and behaviour associated with ecological specialisation. Rails show resilience in diverse conditions and can be found in different habitats/continents because niche partitioning (space and time) is linked to adaptation of organismal traits (structural or behavioural). Morphological divergences and convergence have obscured the relationships and biogeographic patterns within Rallidae, especially among endemic island taxa or archipelago genera and extended to continental relatives. This corresponds to a spatial and temporal dependency of historical rail diversification with increasing rates focusing mainly at species-level in different geographical scales.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2014.09.008.

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