ORIGINAL ARTICLE

Mainland colonization by island lizards

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ABSTRACT

Aim We investigate biogeographic relationships within the lizard genus *Anolis* Daudin, 1802 to test the hypothesis that the mainland (Central and South American) Norops-clade species descended from a West Indian *Anolis* ancestor. Previous hypotheses have suggested that close island relatives of mainland Norops species (the Cuban *Anolis sagrei* and Jamaican *A. grahami* series) represent over-water dispersal from a mainland ancestor. These previous hypotheses predict that the *A. sagrei* and *A. grahami* series should be phylogenetically nested within a Norops clade whose ancestral geography traces to the mainland. If Norops is West Indian in origin, then West Indian species should span the deepest phylogenetic divergences within the Norops clade.

Location Central and South America and West Indian islands.

Methods The phylogenetic relationships of *Anolis* lizards are reconstructed from aligned DNA sequences using both parsimony and Bayesian approaches. Hypotheses are tested in two ways: (1) by reconstructing the ancestral geographic location for the Norops clade using Pagel & Lutzoni's (2002) Bayesian approach, and (2) by testing alternative topological arrangements via Wilcoxon Signed-Ranks tests (Templeton, 1983) and Shimodaira–Hasegawa tests (Shimodaira & Hasegawa, 1999).

Results Our evidence supports an origin of mainland Norops anoles from a West Indian ancestor. A West Indian ancestor to the Norops clade is statistically supported, and alternatives to the biogeographic pattern [Cuban (Jamaican, Mainland)] are statistically rejected by Shimodaira–Hasegawa tests, although not by Wilcoxon Signed-Ranks tests.

Main conclusions Our data support the hypothesis of a West Indian origin for mainland Norops. This result contradicts previous hypotheses and suggests that island forms may be an important source for mainland biodiversity.

Keywords

Anolis, Central America, *Norops*, Polychrotinae, South America, Squamata, West Indies.

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INTRODUCTION

Islands are generally colonized from mainland areas. Classic examples of islands colonized by mainland species include the flora and fauna of the Galápagos, Hawaii, Krakatau, and the Greater Antilles (Carlquist, 1974; Brown & Lomolino, 1998; Cox & Moore, 2000; Woods & Sergile, 2001 and references therein). By contrast, mainland areas are rarely colonized by island taxa (Brown & Lomolino, 1998; Cox & Moore, 2000), although some examples are known. For example,

Eleutherodactylus frogs of the subgenus *Syrrhophus* and the turtle *Trachemys scripta* colonized mainland America from Cuba (Seidel, 1988, 1996; Hedges, 1989; Hass & Hedges, 1991; Hedges *et al.*, 1992), and African chameleons are colonists from Madagascar (Raxworthy *et al.*, 2002; Townsend & Larson, 2002).

Several explanations for the rarity of island-to-mainland dispersals have been proposed (e.g. Carlquist, 1974; Brown & Lomolino, 1998; Cox & Moore, 2000). One explanation relies on sheer numbers: by nature of their small size, islands contain

few individuals and species available as colonists. Another explanation is that islands have less diverse biotic communities and may have underutilized resources – or 'empty niches' – available to arriving colonists. A third possibility is that, because of the greater species richness of continental areas, selective pressures are more intense in mainland communities favouring the evolution of species with greater competitive abilities than species that have evolved in less-diverse island communities. As a result, mainland species may have greater ability to invade island areas than vice-versa.

West Indian *Anolis* (Daudin, 1802) lizards are an appropriate group to examine the dynamics of colonization between mainland and island areas. About 365 species of anoles are distributed throughout the south-eastern USA, Central and tropical South America, and the West Indies. The traditional view is that all West Indian anoles are the result of mainland-to-island (or inter-island) colonizations (Etheridge, 1960; Williams, 1969, 1976, 1983, 1989; Guyer & Savage, 1986).

However, there is reason to question whether the mainland-to-island paradigm applies to all anoles. First, dispersal is clearly not unidirectional, as evidenced by the existence of the green anole (*A. carolinensis*) in Florida. This species is part of a largely Cuban clade, is closely related to the Cuban species *A. porcatus* (Williams, 1969; Buth *et al.*, 1980; Glor *et al.*, in press), and has been in Florida for at least 10,000 years (Auffenberg, 1956; Auffenberg & Milstead, 1965) and probably much longer (Buth *et al.*, 1980; Glor *et al.*, in press). Second, recent molecular studies suggest that one particularly diverse mainland clade of anoles (the Norops clade) is derived from a West Indian ancestor (Jackman *et al.*, 1997; Nicholson, 2002). If this hypothesis is correct, then West Indian anoles not only colonized mainland areas, but also diversified extensively following colonization. We report the results of a molecular phylogenetic analysis that reconstructs historic geographic distributions of West Indian anoles to test the hypothesis that island-to-mainland colonization has occurred and has been important in the evolution of anole diversity.

METHODS

The focus of this study is on lizards of the Norops[1] clade of *Anolis*. Norops occurs both on the mainland and in the West Indies. Of *c.* 152 recognized species of Norops, 129 occur on mainland Central and South America and 23 occur in the West Indies. Of the 23 West Indian species, 16 species occur on

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[1]The current taxonomy of anoles is unresolved. One clade of anoles has been recognized as the genus *Norops* Wagler, 1830 (Guyer & Savage, 1986) or the beta section of *Anolis* (Etheridge, 1960) (Fig. 1). In this paper, we use the term Norops (not italicized), followed by the species name (e.g. Norops *Anolis sagrei* or N. *A. sagrei*) to distinguish this clade of anoles from other *Anolis* species. This clade is well supported (Etheridge, 1960; Guyer & Savage, 1986; Jackman *et al.*, 1997, 1999; Nicholson, 2002); however, we use Norops as a clade name only, not as a genus in the strict taxonomic sense because the latter usage would render remaining members of the genus *Anolis* paraphyletic.

Cuba or nearby small islands, seven on Jamaica or nearby small islands (Schwartz & Henderson, 1991; Powell *et al.*, 1996; Nicholson, 2002), and one species on both. Previous studies that postulated a mainland origin for Norops either did not use cladistic analyses (Etheridge, 1960; Williams, 1969, 1976, 1983, 1989) or did not thoroughly sample some major clades of *Anolis* (Gorman *et al.*, 1984; Guyer & Savage, 1986).

To reconstruct the origin of mainland and West Indian taxa, we used a phylogeny produced for the entire genus by combining DNA sequences of Jackman *et al.* (1999, 2002; 57 species) with new data for 132 species. We then examined relationships among mainland and West Indian Norops in greater detail using a mtDNA phylogeny of Norops analysed independently and in combination with Nicholson's (2002) nuclear DNA sequences.

Taxon sampling

We sampled 51 of the 54 species in Nicholson's (2002) study of Norops based on the nuclear ITS-1 region excepting three ingroup species (Norops *Anolis exsul*, N. *A. compressicauda*, and N. *A. gracilipes*) that were not available. Individuals were the same between these studies except for three members of the N. *A. sagrei* series (N. *A. ahli*, N. *A. ophiolepis*, and N. *A. sagrei*), and all members of the N. *A. grahami* series (N. *A. garmani*, N. *A. grahami*, N. *A. lineatopus*, N. *A. reconditus*, and N. *A. valencienni*); data for these species come from Jackman *et al.* (1999, 2002). Our analyses also include new sequences from 79 non-Norops species from the West Indies and mainland areas for a total of 189 species (187 ingroup and two outgroup species: *Basiliscus plumifrons*, and *Polychrus acutirostris*). This sampling regime is nearly four times that of previous studies of *Anolis* and spans all of the major groups that have been proposed within *Anolis* (e.g. Etheridge, 1960; Guyer & Savage, 1986; Savage & Guyer, 1989).

Laboratory protocols

Following Jackman *et al.* (1999), we sequenced the mitochondrial ND2 gene, five tRNA's ($tRNA^{Trp}$, $tRNA^{Ala}$, $tRNA^{Asn}$, $tRNA^{Cys}$, $tRNA^{Tyr}$), the origin of light-strand replication, and a portion of the CO1 gene. Genomic DNA was isolated from all individuals using DNeasy Kits (Qiagen). Amplification of gene products was performed as in Townsend & Larson (2002) with an annealing temperature of 50 °C. Negative controls were included with all PCR amplifications to confirm the absence of contaminants. Correct amplification of PCR products was verified by visualization on 0.8% agarose gels stained with ethidium bromide. PCR products were then cored from the agarose gels and purified using Viogene Gel-M purification kits (Viogene, Inc., Taipei, Taiwan). Sequencing reactions were conducted with the purified PCR products and BigDye chemistry (Applied Biosystems, Foster City, CA, USA). Sequencing reactions were run on an MJ Research Basestation automated sequencer (MJ Research, San Francisco, CA, USA). DNA sequence fragments were edited using Cartographer (MJ

Research) and aligned manually. Alignment of tRNA sequences utilized secondary structural models (Kumazawa & Nishida, 1993; Macey *et al.*, 1997). All sequences are deposited in GenBank (new sequences produced for this publication are AY909735-AY909789).

Phylogenetic analyses

The mtDNA data gathered for this study were combined with sequences from Jackman *et al.* (1999, 2002) to reconstruct a phylogeny of the genus *Anolis* that includes all species for which mtDNA sequence from the *ND2* region is available. Phylogenetic analyses within Norops were conducted on the mtDNA sequences alone and in combination with Nicholson's (2002) nuclear ITS-1 DNA sequences. Some taxa present in the comprehensive *Anolis* analyses are missing in the combined ITS-1 + mtDNA analyses because ITS-1 data were not available for some Norops species. Sequences were analysed using the programs PAUP* (Swofford, 2000), and MrBayes (version 3.1, Huelsenbeck & Ronquist, 2001) for parsimony and Bayesian methods, respectively. Regions with ambiguous alignment were excluded. For Bayesian analyses, alternative hierarchical models of evolution were evaluated using ModelTest 3.0 (Posada & Crandall, 1998). The selected model and parameter settings were implemented in Bayesian analyses performing 1,000,000 generations with trees sampled every 5000 generations post-burn-in (evaluated post-Bayesian analysis via inspection of plots of ln-likelihood score vs. generation for the plateau or stabilization of likelihood scores). The Bayesian analysis was repeated three times to avoid searching only within local optima. Parsimony analyses were conducted by performing a heuristic search with 1000 random taxon additions and TBR branch swapping with all characters equally weighted. Node support was evaluated using posterior probabilities (Bayesian analysis) and bootstrap analysis (parsimony analysis; Felsenstein, 1985). Bootstrap analysis was conducted using PAUP* (Swofford, 2000) by performing 1000 replicates each with three random taxon additions. We recognize that recent studies differ on the credibility of Bayesian posterior probability support of nodes (Huelsenbeck *et al.*, 2002; Suzuki *et al.*, 2002; Wilcox *et al.*, 2002; Alfaro *et al.*, 2003; Douady *et al.*, 2003; Erixon *et al.*, 2003; Simmons *et al.*, 2004). We, therefore, have not relied solely on Bayesian posteriors to assess node support, but reference parsimony bootstrap support as well.

Statistical analyses

Ancestral-state reconstruction was performed on the mtDNA phylogeny including all available *Anolis* sequences. This analysis was conducted using a Bayesian tree-sampling methodology (Lutzoni *et al.*, 2001; Pagel & Lutzoni, 2002) to determine whether the most recent common ancestor to Norops was West Indian or mainland using the programme Mesquite (Maddison & Maddison, 2004). This approach is desirable because it explores inconsistency between phyloge-

netic reconstructions by virtue of examining multiple trees (in this case all 539 post-burn-in trees from the Bayesian analysis) as opposed to reconstructing ancestral states on a single tree. The programme Mesquite (Maddison & Maddison, 2004) facilitates this procedure by allowing the user to import all trees of interest and then to reconstruct the ancestral states on all nodes across all trees via likelihood probabilities. In this case, we coded all taxa as being either mainland or West Indian rather than coding for specific countries or geographic regions (such as separate mainland geologic 'blocks'). This coding corresponds to the published hypotheses (Williams, 1969; Guyer & Savage, 1986). The geology of the region is poorly constrained and controversial in some aspects, so a simple, broad approach was preferred.

Alternative hypotheses of intra-Norops relationships were tested using Wilcoxon Signed-Ranks tests (Templeton, 1983) as implemented in PAUP* (Swofford, 2000) and Shimodaira–Hasegawa tests (Shimodaira & Hasegawa, 1999) as implemented in the programme SHTests (Rambaut, 2000).

RESULTS

mtDNA results

New mtDNA sequences from 132 species (53 Norops, 79 non-Norops) were combined with 57 previously published anole sequences for a total of 1483 aligned bp of mtDNA. Seventy-five sites were unalignable (excluded positions of mtDNA: 1056–64, 1097–1104, 1117–1120, 1190–1192, 1279–1298, 1319–1326, 1358–1362, 1369–1379, 1387–1393), leaving 1408 included base pairs, 979 of which were parsimony informative. Uncorrected sequence divergence ranged from 4.1% to 27.7% within the ingroup, and as high as 28.5% between ingroup and outgroup taxa. The combined data matrix consisted of 187 ingroup taxa, two outgroup taxa (*Basiliscus plumifrons* and *Polychrus acutirostris*), and 1483 bp of mtDNA sequences.

The mtDNA sequences presented in this study were combined with other *Anolis* sequences from Jackman *et al.* (1999, 2002). Likelihood-ratio tests for the combined data matrix favoured the GTR + I + Γ model. In the Bayesian analysis, the four chains converged on a stable equilibrium point by *c.* 100,000 generations for two of the runs, and by 120,000 generations for the third run. This analysis produced a well-resolved majority-rule consensus tree (539 trees, post-burn-in from three runs), with many strongly supported nodes (Fig. 1). Parsimony analysis yielded 88 most-parsimonious trees with a length of 23,022 steps, with topological features largely concordant with the Bayesian analysis.

A West Indian ancestor to Norops was reconstructed on all of the trees (Fig. 1). A West Indian ancestor was reconstructed also for the clade containing the Jamaican and mainland Norops species, although in one of the 539 trees the reconstruction was equivocal (i.e. neither a West Indian nor a mainland ancestor reconstructed with a probability > 0.95). A mainland ancestor was reconstructed in 538 of 539 trees for the node leading to all mainland Norops. To determine the
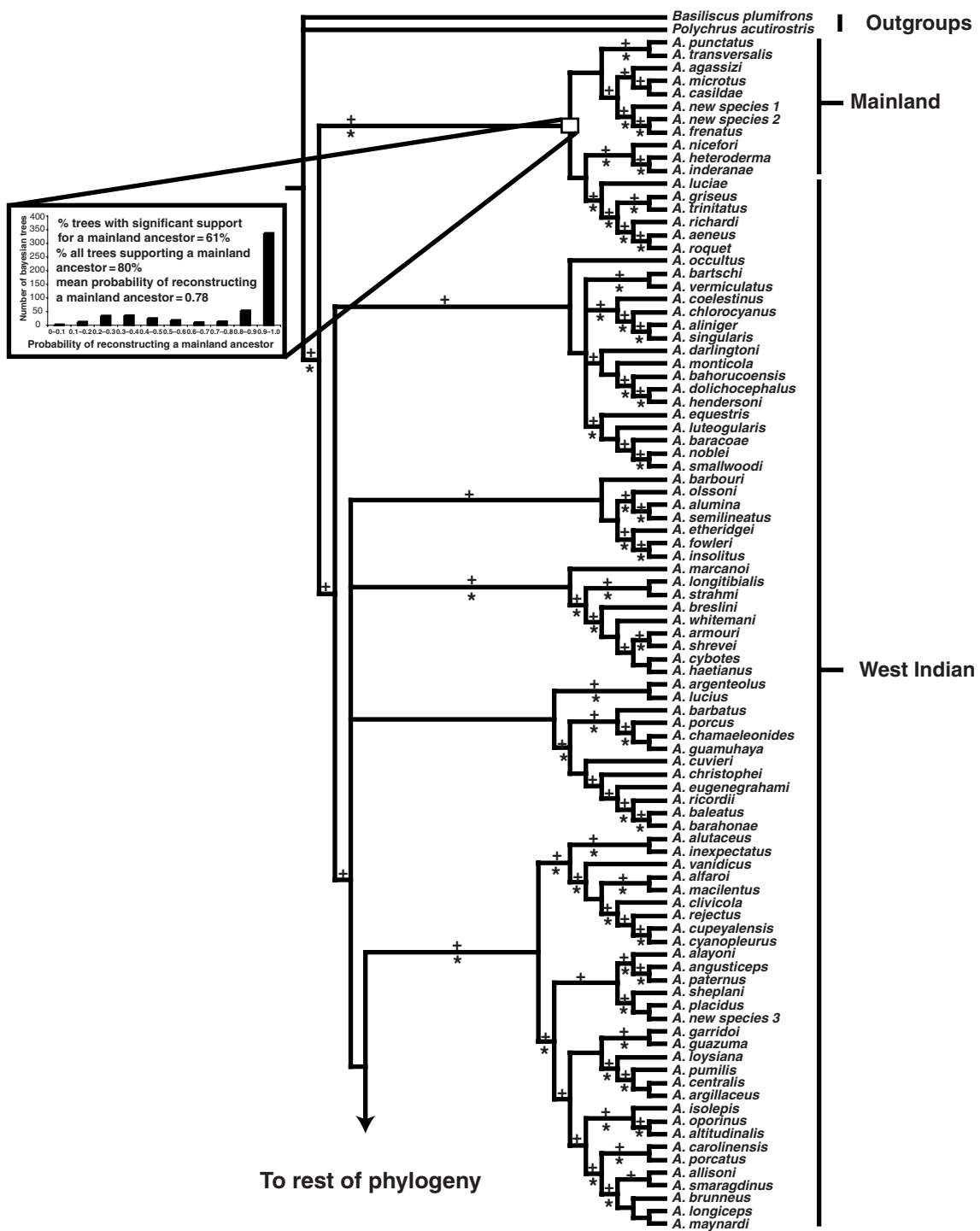
Figure 1 (a and b) Results from the phylogenetic analysis of the full *Anolis* Daudin, 1802 data set [Norops mtDNA sequences + other *Anolis* sequences (Jackman *et al.*, 1999, 2002)]. The tree shown is the 50% majority-rule consensus tree constructed from 539 Bayesian trees from three independent Bayesian searches. The length of this tree prohibits the addition of visible node support values. Therefore, the following symbols are used: '+' above the nodes indicates Bayesian posterior probabilities of 90–100; '*' below the nodes indicates parsimony support (bootstrap proportions) of 80–100. The geographic area to which these taxa belong is indicated to the right of the tree. The Norops subclade is indicated to the far right (see text for details). Ancestral-state reconstruction is indicated by the boxed figures showing the probabilities of reconstructing West Indian or mainland ancestors as well as the number of Bayesian trees supporting those reconstructions; a probability ≥ 0.95 was considered significant. Ancestor reconstruction was performed following the method of Pagel & Lutzoni (2002) as implemented in the programme Mesquite (Maddison & Maddison, 2004).
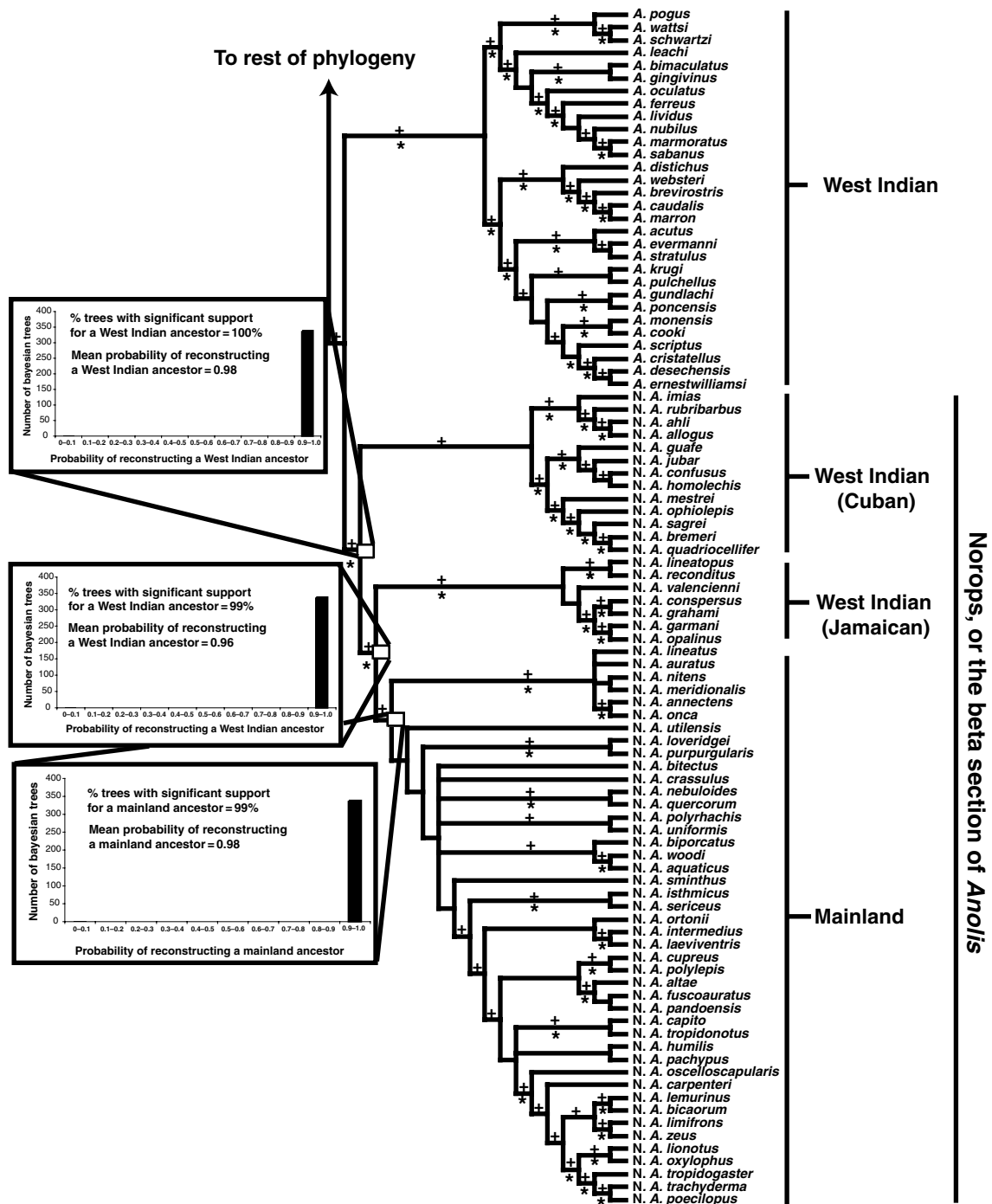
Figure 1 *continued*

number of mainland and island colonization events, we reconstructed the geographic location of an ancestral node not involving *Norops*; the major bifurcation separated a mainland clade and a West Indian clade. This node (Fig. 1) was reconstructed usually as mainland (61% of reconstructions vs. 2% of the trees significantly reconstructing a West Indian location, and the remaining 37% of the trees not significantly favouring either location). Examination of the probability

values across all trees shows that most (80%) trees had a greater than 50% probability that the ancestral geographic location was mainland.

Norops combined-data analysis

Nicholson's (2002) nuclear ITS-1 data set combined with the mtDNA data set presented above for *Norops* taxa (plus

A. frenatus and *A. cristatellus* as outgroups) produced a single data matrix comprising 2416 characters. Unalignable characters were removed (1037–41, 1059–61, 1098–1101, 1279–85, 1312–13, 1362–77, 1467–69*, 1664–99, 1747–1843, 1859–1922, 1932–33, 2236–81, 2297–2350; numbers refer to aligned positions in a data matrix available from the authors, and the star marks the end of the mtDNA data set and the beginning of the ITS-1 data set), leaving 2077 included bp, 1179 of which were parsimony informative. Likelihood-ratio tests for the combined data matrix again favoured the GTR + I + Γ model. The resulting tree (Fig. 2) from the Bayesian analysis is largely consistent with results of the mtDNA-only analyses (results not shown) and differs only by being better resolved than the results for mtDNA alone.

Parsimony analysis yielded a single most-parsimonious tree of length 7901 steps (results not shown). The parsimony tree is consistent with those produced from the parsimony and Bayesian analyses of the mtDNA alone and the Bayesian analysis of the combined data, and it differs primarily in resolution of polytomous branches from the mtDNA parsimony analysis. Most, but not all, nodes are significantly supported by posterior probabilities, and parsimony support is better than in the analysis of mtDNA alone, but several branches remain poorly supported.

Three geographically circumscribed clades [Cuba (Jamaica, and Mainland)] are identical to the mtDNA results. The pattern among these geographic areas was the same among all analyses and was [Cuba (Jamaica, Mainland)]. Both alternative
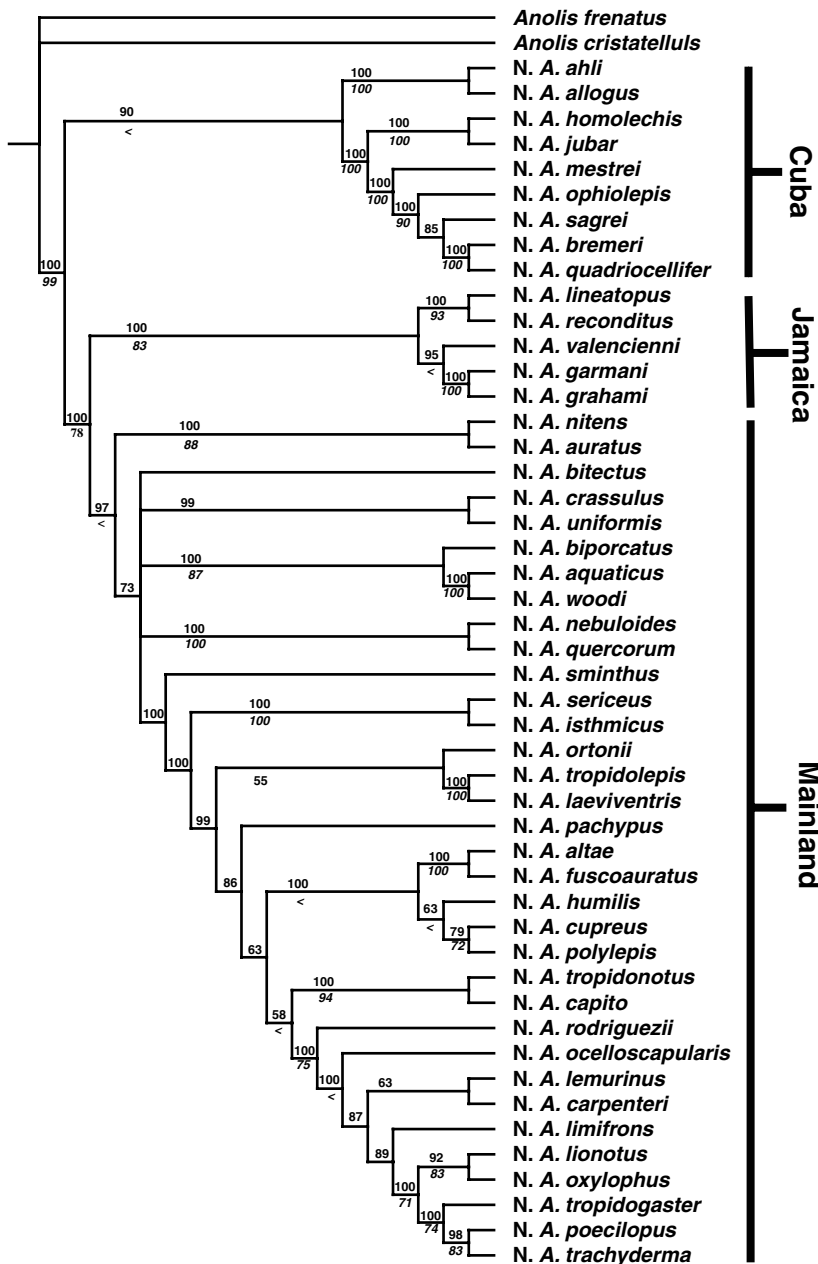

Figure 2 Results from phylogenetic analysis of the combined (mtDNA + nuclear ITS-1 DNA sequences) Norops data set. Some Norops taxa from Fig. 1 do not appear in this tree because ITS-1 data were not available for them (Nicholson, 2002). The tree shown is the 50% majority-rule tree constructed from 901 post-burn-in Bayesian trees. Bayesian posterior probabilities are shown above the nodes. Parsimony support values (bootstrap proportions) are shown below the nodes where Bayesian and parsimony analyses were identical. The general distribution of these groups is indicated to the far right.

hypotheses of relationships among these three clades {alternative 1: [Jamaica (Cuba, Mainland)]; alternative 2: [Mainland (Jamaica, Cuba)]} were rejected by the Shimodaira–Hasegawa test (Diff $-\ln L = 18.60$, $P < 0.02$; Diff $-\ln L = 16.75$, $P < 0.04$, respectively) but not by the Wilcoxon Signed-Ranks tests ($P \gg 0.05$).

DISCUSSION

Our study rejects the hypothesized mainland origin for West Indian Norops in favour of a West Indian origin for mainland Norops. First, Bayesian and parsimony-based analyses for the entire genus *Anolis* reveal that Norops forms a clade nested within a branch that is primarily West Indian. Ancestral-state reconstruction confirms a West Indian ancestor for Norops. Moreover, our phylogenetic analyses within Norops reveal that mainland species form a monophyletic group nested within a group whose other members are West Indian. Alternative scenarios were rejected by the Shimodaira–Hasegawa test, although not by the highly conservative Templeton test.

It seems unlikely that further sampling would alter our finding that mainland Norops are derived from a West Indian ancestor. Our study – which includes more than half of the 365 species of anoles – is by far the most comprehensive phylogenetic analysis of *Anolis*. Our sampling of Caribbean taxa is nearly exhaustive, but the sampling of mainland fauna is less complete. In theory, our conclusions could change if further sampling found Norops taxa branching near the root of the tree or mainland non-Norops taxa grouped with West Indian taxa near the tips of the branches. Both outcomes are extremely unlikely. Our sampling of mainland Norops was comprehensive and included representatives of all major taxonomic groups; moreover, this analysis and others (Etheridge, 1960; Guyer & Savage, 1986; Jackman et al., 1997, 1999; Nicholson, 2002) support monophyly of Norops. Thus, it is unlikely that the additional sampling of Norops would change the phylogenetic position of this clade as a whole. Furthermore, all mainland non-Norops form a single clade, Dactyloa (see Savage & Guyer, 1989, who summarized the morphological work of Etheridge, 1960; Williams, 1976; and Guyer & Savage, 1986). Our molecular data, including 11 of 57 'dactyloid' species, supports monophyly of this group. Because it is consistently diagnosed by morphological and molecular characters, Dactyloa is almost certainly monophyletic, and further sampling for molecular phylogenetic analyses would not alter the phylogenetic position of the group as a whole.

Our results counter the traditional view that mainland areas are rarely successfully colonized by island species. Two colonizations from islands to the mainland are supported for *Anolis*: the Norops clade to Central and South America, and the ancestor of *A. carolinensis* to the south-eastern USA [a third possible case (Fig. 1) which is unlikely, but conceivable, is discussed below]. One explanation for the rarity of island to mainland colonizations is that island faunas inhabit smaller areas with lower species diversity and abundance, and would have difficulty invading the more competitive and diverse mainland communities. However, recent studies show that the West Indian anole radiation has produced an extremely species-rich community with extensive interspecific interactions (Losos, 1994; Roughgarden, 1995). Consequently, West Indian anole species may not be at a disadvantage relative to mainland counterparts; indeed, West Indian species have been successfully introduced to several locations. Cuban Norops *A. sagrei* has been introduced to mainland and other island communities and has thrived in these new areas (Campbell, 2003). Other similar examples include the successful anole invaders of Florida (*Anolis chlorocyanus*, *A. cristatellus*, *A. cybotes*, *A. distichus*, *A. equestris*, and *A. garmani*) (Florida Fish and Wildlife website http://wld.fwc.state.fl.us/critters/exotics/exotics.asp; Bartlett & Bartlett, 1999). Other complex island communities may produce species capable of invading and proliferating in mainland communities, thereby producing a considerable diversity of species as observed in Norops.

Given that island-to-mainland colonization has occurred multiple times in *Anolis*, is there any evidence for mainland-to-island colonization? Such colonization must have occurred early in the evolutionary history of *Anolis*, given that all close relatives of anoles occur in the mainland Neotropics (Schulte et al., 2003). In addition, small Atlantic and Pacific islands near the mainland have been colonized by Norops, as illustrated by *A. agassizi* on Malpelo and *A. townsendi* on Cocos Island, but we have no evidence for mainland Norops colonizing the West Indies. The traditional view (Williams, 1969; Guyer & Savage, 1986) suggests two mainland-to-West Indies colonizations, one resulting in the *roquet* group of the southern Lesser Antilles and another resulting in the rest of the West Indian radiation. Our analysis indicates support for dispersal from the mainland to the southern Lesser Antilles, although the support is not unanimous [2% of the Bayesian trees supported dispersal from the Lesser Antilles to the mainland by the *roquet* group, while other trees did not significantly favour either scenario (Fig. 1)].

Our results indicate that colonization of mainland areas by island forms may have important and previously unappreciated evolutionary outcomes. Although much attention has focused on the ecological and evolutionary diversity of West Indian anoles, mainland anoles are equally diverse: 197 species are known (roughly 45 non-Norops, 152 Norops clade species, and many more probably remain to be discovered), compared with the 154 species currently recognized in the West Indies. In addition, the ecological and morphological diversity of these mainland forms is as great as that exhibited by the West Indian radiations (Irschick et al., 1997; Vitt et al., 2002, 2003a,b). It is startling to realize that much of this mainland diversity (the Norops clade), roughly equal to that in the West Indies, is apparently derived from a single colonization from the West Indies.

Rapid adaptive radiations may occur on continents as well as islands, although the best-known examples are from islands (Cox & Moore, 2000). Many textbook cases of adaptive radiation occur on islands, such as Darwin's finches, Hawaiian silverswords, Rift Lake cichlids (lakes being islands surrounded

by inhospitable environments), and West Indian anoles. A number of explanations have been offered for why adaptive radiation occurs so readily on islands, including ample resources and lack of competitors. However, emerging information from our studies (and references within) suggests that mainland anoles may represent a continental adaptive radiation equally as diverse as the island radiations, although this group is comparatively unstudied. If continental adaptive diversity of anoles is confirmed, adaptive radiation of anoles does not depend upon island settings. Rather, some factor intrinsic to anole biology must hold the key to explaining why this group is prone to adaptive radiation.

Thorough evolutionary studies of mainland anoles comparable with those already conducted on West Indian anoles are needed to explain these patterns and the mechanisms generating them. Phylogenetic information for additional mainland taxa combined with ecologic studies of mainland anoles would permit assessment of whether similar evolutionary patterns indeed exist between West Indian and mainland taxa.

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