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Why is Madagascar special? The extraordinarily slow evolution of pelican spiders (Araneae, Archaeidae)

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Although Madagascar is an ancient fragment of Gondwana, the majority of taxa studied thus far appear to have reached the island through dispersal from Cenozoic times. Ancient lineages may have experienced a different history compared to more recent Cenozoic arrivals, as such lineages would have encountered geoclimatic shifts over an extended time period. The motivation for this study was to unravel the signature of diversification in an ancient lineage by comparing an area known for major geoclimatic upheavals (Madagascar) versus other areas where the environment has been relatively stable. Archaeid spiders are an ancient paleoendemic group with unusual predatory behaviors and spectacular trophic morphology that likely have been on Madagascar since its isolation. We examined disparities between Madagascan archaeids and their non-Madagascan relatives regarding timing of divergence, rates of trait evolution, and distribution patterns. Results reveal an increased rate of adaptive trait diversification in Madagascan archaeids. Furthermore, geoclimatic events in Madagascar over long periods of time may have facilitated high species richness due to montane refugia and stability, rainforest refugia, and also ecogeographic shifts, allowing for the accumulation of adaptive traits. This research suggests that time alone, coupled with more ancient geoclimatic events allowed for the different patterns in Madagascar.

KEY WORDS: **Biogeography, divergence time estimation, paleoendemics, phylogenetics, trait diversification.**

Madagascar is known for its high endemism and in situ radiations, with many groups undergoing remarkable diversification (Vences et al. 2009). Although Madagascar is an ancient fragment of Gondwana, the majority of taxa studied thus far appear to have reached the island through dispersal, typically from Africa, that occurred intermittently from Late Cretaceous and Cenozoic times, frequently followed by diversification (Yoder and Nowak 2006; Crottini et al. 2012; Samonds et al. 2012, 2013). Several hypotheses have been proposed to explain the mechanism for generating high species richness in Madagascar (Vences et al. 2009), which typically reflect more recent events, some centering on Plio-Pleistocene climate cycles. These models include the "western rainforest refugia" (Vences et al. 2009), an instance of the more general "rainforest refugia" model (Moritz et al. 2000), which posits that at one time the Madagascan rainforests were more widespread and later contracted to the East, with allopatric speciation occurring following isolation in western relictual rainforest patches. Alternatively, the "montane refugia" mechanism suggests that speciation occurred through vicariance when lineages became isolated as the forests contracted around high-elevation massifs (Diamond and Hamilton 1980). Montane areas may not just act as refugia, but also as areas of stability, allowing for lineages to persist (Fjeldså 1994; Fjeldså and Bowie 2008; Fjeldså et al. 2012).

However, there are some examples of lineages in Madagascar that reflect its ancient origins (Noonan and Chippindale 2006;

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Ali and Krause 2011; Wood et al. 2013), originating between 165 million years ago when Madagascar first began to break away from Africa (Rabinowitz et al. 1983) until it became isolated in the Cretaceous (Hay et al. 1999; Case 2002). In the Paleogene, as Madagascar shifted in latitude after tectonic isolation, moving northward through the 30°S arid belt, it developed its modern ecogeographic regions (Fig. 6A): the southern spiny dry biome is hypothesized to be the oldest region, with the western deciduous forests developing in the mid-Paleocene, and the eastern rainforests developing in the Eocene with the onset of trade winds (Wells 2003). Termed the "ecogeographic constraint" mechanism, as these regions developed, organisms may have invaded or adapted to this new habitat, resulting in different communities of species in different ecogeographic regions (Yoder and Heckman 2006). Even earlier, during the late Cretaceous, the landscape sustained extensive alteration as a result of volcanism and basalt flows associated with the separation of India and Madagascar (Wells 2003). Thus, ancient lineages on Madagascar may have experienced a very different history compared to more recent arrivals, as such lineages would have encountered dramatic geoclimatic shifts over long time periods. The current study focuses on the signature left by such ancient events: we examine the timing of divergence to explain how evolution proceeded in Madagascar and then determine whether the pattern of diversification on Madagascar is unusual by comparing Madagascan lineages with close relatives in Australia and southeastern Africa.

Southeastern Africa and Australia, compared to Madagascar, have experienced relatively stable geological and climatological environments until the more recent time period of the Miocene. Warm temperate rainforests dominated Australia from at least the Mesozoic up until the early Miocene when the climate became drier and seasonal (Crisp et al. 2004; Hopper and Gioia 2004). In southern Africa, during the Cretaceous, a warm, humid climate pervaded (Partridge and Maud 2000), and a mesic climate likely remained in southeastern Africa through the K-T boundary and until the present day following uplift during Gondwanan fragmentation that resulted in a climate gradient with a more mesic east (Tyson and Partridge 2000). However, starting in the Miocene, geological changes fragmented the landscape due to uplift and subsequent erosion of the Great Escarpment (Partridge and Maud 2000; Tyson and Partridge 2000). Therefore, based on these differences, our hypothesis is that more recent Miocene geologic or climatic events contributed to distribution patterns in southeastern African and Australian lineages, whereas in Madagascar species diversity has been shaped by more ancient events.

Archaeid spiders, commonly called pelican or assassin spiders, are an ancient paleoendemic group that have existed since Pangaean times (Wood et al. 2013). Archaeid spiders have distinct Northern Hemisphere lineages, now extinct and known only from fossils dated from the Eocene to the Jurassic (Koch and Berendt 1854; Penney 2003; Selden et al. 2008). Although, the monophyletic extant Southern Hemisphere lineage is limited to Australia, South Africa, and Madagascar (Wood et al. 2012). A divergence dating study concluded that the split between the extinct northern and extant southern faunas likely relates to Pangaea breaking into Gondwana and Laurasia in the Jurassic (Wood et al. 2013). Further study of extant archaeid spiders offers the possibility to better understand Madagascan diversification patterns in an ancient group that has experienced radical changes in climate and geology over an extended time period.

Archaeid spiders are an excellent group for addressing questions about diversification processes on Madagascar given that there are close relatives on Australia and southeastern Africa that serve for comparison. Archaeids are morphologically and behaviorally bizarre due to their highly modified carapace and chelicerae "jaws" giving them the appearance of a "neck" and "head" (Fig. 1). This morphology directly relates to their unique predatory strategy (Legendre 1961; Wood et al. 2012): they prey only on other spiders, and the long "neck" and chelicerae allow for attacking prey at a distance. There is considerable morphological variation in their carapace shape, ranging from species with short, thick "necks" to species with extremely long, thin "necks," and there is also variation in other traits, such as "head" shape and carapace tilt (Fig. 1). In particular, the Madagascan archaeids seem to have a greater degree of morphological and habitat diversity than their non-Madagascan relatives. Another notable difference is that Madagascan archaeid species occur in sympatry (H. M. Wood, pers. obs.), whereas in Australia and southeastern Africa, species tend to be allopatric (Lotz 1996, 2003, 2006; Rix and Harvey 2011, 2012a,b), and adaptive trait diversity may facilitate coexistence of the Madagascan species. These attributes suggest that different diversification processes have been involved in shaping the diversity of the Madagascan archaeids.

The current study sets out to test whether patterns of trait diversification and species distributions in Madagascar can be explained by ancient geoclimatic events rather than more recent events. We do so by examining (1) the timing of divergence; (2) the differences in distribution patterns compared to non-Madagascan relatives, and how distribution patterns relate to topological and climatic features; (3) the differences in rates of trait evolution compared to non-Madagascan relatives, and whether these traits are adaptive, to understand how these traits are evolving. Our methods include dated phylogenetic reconstructions, creating maps of species richness and endemicity, performing ancestral area reconstructions of ecogeographic regions, evaluating patterns of sister-species distributions, and estimating rates of trait evolution.

Methods

MORPHOLOGY AND DNA SEQUENCE COLLECTION

To examine archaeid relationships, we included 81 terminals representing 52 archaeid species from Madagascar, Australia, and southeastern Africa, comprising the four known extant genera: *Eriauchenius* (Cambridge 1881), *Austrarchaea*, *Afrarchaea* (Forster and Platnick 1984), and *Zephyrarchaea* (Rix and Harvey 2012a) as well as the monophyletic "Gracilicollis Group" (Wood 2008) that is currently considered part of *Eriauchenius.* Of the known Madagascan species, 18 of 21 described are included, plus an additional 15 undescribed, for a total of 33 species (out of 37 known). Twelve African (out of 12 known species) and seven Australian (out of 38 known species) are included. Although we include relatively few Australian species, we were able to include at least two species from each of the three major Australian clades (Rix and Harvey 2011, 2012a,b). Five fossil archaeid taxa, representing five of 11 fossil genera, were included using only morphological characters. Archaeids belong to the Palpimanoidea (Wood et al. 2012): the outgroup taxa include 13 terminals representing the remaining four Palpimanoidea families, the family Austrochilidae, and the tree is rooted with the Haplogynae Segestriidae, for a total of 99 terminals (Table 1).

The morphological characters from Wood et al. (2012) were used to score all species and outgroups. Molecular data for the austrochilid was acquired from GenBank, whereas the molecular data for the remaining specimens were gathered following the methods of Wood et al. (2012). A suite of primers was used to amplify a portion of the mitochondrial protein coding gene Cytochrome c Oxidase subunit 1 (COI), the nuclear protein-coding gene Histone-3 (H3), and the ribosomal nuclear genes 28S and 18S. Some specimens sequenced for this study were difficult to amplify and/or sequence for some markers, so that a few taxa are incomplete for some regions or markers (see Table 1). All DNA sequences have been deposited in GenBank under accession numbers **KP201206-KP201459** (Table 1).

Nonprotein coding genes were aligned using the Mafft (Katoh et al. 2002) online server (http://mafft.cbrc.jp/alignment/server/) using the E-INS-i strategy, which operates best on sequences with conserved domains and long gaps. The gap open penalty and the offset value were set to their defaults of 1.5 and 0.123, respectively. The best-fit substitution model and the data partitions were estimated for the molecular data using PartitionFinder version 1.1.0 (Lanfear et al. 2012) for 28S, 18S, and each of the three codon positions in the protein coding genes, using greedy search for MrBayes models, using BIC criteria, and resulting in the final concatenated total evidence dataset having the following four partitions: morphology; COI codon position 3; COI codon positions 1 and 2 and H3; 18S and 28S. For the morphology partition, the standard discrete Markov (Mkv) model (Lewis 2001) was used with rates set to gamma. The best-fit models for the remaining three partitions were GTR + G, GTR + I + G, and K80 + I + G.

PHYLOGENETIC ANALYSIS AND DIVERGENCE DATING

Analyses were performed using Bayesian methods on the morphological matrix, the molecular concatenated data, and the total evidence data containing the molecular and morphological characters. Analyses were implemented in MrBayes version 3.2.2 (Ronquist and Huelsenbeck 2003) using four chains, with the analysis run twice simultaneously, and the starting trees randomly generated. Analyses were run for 10–20 million generations, depending on how quickly the analysis converged, with sampling every 1000th generation. All analyses were checked to ensure that the deviation of split frequencies was below 0.01. The two simultaneous analyses were evaluated for convergence using Tracer version 1.4 (Rambaut and Drummond 2007). The burn-in value was visualized and determined by summarizing posterior distributions of scalar values, resulting in a final consensus tree with node support expressed as posterior probabilities (pp).

Figure 1. **An example of a short and long "necked" species from Madagascar, lateral view, legs removed, (A) ♂ *Eriauchenius* sp.11. (B) ♀ *Eriauchenius* sp.10. Scale bars = 0.5 mm.**

Table 1. List of vouchers used for molecular data for phylogenetic analysis. Numbers in parentheses following species name denote the individual specimen. Unless otherwise specified the voucher number is from the California Academy of Sciences Entomology Dept (CASENT); NMBA = National Museum, Bloemfontein; MAD = Madagascar; SA = South Africa; AU = Australia; NA = missing.

Species names	Extraction code	Voucher number	GenBank Accession Number			
			CO1	28S	18S	H3
Outgroups						
Segestriidae						
Segestria sp.	Sege43	9024001	KP201206	KP201410	KP201340	KP201275
Austrochilidae						
Hickmania troglodytes		GenBank	FJ948985	FJ948945	FJ948862, FJ948903	FJ949025
Mecysmaucheniidae						
Aotearoa magna	hw0050	9028246	JX240238	JX240275, JX240289	JX240258	JX240308
Zearchaea sp.	hw0051	9028243	JX240242	JX240279, JX240293	JX240262	JX240311
Chilarchaea quellon	hw0029	9028089	JX240241	JX240278, JX240292	JX240261	JX240310
Mecysmauchenius segmentatus	hw0098	9028435	JX240240	JX240277, JX240291	JX240260	JX240309
Huttoniidae						
Huttonia sp. 1	hwHutt41	9028231	JX240237	JX240288	JX240257	JX240307
Huttonia sp. 2	hw0126	9034307	KP201269	KP201457	KP201404	NA
Palpimanidae						
Palpimanus sp. 1	hw0082	9024279	JX240235	JX240274, JX240286	JX240255	JX240305
Palpimanus sp. 2	hw0073	9024208	KP201233	KP201432	KP201370	KP201301
Palpimanidae sp. 1	hw0086	9029145	KP201208	KP201412	KP201342	KP201276
Palpimanidae sp. 2	hw0147	9053299	KP201273	KP201459	KP201408	NA
Stenochilidae						
Colopea sp.	hw0081	9028424	JX240236	JX240287	JX240256	JX240306
Ingroup, Archaeidae						
Zephyrarchaea mainae (1)	hw0080	9028364	KP201209	KP201413	KP201343	NA
Zephyrarchaea mainae (2)	hw0075	9028389	JX240252	JX240302	JX240272	NA
Zephyrarchaea barrettae	hw0078	9028379	KP201240	KP201438	KP201377	NA
Austrarchaea davisae	hwAu066	9023672	JX240251	JX240283, JX240301	JX240271	JX240319
Austrarchaea tealei	hw0091	9028385	KP201229	NA	KP201366	KP201298
Austrarchaea sp. 1	hw0077	9028390	KP201230	KP201429	KP201367	NA
Austrarchaea nodosa (1)	hwAu084	9018966	KP201244	KP201441	KP201380	NA
Austrarchaea nodosa (2)	hw0074	9028388	JX240250	JX240300	JX240270	NA
Austrarchaea harmsi	hw0093	9028427	KP201225	NA	KP201362	KP201294
Eriauchenius legendrei (1)	hw0014	9018992	JX240245	JX240296	JX240265	JX240314
Eriauchenius legendrei (2)	hw0012	9018990	KP201227	KP201427	KP201364	KP201296
Eriauchenius legendrei (3)	hw0025	9019011	KP201207	KP201411	KP201341	NA
Eriauchenius sp. 1	hw0066	9028331	KP201239	KP201437	KP201376	KP201307
Eriauchenius sp. 2	hw0154	9046596	NA	NA	NA	KP201339
Eriauchenius vadoni (1)	hw0065	9028339	KP201246	NA	KP201382	KP201312
Eriauchenius vadoni (2)	hw0024	9019018	KP201214	KP201415	KP201347	NA
Eriauchenius sp. 3	hw0089	9015493	KP201226	KP201426	KP201363	KP201295
Eriauchenius borimontsina	hwsp11	9015520	DQ914571	KP201422	KP201354	KP201288
Eriauchenius tsingyensis (1)	hw0090	9028376	KP201228	KP201428	KP201365	KP201297
Eriauchenius tsingyensis (2)	hw0056	9028295	KP201211	NA	KP201344	KP201278
Eriauchenius anabohazo	hwsp2A	9002611	DQ914573	NA	NA	NA
Eriauchenius griswoldi (1)	hw0010	9018988	KP201237	NA	KP201374	KP201305
Eriauchenius griswoldi (2)	hw0009	9018987	KP201247	KP201443	KP201383	KP201313
Eriauchenius griswoldi (3)	hw0039	9019020	KP201251	KP201444	KP201387	KP201317
Eriauchenius lavatenda (1)	hw0003AB	9018981	JX240243	JX240294	JX240263	JX240312
Eriauchenius lavatenda (2)	hw0064	9028335	KP201242	KP201439	KP201378	KP201309

(continued)

Table 1. continued.

Species names	Extraction code	Voucher number	GenBank Accession Number			
			CO1	28S	18S	H3
Eriauchenius gracilicollis (1)	hw0001AB	9018979	KP201222	KP201424	KP201359	KP201292
Eriauchenius gracilicollis (2)	hw0002	9018980	KP201219	KP201419	KP201351	KP201285
Eriauchenius spiceri	hwsp3	9001002	DQ914568	NA	KP201355	KP201289
Eriauchenius voronakely (1)	hwsp9	9009659	DQ914564	KP201421	KP201353	KP201287
Eriauchenius voronakely (2)	hw0007	9018985	KP201243	KP201440	KP201379	KP201310
Eriauchenius voronakely (3)	hw0023	9018985	KP201223	KP201425	KP201360	NA
Eriauchenius namoroka	hwsp7	9018916	DQ914567	KP201423	KP201356	KP201290
Eriauchenius halambohitra	hwsp8	9004603	DQ914566	KP201420	KP201352	KP201286
Eriauchenius sp. 4 (1)	hw0057	9028293	JX240244	JX240295	JX240264	JX240313
Eriauchenius sp. 4 (2)	hw0128	9028332	KP201271	KP201458	KP201406	KP201336
Eriauchenius ambre	hw0008	9018986	KP201235	KP201434	KP201372	KP201303
Eriauchenius jeanneli (1)	hw0011AB	9018989	KP201245	KP201442	KP201381	KP201311
Eriauchenius jeanneli (2)	hw0026	9019010	KP201221	NA	KP201358	NA
Eriauchenius workmani (1)	hw0006	9018984	JX240246	JX240280, JX240297	JX240266	JX240315
Eriauchenius workmani (2)	hw0070	9028321	KP201236	KP201435	KP201373	KP201304
Eriauchenius workmani (3)	hw0069	9028309	KP201232	KP201431	KP201369	KP201300
Eriauchenius sp. 5 (1)	hw0005	9018983	KP201234	KP201433	KP201371	KP201302
Eriauchenius sp. 5 (2)	hw0004	9018982	KP201216	KP201417	KP201349	KP201282
Eriauchenius sp. 6	hw0071	9028370	KP201238	KP201436	KP201375	KP201306
Eriauchenius sp. 7	hw0122	9015039	KP201272	NA	KP201407	KP201337
Eriauchenius sp. 8	hw0123	9018159	KP201266	NA	KP201401	KP201332
Eriauchenius sp. 9	hw0125	9028371	KP201274	NA	KP201409	KP201338
Eriauchenius sp. 10 (1)	hw0129	9028340	KP201270	NA	KP201405	KP201335
Eriauchenius sp. 10 (2)	hw0131	9028313	KP201267	NA	KP201402	KP201333
Eriauchenius mahariraensis	hw0092	9028297	KP201210	NA	NA	KP201277
Eriauchenius sp. 11 (1)	hw0061	9028315	JX240247	NA	JX240267	JX240316
Eriauchenius sp. 11 (2)	hw0087	9028300	KP201212	NA	KP201345	KP201279
Eriauchenius bourgini	hw0121	9014938	KP201268	NA	KP201403	KP201334
Eriauchenius sp. 12	hw0058	9012346	KP201224	NA	KP201361	KP201293
Eriauchenius sp. 13 (1)	hw0063	9028360	KP201250	NA	KP201386	KP201316
Eriauchenius sp. 13 (2)	hw0067	9028299	KP201218	NA	NA	KP201284
Eriauchenius sp. 14 (1)	hw0062	9028290	KP201249	NA	KP201385	KP201315
Eriauchenius sp. 14 (2)	hw0085	9028425	KP201220	NA	KP201357	KP201291
Eriauchenius sp. 15	hw0059	9009481	KP201248	NA	KP201384	KP201314
Eriauchenius ratsirarsoni (1)	hw0072	9028378	KP201241	NA	NA	KP201308
Eriauchenius ratsirarsoni (2)	hw0068	9028298	KP201253	NA	NA	KP201319
Afrarchaea woodae (1)	hw57Af1	9018957	JX240249	JX240282, JX240299	JX240269	JX240318
Afrarchaea woodae (2)	hw0110	9028446	KP201261	NA	KP201396	KP201327
Afrarchaea entabeniensis (1)	hw60Af4	9018960	KP201217	KP201418	KP201350	KP201283
Afrarchaea entabeniensis (2)	hw61Af4	9018961	KP201215	KP201416	KP201348	KP201281
Afrarchaea sp. 1	hw0106	9028441	KP201257	KP201449	KP201392	KP201323
Afrarchaea sp. 2	hw0103	9028445	KP201254	KP201446	KP201389	KP201320
Afrarchaea bergae (1)	hw59Af3	9018959	JX240248	JX240281, JX240298	JX240268	JX240317
Afrarchaea bergae (2)	hw62Af3	9018962	KP201231	KP201430	KP201368	KP201299
Afrarchaea ngomensis	hw0111	9034605	KP201262	KP201453	KP201397	KP201328
Afrarchaea royalensis (1)	hw0109	9028449	KP201260	KP201452	KP201395	KP201326
Afrarchaea royalensis (2)	hw0104	9028451	KP201255	KP201447	KP201390	KP201321
Afrarchaea lawrencei	hw0107	9028444	KP201258	KP201450	KP201393	KP201324
Afrarchaea harveyi (1)	hw0108	9028452	KP201259	KP201451	KP201394	KP201325

(continued)

Table 1. continued.

Species names	Extraction code	Voucher number	GenBank Accession Number			
			CO1	28S	18S	H3
Afrarchaea harveyi (2)	hw0105	9028447	KP201256	KP201448	KP201391	KP201322
Afrarchaea harveyi (3)	hw0113	9034608	KP201264	KP201455	KP201399	KP201330
Afrarchaea sp. 3	hw58Af2	9018958	KP201252	KP201445	KP201388	KP201318
Afrarchaea cornutus (1)	hw0117	9034612	KP201265	KP201456	KP201400	KP201331
Afrarchaea cornutus (2)	hw0112	9028443	KP201263	KP201454	KP201398	KP201329
Afrarchaea sp. 4	hw0027	NMBA10466	KP201213	KP201414	KP201346	KP201280

Numbers in parentheses following species name denote the individual specimen. Unless otherwise specified the voucher number is from the California Academy of Sciences Entomology Department (CASENT); NMBA, National Museum, Bloemfontein; MAD, Madagascar; SA, South Africa; AU, Australia; NA, missing.

To examine the timing of divergence, a time-calibrated phylogeny was created by treating archaeid fossil taxa as noncontemporaneous tips following the methods of Pyron (2011) and Wood et al. (2013). For each terminal fossil, the geological stage and reference are listed: (1) *Archaea paradoxa*, *Baltarchaea conica*, and *Myrmecarchaea* sp., from Baltic amber, Eocene, Lutetian, 44–49 Ma (Penney et al. 2011); (2) *Burmesarchaea grimaldii*, from Burmese amber, Cretaceous: Cenomanian-Turonian, 88–95 Ma (Penney 2003); (3) *Patarchaea muralis*, compression fossil, Middle Jurassic (Chen et al. 2004; Gao and Ren 2006), 161–176 Ma (based on www.geosociety.org/science/timescale/ last accessed August 8, 2014). The fossil age input was the median of the estimated range, for example, 46.5 Ma for the Baltic amber fossils. The root age was constrained, being treated as a normal distribution with a mean of 225 Ma with soft upper and lower bounds (standard deviation = 30; 5–95% bounds = 175.7–274.3 Ma), based on the age of the oldest Araneomorphae fossil (Selden et al. 1999), which is also close in age to the oldest Mygalomorphae fossil (Selden and Gall 1992; Penney et al. 2003). The breadth of this prior constraint was intentionally large to contain the true age of Araneomorphae divergence and so as not to bias the study.

We estimated the mean node ages and their 95% Bayesian credible interval (CI) using a relaxed clock model implemented in BEAST (Drummond and Rambaut 2007). The taxa, molecular markers, and partitions used for the phylogenetic analysis were also used for the BEAST analysis except duplicate species were pruned so that only one representative per species remained. The same partition models from the Bayesian phylogenetic analysis were used except that partition 2 and 3 (representing COI and H3) were changed to the simpler Hasegawa–Kishino–Yano (HKY) model. This was done to provide an analysis with a much lower chance of convergence problems and parameter nonidentifiability as these partitions were conserved, not having enough variation for their parameters to reach convergence. The molecular clock model was set to relaxed, uncorrelated lognormal and the tree prior was set to speciation, birth–death process. Five MCMC analyses were run for 30 million generations, sampling the chain every 1000 generations. Log files were visualized in Tracer version 1.4 to ensure that the effective sample size of the combined log files reached 200 for all parameters (Drummond et al. 2006). The burn-in was removed from each independent run and the resulting tree files were combined. Because mitochondrial DNA markers can lead to age overestimations under certain conditions (Near et al. 2012), this analysis was repeated excluding COI. Additionally, the original analysis was also performed using the independent gamma rates (IGR) model in MrBayes version 3.2.2 (Ronquist et al. 2012b) following the methods of Ronquist et al. (2012a), however the results were not realistic (see Supporting Information).

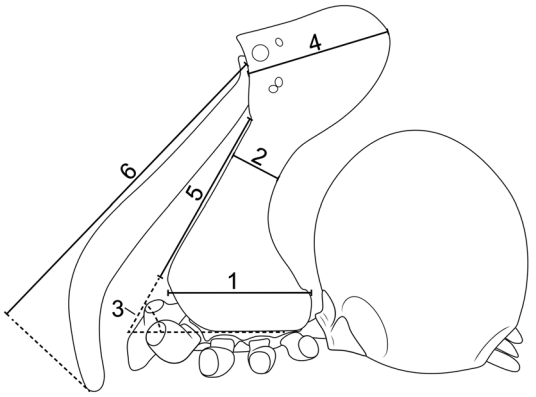

Figure 2. **Diagram showing the measured morphological traits, lateral view, legs removed. (1) Carapace length, (2) carapace constriction, (3) carapace angle, (4) "head" length, (5) "neck" length, (6) chelicerae length. Measurement 7, femur I length, not shown.**

MEASUREMENTS AND HABITAT DATA

We measured seven morphological traits of the cephalothorax and one measurement of standard length per species (Fig. 2). The specific traits measured were: (1) carapace length; (2) carapace

constriction, defined as the depth from anterior to posterior of the narrowest portion of the "neck" in the lateral habitus view; (3) carapace angle, defined as the angle between the posterior edge of the lateral side of the carapace (the portion above coxae II and III) and the anterior edge of the "neck" in the lateral view; (4) anterior "head" length, defined as the length between the clypeus and the posterior edge of the "head," taken perpendicular to the cheliceral foramen in the dorsal view; (5) "neck" length, defined as the length from the bottom edge of the cheliceral foramen to the bottom edge of the carapace, taken in the anterior view; (6) chelicerae length; (7) length of femur I. Carapace width was used as the measurement for size. These traits were selected because of their ecological and functional significance in predatory attacks (Wood et al. 2007; Wood 2008). Measurements were taken, when possible, for five males and five females per species, and all traits were natural log transformed and averaged per species. The effect of size was removed by performing a phylogenetic linear regression on each measurement against the size measurement, and then retaining the residual values for each species (Revell 2009). The size-corrected residuals were used as inputs for a phylogenetically corrected principal components analysis and the resulting eigenstructure and scores were extracted for each species. Even though Australian species are undersampled, we feel that we have adequately sampled the morphospace, as we have a range of morphologies including long and short "necked" species from the three major Australian clades (Rix and Harvey 2011, 2012a,b).

Habitat data were used to examine whether Madagascar species have a greater rate of habitat evolution than their non-Madagascan relatives. Habitat was assessed based on the collection methods used to obtain the specimens, which explicitly records habitat of occurrence based on the techniques used. Habitat was broken into two categories, (1) up in the vegetation or (2) down on the forest floor, per specimen, and was then treated as a continuous trait, per species, of the percentage of time collected in the vegetation. A specimen was recorded as being in the vegetation if it was collected either by beating vegetation or by hand in the vegetation, and as being on the ground if it was collected from either pitfall traps, sifting litter, sweeping, or turning over rocks and logs. Per species, these values were turned into a percentage by dividing the specimens collected in vegetation by the total number of observations. Collection methods were examined mostly from the California Academy of Sciences (CAS) collection, but also from field expeditions made during the course of this study, and from the literature. There was an average of 19 observations per species with a range of 1–215. The species that did not have any recorded habitat data were pruned from the phylogeny for any subsequent analysis that examined habitat. Our characterization of habitat is a simplified version and thus, an underestimation of true habitat diversity: observations of HMW suggest there may be more habitat niches, however, currently, we do not have enough data to test this. Eighteen species in the dataset had less than five habitat observations. Although this lack of data is acknowledged, we still believe there are real differences between habitats among species.

LINEAGE AND TRAIT DIVERSIFICATION

Rate of lineage diversification was tested using the gamma statistic (Pybus and Harvey 2000) to examine how lineage diversification proceeded through time. Negative values of gamma indicate that internal nodes are disproportionally placed closer to the root than expected under the Yule model of speciation, suggesting that diversification rates are slowing over time. The Monte Carlo constant rates test (MCCR), which takes incomplete lineage sampling into account, was implemented in the R package LASER (Rabosky 2006) to identify the critical value for rejecting a constant diversification rate. The MCCR test was performed 5000 times for 37 total taxa with four taxa randomly removed from the phylogeny, mimicking the incomplete taxa sampling of the empirical Madagascar archaeid dataset (non-Madagascan archaeids were pruned from the phylogenies). Then the gamma statistic was calculated for 500 randomly sampled phylogenies from the post-burn-in BEAST output using "gammaStat" in the R package "ape" (Paradis et al. 2004).

We also tested rates of trait evolution in morphology and habitat and predicted that there would be greater rates in the Madagascar lineages compared to the non-Madagascan lineages. Maximum-likelihood rates of morphological evolution were calculated from the first two PC axes, the individual measurements, and the habitat data using the censored rate test implemented in the program Brownie version 2.1 (O'Meara et al. 2006). This program takes into account the lack of independence between species due to phylogenetic structure as well as time since divergence. The censored rate test was used because this method independently calculates the rate of evolution of groups in different parts of the phylogeny. In a pairwise fashion we compared the rate of diversification in lineages from two different areas (i.e., Madagascar compared to South Africa and Madagascar compared to Australia) by statistically testing whether a single rate model is worse than a multiple rate model whereby each compared group is allowed its own rate of evolution. The maximum-likelihood estimates of the rate of morphological and habitat evolution were compared using the Akaike Information Criterion (AIC) and likelihood ratio test (LRT). Due to small sample sizes, we used the AICc and performed 1000 parametric bootstrapping replications on the LRT. To account for uncertainty in branch lengths and phylogenetic topology this analysis was performed on 500 randomly sampled phylogenies from the BEAST output and results were averaged. Outgroups, fossils, and duplicate species were pruned from the phylogenies.

MORPHOLOGICAL ADAPTATION

Natural history and laboratory observations suggest that archaeids, regardless of the carapace shape, prey upon all types of spiders, rather than specific spider groups (e.g., orb-weavers, hunters, sheet-weavers) (Wood et al. 2012). However, morphological traits could instead be linked to habitat rather than prey type, and correlations between morphology and the environment may suggest adaptation. We examined whether morphology was correlated with habitat using phylogenetic generalized least-squares regression (PGLS) (Martins and Hansen 1997). The PGLS analyses were first performed on the BEAST consensus phylogeny assuming different models of evolution, that is, Brownian (Felsenstein 1985), Pagel's lambda (Pagel 1999), accelerate or decelerate (ACDC; Blomberg et al. 2003), and single-peak Ornstein–Uhlenbeck (Butler and King 2004), which then were compared for best fit using the AIC criteria. Then, assuming the best model, PGLS was performed using 500 randomly sampled phylogenies from the BEAST output and results are reported as averages. PGLS was performed treating the separate morphological PC axes as the response variable and habitat (percentage of time found in vegetation) as the explanatory variable. These analyses were performed twice: for all archaeids, and for only the Madagascan archaeids (with pruning of non-Madagascan archaeids). Analyses were performed using the R packages "ape" and "nlme" (Paradis et al. 2004; Pinheiro et al. 2007).

SPECIES RICHNESS AND ENDEMICITY

Distribution patterns on Madagascar were examined to better understand where species were accumulating. We were specifically interested in examining whether montane areas in Madagascar correspond to distribution patterns, as many archaeids occur at higher elevations. The majority of the species distributions were based on sampling that was performed for over 10 years at over 200 localities throughout Madagascar by the CAS Madagascar Arthropod Inventory Survey. Sampling techniques followed a systematic protocol that used a variety of collecting techniques so as not to bias the study toward certain habitats or localities (Fisher 2005). Distributional data were treated as points per species and were translated into a one-quarter degree square grid that was mapped onto Madagascar using the R packages "raster" (Hijmans 2013) and "sp" (Pebesma and Bivand 2005; Bivand et al. 2013). We then calculated species richness and corrected weighted endemism (CWE) per grid cell. Species richness is a measure of the total number of species per grid cell (Linder 2001). "Weighted endemism" (WE) is similar to species richness except that the totaled per species values are weighted by the total number of grid cells occupied by a species, so that a species that occupies four grid cells will be assigned a value of 0.25 per occupied grid cell. CWE was then calculated by dividing WE (combined for all species in the cell) by the total number of species per grid cell (Crisp et al. 2001). We then performed a linear regression of the dependent variables of species richness and CWE against altitude. The altitude variable was the maximum extracted per grid cell. Species richness and CWE were calculated for 36 of 37 total Madagascan species. The species *Eriauchenius pauliani* was excluded from the spatial analyses as it has not been collected since the advent of GPS, so that we do not have comparable precision to those of other *Eriauchenius*.

ANCESTRAL RANGE RECONSTRUCTIONS

An ancestral area reconstruction was performed for two purposes: (1) to examine shifts into new ecogeographic regions, and (2) to compare ecogeographic distributions among close relatives. Biogeographic regions were based on Du Puy & Moat's (P&M) vegetation types (1996), which correspond to the ecogeographic regions in Madagascar (Fig. 6A), and were classified into three areas: rainforests (P&M vegetation types: evergreen humid at low, mid, and montane elevations, and evergreen sclerophyllous woodland); western deciduous forests (P&M vegetation type: deciduous, seasonally dry); southern spiny dry forests (P&M vegetation type: deciduous dry). Ancestor reconstructions were implemented in the R package "BioGeoBEARS" (Matzke 2014), which reproduces the biogeography programs LAGRANGE (Ree and Smith 2008), DIVA (Ronquist 1996), and BayArea (Landis et al. 2013), while also allowing for cladogenesis (e.g., founder events) by introducing an additional parameter "j." We used the BEAST consensus phylogeny with pruning of the non-Madagascan taxa and duplicate taxa, and used likelihood, Bayesian, and parsimony methods, with and without the "j" parameter. The best model was selected using the AICc criterion and the LRT.

Results

PHYLOGENETIC ANALYSIS AND DIVERGENCE DATING

Our alignment resulted in a total evidence concatenated dataset with 5599 characters, consisting of 126 morphological characters, 658 base pairs (bp) for COI, 328 bp for H3, 2572 bp for 18S, 1915 bp for 28S. The concatenated dataset had 3342 variable sites, and 2795 phylogenetically informative sites. The total evidence phylogeny is shown in Fig. 3 and the phylogenies from the molecular-only and the morphology-only analyses, including a discussion of differences, are in the Supporting Information. We used the total evidence analysis as the best estimate of the phylogenetic relationships because this analysis incorporates multiple lines of evidence. The total evidence analysis recovered a monophyletic Archaeidae, a monophyletic grouping of the extant archaeids, and a monophyletic grouping of the fossil archaeids. Among the

extant archaeids, the Australian clade is sister to the Madagascar + Africa clades. The Madagascar clade is paraphyletic with respect to southeastern Africa. With the exception of the fossil taxa, the majority of the branches are well supported with pp greater than 0.95. The monophyletic extant archaeids have branch support of 0.84. We do not think this is problematic in that extant archaeid monophyly is strongly supported by molecular data (pp = 1.0) and morphological data (pp = 1.0).

Regarding the estimation of timing of diversification, there were moderate amounts of rate heterogeneity, meaning that the data are not clock-like: the mean coefficient of variation was 1.041 and the mean ucld.stdev was 0.843. There was not strong evidence for autocorrelation (mean covariance = 0.041). The resulting summary chronogram is presented in Fig. 4. The analysis with COI excluded had weaker branch support at some nodes, but there were no topological conflicts, and the mean divergence date estimations were only slightly younger, and therefore, did not alter our major conclusions (see Supporting Information).

Mean values indicate that archaeid origination began to diversify in the Jurassic-Triassic (Fig. 4, node 1, mean = 205 Ma, 95% CI = 176–237). Diversification of the extant archaeids occurred in the Jurassic with the Australian clade splitting with the Madagascar + South African clade (node 2, mean = 177 Ma, 95% CI = 137–217). The diversification event that gave rise to the Madagascan and southeastern Africa genera occurred 151 Ma (node 3, 95% CI = 115–191), with diversification of the Madagascar "Gracilicollis Group" occurring 116 Ma (node 4, 95% CI = 79–157) and diversification of Madagascan *Eriauchenius* occurring 108 Ma (node 5, 95% CI = 75–143). *Eriauchenius* diverged from *Afrarchaea* a mean of 136 Ma (node 6, 95% CI = 100–173). *Afrarchaea* began to diversify 82 Ma (node 7, 95% CI = 47–120), and the Australian clade began to diversify 89 Ma (node 8, 95% CI = 45–134). The 95% CI are broad in the majority of estimated divergences.

LINEAGE AND TRAIT DIVERSIFICATION

We ran all subsequent analyses with the individual measurements and the scores from the first two morphological PC axes, which had eigenvalues greater than one, and explain 65.2% and 14.3% of the data (Fig. 5), and combined 79.5%. PC1 describes the elongation and constriction of the "neck," chelicerae, and legs from the following measurements: carapace constriction, "neck" length, chelicerae length, and femur I length. PC2 describes the angle of carapace tilt.

The gamma statistic was calculated for 500 randomly sampled phylogenies and compared with the recovered critical value from the MCCR test. The majority (92.6%) of the 500 sampled phylogenies had a gamma statistic that was less than the critical value (= −1.787), suggesting that rates of lineage diversification are slowing over time in the Madagascan archaeids (see Fig. S4).

Madagascan archaeids consistently showed a higher rate of trait and habitat diversification compared to the Australian and South African clades (Table 2). These findings are strongly supported (P-value < 0.05) in PC1, carapace length, carapace constriction, "neck" length, and habitat. Although weakly supported, Madagascar also shows a higher rate of diversification in chelicerae length and femur length. The greatest rate difference recovered was for the habitat trait, followed by carapace constriction. Because Madagascan archaeids are a paraphyletic group, having two distinct clades, with the southeastern African *Afrarchaea* nested within, we performed an additional trait diversification analysis treating Madagascar as two groups. The results of this analysis can be found in the Supporting Information, and did not alter our major conclusions.

MORPHOLOGICAL ADAPTATION

Brownian motion and early burst (ACDC) models were the best fit, with Pagel's lambda having a slightly higher AICc score, and the Ornstein–Uhlenbeck model performed the worst. For this reason PGLS analysis was performed assuming a Brownian motion model, and results are reported as averages of 500 randomly sampled phylogenies (Table 3). There was a strong correlation between PC1 and habitat, confirming that archaeids that live in the vegetation, compared to those that live on the ground, have longer, more constricted "necks," and longer chelicerae, "heads," and legs.

SPECIES RICHNESS AND ENDEMICITY

Many archaeid species appeared to be microendemics, with 18 of 36 species occupying two or less adjacent grid cells. Because of the intensive sampling effort through CAS and because local endemics were not collected in more distant areas, we tentatively conclude that many Madagascan archaeid species are true local endemics, rather than being artifacts of biased sampling. Species richness measurements ranged from 1 to 8 (average = 2.37) per grid cell on Madagascar, with the highest values occurring in Ranomafana and Masoala national parks (Fig. 6B). Other areas of high species richness include portions of the eastern rainforests, Parc National Montagne d'Ambre in the far North, and Parc National Namoroka in the West. Calculations of CWE reveal that the highest values are found in the southeast (Fig. 6C).

There was no statistical support for a linear relationship between species richness and altitude (P-value: 0.0973, adjusted R^2: 0.0399), although the mid-elevations from 900 to 1500 m have the greatest number of species (Fig. 7B). However, there was support for a positive relationship between CWE and altitude, both with and without an outlier point removed—with outlier:

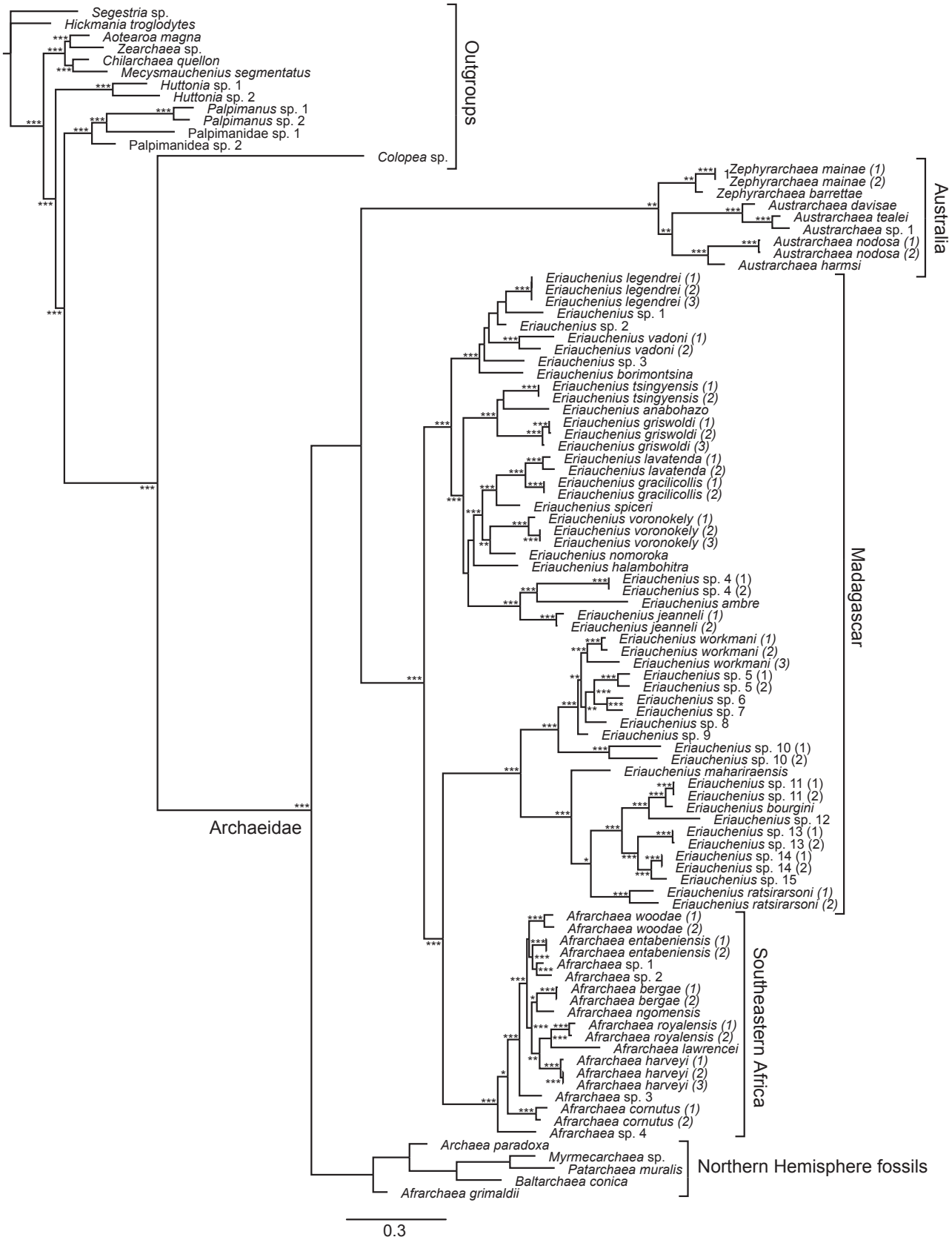

Figure 3. **Total evidence phylogeny from Bayesian analysis of molecular and morphological data. Numbers in parentheses following species name denote the individual specimen, see Table 1. Posterior probabilities are as follows, greater than or equal to: (*) 0.90; (**) 0.95; (***) 0.99.**

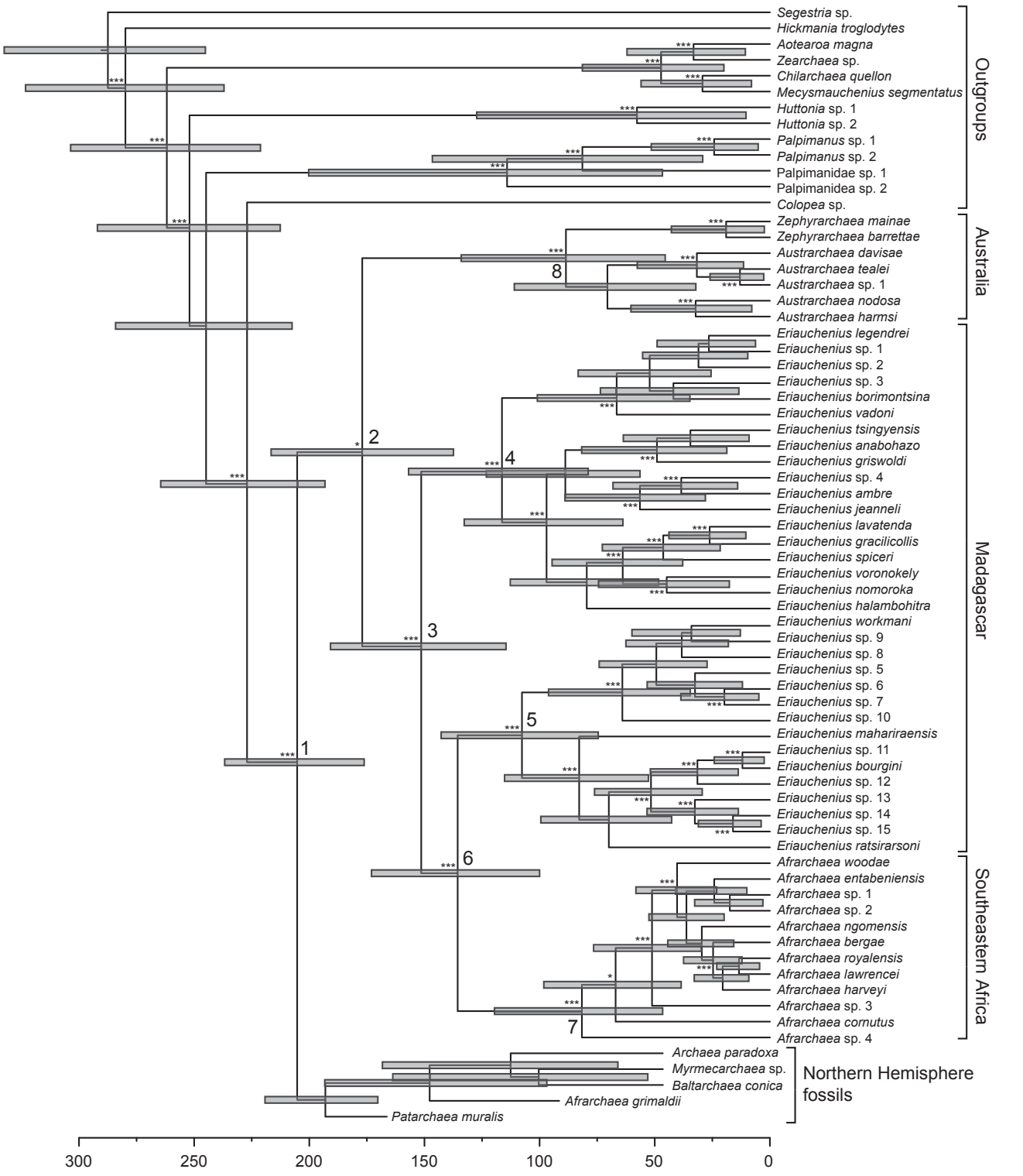

Figure 4. **Dated phylogeny with branch lengths drawn to reflect BEAST divergence age estimation. Error bars reflect the 95% Bayesian credible interval (CI). Numbers next to nodes follow the discussion in the text. Posterior probabilities are as follows, greater than or equal to: (*) 0.90; (**) 0.95; (***) 0.99. Scale at bottom = millions of years before present.**

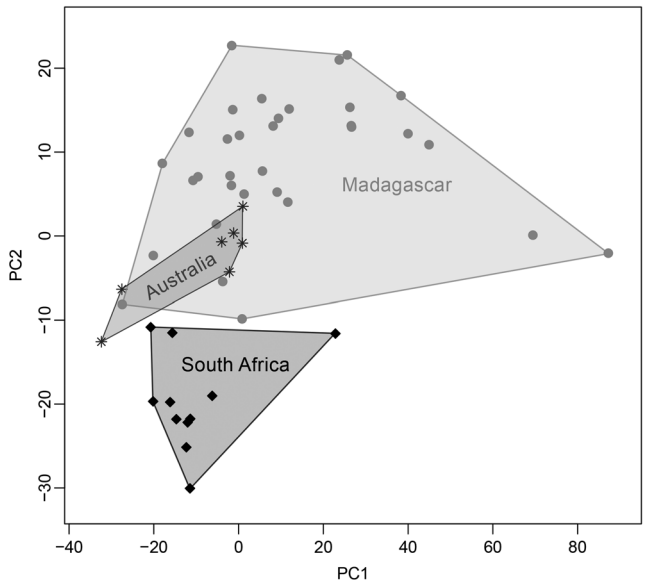

Figure 5. Morphospace plot of first two principal components for seven phylogenetically size-corrected traits.

P-value: 0.000479, adjusted R^2: 0.2273; without outlier: *P*-value: 0.00000055, adjusted R^2: 0.433 (Fig. 7A).

ANCESTRAL RANGE RECONSTRUCTIONS

The ancestral area reconstruction method using the likelihood dispersal-extinction-cladogenesis (DEC) model (Ree and Smith 2008) was selected as the best model, having the lowest AICc score. The LRT found there was no significant difference (*P*-value = 1) between DEC and DEC + *j* (*j* = the cladogenesis parameter), which makes sense because "*j*" was estimated to be close to zero ($j = 0.0086$). For the DEC model, the estimated rate of dispersal was 0.0018 and the estimated rate of extinction was essentially zero. The ancestral reconstruction (Fig. 6D) supports two main findings: (1) there were several range expansions to different ecogeographic regions, including a shift to the western deciduous forests within the "Gracilicollis Group" (nodes 1–2 in Fig. 6D); (2) the estimated rate of dispersal is low suggesting that species have mostly retained the same ecogeographic ranges as their ancestors.

Discussion

The motivation for this study was to unravel the signature of diversification in an ancient lineage by examining an area known for major geoclimatic upheavals (Madagascar) and then comparing the pattern of diversification in Madagascar with lineages in other areas where the environment has been relatively stable. First, we examined timing of divergence to explain how evolution proceeded in Madagascar. Our estimated divergence dates for the deep nodes within the archaeids are validated by the findings of Wood et al. (2013), whereas our mean value estimations are older, there is broad overlap in the 95% CI. The current study and Wood et al. (2013) both recovered estimated divergence dates that are consistent with the timing of continental breakup, although the 95% CI are very broad. Wood et al. (2013) suggested that the southeastern African *Afrarchaea* formed following a dispersal event from Madagascar to Africa, however, the current study recovered an older estimated divergence for the South African clade. Rifting began between Africa and Madagascar around 165 Ma (Rabinowitz et al. 1983), suggesting that vicariance is a plausible explanation for the African clade. Although *Afrarchaea* is only known to occur in eastern South Africa, whereas a vicariance scenario suggests they should occur in Afromontane areas throughout Africa (White 1978); see Wood et al. (2013) for a discussion of global extinction within archaeid spiders. Regardless, species diversification in the Madagascan archaeids is due, not to founder effects from a recent dispersal, but instead due to ancient processes, with adaptive diversification occurring over long periods of geologic time.

Additionally, the majority of shallower divergences among Madagascan sister-species pairs are older than could be caused by Pleistocene climate fluctuations. The age of the most recent sister-species divergence on Madagascar, between *Eriauchenius bourgini* and *Eriauchenius* sp.11 (mean = 11.9 Ma, 95% CI = 2.5–24.2), has the 95% CI lower bound extending into the Pleistocene and the upper bound into the Oligocene. This is the youngest sister-species pair and the majority of estimated divergences of the remaining pairs do not extend into the Pleistocene. These findings contrast with some of the hypothetical diversification mechanisms suggested for Madagascar that explain the production of current biodiversity according to worldwide Pleistocene climate fluctuations. In fact, of the few phylogenetic studies of Madagascan taxa that estimate sister-species divergence times or genetic divergences, all have recovered divergences that are incompatible with Pleistocene climate cycles, suggesting more ancient processes are occurring in the Madagascan biota (Townsend et al. 2009).

Second, we examined topological and climatic features that may be responsible for the timing of divergence and distribution patterns. Montane areas on Madagascar may be important in explaining why certain areas have high amounts of species richness, with sometimes up to eight species per cell (Fig. 6B). We found support for a positive correlation between endemicity and elevation (Fig. 7A), consistent with the hypothesis that montane areas support short-range endemics by allowing these lineages to persist in a stable area despite global climate instability (Fjeldså and Bowie 2008; Fjeldså et al. 2012). Although we did not recover statistical support for a linear relationship between elevation and species richness, species richness was greatest at

Table 2. Rates of morphological evolution from the censored rate test comparing a single rate model with a multiple rate model for Madagascar lineages versus South African and Australian lineages.

Trait	1-Rate estimation	Clade	2-Rate estimation	ΔAICc	*P*-value
PC1	5.44	Madagascar South Africa	6.64 1.81	3.17*	0.043*
PC1	5.71	Madagascar Australia	6.64 1.31	3.00	0.053
PC2	1.08	Madagascar South Africa	1.14 0.91	−1.99	0.63
PC2	1.02	Madagascar Australia	1.14 0.44	−0.036	0.22
Habitat	1.90×10^{-3}	Madagascar South Africa	2.70×10^{-3} 1.60×10^{-5}	45.25*	<0.0001*
Habitat	2.30×10^{-3}	Madagascar Australia	2.70×10^{-3} 1.00×10^{-3}	−0.17	0.23
1. Carapace length	5.62×10^{-5}	Madagascar South Africa	6.56×10^{-5} 2.78×10^{-5}	0.41	0.17
1. Carapace length	5.50×10^{-5}	Madagascar Australia	6.56×10^{-5} 5.09×10^{-6}	8.58*	0.0045*
2. Carapace constriction	4.51×10^{-4}	Madagascar South Africa	5.56×10^{-4} 1.34×10^{-4}	4.10*	0.025*
2. Carapace constriction	4.77×10^{-4}	Madagascar Australia	5.56×10^{-4} 1.02×10^{-4}	3.39*	0.041*
3. Carapace angle	7.64×10^{-5}	Madagascar South Africa	9.34×10^{-5} 3.15×10^{-5}	1.65	0.088
3. Carapace angle	8.10×10^{-5}	Madagascar Australia	9.14×10^{-5} 3.23×10^{-5}	0.76	0.19
4. Anterior head	1.49×10^{-4}	Madagascar South Africa	1.62×10^{-4} 1.10×10^{-4}	−1.65	0.49
4. Anterior head	1.43×10^{-4}	Madagascar Australia	1.62×10^{-4} 5.48×10^{-5}	0.37	0.17
5. Neck length	7.35×10^{-4}	Madagascar South Africa	8.96×10^{-4} 2.52×10^{-4}	2.92*	0.046*
5. Neck length	8.03×10^{-4}	Madagascar Australia	8.96×10^{-4} 3.66×10^{-4}	−0.35	0.25
6. Chelicerae length	3.43×10^{-4}	Madagascar South Africa	4.17×10^{-4} 1.21×10^{-4}	2.73*	0.05
6. Chelicerae length	3.76×10^{-4}	Madagascar Australia	4.17×10^{-4} 1.82×10^{-4}	−0.60	0.29
7. Femur I	6.63×10^{-4}	Madagascar South Africa	8.01×10^{-4} 2.47×10^{-4}	2.33*	0.06
7. Femur I	7.07×10^{-4}	Madagascar Australia	8.01×10^{-4} 2.59×10^{-4}	0.61	0.15

[1]**Values with an asterisk (*) have an ΔAICc score greater than 2 or a *P*-value less than 0.05.**

the mid-elevations (Fig. 7B), suggesting that montane areas are accumulating species. Montane areas may facilitate speciation by isolation, due to climate shifts causing forest contraction into montane refugia; additionally, montane areas may also allow lineages to persist due to local topographic complexity that may moderate global climate (Fjeldså and Lovett 1997; Fjeldså and Rahbek 2006). An example of the importance of montane areas to archaeid diversification is from areas in the southeast: the species *Eriauchenius* sp.15 is endemic to the Andohahela massif and is sister to *Eriauchenius* sp.14, endemic to the Andrigitra massif (mean divergence = 16.0 Ma, 95% CI = 3.8–31.1 Ma); the sister species to this pair, *Eriauchenius* sp.13, is endemic to the Andohahela massif (mean = 32.6 Ma, 95% CI = 13.7–53.3 Ma). Furthermore, an additional species *E. pauliani*, which was not included in

Table 3. Results from phylogenetic generalized least-squares regression (PGLS), with morphological traits treated as the response variable and habitat as the explanatory variable.

	PC1	PC2	1. Carapace length	2. Carapace constriction	3. Carapace angle	4. Anterior head	5. Neck length	6. Chelicerae length	7. Femur I
For all archaeid taxa									
P-value	0.0020*	0.0222*	0.4219	0.0063*	0.3870	0.0055*	0.0017*	0.0023*	0.0004*
Slope	20.9739*	8.1927*	0.0183	−0.1835*	−0.0249	0.1146*	0.2609*	0.1672*	0.2812*
For only Madagascar archaeids									
P-value	0.0105*	0.0521	0.4279	0.0168*	0.6046	0.0079*	0.0093*	0.0121*	0.0049*
Slope	21.5945*	7.3118	0.0213	−0.1990*	−0.0174	0.1248*	0.2605*	0.1628*	0.2706*

Results are averages from analyses using 500 randomly sampled ultrametric phylogenies. Values with an asterisk (*) have a *P*-value less than 0.05.

the phylogeny due to a lack of recently collected material, is also only known to occur in Andohahela: morphology suggests that it is a close relative of the previously mentioned species. Madagascar archaeid diversification events may be due to ancient events involving montane areas, as has been suggested for Madagascan *Brookesia* chameleons (Townsend et al. 2009). Montane areas are also important to Madagascan cophyline frogs diversification (Wollenberg et al. 2008), however, this study did not estimate timing of divergence. In Madagascar, as in the Afromontane biota, long-term stability around montane areas may create the scenario where the ancient sites of diversification overlap with more recent sites of diversification (Fjeldså and Lovett 1997).

Species distribution patterns are also consistent with the "rainforest refugia" mechanism (Moritz et al. 2000), however, again, likely due to more ancient climate patterns. Given that many of the montane areas in Madagascar have rainforests, the rainforest refugia mechanisms is likely intertwined with the role of montane areas in preserving and generating diversity. Many of Madagascan archaeids and their ancestors occur in the rainforest ecogeographic region (Fig. 6D), with limited dispersal to different ecogeographic regions. The Madagascan rainforest species are typically separated from sister species by large distances, with some apparent microendemics known from only localized areas. Because the rainforest is reconstructed as the ancestral habitat for Madagascan archaeid species (Fig. 6D), and because many current species are living in rainforests isolated from their close relatives, it may be that fragmentation of these forests allowed for allopatric speciation. We have illustrated several cases that support this theory. *Eriauchenius* sp.4 is known from the eastern rainforest (Masoala and Andasibe), and the sister species, *Eriauchenius ambre* is endemic to the rainforests on Montagne d'Ambre in the far north, a massif surrounded by deciduous forests. Another example, *E. bourgini* is endemic to the Ambohitantely rainforests in the central plateau and around La Mandraka (vague locality, approximately 40 km east of Antananarivo), and the sister species *Eriauchenius* sp.11 is only known from Masoala in the northeast, and there are no records of either species occurring in-between. The same is true for *Eriauchenius* sp.7, which is only known from the rainforests of Ambohitantely and approximately 75 km to the east, and the sister species, *Eriauchenius* sp.6, is only known from high elevation areas in Ranomafana. In fact, the rainforests of Ranomafana have eight co-occurring species: this is not an in situ radiation, but instead all have sister species occurring in distant areas. It is worth mentioning that within the western deciduous forests species are also in allopatry with their closest relatives. For example, *E. anabohazo* is known only from the northwest and its sister species *E. tsingyensis* is known only from the central-west, and the sister species to the pair, *E. griswoldi*, is known only from the south-central west. A more general model of allopatric speciation due to isolation of all Madagascar forest types likely

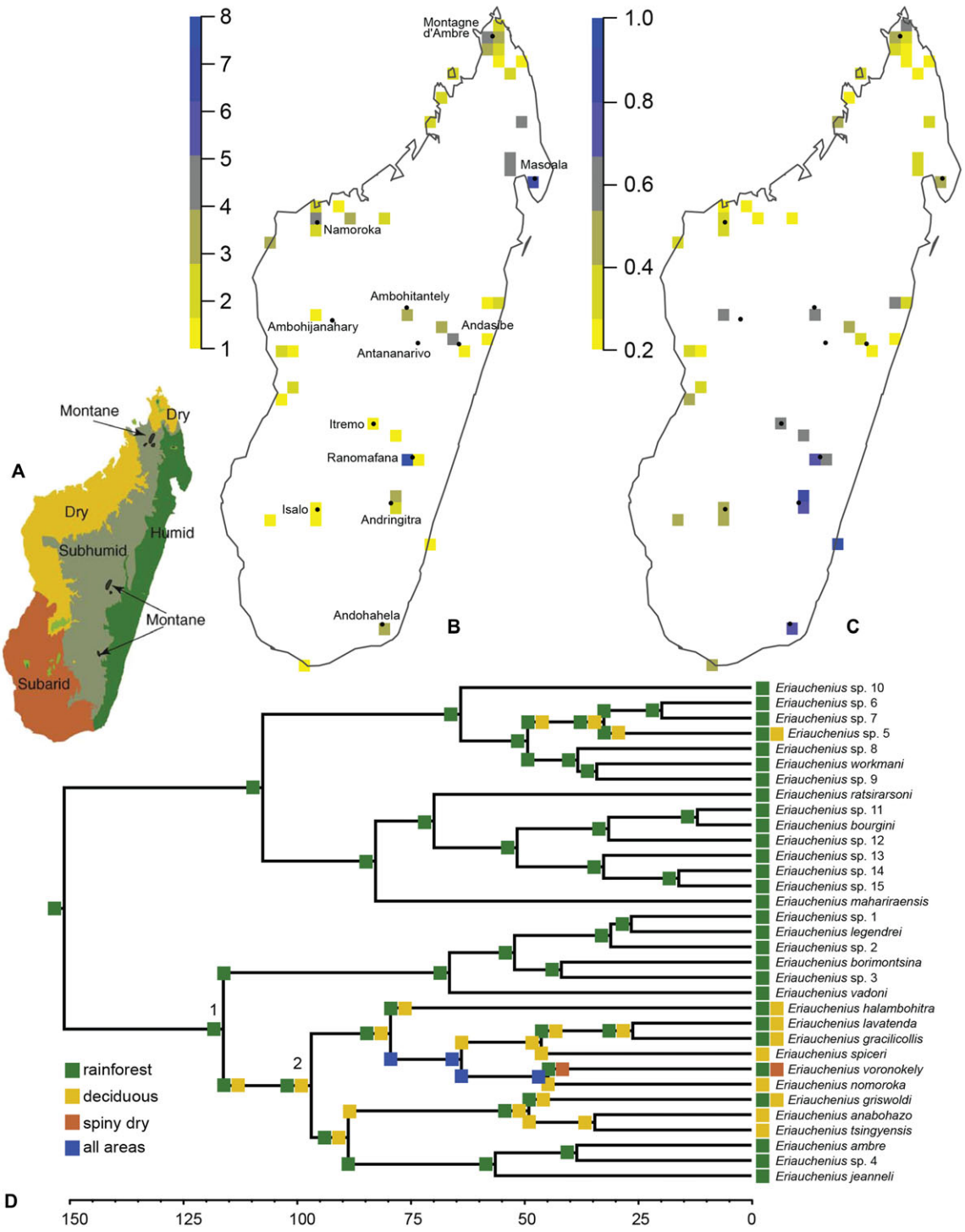

Figure 6. (A) Simplified version of ecogeographic regions of Madagascar, figure taken from Vences et al. (2009). For the ancestral area reconstruction, based on Du Puy and Moat's (1996) vegetation types, "humid" and "montane" correspond to rainforests, "dry" corresponds to deciduous forests, and "subarid" corresponds to the spiny dry forests. Grid showing (B) species richness and (C) corrected weighted endemism (CWE) in Madagascar. Black dots, which are labeled in (B), correspond to Madagascar landmarks: all points represent national parks except for Antananarivo, the capital city. (D) Ancestral area estimation of Madagascan archaeids, scale = millions of years before present. Node numbers follow discussion in manuscript. Colored squares at terminal tips represent the distribution of extant taxa and colored squares at nodes represent ancestral range inheritance scenarios. A single square at an internal node marks when the two descendant lineages have the same inferred range. When the inferred range of the descendants is different, then the ancestral state is shown in the middle and the descendant lineages are shown on either side. Branch support values mimic Figure 4.

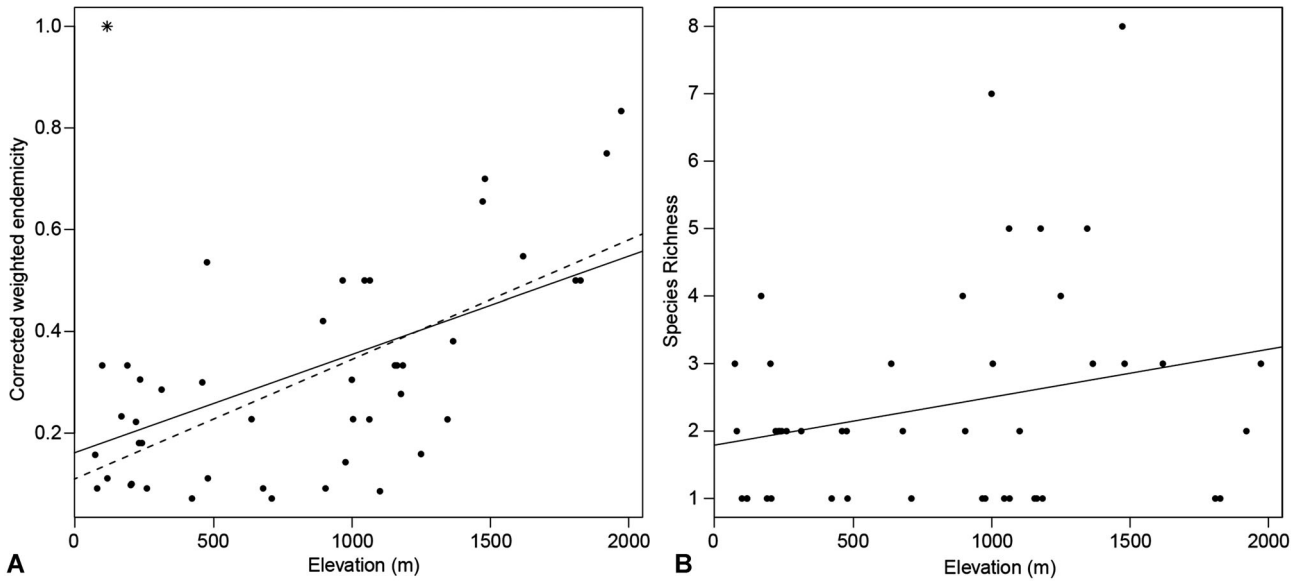

Figure 7. **(A) Linear relationship between corrected weighted endemism (CWE) and elevation (m). Solid line: with outlier, shown as asterisk (*), *P*-value = 0.000479, adjusted R^2 = 0.227. Dashed line: without outlier, *P*-value = 0.00000055, adjusted R^2 = 0.433. (B) Linear relationship between species richness and elevation (m), not statistically significant. Solid line: *P*-value = 0.0973, adjusted R^2 = 0.03991.**

contributes to diversification. These distribution patterns, coupled with divergence times, are suggestive that fragmentation of habitat has occurred over large time spans in Madagascar's history.

Regarding climate shifts, as Madagascar moved northward after tectonic isolation, it developed its modern ecogeographic regions (Wells 2003) and as these ecogeographic regions emerged, organisms may have invaded and adapted to this new habitat. We found that within the "Gracilicollis Group" (Fig. 6D, node 1) an ancestor shifted to the western deciduous forests (Fig. 6D, node 2; mean = 97.0 Ma, 95% CI = 63.8–132.7 Ma). This timing is congruent with the development of the western deciduous forests in the mid-Paleocene. However, the ancestral state reconstructed for Madagascar archaeids is rainforest (Fig. 6D), and the modern rainforests are hypothesized to not have developed until the Eocene (Wells 2003). This inconsistency is likely due to current climate conditions being used to represent past conditions. Furthermore, the fact that archaeids are now in the rainforests may simply be an artifact of these regions being relatively stable montane sites. Several additional instances of range expansions into different ecogeographic regions are supported, such as the species *E. voronokely* that moved into the spiny southern dry forests and *Eriauchenius* sp.5 that moved into the deciduous forests. However, while shifts into different ecogeographic regions appear to have occurred in archaeid diversification, there are fewer shifts into new ecogeographic regions compared to the number of diversification events within the same ecogeographic region.

By comparison, in Australia, archaeids are "characterized by mostly short-range endemic (Harvey 2002; Harvey et al. 2011) allopatric taxa, many of which are restricted to individual mountains or montane systems, and all of which are closely tied to mesic and/or refugial habitats (see Rix and Harvey 2011)" (from Rix and Harvey 2012c). Warm temperate rainforests dominated Australia up until the early Miocene, when mesic habitats underwent contraction into refugia (Crisp et al. 2004; Hopper and Gioia 2004). Rix and Harvey (2012c) showed that speciation events within the Australian archaeids are congruent with the timing of contraction and fragmentation in the Miocene. Although our study recovers older divergences for the deeper nodes in the Australian archaeids, we still recover the shallow divergences as occurring in the Miocene. See Supporting Information for an additional divergence dating analysis that includes additional Australian taxa from Rix and Harvey (2012c).

Similar patterns are revealed in the southeastern African archaeids: species are typically allopatric and the more shallow diversification events occurred in the late Oligocene/early Miocene. Archaeids are only known to occur in the eastern parts of South Africa, which have likely remained mesic from Gondwanan times to the present day (Tyson and Partridge 2000). In the Miocene uplift of the Great Escarpment occurred, followed by erosion, which fragmented the landscape (Partridge and Maud 2000). The four oldest *Afrarchaea* divergences (Fig. 4) gave rise to species that are distributed around the eastern and southeastern coasts. The remaining species diverged in the Miocene and typically occur more inland in areas that are part of the Great Escarpment.

Third, the results of this study reveal that Madagascan archaeids show different trait diversification patterns compared to their non-Madagascan relatives. Madagascan archaeids occupy

a greater degree of morphospace (Fig. 5) and they have a greater rate of diversification in morphological and habitat traits (Table 2). Regarding lineage diversification, the results suggest that Madagascan archaeids have experienced a slowing down of lineage diversification, consistent with adaptive radiation; however, this slowing-down pattern is common and there may be alternative explanations than niche saturation (Moen and Morlon 2014). There is a high amount of sympatry in the Madagascan archaeids: authors CEG and HMW have spent over eight combined months collecting in various localities in Madagascar and have directly observed sympatry among species (e.g., with different species co-occurring in the same microlocality, such as on one tree, at the same time). Although allopatry is the typical pattern among non-Madagascan archaeids (Lotz 1996, 2003, 2006; Rix and Harvey 2011, 2012a,b; H. M. Wood, pers. obs.). Closely related sympatric species are likely in competition and character displacement mitigates this competition (Schluter and McPhail 1993), so that the greater rate of trait diversification in the Madagascan lineages may be due to character displacement in sympatry. Although, instead of character displacement, this could also be due to ecological divergence that occurred in allopatry, prior to secondary contact, over very long periods of time. Although it is not possible from the current distribution to determine whether the changes in morphology and niche occurred while currently sympatric species coexisted or when they were in allopatry, it seems likely that this trait diversity promotes coexistence of species in modern Madagascan communities.

The examined morphological traits appear to be adaptive, evidenced by the strong correlation found between morphology and habitat: species with longer "necks," chelicerae, "heads," and legs, occur more often in the vegetation (Table 3). The reasons for this adaptation may be that archaeids in the vegetation are preying on a different composition of spider fauna, for example, a greater degree of orb-weaver spiders and their relatives, compared to archaeids on the ground, where there are likely more cursorial spiders, making it advantageous to have different morphologies depending on their habitat. Another reason could be that archaeids have different functional lifestyles in the vegetation than on the ground. Life in the open vegetation may be more conducive for allowing morphological traits to elongate, whereas in dense leaf litter on the ground, morphologies may be constrained. This is supported by previous studies that have found that organisms living in open habitats tend to have longer limbs (Adams 1984; Niemi 1985; Villani et al. 1999; Melville and Swain 2000). Thus, the Madagascan archaeids appear to have undergone increased rates of evolution in adaptive traits compared to their relatives, which may be caused by adaptation over long periods of time and may allow sympatric species to coexist.

Thus, it appears that geoclimatic events in the Miocene contributed to the present-day distributions of many of the African and Australian species. However, in the Madagascan taxa there seems to be no single event associated with divergence, instead divergence is spread out over long periods of time. Although in all areas there is a similar pattern where sister species tend to be allopatrically isolated, with one species per locality, it is only in Madagascar that there are areas with high archaeid species richness (and associated sympatry), suggesting that time alone, coupled with more ancient geoclimatic events allowed for the different patterns in Madagascar, including greater rates of adaptive trait evolution. The main storyline for Madagascar involves groups dispersing there because the Cenozoic with the majority of the biota composed of neoendemics (Yoder and Nowak 2006; Crottini et al. 2012; Samonds et al. 2012, 2013). We provide evidence that the Madagascar saga is more complex: the diversity and trait variation that has evolved in Madagascan archaeids is a result of extremely slow processes since the Mesozoic. For those lineages that have been on Madagascar since preisolation times, ancient geoclimatic events over long periods of time may have facilitated the buildup of high species richness due to montane refugia and persistence, rainforest refugia, and also ecogeographic shifts, allowing for the accumulation of adaptive traits. This research suggests that one overlooked factor causing Madagascar's high species richness and remarkable diversifications (both adaptive and non-adaptive), compared to other parts of the world, may relate to its having more ancient patterns of geoclimatic events.

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DATA ARCHIVING

Data available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.34qm4.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

1. Divergence dating using IGR model in MrBayes version 3.2.2 (Ronquist et al. 2012).
2. Molecular-only and morphology-only phylogenetic analyses.
3. Divergence dating with COI excluded.
4. Lineage diversification.
5. Trait diversification rates treating Madagascar as two groups.
6. Divergence dating analysis with additional Australian archaeids.

Table S1. Rates of morphological evolution from the censored rate test comparing a single rate model with a multiple rate model for the two different Madagascar clades versus South African and Australian lineages.

Figure S1. Dated phylogeny from the MrBayes analysis, using the IGR model, with branch lengths drawn to reflect divergence age estimation.

Figure S2. Phylogeny from Bayesian analysis of molecular data.

Figure S3. Phylogeny from Bayesian analysis of morphological data.

Figure S4. Dated phylogeny from analysis with COI excluded, with branch lengths drawn to reflect BEAST divergence age estimation.

Figure S5. Plot showing density of the estimated gamma variable for 500 randomly sampled ultrametric phylogenies of the Madagascan taxa.

Figure S6. Dated phylogeny, including additional Australian archaeids, with branch lengths drawn to reflect BEAST divergence age estimation.