Biogeographic Analysis Reveals Ancient Continental Vicariance and Recent Oceanic Dispersal in Amphibians

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Abstract.—Amphibia comprises over 7000 extant species distributed in almost every ecosystem on every continent except Antarctica. Most species also show high specificity for particular habitats, biomes, or climatic niches, seemingly rendering long-distance dispersal unlikely. Indeed, many lineages still seem to show the signature of their Pangaean origin, approximately 300 Ma later. To date, no study has attempted a large-scale historical-biogeographic analysis of the group to understand the distribution of extant lineages. Here, I use an updated chronogram containing 3309 species (~45% of extant diversity) to reconstruct their movement between 12 global ecoregions. I find that Pangaean origin and subsequent Laurasian and Gondwanan fragmentation explain a large proportion of patterns in the distribution of extant species. However, dispersal during the Cenozoic, likely across land bridges or short distances across oceans, has also exerted a strong influence. Finally, there are at least three strongly supported instances of long-distance oceanic dispersal between former Gondwanan landmasses during the Cenozoic. Extinction from intervening areas seems to be a strong factor in shaping present-day distributions. Dispersal and extinction from and between ecoregions are apparently tied to the evolution of extraordinarily adaptive expansion-oriented phenotypes that allow lineages to easily colonize new areas and diversify, or conversely, to extremely specialized phenotypes or heavily relictual climatic niches that result in strong geographic localization and limited diversification. [Amphibians; caecilians; dispersal; frogs; historical biogeography; oceanic dispersal; salamanders; vicariance.]

Amphibians are one of the most diverse and conspicuous radiations of terrestrial vertebrates, with over 7000 described species in most habitats on most continents (AmphibiaWeb 2014). Recent studies have investigated historical patterns of diversification in the group (Roelants et al. 2007; Wiens 2007), as well as the biogeographic distribution of species richness (Wiens et al. 2009; Pyron and Wiens 2013). Similarly, many recent studies have examined the complex biogeographic history of some broadly distributed amphibian subgroups, such as toads (Pramuk et al. 2008), hylid frogs (Smith et al. 2005), ranoid frogs (Bossuyt et al. 2006), dendrobatid frogs (Santos et al. 2009), caecilians (Zhang and Wake 2009b), and salamandrids (Weisrock et al. 2001; Zhang et al. 2008). Other studies examined early biogeographic history, finding evidence for Gondwanan vicariance of major lineages (Biju and Bossuyt 2003; Van Bocxlaer et al. 2006) and a Pangaean origin of early amphibians (Roelants and Bossuyt 2005; San Mauro et al. 2005).

To date, no study has performed a comprehensive evaluation of amphibian biogeography using a large-scale phylogeny sampling all major geographic radiations in all major lineages, with explicit ancestral-area estimations. The biogeographic history of amphibians is of particular interest due to the potentially constrained nature of their movements and dependence on homeostasis in local environments. Amphibians show remarkable stasis in ecological niches, suggesting that intercontinental dispersal will have been historically constrained between similar climatic zones (Wiens 2011a). Recent evidence suggests that transitions between tropical and temperate areas

are reduced due to niche conservatism (Wiens et al. 2006; Pyron and Wiens 2013). However, the diversity of areas, habitats, and climates inhabited by modern amphibians indicates that dispersal must have occurred a number of times (Buckley and Jetz 2007).

One recent analysis (Pyron and Wiens 2013) used a dated tree containing approximately 41% of extant amphibians (2871 species), and estimated ancestral areas using maximum likelihood (ML). However, the purpose of that study was simply to identify the earliest colonization of major ecoregions, not to describe the biogeographic history of amphibians or estimate dispersal and vicariance patterns between ecoregions. Additionally, the effectiveness of traditional ML methods for estimating ancestral areas is limited (Ree et al. 2005), as they make assumptions that do not comport with historical processes in biogeography (e.g., assuming that ranges can shift instantaneously). Newer algorithms explicitly designed for biogeographic reconstruction now allow for processes such as dispersal, extinction, and cladogenesis (DEC) within and among regions, increasing power to estimate ancestral areas (Ree and Smith 2008).

Recent authors have also pointed out that even these DEC models are limited in terms of how biogeographic history can unfold (Matzke 2013b). Specifically, DEC models disallow "founder-event" speciation, where a lineage newly colonizes one area from another (such as an island). Under the DEC models, for range B to be colonized from range A, the range of the lineage must expand (via dispersal) to A + B. Allowing the ancestral area to be A alone with a "jump" colonization to B significantly increases both

numerical model-fit in many cases, and consilience with traditional biogeographic understanding (Matzke 2012). Such processes are relatively common for other terrestrial vertebrates, such as squamates (Raxworthy et al. 2002; Vidal et al. 2008; Townsend et al. 2011). Contrastingly, many studies have assumed that long-distance over-water dispersal was essentially impossible for amphibians due to salt intolerance (Bossuyt and Milinkovitch 2001; Wilkinson et al. 2002; Van Bocxlaer et al. 2006). However, recent evidence increasingly suggests a role for oceanic dispersal in explaining distributional patterns (Vences et al. 2003; de Queiroz 2005), which might be obscured by DEC models.

These issues can be most directly addressed in a large-scale phylogenetic framework using explicit biogeographic analyses. Here, I present such an analysis, based on a dated phylogeny containing 3309 species, approximately 47% of approximately 7000 extant amphibians. With data on the occurrence of these species in 12 major global ecoregions, I use explicit biogeographic methods to estimate ancestral areas across the tree. Given a time scale for both amphibian evolution and the motion of continents, I evaluate support for dispersal versus vicariant explanations for the distribution of major lineages. Finally, I evaluate the potentially under-appreciated role of extinction from intervening areas for explaining intercontinental disjunctions (Chen et al. 2013), and founder-event speciation for explaining oceanic-dispersal patterns (Matzke 2013a).

The ancient origin of amphibians provides a classic null model; a vicariant-origin hypothesis for their biogeographic distribution. Nearly all studies have placed the crown-group age of extant amphibians in the Carboniferous to Permian, between 359 and 252 Ma (San Mauro et al. 2005; Marjanovic and Laurin 2007; Roelants et al. 2007; Pyron 2011). This coincides closely with the age of Pangaea (Lomolino 2010), and strongly suggests that the ancestral lineages of caecilians, salamanders, and frogs were present on a landmass containing both the Laurasian and Gondwanan supercontinents. Thus, continental drift provides a preliminary explanation, against which recent dispersal can be contrasted, using numerical methods. New algorithms incorporating founder-event speciation models further facilitate this (Matzke 2013a).

I find that the early biogeographic history of amphibians (Paleozoic to Mesozoic) is indeed strongly dominated by Pangaean, Laurasian, and Gondwanan vicariance, and that this signature is still present in the distribution of most major extant lineages. However, a secondary wave of Cenozoic dispersal events in many clades, including over-land range expansion, land-bridge colonization, and short-distance oceanic movements, has also exerted a powerful influence on the global distribution of many clades. Furthermore, there are at least three well-supported instances of long-distance oceanic dispersal of major lineages, but founder-event speciation is not a dominant force. The ability of some lineages to disperse and diversify

seems to be related to specialization of both ecological niches (where a restricted niche limits distribution and increases extinction) and phenotypic adaptations (where certain ecomorphologies are more or less suited to dispersal and colonization). Both ecological and evolutionary processes affecting speciation, extinction, and dispersal have had a strong impact over long periods of time on the diversity and distribution of amphibians.

MATERIALS AND METHODS

Phylogeny

The phylogeny used here is an update of a previous tree and set of divergence times (Pyron and Wiens 2011; 2013), updated to incorporate additional recent sequence data. Most families, subfamilies, and genera are represented, notable exceptions being the recently described Chikilidae (Kamei et al. 2012) and Odontobatrachidae (Barej et al. 2014). Following the protocols detailed in recent supermatrix-based studies (Pyron 2011, 2013; Pyron and Wiens 2011; I searched GenBank by family (stopping in February 2013), adding in sequence data for nine nuclear genes: C–X–C chemokine receptor type 4 (CXCR4), histone 3a (H3A), sodium–calcium exchanger (NCX1), pro-opiomelanocortin (POMC), recombination-activating gene 1 (RAG1), rhodopsin (RHOD), seventh-in-absentia (SIA), solute-carrier family 8 (SLC8A3), and tyrosinase (TYR), and three mitochondrial genes: cytochrome b (cyt-b), and the large and small subunits of the mitochondrial ribosome genes (12S/16S; omitting the adjacent tRNAs as they were difficult to align and represented only a small amount of data).

Unlike previous studies (Wiens et al. 2005; Pyron and Wiens 2011), I did not attempt to partition 12S/16S into stems and loops, due to the difficulty of identifying secondary structures conserved over the time-scales involved. The final matrix contained 3309 taxa (compared with 2871 previously) plus the outgroup *Homo sapiens*, measuring 12,809 bp with an average of 20% completeness. Note that this completeness is a relative figure; each taxon is represented on average by 2618 bp (range 249–11,413 bp) from an average of four genes. Amphibians have shown strong concordance between analyses of many nuclear genes for representative taxa to examine higher level relationships (Frost et al. 2006; Roelants et al. 2007), species-level examination of relationships within families and genera (Faivovich et al. 2005; Grant et al. 2006), and supermatrix approaches such as this one combining available data (Pyron and Wiens 2011). This consistency suggests that the approach used here should yield accurate estimates of topology and branch lengths, even if some taxa are represented by only a small amount of data (Wiens and Morrill 2011). Indeed, the results obtained here are overall very similar to previous studies (see below). All data are available from http://www.sysbio.oxfordjournals.org/, and DataDryad repository http://dx.doi.org/10.5061/dryad.jm453.

I performed phylogenetic analyses of the 12-gene concatenated matrix using Maximum Likelihood (ML). I assessed node support using the nonparametric Shimodaira–Hasegawa-Like (SHL) implementation of the approximate likelihood-ratio test (aLRT; Anisimova and Gascuel 2006). The SHL approach has at least two major advantages over nonparametric bootstrapping for large ML trees: (i) values are robust to model violations and have the same properties as bootstrap proportions for all but the shortest branches (Anisimova and Gascuel 2006; Anisimova et al. 2011; Pyron et al. 2011) and (ii) values for short branches may be more accurate than bootstrap proportions, as support is evaluated based on whole-alignment likelihoods, rather than the frequency of resampled characters (Anisimova and Gascuel 2006; Guindon et al. 2010; Simmons and Norton 2014). Additionally, the SHL approach is orders of magnitude faster than traditional bootstrapping (Anisimova and Gascuel 2006; Guindon et al. 2010; Anisimova et al. 2011), and it appears to be similarly robust to matrices with extensive missing data (Pyron et al. 2011; 2013). As in previous studies, I take a conservative view, considering SHL values of 85 or greater (i.e., a 15% chance that a branch is "incorrect") as strong support (Guindon et al. 2010; Anisimova et al. 2011; Pyron et al. 2011).

Estimation of SHL values involved a two-stage strategy. I first performed initial ML tree inference using the program RAxML-Light v1.0.7 (Stamatakis et al. 2012), a modification of the original RAxML algorithm (Stamatakis 2006). This program uses the GTRCAT algorithm for all genes and partitions, a high-speed approximation of the GTR+Γ model (general time-reversible with gamma distribution of rate heterogeneity among sites). To generate an initial ML estimate for final optimization and support estimation, I performed 101 ML searches from 101 randomized parsimony starting trees generated under the default parsimony model in RAxMLv7.2.8. This number is likely to be sufficient when data sets contain many characters that have strong phylogenetic signal (Stamatakis A., personal communication). The data analyzed here have formed the core of essentially all previous molecular studies of amphibian phylogeny; that they possess strong phylogenetic signal is an assumption, but does not appear to be unwarranted. The concordance between the results here and previous topologies (e.g., Roelants et al. 2007; Pyron and Wiens 2011) suggests that the tree was not strongly impacted by searches stuck on local optima, and that it should be a good approximation of the ML tree.

I then performed a final topology optimization and assessed support by passing the best ML estimate of the phylogeny (based on GTRCAT) from RAxML-Light to RAxMLv7.2.8, which does an additional search (using the GTRGAMMA model) to produce a nearest-neighbor interchange (NNI)-optimized estimate of the ML tree. This optimization is needed to calculate the SHL version of the aLRT for estimating support values (Anisimova and Gascuel 2006), which are then calculated by RAxML. This strategy approximates a test of the null hypothesis that the branch length subtending each node equals 0 (i.e., that the node cannot be resolved) with a test of the more general null hypothesis that "the branch is incorrect" relative to the four next suboptimal arrangements of that node relative to the NNI-optimal arrangement (Anisimova and Gascuel 2006). Based on initial analyses, generating sufficient ML bootstrap replicates for a tree of this size proved computationally intractable, so I rely on SHL values alone to assess support. These analyses were performed on a 360-core SGI ICE supercomputing system at the High-Performance Computing Center at the City University of New York. The final analysis was completed in approximately 17 days of computer time using approximately 102 nodes.

Divergence Times

I estimated divergence times for this tree topology using a C++ implementation of r8s (Sanderson 2002) called "treePL" (Smith and O'Meara 2012). This algorithm estimates evolutionary rates and divergence dates on a tree given a set of fossil constraints and a smoothing factor determining the amount of among-branch rate heterogeneity. Other approaches such as BEAST or MrBayes are computationally intractable for data sets of this size. As in previous studies (Pyron and Wiens 2013), analyses were run with fixed-age constraints (secondary calibrations) on the nodes listed below, given the computational difficulties of dating trees of this size using minimum and maximum ages (Britton et al. 2007), and the existence of robust divergence-time estimates for major amphibian lineages (Wiens 2011b). This ensures that age-estimates for the large-scale tree presented here fit broadly within existing fossil-calibrated temporal frameworks for amphibian evolution.

This strategy incorporates a strong constraint on the root (Sanderson 2002; Pyron 2010) and some other nodes, while estimating the rest. Based on previous recommendations (Benton and Donoghue 2007; Donoghue and Benton 2007), I constrained the Amniote–Amphibia divergence (the root of the tree) at 330.4 Ma. This is based on the oldest known fossils of Lepospondyli, the putative sister-group to Lissamphibia (Carroll and Chorn 1995; Vallin and Laurin 2004; Pyron 2010; 2011). Slightly older ages (up to 350.1 Ma) are possible based on the oldest tetrapodomorphs (Carroll 2009), but this represents a conservative minimum (see section below on error and precision). The fossil age-estimate for this clade is broadly consistent with several recent estimates based on molecular clock analyses (Zhang et al. 2005; Alfaro et al. 2009; Pyron 2010; 2011).

I determined the optimal smoothing factor empirically using cross-validation (Sanderson 2002), with the root age fixed (see below) due to computational constraints. I tested six values for the smoothing parameter (0.01, 0.1, 1, 10, 100, and 1000), graduated by orders of magnitude across a reasonable range given empirical

data sets (Sanderson 2002). The cross-validation analysis yielded an optimal smoothing-parameter value of 0.1. To estimate the ages of internal nodes of interest, I then fixed a series of nodes above the family level, using dates from a recent study of the origins of the major lissamphibian groups (Wiens 2011b).

I identified nodes that spanned the temporal and taxonomic breadth of the higher level structure of the tree, but that were not too close together (i.e., I did not constrain all possible nodes, nor any direct ancestor–descendant pairs). In some cases, the shape of the trees necessitated constraining the stem-group age of the most recent common ancestor (MRCA) of some families in order to enforce the necessary constraint. However, all crown-group ages and most stem-group ages were freely estimated for the nodes of interest (i.e., families). As in Pyron and Wiens (2013), I fixed the following internal nodes using estimated ages from Wiens (2011b):

1. Cryptobranchoidea

   The MRCA of Hynobiidae and Cryptobranchidae: 164.50 Ma.

2. Sirenoidea

   The MRCA of Sirenidae and the noncryptobranchoid caudates: 199.59 Ma.

3. Salamandroidea

   The MRCA of Salamandridae and Ambystomatidae: 167.22 Ma.

4. Plethodontoidea

   The MRCA of Rhyacotritonidae, Amphiumidae, and Plethodontidae: 133.03 Ma.

5. Leiopelmatoidea

   The MRCA of Ascaphidae and Leiopelmatidae: 202.04 Ma.

6. Pipoidea

   The MRCA of Pipidae and Rhinophrynidae: 190.42 Ma.

7. Discoglossoidea

   The MRCA of Discoglossidae, Alytidae, and Bombinatoridae: 160.07 Ma.

8. Pelobatoidea

   The MRCA of Scaphiopodidae, Pelodytidae, Pelobatidae, and Megophryidae: 155.73 Ma.

9. Ranoidea

   The MRCA of Ranidae and Microhylidae (including numerous other families): 111.90 Ma.

10. Hyloidea

    The MRCA of Bufonidae and Hylidae (including numerous other families): 73.53 Ma.

11. Gymnophiona

    The MRCA of extant caecilians: 108.65 Ma.

This time scale is very similar to the stratigraphic and paleontological framework for amphibians described in several recent reviews of lissamphibian origins (Marjanovic and Laurin 2007; Roelants et al. 2007; Pyron 2011). Other studies have looked at broad-scale age-estimates in amphibians, and some have found older ages for major groups such as caecilians (Zhang and Wake 2009a, 2009b; San Mauro 2010; Pyron 2011). However, these studies generally lacked wide taxonomic sampling or were based primarily on fast-evolving mitochondrial genes, so those ages were not used here.

Geographic Areas

To reconstruct the timing of colonization and length of occupancy of the various temperate and tropical ecoregions, I used range maps from the IUCN Global Amphibian Assessment (http://www.iucnredlist.org/initiatives/amphibians) to assign species to one or more regions in a global set of 12 biogeographic provinces (data given in Dryad repository: http://dx.doi.org/10.5061/dryad.jm453). Maps were available for 6576 species (~87% of extant species), including the 3309 in the tree. The 12 regions follow from commonly used definitions in herpetology and biogeography (Duellman 1999; Schultz 2005; Vitt and Caldwell 2009; Lomolino 2010). Although some ambiguity about the limits of these regions exists, they correspond closely with both geography and species distributions, and represent major areas of amphibian diversity and endemism (Duellman 1999). They include all major plates harboring endemic amphibian faunas (e.g., South Asia and South America), as well as major climatic subdivisions within those plates (e.g., Temperate South America and Eastern Palearctic). The areas are:

Tropical South America.—Tropical regions of South America, ranging from the Colombia-Panama border to the latitudinal level of Buenos Aires, excluding the high-elevation southern Altiplano (see below under Temperate South America). I defined the boundary between Middle and South America as the Panama/Colombia border.

Tropical Middle America.—Including Central America, Baja California Sur, and tropical regions of Mexico, including Sonora on the Pacific coast, and Tamaulipas on the Gulf coast.

Temperate South America.—Southern South America, including Patagonia, the Pampas of Argentina and Uruguay, and the high-elevation Altiplano extending into Bolivia and southeastern Peru.

West Indies.—The Caribbean Islands, including the Antilles and the Bahamas. Does not include coastal

islands such as Trinidad, Bonaire, Curacao, Aruba, or Cozumel.

Nearctic.—Temperate North America, including the continental United States, Canada, the central Mexican Plateau, and northern Baja California.

Afrotropical.—Sub-Saharan Africa and the southern Arabian Peninsula (i.e., Yemen and southern Oman).

Western Palearctic.—Europe (i.e., west of the Caspian Sea), North Africa, the northern portion of the Arabian Peninsula, and western Iran (Zagros mountains).

Eastern Palearctic.—Temperate Asia east of the Caspian Sea, excluding the tropical provinces of southern China (Yunnan, Guangxi, southern Sichuan, Guangdong, Hainan, Hong Kong, Macau, and Fujian) and including the major islands of Japan (but not the southern Ryukyu Islands). Includes Afghanistan and southeastern Iran.

Madagascar.—Including Madagascar and adjacent islands (i.e., Mauritius, the Seychelles, and the Comoros).

Australasia.—Includes Australia, New Zealand, New Guinea, and islands to the east (e.g., Solomon Islands, Fiji, Vanuatu, and New Caledonia). Includes the Maluku Islands. Separated from *Southeast Asia* by Weber's line (Lomolino 2010).

Southeast Asia.—Tropical East Asia, from Myanmar to the Lesser Sunda islands, including southeast China (Yunnan, Guangxi, Guangdong, Hainan, Hong Kong, Macau, and Fujian provinces), Taiwan, the southern Ryukyu Islands, and the Philippines. Separated from *Australasia* by Weber's line (Vitt and Caldwell 2009).

South Asia.—The Indian subcontinent, from Pakistan to Bangladesh, including Sri Lanka, Nepal, and Bhutan.

I first used these data to test two basic hypotheses regarding the biogeographic distribution of diversity through space and time, which have not necessarily received much attention in the past. First, I determine whether the age of clades is related to the number of areas they occupy. As every clade must have originated in a single area, a nonsignificant result would indicate that older clades are not more likely to have expanded to more areas. Thus, occupancy of more areas must represent time-independent vicariance or dispersal patterns (e.g., a single recent wave). In contrast, a significant relationship would indicate that older clades are more likely to occupy more areas, either due to increased vicariance over time (as expected for clades that originated on fragmenting landmasses) or greater dispersal over time. Discrimination between these will be possible with an estimate of the relative importance of vicariance versus dispersal, and it is possible that both explanations could contribute to a significant relationship.

Second, I test for a positive relationship between the number of areas occupied, and the number of species

in clades. A nonsignificant result would indicate that occupying more biogeographic areas is not a predictor of higher species richness; that a clade with 1000 species is just as likely to occupy 1 or 10 ecoregions. In contrast, a significant result would suggest that occupying more global ecoregions is a strong predictor of species richness. This could be due either to a greater ecological carrying capacity for the clade as a whole (e.g., if 10 areas can each support 100 species), or if colonizing new areas increases net diversification rates (e.g., due to increased ecological opportunity). These are also not mutually exclusive, and it would be difficult to discriminate between them based on the analyses presented here.

I use the 66 family-level clades present in the tree as defined in previous analyses (Pyron and Wiens 2011), with crown-group age-estimates taken from the chronogram, and the number of species and areas occupied taken from the 6576 species with range information described above. Note that families are a relatively arbitrary taxonomic unit, and biases in how families are described could theoretically affect analyses such as these (Rabosky et al. 2012). For instance, families could have been defined endemic to single ecoregions (as is the case for some Malagasy taxa such as Mantellidae), erasing the relevant signal. However, most families have not been defined based on biogeographic criteria, and such a definition would induce a Type II, rather than Type I error. Thus, I regard families as an appropriate preliminary scale at which to test these hypotheses. These tests were conducted in R (R Core Development Team 2014).

Biogeographic Analyses

Numerous analytical methods for historical biogeography exist, accounting for processes such as DEC (Ronquist 1994; Ree et al. 2005; Landis et al. 2013). All of these models contain conceptually similar elements, and have been unified in the R package "BioGeoBEARS" (Matzke 2013b). This provides a flexible framework for comparing alternative models in a mathematically explicit context to explore alternative biogeographic scenarios. I concentrate primarily on a comparison between the DEC model (Ree and Smith 2008) and the DECj model, incorporating founder-event speciation allowing dispersal without range expansion (Matzke 2012).

The primary limitation in statistical analysis of ancestral areas is rarely the size of the tree, but the number of areas. The 12 areas coded here yield 2^{12} possible combinations of presence/absence in each area (4096 total), which produces a transition matrix of 4096×4096 entries (16,777,216 total), which has to be exponentiated across each branch in the tree for ML optimization. This is infeasible with current hardware and matrix-handling algorithms. However, tractable analyses can be performed by reducing both the number of total areas and the number of areas that can be

occupied simultaneously by lineages. I addressed this in four ways.

First, I performed a "traditional," nonbiogeographic inference of ancestral states using ML in the program Mesquite v2.75 (Maddison and Maddison 2011). This strategy uses the Mk1 model (a single transition rate between all states), assuming lineages inhabit only one area at a time. This was a historically common way of estimating ancestral areas, to which the explicitly biogeographic models were developed in response (Ree et al. 2005). Amphibians were previously analyzed using this approach to infer the earliest colonization of the 12 ecoregions (Pyron and Wiens 2013). As the ML methods do not accommodate multiple states, I reduced the tree to the 3126 species endemic to a single ecoregion. I used a standard likelihood-threshold of 2 units to select between alternative estimations. Note that this analysis is almost entirely exploratory, and discussed below only in reference to the explicitly biogeographic DEC/DECj analyses. The only advantage offered by this strategy is the potential to identify separate invasions of areas merged in subsequent analyses (e.g., Eastern and Western Palearctic).

Second, caecilians only occur in 6 of the 12 areas listed above (Tropical South America, South Asia, Southeast Asia, Africa, Tropical Middle America, and Madagascar). Thus, I extracted the subtree for caecilians (55 species) and ran the DEC/DECj models for that subtree separately, using those six areas. The maximum range size was set to 2, the maximum number of areas occupied by any of the terminal species. In reality, only one species in the analysis (*Oscaecilia microcephala*) occurs in two areas: Tropical South America and Tropical Middle America; all others are endemic to single ecoregions.

Third, this strategy was repeated with salamanders, for a subtree containing 469 species. Salamanders also only occur in 6 of the 12 ecoregions: Nearctic, Eastern Palearctic, Western Palearctic, Southeast Asia, Tropical Middle America, and Tropical South America. As with caecilians, the majority of species are endemic to single ecoregions; only a few occur in 2, and the maximum number of areas was thus set to 2.

Fourth, I analyzed all amphibians concurrently. As frogs occur in all 12 ecoregions, reducing the tree for a frogs-only analysis would offer little benefit over a full-tree analysis with fewer areas. I performed one for comparison (2785 species; see below), but rely primarily on the whole-tree analysis in the results. Preliminary analyses indicated that no more than eight areas were tractable for ancestral estimations, necessitating the elimination of 4. This requires difficult decisions about merging areas, as the degree of apparent long-term endemism indicates that all 12 ecoregions are distinct biogeographic provinces with unique histories (Duellman 1999).

Thus, I merged the Eastern and Western Palearctic into "Palearctic," and Tropical Middle America, Temperate South America, West Indies, and Tropical South America into "Neotropics." As with caecilians and salamanders,

the majority of species occur in one area, with a small number in 2. Four primarily tropical species occupied a third area (Palearctic). However, ML optimizations failed when the number of areas was set to 3, so these species were restricted to their two main tropical areas (see online Appendix S3), and the maximum number of areas was set to 2. This produced a tractable state space for ML searches.

I then reconstructed ancestral states using the optimx routine in BioGeoBEARS, under both the DEC and DECj models for the three strategies described above. I compared the fit of the two models with respect to the addition of the "j" parameter using a standard likelihood-ratio test to determine which provided a better fit to the data. These were run on the SHL-optimized, dated phylogeny described above. Note that these estimations are the ancestral state probabilities under the globally optimal model, not the locally optimum estimations, or the single best reconstruction of joint history. It is possible to reconstruct character histories in alternative ways, such as the single best joint reconstruction, but this may actually have a very low probability.

Another major consideration for biogeographic inferences is the specification of connectivity matrices and area availability through time. A relatively well-established timeline exists for the emergence of the ecoregions specified here (Lomolino 2010), and BioGeoBEARS (and other programs) allow for parameters such as dispersal multipliers (unequal rates of dispersal between areas, specified a priori), time-stratified dispersal (different dispersal rates through time), and areas allowed (dropout of areas through time). These may be important in scenarios such as island emergence, where a landmass did not exist prior to a specific point in time. However, all of the ecoregions here existed more or less continuously through the history of amphibians (at least in terms of exposed land area, but not necessarily climate), differing primarily in how they were positioned or accreted.

No current methods can merge areas backwards in time, as this requires a more complex partitioning of likelihoods at different time-slices. It would be possible in this case to "erase" areas as they accrete with other areas, such as specifying that Madagascar does not exist prior to 90 Ma, at which point it is simply part of "South Asia" as it existed more than 90 Ma (i.e., India + Madagascar). This would also involve respecifying dispersal multipliers.

There are two problems with this. First, any such modifications run the risk of imposing a specific historical-biogeographic scenario a priori (e.g., if the date is actually 100 Ma, and this difference is enough to alter the results), which would run counter to my goal of assessing alternative dispersal versus vicariant explanations for extant taxa. Second, removing areas backwards in time is not the same as merging them, and is not demonstrably superior in a biological sense to retaining the areas. If a landmass exists as AB from 100 to 50 Ma, then splits into A and B, disallowing "A"

prior to 50 Ma and interpreting "B" as "A + B" is not obviously superior to allowing both "A" and "B" prior to 50 Ma, and interpreting either as "A + B." Thus, I do not impose additional constraints on dispersal or area availability.

Instead, a well-defined temporal paleogeographic framework is needed to interpret the hypotheses I wish to test (Springer et al. 2011). I attempt to frame this as a comparison of dispersal versus vicariance as an explanation for the major distributional patterns of extant amphibians, and DEC versus DECj models as an evaluation of the importance of oceanic dispersal. Thusly, I attempt to interpret these inferences in an explicit hypothesis-testing framework (the null hypothesis being ancient vicariance), rather than a purely narrative approach to the geohistory of the group (Crisp et al. 2011). A complementary part of this analysis is a description of the biogeographic history of amphibians, so as to cast inferred events (e.g., recent dispersals) in an explicit hypothesis-testing framework, to highlight their importance for future studies.

Although some studies attempt to infer paleogeographic scenarios (e.g., the existence of land bridges) from phylogenetic inferences of biogeographic history (Noonan and Chippindale 2006; Evans et al. 2008), I prefer to treat paleogeography as essentially fixed, given the endemism present in the ecoregions as defined, and the large amount of potential error inherent in phylogenetic inference and divergence-time estimation versus the geological record. This allows for a more direct test of dispersal versus vicariance as explanations for present-day distributions. For the 12 ecoregions as defined above, we can interpret the biogeographic history of amphibians within the following paleogeographic framework (Sanmartin et al. 2001; Lomolino 2010):

1. 0–50 Ma: From the Eocene to the present, most landmasses have occupied their current position. From approximately 20 to 3 Ma, Holarctic (Palearctic + Nearctic) connectivity was enhanced by the Beringian land bridge as a major dispersal route.

2. 90 to 50 Ma: From the Late Cretaceous to the Eocene (across the K–T boundary), India and Madgascar are separated as India rafts toward Asia. Australasia (Australia + New Guinea) separates from Antarctica. Overlapping these previous two periods from approximately 70 to 20 Ma, the de Geer and Thulean land bridges are the primary Holarctic connection.

3. 120 to 90 Ma: From the Early to Late Cretaceous, West Gondwana (South America + Afrotropics) begins to separate, as do India and Madagascar, as both masses begin to drift away from East Gondwana (including Australasia [Australia + New Guinea]).

4. 170 to 120 Ma: From the Middle Jurassic to Early Cretaceous, Gondwanaland (South America, Afrotropics, Madagascar, India, Australia, and Antarctica, etc.) begins to break up, as does Laurasia (Holarctic [Nearctic + Palearctic]). Laurasia and Gondwanaland are mostly separated after the breakup of Pangaea. Most global landmasses are connected prior this point.

5. 300 to 170 Ma: From the Late Carboniferous to the Middle Jurassic, which encompasses the likely origin of amphibians (Pyron 2011), most global landmasses are accreted in the supercontinent Pangaea, comprising Laurasia + Gondwanaland. Lineages dating to this period can thus be considered to have occupied any or all present-day landmasses.

Error and the Illusion of Precision

Biogeographic hypothesis testing is heavily dependent on estimated ages and relationships (Crisp et al. 2011). A framework for accepting and rejecting hypotheses of dispersal versus vicariance is thus needed. As noted above, I begin with the null hypothesis that the present-day distribution of amphibians can be explained by vicariance, given their Pangaean origin. Typically, biogeographic hypotheses such as these are tested by comparing the confidence interval for the estimated date of a biogeographic shift to the estimated age of the geographic event in question. Such confidence intervals are not available for this tree. Even if they were, time scales for amphibians vary enough among studies (see San Mauro et al. 2005; Roelants et al. 2007; Pyron 2011) to influence acceptance or rejection of most biogeographic hypotheses, beyond whatever precision might be implied by the 95% confidence intervals estimated in any given study. Thus, it will be important to evaluate each case individually for temporal and paleogeographic variability. For important nodes, I report the range of dates found across previous studies when assessing alternative scenarios.

Finally, computational limits prevent evaluation of alternative histories across the distribution of ML trees. Error in biogeographic ancestral-area estimations is assessed using the estimates of marginal probability for each state at the internal nodes of the SHL-optimized tree described above. As the state space of potential alternative ranges is typically very large, I will consider a single history with more than 50% marginal probability to be "strongly supported," as even a much lower probability (e.g., ~20%) will still occupy a large plurality of the likelihood. As noted above, these estimations must be interpreted in the context of the temporal paleogeographic framework outlined above. For instance, if a node dated to 150 Ma is estimated to have occurred in Tropical South America, this must be understood as representing "Gondwana," that is, the landmass containing South America at the time. Little

further precision will be possible unless additional fossil evidence is available, which I discuss when available.

RESULTS

Diversity and Distributions

The phylogeny and chronogram are overall very similar to previous studies (Pyron and Wiens 2011; 2013), differing primarily by the inclusion of 528 additional species for increased resolution of biogeographic patterns, and correcting a few instances of misidentified sequences noted by some recent authors (Frost 2011; Blotto et al. 2013). The phylogenies and matrix are included in DataDryad repository: http://dx.doi.org/10.5061/dryad.jm453.

There is a significant positive relationship between the number of areas occupied and the diversity of clades (Spearman's correlation $s = 0.69$, $P < 0.00001$; Fig. 1a). Thus, more diverse clades necessarily inhabit a larger number of global ecoregions; no clades are hyperdiverse in a single ecoregion, and no clades inhabiting many ecoregions are depauperate. No clade inhabiting a single ecoregion has more than 174 species (Mantellidae in Madagascar), whereas no clade inhabiting four or more ecoregions has fewer than 120 species (Caeciliidae). This suggests that there is a strong interplay between a broader biogeographic distribution and increased total diversity. Future studies could test whether or not this is due to an increased rate of speciation related to the colonization of new areas and increased niche breadths (e.g., Goldberg et al. 2011; Etienne and Haegeman 2012).

There is also a significant relationship between clade age and the number of areas occupied ($s = 0.43$, $P = 0.0005$; Fig. 1b). This relationship is not as strong, as older lineages appear only slightly more likely to occupy more areas. A small group of clades (Bufonidae, Hylidae, Microhylidae, and Ranidae) represents apparent outliers, being of intermediate age and occupying more than eight ecoregions each. These may be related to extraordinarily adaptive expansion-oriented phenotypes (see below). The weak but significant relationship here can preliminarily be interpreted as indicating the action of vicariance over time in older clades occupying landmasses that subsequently fragmented. This can be tested further by examining the biogeographic history of these clades.

Caecilians

For the caecilian subtree, the addition of the "j" parameter for founder-event speciation significantly increases the likelihood of the traditional model (DEC ln $L = -63.21$, DECj ln $L = -60.48$, $P = 0.019$; Table 1), with a large proportion on the AIC weight (0.85). The root age of this tree is constrained at 108.65 Ma, similar to several previous studies that yielded a range of 125 to 98 Ma, though significantly younger than some other estimates ranging from 228 to 213 Ma
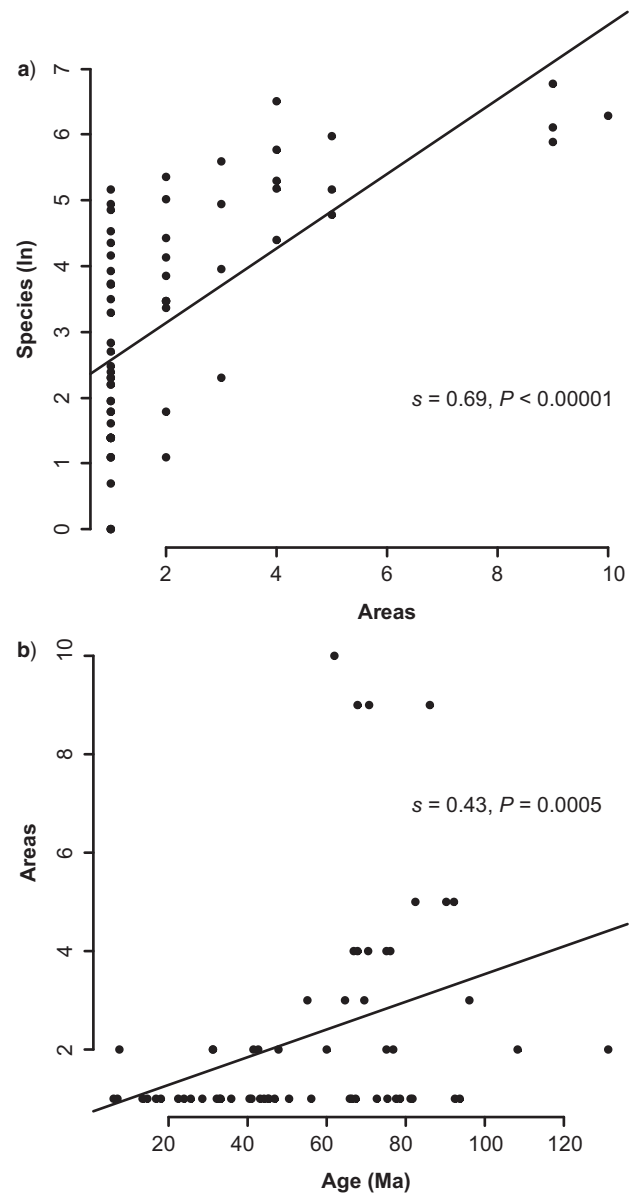

FIGURE 1. Relationship between a) number of areas occupied by a clade and the number of species in that clade, and b) age of a clade and the number of areas occupied by that clade. Significant relationships for both indicate that older clades occupy more areas, which leads to the greater accumulation of diversity over time.

(see review in Pyron 2011). During this period (120 to 90 Ma), South America + Afrotropics (West Gondwana) and India + Madagascar are beginning to separate, but both are relatively proximate to each other and to East Gondwana (Lomolino 2010). Caecilians are known from the Jurassic in the Nearctic (Arizona) and Western Palearctic (Morocco), and from Tropical South America (Bolivia and Brazil) and Western Palearctic (North Sudan) in the Cretaceous (Estes 1981; Jenkins and Walsh 1993; Evans et al. 1996; Evans and Sigogneau-Russell 2001; Gayet et al. 2001). Both the younger age recovered here and other older ages are congruent

TABLE 1. Comparison of DEC and DECj models for caecilians, salamanders, and amphibians as a whole

Model	Ln L	Parameters	d	e	J
Caecilians	$P=0.02$				
DEC	−63.2	2	0.000668	0.000642	0.000000
DECj	−60.5	3	0.000711	0.000526	0.000695
Salamanders	$P=0.04$				
DEC	−216.4	2	0.000687	0.000687	0.000000
DECj	−214.3	3	0.001005	0.000000	0.000488
Frogs	$P>0.05$				
DEC	−1479.8	2	0.000761	0.000761	0.000000
DECj	−1481.8	3	0.000809	0.000809	0.000818
Amphibians	$P>0.05$				
DEC	−1721.2	2	0.000753	0.000753	0.000000
DECj	−1804.3	3	0.000996	0.000982	0.000997

Notes: Parameters are d (dispersal), e (extinction), and j (founder-event speciation). The c parameter (cladogenesis) is integrated out, as the model assumes a fixed tree with all speciation events included, and is thus reconstructing dispersals, extinctions, and jumps across the tree.

with a Pangaean origin and Gondwanan vicariance-diversification scenario (i.e., the null hypothesis).

The estimates from the DECj model corroborate this strongly (Fig. 2). Support for all states and transitions is relatively high (online Appendix S1). The ancestor of extant caecilians is estimated in Tropical South America + South Asia, suggesting a Gondwanan origin by vicariant fragmentation. The origin of a Southeast Asian clade of icthyophiids in the Oligocene is most consistent with overland dispersal after the collision of India with Asia in the Eocene (Hedges et al. 1993). The remaining major events are dated here between approximately 100 and 60 Ma. The most likely (globally optimal marginal estimations) estimates suggest a Gondwanan cradle of diversification for the remaining caecilians in the Afrotropics, Tropical South America, Madagascar, and South Asia. There is a potential secondary recolonization of Afrotropics from Tropical Middle America in the dermophiids after the breakup of West Gondwana. The last major event is the split between the Indian and Seychellois indotyphlids.

An older time-scale for caecilian evolution, as reported in some previous studies (Roelants et al. 2007), has been used to support a Gondwanan vicariance for the majority of these events (Wilkinson et al. 2002; Zhang and Wake 2009b). However, a short-distance trans-Atlantic rafting scenario during the Late Cretaceous, when Africa and South America were still nearby, is implied by these results in Dermophiidae (Dermophis, Geotrypetes, Gymnopis, and Schistometopum). Such an event has also been supported in various terrestrial vertebrates in the Mesozoic and Cenozoic (Flynn and Wyss 1998; Carranza and Arnold 2003; Vidal et al. 2008; Gamble et al. 2011). However, an older date for this group would support a vicariant origin with extinction from intervening areas (e.g., Kamei et al. 2012). More directly, the divergence between the Seychellois and Indian indotyphlids (~62 Ma) is congruent with the

rifting of the Seychelles from India approximately 62 Ma (Collier et al. 2008).

Salamanders

As with the caecilians, the DECj model is significantly more likely than the DEC model ($\ln L = −214.3$ vs. $−216.4$, $P = 0.04$). Stem-group batrachians and salamanders are known from Jurassic deposits in the Nearctic and Palearctic (Anderson et al. 2008; Gao and Shubin 2012), again consistent with a Pangaean origin of amphibians, and a primarily vicariant biogeographic history. Visual representation of the complex bigeographic history for a clade this size is difficult (online Appendix S2), but several major patterns consistent with this interpretation are apparent. I will describe these results briefly here; the full history is given in online Appendices S2–S5.

In contrast to the Gondwanan Cradle evident in the caecilians, the MRCA of salamanders is reconstructed in a Laurasian Cradle (Nearctic + Eastern Palearctic) approximately 209 Ma, again reinforcing a Pangaean origin of early amphibian lineages. Stem-group salamanders are known from the Eastern Palearctic and Nearctic in the Jurassic (Estes 1981; Wang and Evans 2006). In the cryptobranchoids, the hynobiids show a long history in the Eastern Palearctic, with a recent (~16 to 12 Ma), presumably overland dispersal (range expansion) into Southeast Asia. In contrast, the divergence between the Palearctic and Nearctic cryptobranchids (Andrias and Cryptobranchus) dates to approximately 43 Ma, similar to previous studies (Zhang and Wake 2009a; Wiens 2011b). Fossil cryptobranchids from the Paleocene of Eastern Palearctic (Mongolia) and the Nearctic (western Canada) suggest a Beringian dispersal (Vasilyan et al. 2013), with Miocene lineages in the Germany and Ukraine potentially representing a separate invasion of the Western Palearctic with subsequent extinction (Estes 1981).

Sirenoidea (all salamanders excluding cryptobranchoids) are estimated solely in the Nearctic (part of a fragmenting Pangaea), with the sirenids (endemic to the Nearctic) forming the sister lineage of a large number of Holarctic clades. The dicamptodontids are Nearctic, whereas the ambystomatids are primarily Nearctic with a recent (presumably overland) expansion into the margins of Tropical Middle America, approximately 10 Ma. Divergence between the Nearctic dicamptodontid + ambystomatid clade and the primarily Palearctic salamandrids (Salamandroidea) is also consistent with a vicariant origin while Laurasia was fragmenting. The salamandrids show movement between the Western and Eastern Palearctic and the Eastern Palearctic and Southeast Asia frequently throughout the Cenozoic, presumably as a result of overland dispersal (range expansion). One apparent recolonization of the Nearctic (Notophthalmus and Taricha) is reconstructed between 66 and 37 Ma. A trans-Atlantic land-bridge dispersal seems the most likely scenario based on this time-scale, and the presence of
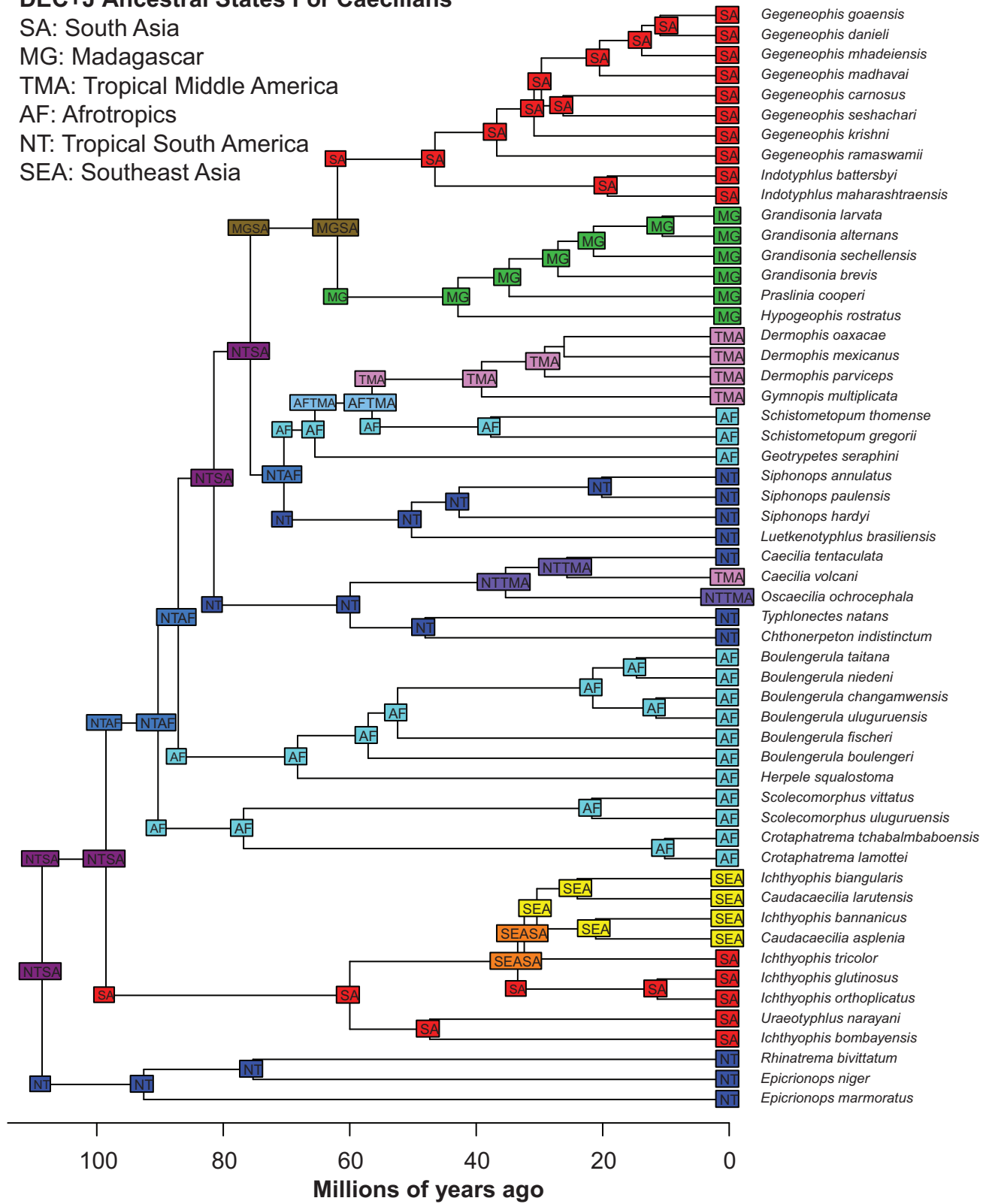
FIGURE 2. Ancestral-area estimations for 55 species of extant caecilians, using the DECj model in BioGeoBEARS. States at nodes represent the ancestral area before the instantaneous speciation event, whereas those on branches (corners) represent the state of the descendant lineage immediately after speciation. Some "corner" labels have been removed to reduce clutter in all cases where they are identical to the state at both the ancestral and descendant node. Similar histories for salamanders, frogs, and amphibians as a whole are given in online Appendices S1–S5.

Paleocene and Eocene salamandrid fossils from the Western Palearctic (Estes 1981).

The majority of the remaining salamanders (proteids, rhyacotritonids, amphiumids, and plethodontids) are Nearctic, and are reconstructed as such, with a few notable exceptions. An apparent recolonization of the Western Palearctic by *Proteus* dates to approximately 108 Ma, after the breakup of Laurasia. Recent studies have recovered both older and younger dates for this divergence (Roelants et al. 2007; Wiens 2011b). The geographic position of *Proteus* and *Necturus* would most simply suggest a trans-Atlantic land-bridge dispersal shortly after the initial breakup of Laurasia. A fossil *Necturus* is known in the Nearctic (Canada) from the Paleocene (Holman 2006). This will likely remain ambiguous pending further data.

Within Plethodontidae, there are two apparent, similarly timed recolonizations of the Palearctic, by *Hydromantes* (Western Palearctic: France and Italy) approximately 33 to 19 Ma, and by *Karsenia* (Eastern Palearctic: Korea) approximately 53 to 51 Ma. The restricted distributions and broad time-scales involved again make reconstructing exact routes (Pacific or Atlantic) equivocal (see Vieites and Wake 2007), and most fossil material is recent, from the Miocene or later (Holman 2006).

Within the remaining New World plethodontids, the time-scale here suggests a relatively early (presumably overland) dispersal into Tropical Middle America (Bolitoglossinae), approximately 80 to 73 Ma. This time-scale is congruent with many recent studies (Roelants et al. 2007; (Wiens, 2011b)). The landmass associated with present-day Central America (e.g., southern Mexico) was not fully emergent during much of the Late Mesozoic and Early Cenozoic, suggesting that the initial stages of the extremely diverse bolitoglossine radiation may have been in a relatively small geographic area. The colonization of South America by *Bolitoglossa* approximately 25 to 20 Ma is congruent here with previous studies (Elmer et al. 2013). However, given the proximate geographic locations of the landmasses (Central and South America), this history is consistent with a relatively short-distance oceanic dispersal between the adjacent continents (as in frogs; Heinicke et al. 2007; see below), rather than the scenario proposed by previous authors, that the Isthmus of Panama arose earlier than the widely accepted date of approximately 3 Ma (Elmer et al. 2013).

Whole-Tree Analysis

For amphibians as a whole, the DEC model is actually a significantly better fit ($-\ln L = -1721.2$) than the DECj model ($-\ln L = -1804.3$, $P > 0.05$), suggesting that founder-event speciation is not as common in frogs compared with caecilians and salamanders (online Appendix S4). This is mirrored by the frog subtree (Table 1; online Appendix S3), which is essentially identical to the whole-tree analysis, and is not discussed in detail. The results for frogs from the whole-tree analysis are examined in more detail below; the results for caecilians and salamanders are very similar to the subtree analyses (online Appendices S1–S5). The differences relate to the lumping of some areas (e.g., Tropical Middle America with Tropical South America) and the change in number of areas at some nodes (e.g., Palearctic for the ancestor of salamanders in the whole tree vs. Nearctic + Palearctic in the subtree). The main biogeographic events are similar for both groups, as the time-scale and geographic areas are the same, just in slightly different configurations.

Frogs

The MRCA of frogs dates to the Late Triassic approximately 219 Ma, similar to several recent studies (Roelants and Bossuyt 2005; Roelants et al. 2007; Pyron 2011), and suggesting a mid-to-late Pangaean origin of extant frogs. Fossils of stem anurans are known from Early Triassic (~250 Ma) from deposits in Madagascar and Poland, with a few Holarctic crown-group frogs known from the Jurassic (Evans and Borsuk-Bialynicka 1998). The DEC estimates place the MRCA of frogs in the Neotropics + Palearctic (presumably other areas would be included if allowed in the analysis), corroborating a Pangaean origin. The long time-periods and extinctions from intervening areas involved in interpreting estimations at this temporal scale yield some unusual, but intuitive results.

The basal lineage Leiopelmatoidea (*Ascaphus* + *Leiopelma*) is reconstructed in Australasia (New Zealand, *Leiopelma*) + Nearctic (Pacific Northwest, *Ascaphus*) around the initial breakup of Pangaea, suggesting a vicariant origin. These two landmasses were never geographically proximate, implying that the ancestral lineage had a broader distribution in Pangaea spanning Laurasia and Gondwana, and that extinction from intervening areas has eliminated the remnants of this clade on other landmasses. Indeed, leiopelmatids are known from Temperate South America in the Jurassic (Sanchiz 1998). Both lineages inhabit a relictual temperate niche that is associated with higher rates of extinction (Pyron and Wiens 2013).

The remaining major frog lineages diversified approximately 170 to 120 Ma, after the initial breakup of Pangaea, whereas Laurasia and Gondwanaland were still primarily accreted. The superfamily Discoglossoidea (Bombinatoridae, Alytidae, and Discoglossidae) shows this signature, with a long history in the Palearctic, and recent (presumably overland) dispersal into Southeast Asia by a few bombinatorid lineages. Pipoidea (Rhinophrynidae + Pipidae) shows the classic signature of West-Gondwanan vicariance (Bewick et al. 2012), with the ancestral lineage in Tropical South America, and divergence between the African and New World pipids approximately 131 Ma. Pipoids have a broadly distributed fossil record in the Nearctic, Western Palearctic, Tropical South America, Afrotropics, and Temperate South America (Sanchiz 1998).

Similarly, Pelobatoidea (Scaphiopodidae, Pelodytidae, Pelobatidae, and Megophryidae) is reconstructed in the Nearctic + Palearctic (Laurasia), with a basal divergence (presumably vicariant) between the Nearctic scaphiopodids and the remainder of the Palearctic pelobatoids as Laurasia is breaking up. A relatively early colonization of Southeast Asia is reconstructed for the megophryids approximately 126 to 99 Ma. This resulted in several recolonizations of the Palearctic in a number of megophryid lineages, presumably via overland dispersal (range expansion) back into temperate East Asia (i.e., Eastern Palearctic).

Neobatrachian frogs show strong evidence of a Gondwanan Cradle, reconstructed in Tropical South America + Africa approximately 152 Ma, prior to its final breakup. The basal Neobatrachian lineage (Heleophrynidae) is endemic to southern Africa. Sooglossoidea is reconstructed in Madagascar + South Asia, with Nasikabatrachidae in southern India and Sooglossidae in the Seychelles (Biju and Bossuyt 2003). Their divergence approximately 99 Ma predates the rifting of those landmasses, potentially suggesting a vicariant origin of the sooglossoids similar to the indotyphlopid caecilians. Sooglossoidea is the sister-group to Ranoidea, but this placement has varied in previous analyses (see Pyron and Wiens 2011).

The remaining frog lineages (Ranoidea and Hyloidea) contain the majority of species, and continue to show the strong signature of a Gondwanan Cradle. Although neobatrachian frogs have a relatively rich fossil record (Sanchiz 1998), assignment of taxa to extant groups as defined here becomes more difficult (Ruane et al. 2011). Thus, we can rely less on fossil information to discriminate among alternate historical scenarios for these groups.

Ranoidea is reconstructed in the Afrotropics, and ancestral-area and divergence-time estimates show similar patterns to previous estimations (Bossuyt et al. 2006; Wiens et al. 2009). There are numerous ranoid lineages endemic to Africa including Brevicipitidae, Hemisotidae, Arthroleptidae, and Hyperoliidae. Among these is a recent (~31 Ma), presumably over-water dispersal to Madagascar and the Seychelles (*Tachycnemis* and *Heterixalus*).

Microhylidae presents a challenging biogeographic scenario, occupying a traditionally Gondwanan position with extant lineages in the Nearctic, Neotropics, Afrotropics, Madagascar, India, Southeast Asia, Palearctic, and Australasia. Divergence-time estimates for the group have varied, but typically date to the Late Cretaceous (Van Bocxlaer et al. 2006; van der Meijden et al. 2007; de Sa et al. 2012). I corroborate this here, with an estimate of approximately 86 Ma. By this time, all major Gondwanan landmasses were separated, including South America from Africa, India from Madagascar, and Australia from Antarctica. As noted by previous authors, a far more ancient origin would be required to safely assume a vicariant origin of major lineages (van der Meijden et al. 2007), and few fossils are known.

The ancestral-area estimates for early branches in the group do not intuitively suggest a straightforward historical-biogeographic scenario, which is coincident with relatively low support for the backbone of the family (de Sa et al. 2012). A rapid diversification in the Late Cretaceous has resulted in numerous subfamilies endemic to areas such as the Neotropics, South Asia, Africa, and Madagascar, some of which are sister-groups (e.g., Melanobatrachinae + Otophryninae; Cophylinae + [Hoplophryninae + Gastrophryninae]), but none of which imply a straightforward vicariance scenario. There are multiple estimated colonizations of Madagascar, South Asia, Southeast Asia, the Neotropics, and the Palearctic. All Nearctic species result from a single, presumably overland dispersal (range expansion) in Gastrophryninae. All Australasian species arise from a single lineage (Asterophryninae).

It is difficult to rule out an early vicariant origin of some major lineages on Gondwanan landmasses, though overseas dispersal remains a strong possibility in many cases (van der Meijden et al. 2007). In addition, there are multiple clear cases of presumably overland dispersal (range expansion), such as from the Neotropics to the Nearctic, and several instances of Palearctic and South Asian colonization from Southeast Asia. Resolving the biogeographic history of microhylids will likely remain difficult pending better resolution of higher level relationships and additional fossil evidence (de Sa et al. 2012).

A similar conundrum is observed in the remainder of the ranoid frogs, dating to approximately 101 Ma. The divergence times and ancestral states are similar to recent studies (Bossuyt et al. 2006; Wiens et al. 2009), suggesting a post-Gondwanan origin of most major lineages, but not unambiguously rejecting a vicariant origin. The group is strongly supported as originating in the Afrotropics where most of the early branching lineages are found (Ptychadenidae, Phrynobatrachidae, Conrauidae, Petropedetidae, and Pyxicephalidae), with a very recent (presumably over-water) dispersal into Madagascar (*Ptychadena mascareniensis*), and a relatively recent (~29 Ma) colonization of South Asia (Micrixalidae), presumably also through over-water dispersal. The remaining families (Ceratobatrachidae, Nyctibatrachidae, Ranixalidae, Dicroglossidae, Ranidae, Rhacophoridae, and Mantellidae) show rapid movements among Afrotropics, South Asia, Southeast Asia, Australasia, Neotropics, Nearctic, and Palearctic.

Many of these presumably represent over-land dispersal (range-expansion) events, though some seem to indicate over-water (e.g., Afrotropics from Southeast Asia by *Amnirana* [*Hylarana*] and *Chiromantis*) or land-bridge dispersal (e.g., New World *Rana* [sensu stricto]). As with the microhylids, the backbone of this ranoid subgroup is poorly supported, suggesting a rapid radiation during a time-period that renders discriminating between vicariance and dispersal hypotheses ambiguous. It will be difficult to arrive at a robust conclusion regarding the biogeographic history

of the group without improved resolution of higher level relationships (perhaps sampling more taxa or characters), and additional fossil data.

The sister-group to Hyloidea is Calyptocephalellidae + Myobatrachidae, presenting a similar situation to Leiopelmatoidea (*Ascaphus* + *Leiopelma*), with a divergence between Australasian taxa (Australo-Papuan myobatrachids) and the calyptocephalellids (*Telmatobufo* and *Calyptocephalella*) found in Temperate South America. This split dates to the Early Cretaceous (~110 Ma), after the initial breakup of Gondwanaland, but with South America still relatively proximate to East Gondwana, which still contained the Australasian landmass. Thus, a vicariant origin of these lineages seems most likely (particularly allowing that the divergence might be somewhat older), with extinction from the intervening landmasses (i.e., Antarctica). Fossils for both groups are primarily Cenozoic and found mostly in the range of extant lineages (Sanchiz 1998), offering little insight. As with the leiopelmatoids, the calyptocephalellids inhabit a relictual temperate niche associated with higher extinction rates (Pyron and Wiens 2011).

In contrast to the ranoids, the remaining frogs (Hyloidea) are firmly rooted in the Neotropics, with the stem-group ancestor of Hyloidea + (Calyptocephalellidae + Myobatrachidae) having persisted there since approximately 144 Ma. The majority of hyloid frogs are Neotropical (as coded for this analysis, including Temperate South America, Tropical Middle America, and the West Indies), with a several relatively recent (Eocene or later) expansions (presumably overland dispersal [range expansion]) into the Nearctic. These include species in *Eleutherodactylus* [*Syrrhopus*], *Craugastor*, *Acris* + *Pseudacris*, *Smilisca*, *Hyla*, and *Bufo* [*Rhinella*, *Incilius*, and *Anaxyrus*]. There are several apparent major long-distance movements as well (see below). The first is the colonization of Australasian (Australia + New Guinea) by the pelodryadine hylids approximately 61 to 52 Ma, at which time most major landmasses approximated their present-day position. This would strongly suggest an over-water oceanic dispersal from South America to Australia during the Paleocene–Eocene.

Within the hyline hylids, there is a colonization of the Palearctic (and subsequently, Southeast Asia) from the Neotropics approximately 37 to 35 Ma, potentially suggesting an oceanic dispersal (Smith et al. 2005). From that lineage, there is then a strongly supported recolonization of the Nearctic, presumably via land-bridge dispersal (range expansion). Incredibly, there is then a subsequent recolonization of the Palearctic (East Asia) from that lineage. Presumably this would indicate Pacific (Beringian) or Atlantic (de Geer or Thulean) land bridges. However, it is also possible to imagine scenarios of a broader Holarctic distribution of these early hyline lineages, from which extinction in intervening areas during the Eocene and Oligocene yielded the observed pattern, rather than multidirectional dispersal routes across land bridges.

The last major clade in hyloids exhibiting major movement is the toads (Bufonidae), which exhibit a nearly cosmopolitan distribution (Pramuk et al. 2008; Van Bocxlaer et al. 2010). The early branching toad lineages are Neotropical, with a few relatively recent (Eocene or later) movements (presumably over-land dispersal [range expansion]) into the Nearctic. The Old World representatives of this group stem from a lineage reconstructed to have colonized Africa + Palearctic from Tropical South America approximately 38 to 36 Ma, which would strongly suggest a trans-Atlantic oceanic dispersal from South America to Africa. Although this is an unusual route, the reverse is relatively common in other terrestrial vertebrates (Carranza and Arnold 2003; Le et al. 2006; Gamble et al. 2008; Vidal et al. 2008). A land-bridge dispersal from the Nearctic cannot be ruled out, however. From this lineage that recolonized Afrotropics + Palearctic, there are several subsequent colonizations (presumably over-land dispersal [range expansion]) of South Asia, Southeast Asia, and secondary recolonizations of Afrotropics. These rapid movements are associated with an expansion-adapted phenotype (Van Bocxlaer et al. 2010), and similar adaptations may be related to expansion in other lineages (see below).

Nonbiogeographic Estimations

Ancestral-state estimates from Mesquite using ML methods are overall fairly similar to the DEC/DECj models. Major features corroborated are a Laurasian Cradle for salamanders and a Gondwanan Cradle for frogs, with ranoids originating in Afrotropics and hyloids in Tropical South America. The primary differences relate to higher ambiguity at internal and root nodes (due to estimates being limited to single areas), and small differences arising from having all 12 areas included. A few additional insights are gained from these estimates (online Appendix S5).

The West Indian anuran fauna comprises a small number of hyloid lineages (*Eleutherodactylus*, *Pristimantis*, *Hypsiboas*, *Osteopilus*, *Leptodactylus*, and *Bufo* [*Peltophryne*]), most of which originated through (presumably over-water) dispersal to the Proto-Antilles during the Eocene to the Miocene (Heinicke et al. 2007). A number of hyloid lineages have also colonized Temperate South America via recent (presumably over-land [range-expansion]) dispersal from Tropical South America, including *Bufo* [*Rhinella*], *Pleurodema*, *Melanophryniscus*, and *Odontophrynus*. There are also a few relatively diverse clades in Temperate South America with more ancient origins, including Calyptocephalellidae, which has a likely Gondwanan-vicariant origin as noted above. Two other clades (Rhinodermatidae + Telmatobiidae and Batrachylidae + Alsodidae) are also relatively ancient and diverse, but appear to have arisen via colonization (presumably over-land dispersal [range expansion]), originating from Tropical South America.

Colonization of Tropical Middle America by caecilians and salamanders was detailed above, but has also occurred extensively in frogs. Microhylids appear to have expanded northward from Tropical South America, presumably via over-land dispersal (range expansion), continuing to the Nearctic. In contrast, *Rana* [*Lithobates*] appears to have expanded south through Tropical Middle America to Tropical South America from the Nearctic, again presumably through over-land dispersal (range expansion). In hyloids, some lineages appear to have colonized Tropical Middle America from Tropical South America via rafting (i.e., over-water dispersal), such as *Diasporus*, *Craugastor*, *Pristimantis*, *Pachymedusa* + *Agalychnis*, *Hypsiboas*, *Scinax*, and *Dendropsophus*, a large clade of Neotropical hylids (described above) that includes a recolonization of the Holarctic, *Leptodactylus*, *Hyalinobatrachium*, *Cochranella*, *Silverstoneia*, *Phyllobates*, *Dendrobates*, *Atelopus*, and *Bufo* [*Incilius*]. All of these date to the Paleocene or later, but some date to the Late Miocene or Early Pliocene, and may thus represent over-land dispersals (range expansion) coinciding with the uplift of the Isthmus of Panama.

Due to the computational constraints mentioned above, the Eastern and Western Palearctic were lumped together into "Palearctic" in the DEC/DECj analyses. However, the 12-area ML analyses reveal that they have distinct histories of colonization in frogs. The clade consisting of Bombinatoridae, Alytidae, and Discoglossidae is centered in the Western Palearctic, having recently colonized Southeast Asia (Bombinatoridae) and the Eastern Palearctic (*Bombina*), presumably via over-land dispersal (range expansion). Pelodytids and pelobatids are exclusively Western Palearctic, whereas the Eastern Palearctic megophryids represent a secondary colonization (presumably via over-land dispersal [range expansion]) from Southeast Asia.

A few Old World microhylid, dicroglossid, ranid, and rhacophorid lineages have also colonized the Eastern Palearctic from Southeast Asia in an apparently similar manner. In contrast (as described above), the genus *Rana* (sensu stricto) exhibits a Holarctic distribution, with lineages in the Nearctic, Western Palearctic, and Eastern Palearctic. Another ranid lineage, *Pelophylax*, has colonized both the Western and Eastern Palearctic from Southeast Asia. As noted above, one hyline lineage has recolonized the Old World from Tropical Middle America, with lineages in both the Western and Eastern Palearctic. These movements date to the Cenozoic, ruling out Laurasian vicariance, and suggesting either over-land dispersal (range expansion), or land-bridge dispersal across the Pacific (Beringian) and Atlantic (de Geer and Thulean).

DISCUSSION

Vicariance, Dispersal, and Extinction

A conservative interpretation of the results can seemingly be divided into two major, fundamental portions. The primary distribution of major amphibian lineages is apparently dominated by Pangaean dynamics (vicariance), including both the initial diversification of amphibians and subsequent Laurasian and Gondwanan fragmentation (Feller and Hedges 1998; Roelants and Bossuyt 2005; San Mauro et al. 2005; Bossuyt et al. 2006; Van Bocxlaer et al. 2006). The secondary distribution of amphibians seems to be driven primarily by dispersal, including over-land range expansion, and land-bridge colonization involving short-distance over-water or stepping-stone events (Bossuyt and Milinkovitch 2001; Heinicke et al. 2007; Pramuk et al. 2008; Van Bocxlaer et al. 2010). That the history of amphibians is a mixture of both vicariance and dispersal is not surprising given their ancient origin (Marjanovic and Laurin 2007; Roelants et al. 2007; Pyron 2011). However, these results reinforce that both ancient vicariance and recent dispersal can have similar impacts on the distribution of extant lineages.

A remaining question is whether or not long-distance oceanic dispersal has had a strong influence on amphibian distributions (de Queiroz 2005). Clearly, this has not been the dominant pattern in amphibians, as the DECj models are only marginally supported for the caecilians and salamanders (albeit significantly), but not frogs or amphibians as a whole (Table 1). Previous research suggests that these models provide a much better fit for the structuring of island assemblages (Matzke 2013b), but the results here suggest they are less important for ancient continental faunas. However, there are several events reconstructed above for amphibians that seemingly suggest that long-distance oceanic dispersals have occurred (Vences et al. 2003).

By long-distance oceanic dispersal, I am referring to the over-water colonization of areas well after their separation from the originating landmass, and which were not proximate during accretion (e.g., Tropical Middle America, the West Indies, and Tropical South America) or supported by stepping stones or land bridges (e.g., de Geer and Thulean [Atlantic] or Beringian [Pacific]). Some potential instances of oceanic dispersal are equivocal, given variability in the time-scales or topologies. The genus *Dermophis* is estimated to have recolonized Tropical Middle America from Africa approximately 65 to 57 Ma, after the separation of West Gondwana. However, the time-scale used here is relatively young compared with other studies (see Pyron [2011] for a review), and this divergence could conceivably have occurred prior to the continental breakup if we allow that the divergence could be somewhat older. I will focus on three Southern Hemisphere dispersal events that seem to be strongly supported as long-distance over-water movements.

First are the Malagasy hyperoliids. In the paleogeographic framework used here, Madagascar + India and Africa had separated from East Gondwana by 120 Ma, and Madagascar and India separated by 90 Ma. Thus, Malagasy lineages originating after those times have a strong likelihood of having

originated via oceanic dispersal (Raxworthy et al. 2002). The Malagasy hyperoliid radiation (*Tachycnemis* and *Heterixalus*) diverged approximately 51 Ma, with extant species arising approximately 31 Ma, and are strongly reconstructed to have originated from the African hyperoliids. Thus, there is little alternative to explain their origin other than oceanic dispersal from Africa to Madagascar. Some authors have suggested that land bridges during the Eocene and Miocene facilitated mammal dispersal (McCall 1997), but more recent simulations and paleogeographic evidence do not support this (Ali and Huber 2010). Microhylids and mantellids also present possibilities for long-distance over-water dispersal to Madagascar (van der Meijden et al. 2007; Wiens et al. 2009), but these are not nearly as unambiguous as the hyperoliids.

Second is the south Asian family Micrixalidae, which is deeply nested within a solely African lineage near the base of Ranoidea (Pyron and Wiens 2011). This group diverged from Petropedetidae approximately 77 Ma, but the crown-group age for the family is approximately 29 Ma. An expansion to South Asia is estimated as early as approximately 84 Ma, but given the length of the stem-group branch, this is difficult to pinpoint. A vicariant origin would necessitate the ancestral lineage having occupied both East and West Gondwana, with subsequent fragmentation and extinction from intervening areas leaving the African and South Asian lineages as the only descendants. However, these landmasses were last proximate (but still fragmented) approximately 120 Ma, whereas the extant *Micrixalus* date to approximately 29 Ma, similar to previous studies (Bossuyt et al. 2006; Wiens et al. 2009). There are no other phylogenetically proximate South Asian lineages, and the placement of the group in an otherwise exclusively African clade is strongly supported. Thus, long-distance over-water dispersal from Africa to South Asia, around the same time and in the same direction as the dispersal of *Tachychnemis* + *Heterixalus* to Madagascar, seems the most likely explanation.

Third are the pelodryadine hylids of Australian and New Guinea. Little mention of the biogeographic history of this group can be found in the literature. This group originated approximately 61 to 52 Ma, and is deeply nested within a group of hyloids that are otherwise reconstructed to have existed solely in Tropical South America after approximately 132 Ma. By the time pelodryadines originated in the early Paleogene, all major continental landmasses occupied more or less their present-day positions, with South America and Australia long separated from Antarctica. The young age of this group (<65 Ma) is supported even by studies estimating relatively old ages for amphibians as a whole (Roelants et al. 2007). Given the complete absence of any other Old World hyloid lineages of a similar age, and the total lack of ambiguity in any biogeographic estimations, it seems logical that the most likely explanation for the origin of this group is a trans-Pacific dispersal event from South America to Australasia approximately 61 to 52 Ma.

There are similarly distributed groups such as iguanians and booids, for which Gondwanan vicariance and over-water dispersal are competing explanations, given the ambiguous time-scale (Keogh et al. 2008; Noonan and Sites 2010). For pelodryadines in particular (and potentially hyperoliids and micrixalids), over-land dispersal could also explain the observed patterns. This would involve a (i) "short hop" from South America to Antarctica, (ii) over-land dispersal across Antarctica, (iii) another "short hop" from Antarctica to Australia, and (iv) extinction from Antarctica. Whether this is more likely than direct dispersal is an open question.

A final point is the importance of extinction from intervening areas in generating large-scale biogeographic patterns. By this, I mean the necessary occurrence of lineages over large areas that have subsequently been lost, resulting in restricted or relictual distributions of descendant lineages. These seem to be more common in ancient lineages, which have dealt with a longer history of geological and ecological change. One example is Leiopelmatidae (New Zealand) + Ascaphidae (Nearctic), which as noted above likely resulted from an originally Pangaean lineage, which has subsequently been lost from the remainder of the Laurasian and Gondwanan landmasses. Another example is Calyptocephalellidae (Temperate South America) + Myobatrachidae (Australasia), which likely originated on Gondwana, but has subsequently been lost from the other remaining fragments.

Although it is unlikely that ancestral lineages occupied the entirety of the supercontinents, this scenario would predict that a rich fossil record of tropical frogs exists in Antarctica. Several of these lineages also exhibit highly restricted temperate climatic niches (see below), suggesting that "ecological vicariance" (Pyron and Burbrink 2010) was a major factor isolating the extant lineages as the remaining Gondwanan fragments became increasingly tropical. Even under relatively simple Laurasian or Gondwanan vicariance scenarios, many lineages would likely have to had much larger ancestral distributions that have suffered extinction from intervening areas to produce present-day patterns.

Ecomorphological Patterns

Amphibians present a dichotomy for biogeographic inference and ecological responses (Ricklefs and Jenkins 2011; Wiens 2011a). A large proportion of their distributional patterns are clearly attributable to long-term occupancy of different tectonic plates and associated vicariance (San Mauro et al. 2005; Bossuyt et al. 2006). In contrast, the present-day distribution of species' ranges and regional species-richness patterns is strongly tied to current or recent climatic conditions (Wiens et al. 2006; Buckley and Jetz 2007; Pyron and Wiens 2013). Community assembly shows a strong signature of both present-day climate and historical influences on phenotypic traits and ecological niches for coexisting species (Ernst and Rodel

2008; Moen et al. 2009; Wiens et al. 2011). Thus, the distribution of amphibians represents a complex interplay between very tightly linked organism–environment interactions across very long periods of time. Diversification and persistence seem to be (perhaps somewhat unsurprisingly) linked to niche breadth and the availability of suitable niches.

Concomitantly, there is an apparently close link between phenotypes, and their ability to colonize and diversify in different regions. A small number of ecomorphs are convergently replicated in communities across the globe (Moen et al. 2009, 2013; Wiens 2011a; Vidal-Garcia et al. 2014). Furthermore, colonization seems to be tightly linked to phenotypes that facilitate range expansion (Van Bocxlaer et al. 2010). Taken together, these factors suggest that ecomorphological variation represents the link between ecological and geographic processes affecting distributions (Ricklefs 2004), by mediating the processes that affect diversity in areas: speciation, extinction, and dispersal (Ricklefs 1987).

This is evident when examining the disparity in diversity and distribution of major amphibian lineages. The most heavily relictual lineages (i.e., ancient, geographically localized groups with few species) seem to fit into two major categories. The first are those with highly specialized phenotypes that originated early, such as caecilians, cryptobranchid, and limbless salamanders (sirenids, proteids, and amphiumids) in the Holarctic, and rhinophrynid, hemisotid, and nasikabatrachid frogs in Tropical Middle America, Afrotropics, and South Asia. The second are those with geographically restricted ecological niches, such as leiopelmatid, heleophrynid, and calyptocephalellid frogs, which inhabit a temperate Gondwanan niche that is overshadowed by the predominantly tropical present-day climates of those landmasses. Similarly, dicamptodontid and rhyacotritonid salamanders and ascaphid frogs inhabit a cool, high-elevation, high-precipitation niche in the Pacific Northwest of the Nearctic, which is highly localized, but presumably occupied a much larger area of Laurasia when those lineages originated.

CONCLUSIONS

The results presented here provide a preliminary overview of the biogeographic history of extant amphibians, analyzed as a single group. Future studies taking a more focused approach to some of the subclades highlighted here may be able to further refine this history. In particular, estimates of variability in paleogeographic scenarios and divergence-time estimates will help to test hypotheses of vicariance and dispersal more precisely. Three major trends are apparent in these coarse-grained analyses. First, the major lineages of extant amphibians originated in Pangaea, and their initial diversification coincides with the breakup of the supercontinent, and the

subsequent fragmentation of Laurasia and Gondwana. Most major clades still bear the biogeographic signature of these early vicariant processes. Second, Cenozoic dispersal has subsequently exerted a similarly strong influence on the distribution of extant amphibians, as numerous lineages have undergone relatively short-distance movements across land bridges or short distances across water. Third, there are a small number of strongly supported instances of long-distance oceanic dispersal, involving movements between Gondwanan landmasses that significantly postdate any geographic proximity of those areas. The inference of numerous ancient supercontinental lineages implies a large role for intermediate extinction in shaping the distribution of extant lineages, and suggests that a rich fossil record may exist in intermediate areas such as Antarctica. Ability to disperse, or conversely, propensity for extinction, seems to be driven by either the evolution of extraordinarily adaptive expansion-oriented phenotypes in some clades, in contrast to extremely specialized body forms or heavily relictual climatic niches in other geographically restricted, depauperate lineages. These observations will hopefully provide a foundation for further analyses of the ecomorphological roots of biogeographic processes and the distribution of amphibians through space and time.

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