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Treating Fossils as Terminal Taxa in Divergence Time Estimation Reveals Ancient Vicariance Patterns in the Palpimanoid Spiders

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Abstract.—Incorporation of fossils into biogeographic studies can have a profound effect on the conclusions that result, particularly when fossil ranges are nonoverlapping with extant ranges. This is the case in archaeid spiders, where there are known fossils from the Northern Hemisphere, yet all living members are restricted to the Southern Hemisphere. To better understand the biogeographic patterns of archaeid spiders and their palpimanoid relatives, we estimate a dated phylogeny using a relaxed clock on a combined molecular and morphological data set. Dating information is compared with treating the archaeid fossil taxa as both node calibrations and as noncontemporaneous terminal tips, both with and without additional calibration points. Estimation of ancestral biogeographic ranges is then performed, using likelihood and Bayesian methods to take into account uncertainty in phylogeny and in dating. We find that treating the fossils as terminal tips within a Bayesian framework, as opposed to dating the phylogeny based only on molecular data with the dates coming from node calibrations, removes the subjectivity involved in assigning priors, which has not been possible with previous methods. Our analyses suggest that the diversification of the northern and southern archaeid lineages was congruent with the breakup of Pangaea into Laurasia and Gondwanaland. This analysis provides a rare example, and perhaps the most strongly supported, where a dated phylogeny confirms a biogeographical hypothesis based on vicariance due to the breakup of the ancient continental plates. [Biogeography; divergence time estimation; fossils; Gondwana; molecular clock; Pangaea; total evidence; vicariance.]

Evolutionary biologists seek to understand broad evolutionary patterns by examining phylogenetic relationships among extant organisms, yet the majority of all organisms that ever existed have gone extinct (Raup 1993). Studies that focus exclusively on contemporary taxa therefore may produce conclusions of questionable reliability (Lieberman 2002; Quental and Marshall 2010; Crisp et al. 2011). One way of incorporating information from fossils is by including them as calibration points when estimating timing of diversification, this exercise being particularly important for testing hypotheses of vicariance and dispersal. Use of fossils in this way has resulted in productive science; for example, many of the classic examples of vicariance in Gondwanan groups have been overturned as dating information indicates that their distributions are products of more recent dispersals (Queiroz 2005; Upchurch 2008). Examples include the southern beech, *Nothofagus* (Cook and Crisp 2005; Knapp et al. 2005), chameleons (Raxworthy et al. 2002), and plants in the family Melastomataceae (Renner 2004). In amphibians, the Gondwanan vicariance hypothesis was overturned due to their diversification having occurred prior to Pangaean breakup (San Mauro et al. 2005). In addition to providing information on the timing of biogeographic events, inclusion of fossils as calibration points in some cases can provide entirely new insights into biogeographic patterns, particularly when fossil distributions differ from those of contemporary taxa. Indeed, there are now examples where the use of fossil information in divergence time estimations has explained biogeographic disjunctions as not being due to Gondwanan vicariance but instead due to migration across land, and then subsequent extinction in intermediate areas, such as in the angiosperm clade Malpighiaceae (Davis et al. 2002) and in the plant genus *Cornus* (Xiang et al. 2005).

Most quantitative phylogenetic studies to date have made use of fossils by treating them as calibration points in divergence time estimations. Nodal calibrations derived from fossils, employed in programs such as BEAST (Drummond and Rambaut 2007), aim to limit the time-of-origin of a certain clades to times considered reasonable through the use of prior probability distributions. However, treating fossils as calibration points is somewhat problematic. First, even a well-dated fossil with a high-confidence placement on a phylogeny provides only a minimum age of a clade, and the prior probability distribution on the *actual* time of origin of a clade, given the age of the oldest known fossil, is usually determined subjectively. Several suggestions have been made about how to determine the probability distribution on the time of clade origin in a more rigorous and repeatable way (e.g., Marshall 2008), but they require many more data, and

strong assumptions about probability of detection and are not widely employed. Further, the fossils of most interest for use in dating, that is, the earliest known members or relatives of a taxon, often exhibit transitional morphologies, and due to discrepancies in topology among different phylogenetic analyses are thus often placed ambiguously by authorities, sometimes being placed inside a crown clade, but near the base of it, and sometimes being placed below the crown clade, on the stem. In the ideal situation for node calibration methods, a combined phylogenetic analysis of molecular data and morphological data from fossil and living specimens is performed and only the fossil specimens which are confidently placed in the phylogeny are used to inform the node calibrations (Parham et al. 2012). However, the step from the phylogenetic position of a fossil to a probability distribution on the actual time of origin of a clade is still subjective. The most recent and comprehensive review of the "best practices" for justifying fossil calibrations notes that the decision about the distribution of the maximum age of a clade is "intuitive," that "educated guesswork" and "ambiguous assumptions" are relied upon, and that this is a "major limitation" in dating studies (Parham et al. 2012). Further, much information is lost when fossil data are used simply for node calibrations, with all remaining data discarded. Using fossils as calibration points is still worthwhile, but it is important to note that there are possible sources of error (Parham et al. 2012).

Once a dated phylogeny has been obtained, there remains the problem of how to use it in inference of historical biogeography. If a dated tree has only extant taxa at the tips, it is not clear how biogeographic information from fossils should be included. A phylogenetic tree derived from combined analysis of morphology and molecules for fossil and living taxa can include fossil specimens as terminal tips, but these phylogenies are undated because typical methods of divergence date estimation do not allow the use of terminal fossils, which essentially means that only parsimony-based methods of biogeographic inference can be used. Although parsimony-based methods have merit, they ignore dating information, which can be important in reaching the correct biogeographical conclusions (Donoghue and Moore 2003).

A more recent alternative to examining timing of diversification and biogeographic patterns is to incorporate fossils directly into the phylogeny using morphological characters. Recent advances now allow the inclusion of fossils in divergence time estimation as noncontemporaneous terminal tips rather than as node calibration points (Pyron 2011; Ronquist et al. 2012). Full incorporation of fossils into a biogeographic study is crucial when fossil distributions are nonoverlapping with contemporary ranges, as in the case of this study, and to ignore these unique distributions would bias the biogeographic outcome. In this study, we examine the biogeography of a family of spiders (Archaeidae) by incorporating morphological data from fossils directly into the divergence dating analysis. Then, for comparison, we perform additional analyses with the terminal fossils removed and instead estimate rates of diversification using calibration points (derived from other fossils, and both with and without a calibration point based on the age of the removed archaeid fossils). Doing so, we are able to draw conclusions about the impact of incorporating fossils as terminal tips in divergence dating. Furthermore, we attempt to explain a disjunct biogeographic pattern found in archaeid spiders where extant members occur only in the Southern Hemisphere (SH), but an excellent Northern Hemisphere (NH) fossil record exists for the group as well.

The family Archaeidae was first described in the NH from 3 Baltic amber fossils in 1854 (Koch and Berendt) dated to be of mid-Eocene age (Penney et al. 2011). It was not until later that the first living archaeid was found in Madagascar (Cambridge 1881). Since then many more extant species have been discovered from Madagascar, South Africa, and Australia (Forster and Platnick 1984; Lotz 1996, 2003, 2006; Wood 2008; Rix and Harvey 2011), whereas additional fossil species and genera have been found in the north, from Baltic and Burmese amber (Penney 2003; Wunderlich 2004a, 2008), and even compression fossils from Inner Mongolian rocks of Jurassic age (Selden et al. 2008a). Some have suggested that archaeids are a relictual group whose distribution is a product of diversification that predated Pangaean breakup followed by extinction of the northern lineages (Eskov 1987, 1992; Selden et al. 2008a), whereas others have suggested their distribution was due to vicariance relating to Gondwanan breakup (Legendre 1977; Paulian and Viette 2003). However, for any given lineage, in order to properly test for various biogeographic scenarios, the divergence time between lineages on either side of a biogeographic barrier needs to be topologically and temporally examined in the context of geological history (Donoghue and Moore 2003). To do so essentially requires that the NH archaeid fossils be incorporated into the phylogeny as terminal taxa. Formal inference of historical biogeography may reveal that the archaeid spider distribution is a result of vicariance, if it can be shown that northern and southern clades are distinct lineages, thus being topologically congruent, and that the timing of diversification is temporally congruent with Pangaean breakup into Gondwana and Laurasia. Alternatively, incongruencies may suggest alternative scenarios, such as dispersal, if the estimated ages postdate the vicariance event, or such as diversification that predated Pangaean breakup.

A recent study by Wood et al. (2012), which included both fossil and extant archaeid taxa, found that the extant SH archaeids are a distinct monophyletic lineage with respect to the northern fossil archaeids. Given that there are archaeid fossils of Jurassic age and that the extant southern clade is monophyletic, this enigmatic temporally disjunct distribution is suggestive that archaeid biogeography patterns may be explained by vicariance due to Pangaean breakup, which separated the northern and southern fauna. Using the total

evidence morphological and molecular data set of Wood et al. (2012), which includes extant and fossil archaeids, we explore the effects of different ways of calibrating a relaxed molecular clock on estimations of the timing of deep diversification within the Araneomorphae (a spider infraorder) and among archaeid lineages (e.g., with only archaeid fossil taxa as noncontemporaneous terminal tips, or with archaeid and nonarchaeid fossils used to create node calibration points, or a combination of the 2). To do so, we make use of recent advances that allow the inclusion of fossils into divergence time estimation as noncontemporaneous tips (Pyron 2011). These temporal estimations are then used to examine the congruence of biogeographic range estimates with continental breakup among archaeids and their close relatives in the Palpimanoidea.

Methods

Morphological and Molecular Data

Recent phylogenetic analysis of molecular and morphological data by Wood et al. (2012) placed archaeids in the superfamily Palpimanoidea along with 4 other families; Palpimanoidea belongs in the infraorder Araneomorphae, which is comprised of the spider families with derived spinning and respiratory organs, contains all the familiar spiders (excluding tarantulas, trap-door spiders, and their kin) and makes up the majority of spider biodiversity worldwide (Platnick 2012). To examine timing of diversification events, we utilize the total evidence morphological and molecular data set of Wood et al. (2012). This data set contains the 3 known extant archaeid genera that occur in Madagascar, Australia, and South Africa: *Eriauchenius* Cambridge (1881); *Austrarchaea* Forster and Platnick (1984); and *Afrarchaea* Forster and Platnick (1984); as well as the monophyletic "Gracilicollis Group" from Madagascar (Wood et al. 2007; Wood 2008) that is currently placed in *Eriauchenius*. This data set also includes 5 fossil archaeid taxa, made up of 1 taxon from Burmese amber (*Burmesarchaea grimaldii* (Penney 2003); 3 taxa from Baltic amber (*Archaea paradoxa* Koch and Berendt 1854; *Baltarchaea conica* (Koch and Berendt 1854), and *Myrmecarchaea* Wunderlich 2004a); and one compression fossil from Inner Mongolian rocks (*Patarchaea muralis* Selden et al. 2008a). Also in the data set are an additional 22 nonarchaeid taxa representing 18 families, with Hypochilidae, which is inferred to be sister to a clade comprising all other araneomorph families (Platnick 1977), as the outgroup. These additional taxa represent the major clades within the Araneomorphae (Griswold et al. 2005). The data set of Wood et al. (2012) is comprised of 126 morphological characters and a molecular concatenated data set with 5185 characters, consisting of 658 base pairs (bp) for the mitochondrial protein-coding gene Cytochrome c Oxidase subunit 1 (COI), 328 bp for the nuclear protein-coding gene Histone-3, and 2454 and 1745 bp for the ribosomal nuclear genes 18S and 28S, respectively. The fossil archaeid taxa are scored for only morphological characters and lack molecular data. Fossil taxa are missing the following percentages of morphological data: 26% for *Archaea paradoxa*; 42% for *Burmesarchaea grimaldii*; 56% for *Baltarchaea conica*; 60% for *Myrmecarchaea* sp.; and 66% for *Patarchaea muralis*. Extant taxa are missing fewer than 5% of morphological data, with the exception of *Aotearoa magna* missing 11% and *Mesarchaea bellavista* missing 17%. Regarding molecular data, the majority of extant taxa (84%) are missing fewer than 30% of the molecular data, whereas 4 taxa are missing 30–51%, and 1 taxon is missing 73%.

Divergence Time Estimation

Our interest is in examining the impacts of treating fossils as terminal tips in divergence dating and also in determining whether the age of the split between extant and fossil archaeids is congruent with continental drift patterns, in particular the splitting of Pangaea into Laurasia and Gondwana, dated around 180 Ma (Smith et al. 2004). 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). Archaeid fossils were used in 2 different ways: either being included in the analysis as noncontemporaneous terminal tips or they were removed from the analysis and treated as a node calibration that constrained the age of the common ancestor of living archaeids and their sister taxon. Additional calibration information, based on the fossil record, was used to place priors on the root node and 5 additional nodes. These additional fossils were not incorporated into the phylogeny as terminal tips because they were not originally included in the data set of Wood et al. (2012), used in this study. We chose to use these nonarchaeid fossils as calibration points in some analyses in order to make the best use of the most available data.

In total, 5 different divergence dating analyses were performed to compare the effects of incorporating information about archaeids in different ways (as terminal tips or as calibration points), and also to compare the effects of other nonarchaeid nodal calibrations. The 5 different analyses were performed with the following combination of calibration techniques; in all 5 analyses, a broad prior constraint was placed on the root node: (i) the archaeid fossils were treated as terminal tips and no other nonarchaeid calibration points were used; (ii) the terminal archaeid fossils were removed and were instead incorporated into a calibration point based on the age of the oldest archaeid fossil, and in addition 5 nonarchaeid calibration points were used; (iii) the terminal archaeid fossils were removed and were not used as a calibration point; however, 5 nonarchaeid calibration points were used; (iv) the terminal fossils were removed and were incorporated in the analysis as a calibration point based on the age of the oldest archaeid fossil, and no

other calibration points were used; (v) a total analysis that incorporates all available data, which has the archaeid fossils treated as terminal tips as well as all 5 nonarchaeid node calibration points. Additionally, to examine how sensitive our results were to the prior distributions of the calibration points, analysis (ii), which contained only calibration points (1 archaeid and 5 nonarchaeid), was rerun to produce analysis (ii.a), with the lognormal distribution changed as follows: the log of the mean of the distribution of time-before-fossil was changed from 2.0 to 4.0, which moved the mean from 7.39 to 54.60 Ma before the fossil date, and substantially broadened the width of the distribution (95% interval of the distribution changed from 33.5 to 131.1 Ma); this was done for all calibration points except the root, which is already very broad.

In all analyses, both molecular and morphological data were included. This was done following Pyron (2011) using the 1-clock model where the rates for each branch are drawn from a common lognormal-distributed relaxed clock for both morphology and molecules and with the morphological data partition run under the Lewis-Mk model (Lewis 2001). Regarding including fossil taxa as terminal tips, in Pyron (2011), fossil ages were entered as noncontemporaneous tip dates representing millions of years before present and were based on the lower bound of the fossil's age range. Our study differed from Pyron (2011) by treating the tip date as a uniform distribution instead of a point, in order to reflect the uncertainty in the date of the fossil. The distribution spanned the entire estimated age range of the fossil. 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 10 December 2012). To examine how the technique of treating the tip date as a uniform distribution may have affected the uncertainty in the age estimations, we reran analysis (i), called analysis (i.a), with the range of the fossil tip date greatly reduced so that it spanned only 1 myr and was centered on the mean, virtually treating the fossil tip age as a point rather than a range.

For each generation of sampling, the tip date for the 3 Baltic amber fossils was drawn once from the uniform distribution, rather than 3 times independently. This was done because the Baltic amber fossils are from the same geological deposit, so that whatever their true date is, it is the same for all of them. We think that linked tip dating is a more accurate representation of our prior knowledge than independent tip dating of fossils from the same deposit (Fig. 1).

In analyses that made use of calibration points, archaeid fossils and/or 5 additional fossils were used to design node calibration points and the age of the root node was also constrained based on the fossil record. In analyses (ii) and (iv), the terminal archaeid fossils were removed and instead a calibration point was used based on the age of the oldest archaeid fossil. All fossil calibration points (except the root calibration) were treated as lognormal distributions with a hard lower bound, based on the minimum age of the fossil, and a soft 95% upper bound that was approximately the lower bound plus 20–30 Ma (log of the mean time before the fossil age = 2.0, log of the standard deviation = 0.8 or 0.9), described here:

1. (node 24) fossil *Mesozygiella dunlopi* Penney and Ortuño (2006) from the family Araneidae was used to constrain the node for the common ancestor of *Araneus* sp. (Araneidae) and *Mimetus* sp. (Mimetidae), from amber from Álava, Spain, Cretaceous-Aptian, 115–121 Ma (Larrasoaña et al. 2003). Parameters: median = 122.4 Ma, hard lower = 115 Ma, and soft 95% upper = 142.5 Ma. This relationship was based on the findings of Penney and Ortuño (2006).

2. (node 27) fossil Lycosidae gen. et sp. indet. (Penney 2001) was used to constrain the node for the common ancestor of Lycosidae sp. and Gnaphosidae sp., from Dominican amber, Miocene, 15–20 Ma (Iturralde-Vinent and MacPhee 1996). Parameters: median = 22.4 Ma, hard lower = 15 Ma, and soft 95% upper = 42.6 Ma. This relationship was based on the findings of Penney (2001).

3. (node 29) fossil *Nephila jurassica* Selden et al. (2011) from the family Nephilidae was treated as belonging to the superfamily Araneoidea and was used to constrain the node for the common ancestor of the Araneoidea taxa (*Araneus* + *Mimetus* + *Holarchaea* + Parchaeidae) and the RTA clade (*Badumna* + Lycosidae + Gnaphosidae), compression fossil, Middle Jurassic (Chen et al. 2004), 161–176 Ma (based on www.geosociety.org/science/timescale/ last accessed 10 December 2012). Parameters: median = 168.4 Ma, hard lower = 161 Ma, and soft 95% upper = 193.5 Ma. This relationship was based on the findings of Selden et al. (2011).

4. (node 23) fossil *Lebanoecobius schleei* Wunderlich (2004b) from the family Oecobiidae was used to constrain the node for the common ancestor of the oecobiid (*Uroctea* sp.) and the eresidae (*Stegodyphus* sp.), from Lebanese amber, Cretaceous, 125–135 Ma (Penney and Selden 2002; Azar 2007). Parameters: median = 132.4 Ma, hard lower = 125 Ma, and soft 95% upper = 152.5 Ma. This relationship was based on the findings of Wood et al. (2012).

5. (node 21) fossil *Huttonia* sp. from the family Huttoniidae (Penney and Selden 2006) was used

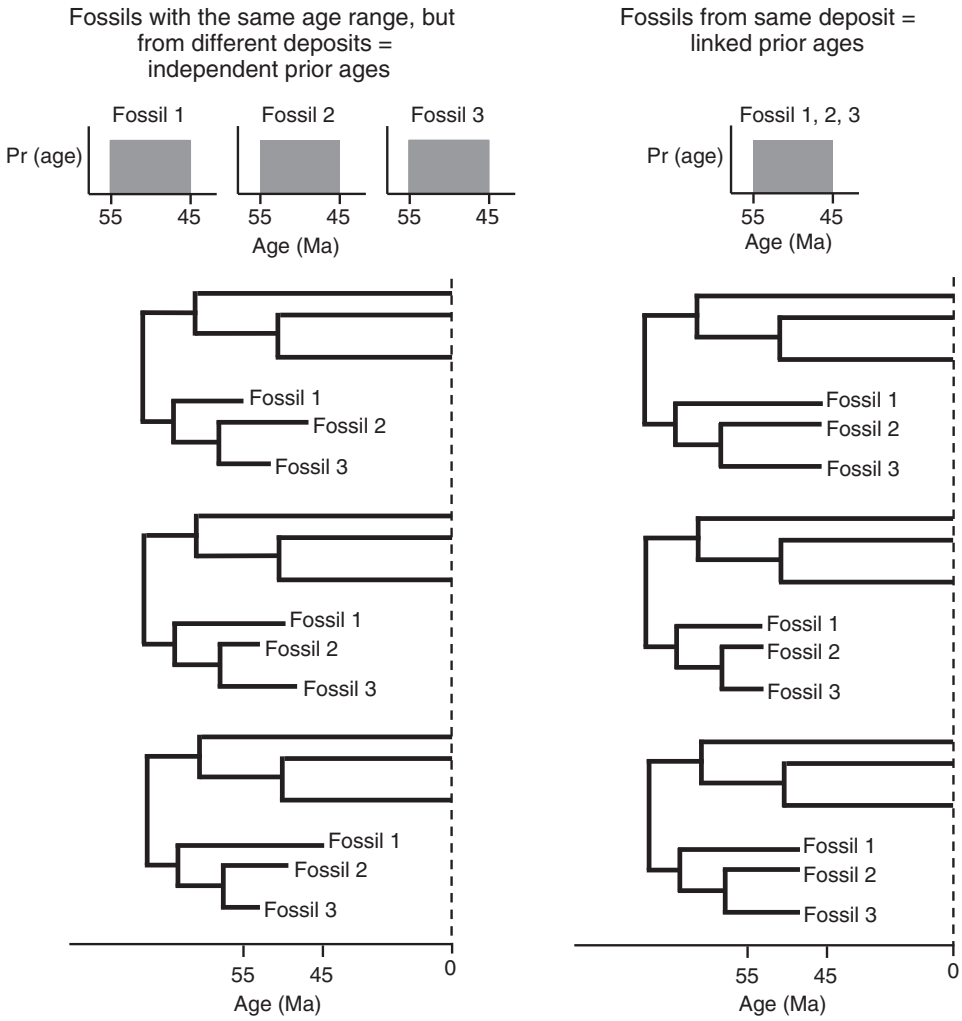

FIGURE 1. Different ways of sampling from the prior distribution for a fossil's age in a Bayesian analysis. Left: Independent sampling—each fossil has the same estimated age and uncertainty, 55–45 myr, but the age of each tip is drawn independently in each step of Bayesian sampling. Right: Linked sampling of fossil tip dates—all 3 fossils are given the same date in each step of Bayesian sampling. Although the date varies uniformly between 55 and 45 Ma, the 3 fossils always have the same date. The latter procedure is appropriate when fossils are from the same deposit.

to constrain the node for the common ancestor of the extant *Huttonia* and the palpimanid (*Palpimanus* sp.), from Canadian amber, Cretaceous, Campanian, 76.5–79.5 Ma (Poinar et al. 2000). Parameters: median = 83.9 Ma, hard lower = 76.5 Ma, and soft 95% upper = 104.0 Ma. This relationship was based on the findings of Wood et al. (2012).

6. (node 15) for the analyses where the terminal fossils were removed and treated as a calibration point, this was based on the age of the oldest archaeid fossil *Patarchaea muralis* and was used to constrain the node for the common ancestor of the extant archaeids and the stenochilid (*Colopea* sp.), compression fossil, Middle Jurassic (Chen et al. 2004, Gao and Ren 2006), 161–176 Ma (based on www.geosociety.org/science/timescale/ last accessed 10 December 2012). Parameters: median = 168.4 Ma, hard lower = 161 Ma, and soft 95% upper = 193.5 Ma.

7. The age of the root (node 36) for the Araneomorphae was constrained to be from 161–392 Ma: the maximum age was based on the oldest known fossil in the sister group of spiders Uraraneida *Attercopus* (Selden et al. 1991; Penney et al. 2003; Penney and Selden 2007; Selden et al. 2008b), which implies that spiders, Araneae, are equally old. The minimum age of the root constraint was based on the oldest fossil spider used as a terminal in this study, *Patarchaea muralis*; the breadth of this constraint was intentionally large to contain the true age of Araneomorphae divergence. The constraint on the root was treated as a normal distribution where the minimum and maximum range was the soft 5–95% upper and lower bounds with a mean of 276.5 Ma, standard deviation of 70.

The molecular clock model was set to relaxed, uncorrelated lognormal and the tree prior was set to Yule process (following Pyron [2011]). In the preliminary analysis of the combined data (v: archaeid fossils as terminal tips+5 node calibrations), the tree prior was set to Birth–Death, and we found that the results did not differ from when it was set to Yule process. Preliminary analyses were also run with the data partitioned for 28S, 18S, and each of the 3 codon positions in the protein-coding H3 and COI genes, as well as the morphological data. We found that regardless of whether codon partitions were removed or were retained, the resulting credibility intervals on the estimated dates were essentially the same with only minor differences. However, in analyses where codon partitions were removed the burn-in was reduced and the effective sample size (ESS) values were greatly improved (in analyses with codon partitions retained, some parameters never reached an ESS of 200), likely because some of the codon partitions were too conserved and did not have enough variation. So, in order to provide an analysis with a much lower chance of convergence problems and parameter nonidentifiability, the codon partitions were removed. All final analyses were run with partitions for each of the molecular markers and for the morphological data. The morphological data were put in one partition, with all characters treated as unordered, with an overall mean rate and gamma-distributed rate variation; an R script was written to convert NEXUS-formatted character data into BEAST's unique format, and to check for and exclude invariant characters. All partitions were unlinked, allowing the relative rates to vary, but were linked to the overall clock. Depending on ESS scores, 4–7 MCMC Bayesian analyses were run in BEAST for 20 million generations, sampling the chain every 1000 generations, resulting in 4–7 files of 20 000 trees. Log files were visualized in Tracer v.1.4 to confirm that the ESS of the combined log files reached 200 for all parameters (Drummond et al. 2006). Typically, the burn-in was set to 10% (but this amount varied depending on the analysis) for each independent run, resulting in a combined file that ranged in size from 72 000 to 121 500 trees. For all analyses, an empty data set containing only the priors was also run for 20 million generations in order to examine the extent to which the data were affecting the results (Drummond et al. 2006) and also to ensure that the prior constraints placed on nodes were what we intended (Heled and Drummond 2012). The final chronogram and node ages were visualized in FigTree v.1.3.1 (Rambaut 2010).

Biogeographic Analysis

The purpose of this analysis is to examine ancestral ranges of archaeid spiders and their relatives within the Palpimanoidea. Because the archaeid fossils occur in geographic areas different than the extant archaeids, it is crucial that they are included in the ancestral reconstructions as terminal tips. Reconstructions of ancestral distributions of palpimanoid clades were performed using the fully resolved BEAST chronogram from analysis (v). Analysis (v) was used for the biogeography analysis because it included the archaeid fossils treated as noncontemporaneous tips, which was crucial for the purposes of this analysis, but also, because it included the nonarchaeid fossil calibration points, we felt that this analysis makes the best use of the most available data. Furthermore, the biogeography analysis was only performed on palpimanoid taxa, and among the Palpimanoidea the results of analysis (i), which did not contain additional node calibration points, compared with analysis (v) only differ in that the 95% Bayesian CI in node 21 is narrower (Table 1). In order to account for uncertainty in branch length, analyses were also performed on 1000 randomly sampled dated phylogenies that were taken from the analysis (v) postburn-in output distribution of phylogenies (Smith 2009). The non-Palpimanoidea were pruned from the BEAST phylogenies.

Families within the Palpimanoidea have highly restricted distributions with the exception of Palpimanidae, which is widespread except for not being known to occur in North America, Australia, or New Zealand. Extant archaeids are only known from South Africa, Madagascar, and Australia, and fossil archaeids are only known from Eurasia and Southeast Asia; mecysmaucheniids are only known from New Zealand and southern South America; huttoniids are only known from New Zealand; and stenochilids are only known to occur in Southeast Asia although they are also found in Australia (Raven R., personal communication), spanning India to the north-east of Australia. Biogeographic regions were based on Cox (2001) zoogeographic regions, with the addition of Madagascar and New Zealand as separate areas. The taxon distributions resulted in 7 areas: Southeast Asia (Oriental in Cox [2001]); Africa; South America; Australia; New Zealand; Eurasia; and Madagascar. We also repeated this analysis using only 2 areas: the NH and SH. Ancestor reconstructions were examined using likelihood methods, implemented in LAGRANGE C++ ver.0.1 (Ree et al. 2005; Ree and Smith 2008), available at http://code.google.com/p/lagrange/ last accessed 10 December 2012, using the default settings. Implementation of the LAGRANGE analyses run on the 1000 randomly drawn phylogenies from the BEAST output used the statistical program R (R Development Core Team 2008).

The only program that can infer vicariance processes explicitly is DIVA (Ronquist 1996; Ronquist and Sanmartín 2011). However, it does not take into account time information, so use of DIVA was de-emphasized in this study. Nevertheless, for completeness, we ran DIVA 1.2 on the same fully resolved BEAST chronogram using both 7 and 2 areas. We also ran DIVA on the same sample of 1000 trees as used for LAGRANGE and summarized the results (Bayes-DIVA) (Nylander et al. 2008; Harris and Xiang 2009).

TABLE 1. Estimates of divergence times in millions of years

Node	Crown group	Analysis (i) terminal fossils only	Analysis (ii) only calibrations	Analysis (iii) only calibrations	Analysis (iv) only calibrations	Analysis (v) fossils + calibrations	Analysis (ii.a) prior sensitivity	Analysis (i.a) range reduced
		Mean [95% CI]	Mean [95% CI]	Mean [95% CI]	Mean [95% CI]	Mean [95% CI]	Mean [95% CI]	Mean [95% CI]
1		54[108,13]	53[94,16]	50[97,15]	49[90,15]	55[104,17]	59[109,16]	56[108,18]
2	Madagascan archaeids	80[141,30]	76[118,35]	73[123,31]	72[113,32]	81[135,34]	85[137,38]	82[140,33]
3	South African archaeids	44[101,7]	40[93,8]	41[90,7]	40[85,5]	42[96,6]	47[103,6]	44[96,8]
4		119[184,64]	114[148,74]	109[164,63]	108[143,65]	116[177,68]	128[177,80]	119[181,67]
5	Madagascan archaeids	64[122,18]	56[98,20]	55[102,16]	54[95,17]	61[118,18]	64[116,19]	65[123,18]
6	Mad + AF archaeids	139[208,83]	**	**	**	135[194,82]	**	141[206,83]
7		48[97,15]	39[71,10]	38[76,11]	37[69,13]	49[95,14]	45[81,15]	49[100,13]
8	Australian archaeids	75[134,29]	59[96,28]	59[101,26]	57[93,27]	81[131,30]	68[111,34]	77[138,29]
9	SH archaeids	164[233,107]	140[162,112]	138[191,91]	137[160,107]	161[221,108]	158[202,121]	165[232,107]
10		89[174,51]	n/a	n/a	n/a	88[170,50]	n/a	88[173,50]
11		105[175,60]	n/a	n/a	n/a	104[170,60]	n/a	105[176,60]
12	NH Archaeids	139[201,91]	n/a	n/a	n/a	136[195,92]	n/a	138[199,92]
13		178[236,126]	n/a	n/a	n/a	175[226,128]	n/a	178[236,128]
14	Archaeidae	211[269,171]	n/a	n/a	n/a	205[255,170]	n/a	212[267,173]
15		236[306,180]	168 [186, 162]	171[227,117]	167 [184, 161]	228[287,181]	197 [240, 168]	1237[305,182]
16		**	178[223,109]	178[247,100]	**	225[308,117]	210[274,139]	**
17	NZ mecysmaucheniids	46[112,7]	40[90,7]	38[92,7]	35[87,4]	42[100,8]	45[97,10]	47[114,10]
18		68[141,18]	57[113,20]	56[116,17]	50[108,13]	62[127,19]	63[124,21]	66[138,20]
19		52[126,9]	44[95,6]	44[99,6]	38[97,8]	48[114,10]	51[111,11]	51[120,10]
20	Mecysmaucheniidae	97[187,36]	80[147,31]	81[149,28]	70[140,26]	87[172,33]	87[157,36]	94[183,36]
21		183[290,54]	85 [110, 77]	85 [108, 77]	140[203,48]	85 [109, 77]	139 [216, 86]	1186[294,57]
22	Palpimanoidea	265[345,198]	199[233,174]	202[265,151]	196[224,171]	253[320,196]	232[285,192]	266[343198]
23		133[245,33]	133 [153, 126]	133 [153, 126]	103[178,28]	133 [155, 126]	168 [213, 132]	1134[247,30]
24		77[150,19]	121 [134, 116]	121 [134, 116]	61[115,18]	121 [135, 116]	140 [169, 121]	81[149,24]
25	Araneoidea	112[194,46]	142[163,121]	142[163,121]	88[145,39]	143[165,121]	162[196,132]	118[196,55]
26		82[158,20]	116[155,57]	115[155,53]	64[120,21]	115[156,55]	133[182,60]	89[160,27]
27		61[136,12]	26 [52, 16]	27 [52, 16]	49[99,11]	27 [53, 16]	63 [115,25]	65[133,17]
28	RTA-clade	104[189,38]	78[146,29]	79[148,31]	80[148,31]	82[150,32]	115[177,53]	106[186,40]
29	Araneoidea + RTA-clade	156[253,77]	166 [179, 161]	166 [179, 161]	121[184,66]	167 [184, 161]	187 [221, 165]	162[250,84]
30	Entelegynae	199[298,104]	184[212,165]	184[219,165]	154[216,88]	194[247,166]	211[258,177]	203[301,110]
31		285[371,212]	220[263,189]	223[283,178]	214[257,181]	272[342,210]	255[313,210]	286[372,216]
32		309[401,230]	243[296,203]	247[314,191]	236[291,193]	296[373,228]	281[348,227]	310[403,234]
33		330[425,244]	264[326,215]	268[341,205]	254[317,206]	317[397,243]	303[376,242]	331[428,250]
34		179[349,33]	146[278,25]	146[281,25]	146[281,25]	153[324,26]	176[321,33]	180[351,32]
35		347[445,256]	282[350,227]	286[366,218]	271[340,217]	334[420,257]	321[399,256]	349[447,261]
36	Root, Araneomorphae	362 [464, 269]	300 [377, 239]	304 [388, 229]	288 [366, 229]	351 [441,270]	338 [420, 268]	365 [466, 274]

Notes: Analyses were constrained in the following ways, nodes follow Figures 2 and 3: (i) only the archaeid fossils as terminal tips; (ii) only node calibrations, including the archaeid fossils incorporated in calibration point; (iii) only node calibrations, but without the calibration point for the archaeid fossils; (iv) only the archaeid calibration point, and all other calibrations removed; (v) all nonarchaeid node calibrations and the archaeid fossils treated as terminal tips; (ii.a) prior sensitivity analysis, log of the mean = 4; (i.a) fossil tip range reduced to span 1 myr. In all analyses, a prior constraint was placed on the root node. Shaded nodes are those that had a prior constraint based on the fossil record; **, represents a node that was not recovered; n/a, represents a node that does not exist because terminal archaeid fossils were not included in the analysis; AF = Africa; Mad = Madagascar; NH = Northern Hemisphere; NZ = New Zealand; SH = Southern Hemisphere.

Results

Divergence Time Estimation

Visualization of the log files from the BEAST analyses in Tracer v1.4 confirmed that the ESSs were sufficient (>200) for all parameters including the age estimations of all nodes. Typically the first 10% of samples were discarded as burn-in, a conservative decision as inspection of the likelihood scores and other various parameters indicated that stationarity was achieved before this. There were moderate amounts of rate heterogeneity, meaning that the data are not clock-like: for all analyses the coefficient of variation ranged from 1.244 to 1.338 and the ucld.stdev ranged from 1.062 to 1.104. There was no evidence for autocorrelation in any analysis (e.g., for analysis (v), mean covariance = 0.145; 95% CI lower = −0.0684, and upper = 0.376). The analyses run on empty data set were compared with the analyses with data in Tracer v1.4 and confirmed that the data were informing the estimates (Supplementary Figs. S7 and S8, http://datadryad.org, doi:10.5061/dryad.7231d). Regarding ensuring that the prior constraints placed on nodes were what we intended, for all calibration points except the root node constraint the expected prior matched the observed prior (Supplementary Figs. S7 and S8). The mismatch observed in the root node constraint is likely because the youngest soft bound on the root constraint, which was left intentionally broad in order not to bias the results and in order to contain the true age of Araneomorphae divergence, overlaps with the oldest soft bound on other node calibrations, which pushed the observed root prior back in time. However, we do not feel this is a problem because the observed prior is still broad, still contains the true age of Araneomorphae divergence and is still reasonable.

The results of node age estimations for all 5 analyses are presented in Table 1 and the resulting chronograms from analyses (v) and (ii) are presented in Figures 2 and 3. In all analyses where fossils are treated as terminal tips (analyses (i) and (v)), the majority of node age estimations are older than node age estimations in analyses where only fossil calibration points are used (analyses (ii), (iii), and (iv)). This is the case for the nodes that are both distal and basal to the terminal fossils (compare analyses (i) and (v) with analyses (ii), (iii), and (iv) for nodes 1–9, 15–20, 22, 30–33, and 35–36 in Table 1). In order to examine how our results changed when the prior distributions of the calibration points were changed, in analysis (ii.a), we found that when the mean was doubled that all resulting mean node estimations were older, as expected, and mimicked the results of analysis (v) more closely.

Regarding branch support values (reported as posterior probabilities, pp), in analysis (v), many of the nodes from which we draw biogeographic conclusions (e.g., nodes 13 and 9) have pp <0.90. We do not think this is problematic. It has been shown by Wood et al. (2012) that extant archaeid monophyly (node 9) is strongly supported by molecular data. Furthermore, morphological data also strongly support archaeid monophyly (including both extant and fossil taxa; node 14), as well as monophyly of the extant archaeids (node 9), with the fossil archaeids falling outside. However, when fossil taxa are incorporated into total evidence analyses of combined morphological and molecular data, branch support values decrease around these nodes, likely due to the smaller number of morphological characters compared with molecular characters. In analysis (ii), which does not include fossil taxa, the branch support values are improved. In this study, the biogeography analyses performed on the 1000 randomly sampled trees take this phylogenetic uncertainty into account, yet still our biogeographic conclusions remain (see below).

Biogeographic Analysis

Results from the LAGRANGE and DIVA biogeographic analyses on the single, fully resolved BEAST chronogram are presented in Figure 4 and Table 2. Results from the LAGRANGE and DIVA analyses on the random sample of 1000 dated phylogenies taken from the BEAST distribution of phylogenies are summarized in Figures 5 and 6. LAGRANGE estimated the global rate of dispersal and extinction to be 0.000536 and 0.0000685 per million years, respectively, for the single chronogram analysis with 7 areas and 0.00147 and 0.0000259 for the single chronogram analysis with 2 areas. For the 1000 randomly sampled phylogenies, the 95% Bayesian CIs on the global rates of dispersal and extinction are between 3.53e-4–6.74e-4 and 6.73e-6–1.11e-3, respectively, for the 7-area analysis, and between 7.73e-4–1.79e-3 and 4.08e-7–3.38e-4 for the 2-area analysis. In other words, the extinction rate is closer to zero than the dispersal rate and is more uncertain in that it varies over several orders of magnitude. Ree and Smith (2008) found that LAGRANGE underestimates global dispersal and extinction rates, with dispersal rates being underestimated by a constant proportion, whereas extinction rates are rarely estimated far from zero. Even though our study includes fossils, our estimated extinction rate is still close to zero.

The dispersal-extinction-cladogenesis model (DEC model) employed by LAGRANGE forces one of the daughter species to inherit a range of only a single area and does not include a mechanism that allows the vicariance scenario where both daughter species inherit ranges of 2 or more areas (Ree et al. 2005; Ronquist and Sanmartín 2011): because of this, at node 13 and node 21, we summed the probabilities of the most likely ancestral splits and we also reported the results from the 2-area analysis (Table 2). Node 13 of the BEAST chronogram analysis deals with the split between the extant SH archaeid taxa and the extinct NH archaeid taxa. In the analysis with 7 areas, the most likely split at this node is (1) Eurasia splitting with Australia+Madagascar, and the second most likely split is (2) Eurasia splitting with

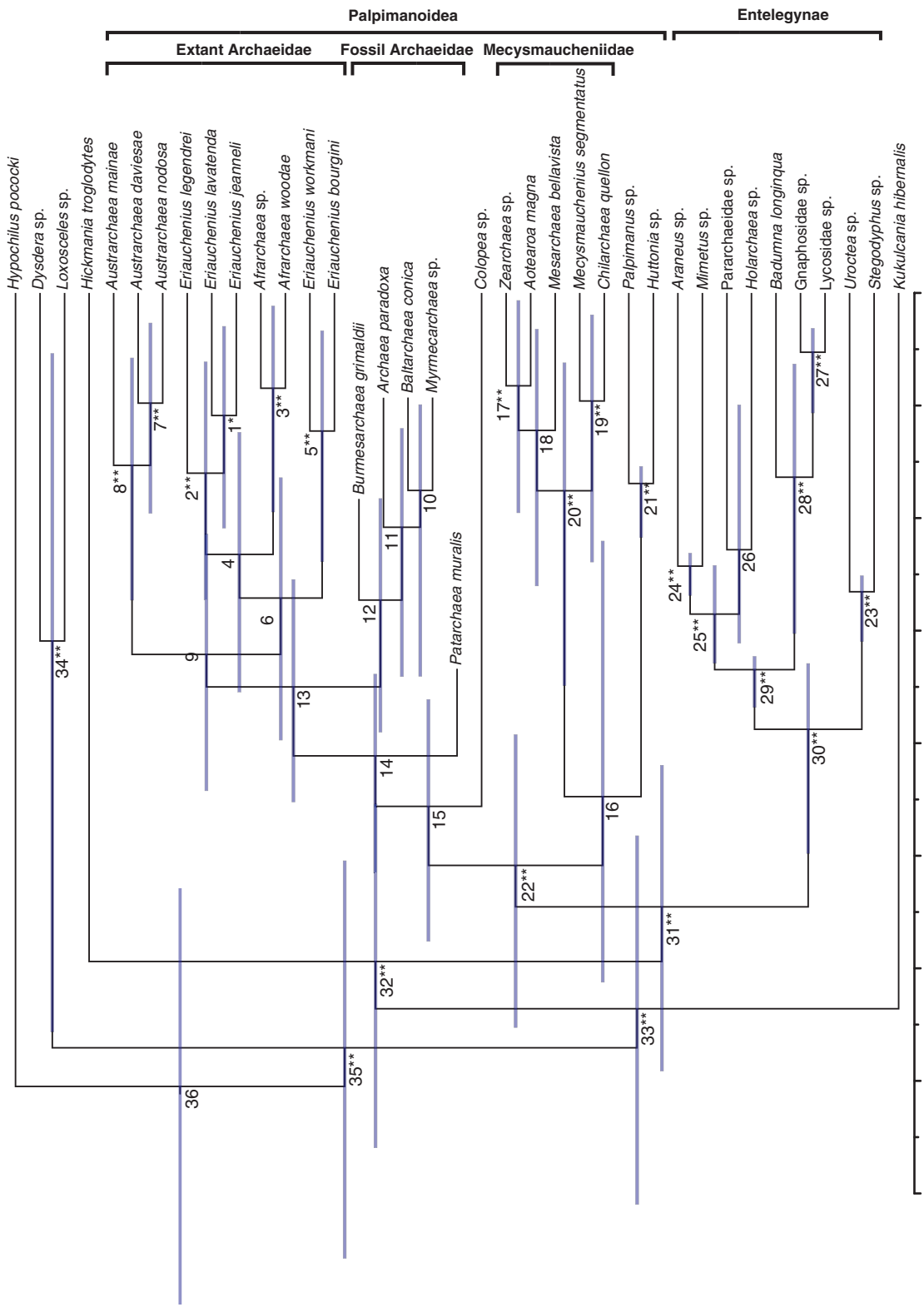

FIGURE 2. Dated phylogeny from analysis (v) with branch lengths drawn to reflect BEAST divergence age estimations. Error bars reflect the 95% Bayesian CI. Numbers next to nodes refer to Tables 1 and 2. All branches with a double asterisk (**) have a posterior probability of greater than 0.95; a single asterisk (*) next to the number signifies, $0.90 < pp < 0.95$; all other branches have $pp < 0.90$. Scale = millions of years before present.

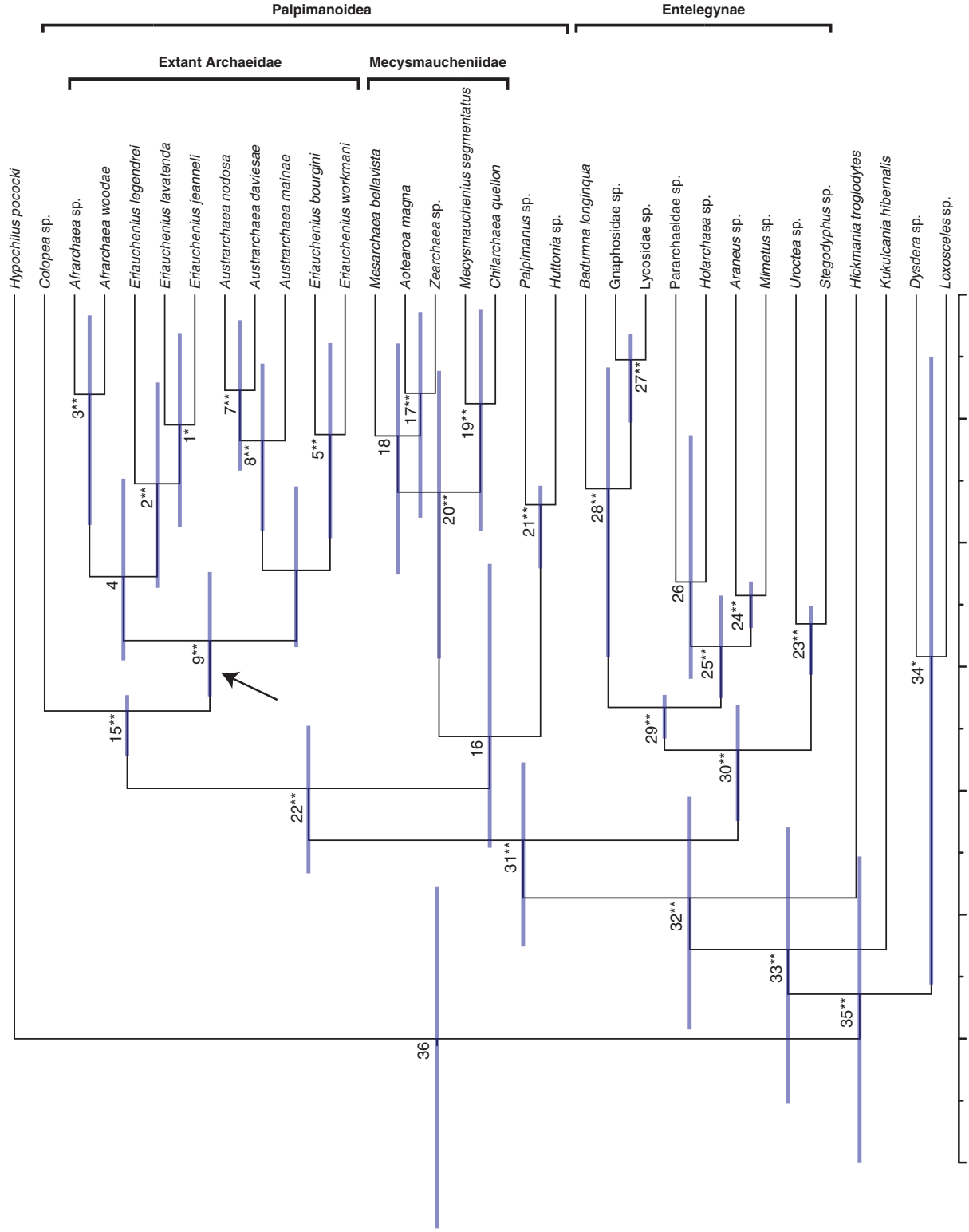

FIGURE 3. Dated phylogeny from analysis (ii) with branch lengths drawn to reflect BEAST divergence time estimations. Error bars reflect the 95% Bayesian CI. Numbers next to nodes refer to Tables 1 and 2; node 6 is not recovered in this analysis. Arrow is pointing to the branch where the fossil archaeids would have diversified. All branches with a double asterisk (**) have a posterior probability of greater than 0.95; a single asterisk (*) next to the number signifies, $0.90 < pp < 0.95$; all other branches have $pp < 0.90$. Scale = millions of years before present.

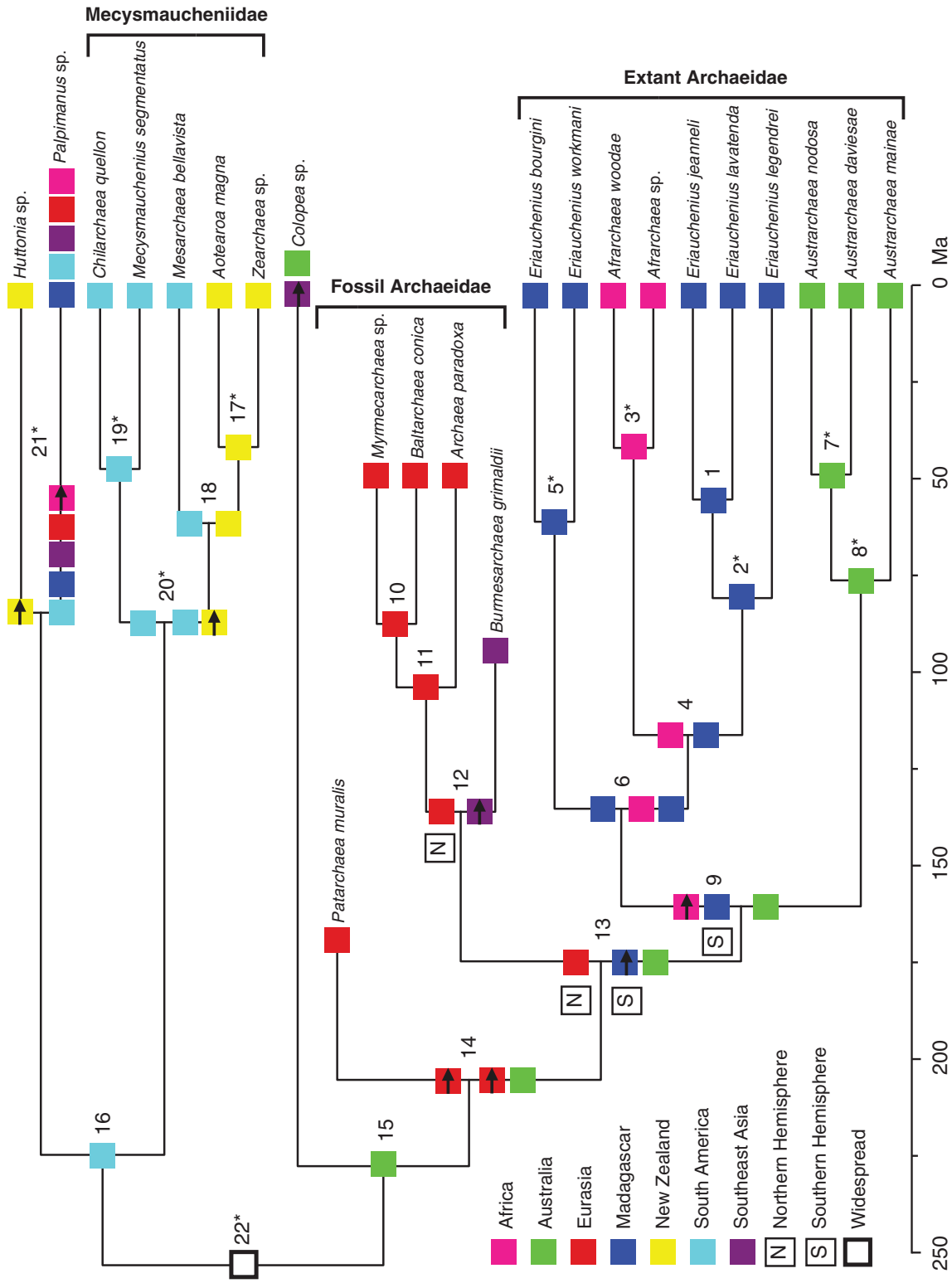

FIGURE 4. Ancestral area estimations from the LAGRANGE 7-area biogeographic analysis, with the ultrametric phylogeny from BEAST analysis (v) used as the input phylogeny. At nodes 9, 12, and 13 results from the LAGRANGE 2-area analysis are also reported. Scale = millions of years before present. Colored squares at terminals represent the distribution of terminal taxa and colored squares at nodes represent ancestral range inheritance scenarios following Table 2. A single square at a node marks when the 2 descendant lineages have the same inferred range. Arrows represent a range expansion or dispersal. Numbers next to nodes follow Tables 1 and 2 and an asterisk (*) next to the number signifies the posterior probability at that branch is greater than 0.95.

TABLE 2. Ancestral area reconstructions with 7-areas, using maximum likelihood (ML) and parsimony (P); node numbers correspond with Figures 2 and 3

Node	ML area reconstruction	Relative Probability	P area reconstruction
1	Mad | Mad	1.00	Mad
2	Mad | Mad	1.00	Mad
3	AF | AF	0.99	AF
4	AF | Mad	0.95	AF + Mad
5	Mad | Mad	1.00	Mad
6	*Mad | AF + Mad	0.60	Mad
	Mad | Mad	0.38	
7	Au | Au	1.00	Au
8	Au | Au	1.00	Au
9	*Au | AF + Mad	0.46	Au + Mad
	Au | Mad	0.43	
	Au | AF	0.07	
10	Eu | Eu	1.00	Eu
11	Eu | Eu	1.00	Eu
12	Eu | SeA	0.97	Eu + SeA
13	*Eu | Au + Mad	0.24	SeA + Au
	Eu | AF + Au + Mad	0.23	Au + Eu
	SeA | AF + Au + Mad	0.14	SeA + Au + Eu
	Eu + SeA | Au	0.08	SeA + Au + Mad
	Eu | Au	0.07	Eu + Mad
	SeA | Au + Mad	0.06	SeA + Eu + Mad
	Eu | AF + Au	0.06	Au + Eu + Mad
	SeA + Eu | Mad	0.04	SeA + Au + Eu + Mad
	Summary:		
	NH | SH	0.92	
	Analysis with only 2 areas:		
	*NH | SH	0.99	NH + SH
14	*Eu | Au + Eu	0.23	Eu
	Eu | Au + Eu + Mad + Af	0.15	Au + Eu
	Eu | Au + Eu + Mad	0.13	SeA + Au + Eu
	Eu | AF + Au + SeA + Mad	0.11	Au + Eu + Mad
	Eu | SeA + Au + Mad	0.05	SeA + Au + Eu + Mad
	Eu | Eu + Au + AF	0.05	
	Eu | SeA + Eu	0.05	
	Eu | SeA + Eu + Au	0.03	
	Eu | Eu	0.03	
15	*Au | Au	0.20	Au
	Au | Au + Eu	0.09	Au + Eu
	Au | AF + Au + Eu + Mad	0.07	SeA + Au + Eu
	Au | Au + Eu + Mad	0.06	
	SeA | Au + Eu + Mad +AF	0.06	
	SeA | SeA	0.05	
	Au | SeA + AF + Au + Eu + Mad	0.04	
	SeA | SeA + AF + Au + Eu + Mad	0.04	
	SeA | Au + Eu + Mad	0.03	
16	*SA | SA	0.24	Various area combinations
	NZ | NZ	0.16	
17	NZ | NZ	1.00	NZ
18	NZ | SA	0.99	NZ + SA
19	SA | SA	1.00	SA
20	*SA + NZ | SA	0.63	SA
	SA | SA	0.36	
21	*NZ | SeA + AF + SA + Eu + Mad	0.34	Various area combinations
	NZ | SeA + SA + Eu + Mad	0.08	
	NZ | SeA + AF + SA + Eu	0.08	
	NZ | AF + SA + Mad + Eu	0.08	
	NZ | AF + SA + SeA + Mad	0.07	
	Summary:		
	NZ | various area combinations	0.65	
22	Summary:		All areas
	Various area combinations		
	No clear patterns		

Notes: For ML: only splits within 2 log-likelihood values are shown; area reconstructions are for 2 descendent daughter branches, at several nodes the results have been summarized by summing the probabilities; (*) marks the preferred area reconstruction depicted in Figure 4. At node 13, results from the 2-area ancestral area reconstruction are also reported. Mad: Madagascar, SeA: Southeast Asia, AF: Africa, SA: South America, Au: Australia, NZ: New Zealand, Eu: Eurasia, NH: Northern Hemisphere, SH: Southern Hemisphere.

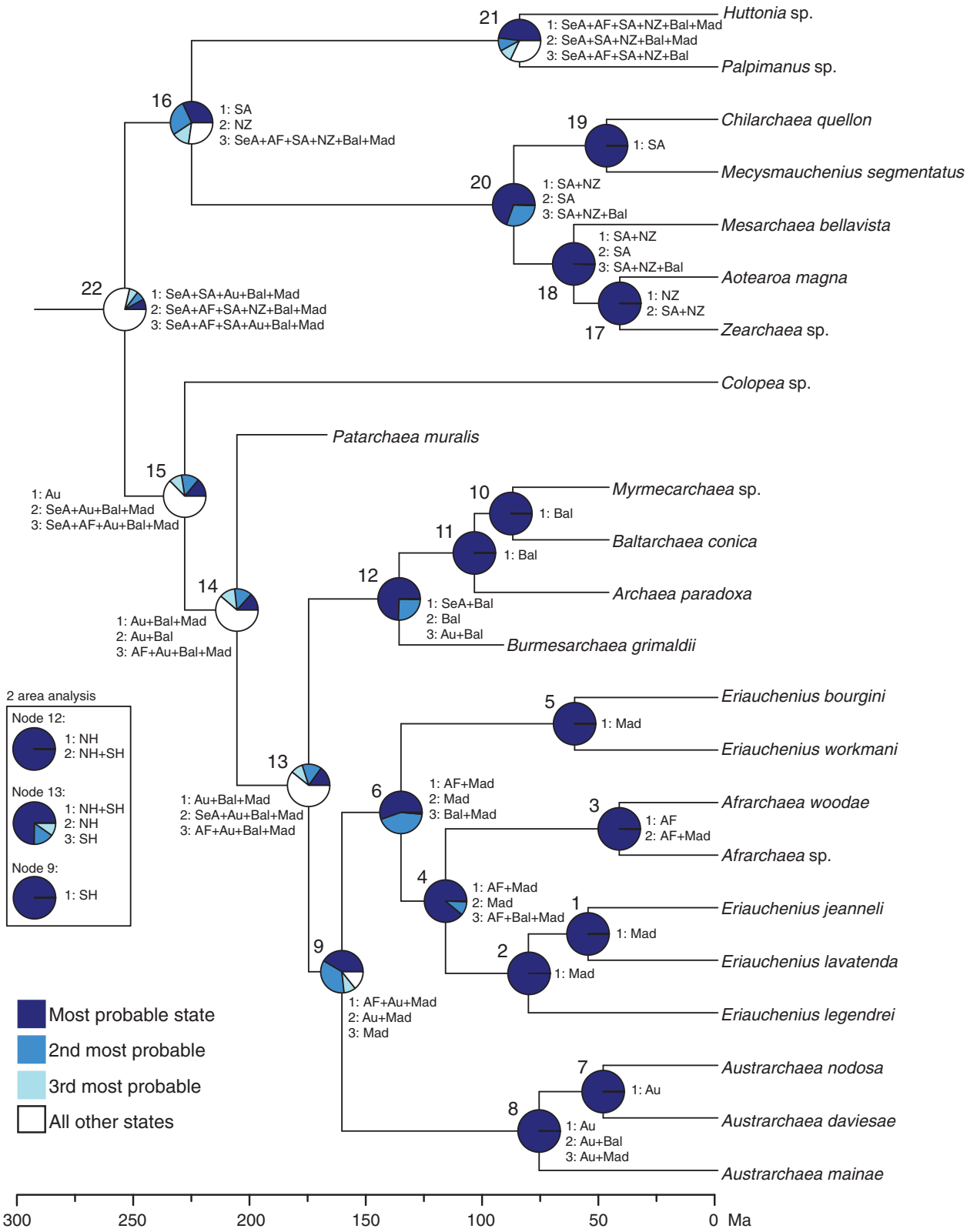

FIGURE 5. Summary of the LAGRANGE ancestral range estimates for the 7-area analysis. LAGRANGE was run on each of 1000 dated phylogenies randomly sampled from the posterior distribution of phylogenies produced during BEAST analysis (v). Pie charts represent the top 3 most likely ancestral geographic ranges at each node. Numbers next to nodes follow Tables 1 and 2. Boxed section summarizes the results from the 2-area analysis for nodes 9, 12, and 13. AF = Africa; Au = Australia; Eu = Eurasia; Mad = Madagascar; NZ = New Zealand; NH = Northern Hemisphere; SA = South America; SeA = Southeast Asia; SH = Southern Hemisphere.

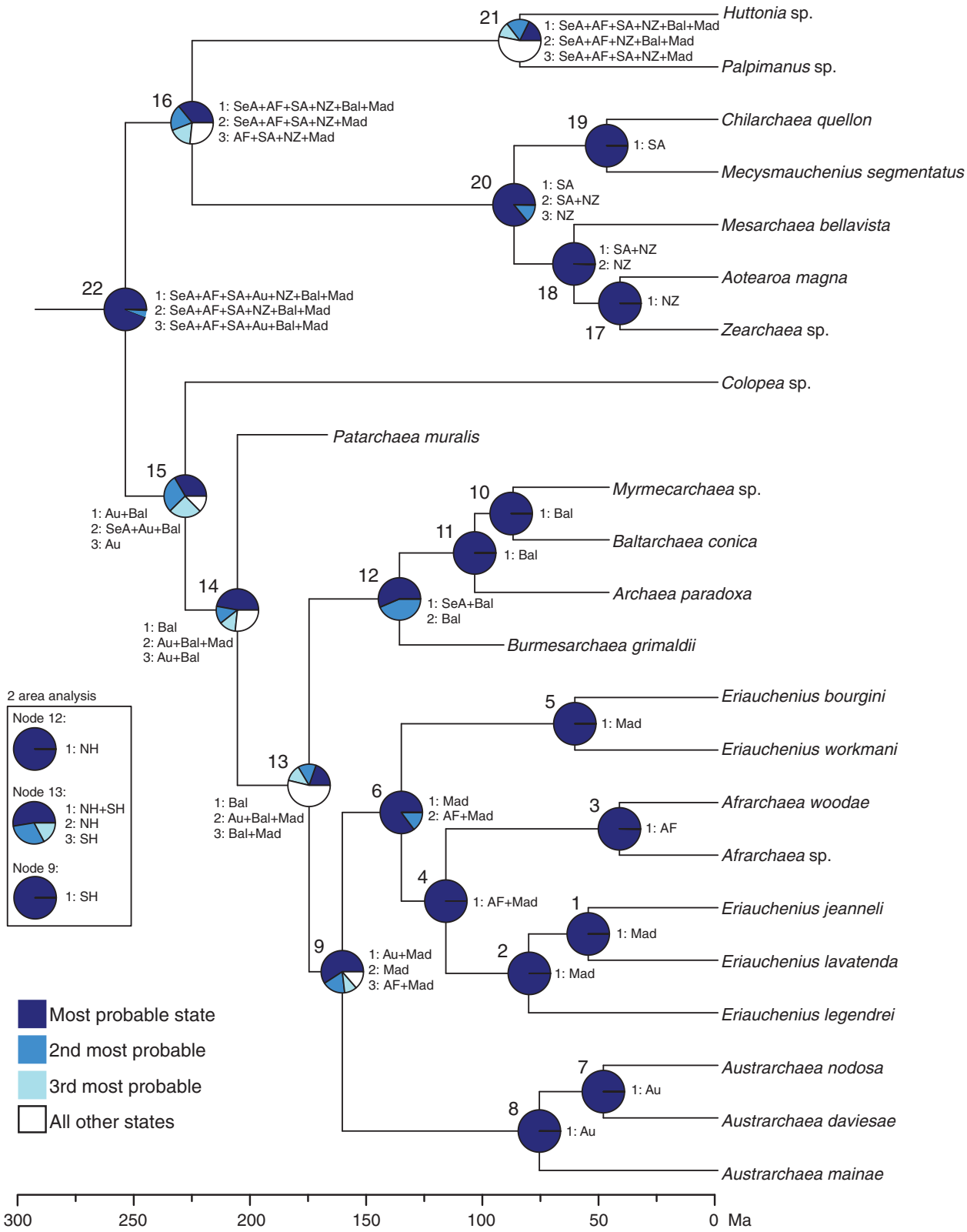

FIGURE 6. Summary of the DIVA ancestral range estimates for the 7-area analysis. DIVA was run on each of 1000 dated phylogenies randomly sampled from the posterior distribution of phylogenies produced during BEAST analysis (v). Pie charts represent the top 3 most likely ancestral geographic ranges at each node. Numbers next to nodes follow Tables 1 and 2. Boxed section summarizes the results from the 2-area analysis for nodes 9, 12, and 13. AF = Africa; Au = Australia; Eu = Eurasia; Mad = Madagascar; NZ = New Zealand; NH = Northern Hemisphere; SA = South America; SeA = Southeast Asia; SH = Southern Hemisphere.

Australia+Madagascar+Africa, but there are other less likely splits, such as Southeast Asia+Eurasia splitting with Australia. Because of the assumption of the DEC model where one of the daughter lineages inherits a range of a single area, LAGRANGE will never produce a result where, for example, Southeast Asia+Eurasia splits with Australia+Madagascar+Africa. Instead, LAGRANGE is forced to infer dispersal or range expansion to explain on descendent branches how lineages came to inhabit 2 or 3 areas. Because at this particular node we are interested in whether the split between the northern extinct archaeids and the southern extant archaeids is an ancient vicariance or dispersal event between Gondwana and Laurasia, the probability scores are summed for all the splits that involve one or more NH areas splitting with one or more SH areas, which equals 0.92 and which accounts for all the likely scenarios at this node. The analysis with only 2 areas, the NH and SH, confirmed these results: in LAGRANGE, the most likely split is between the NH and SH, with a probability score of 0.99; in DIVA, node 13 is reconstructed to be NH+SH. This result is also confirmed in the 2-area LAGRANGE and DIVA analyses on the randomly sampled 1000 dated phylogenies, which report the most likely ancestral state at node 13 to be the NH+SH, and at nodes 9 and 12 to be the SH and NH, respectively, (see boxed section of Figs. 5 and 6). Results for node 21 are also summarized to highlight the general biogeographic patterns and we find that all the likely splits involve New Zealand splitting from multiple areas.

To summarize, the general biogeographic patterns that emerge are that the more recent divergences are restricted to one or 2 areas and the ancestral nodes are widespread or restricted to many areas, a pattern suggestive of vicariance, rather than dispersal or relictualism. The basal nodes within the Palpimanoidea are widespread or ambiguous, and several nodes that are higher up (such as nodes 9 and 13) suggest vicariance events. Southeast Asia, Australia, and Eurasia were important in archaeid distribution patterns and one of these areas likely served as their origin. These biogeographic patterns are upheld in the analyses of the single dated phylogeny as well as the 1000 randomly sampled dated phylogenies.

Discussion

Impact of Treating Fossils as Terminal Tips

Including terminal fossils in divergence dating estimation and biogeographic reconstruction allows a researcher to make the most use of the fossil record and morphological data when available. When archaeid fossils are used as terminal tips, either with or without additional calibration points (analyses (i) and (v)), the estimated node ages for the most part are older than when using those same archaeid fossils only as node-based calibration points based on the age of the oldest archaeid fossil (compare with analyses (ii–iv)). This is particularly noticeable in the deeper diversification events that occur on nodes lower down than the terminal fossils (see nodes 22, 30–33, and 35–36) and suggests that the morphological traits in the terminal fossil taxa are contributing to the results. A different pattern was found in a total evidence dating analysis on Hymenoptera that examined what happens when fossils are treated as terminal tips or as node calibrations (Ronquist et al. 2012): some nodes were younger (outside the Hymenoptera) and some nodes were older (inside the Hymenoptera). In the current study, all archaeid terminal fossils branch off at the same point, whereas in Ronquist et al. (2012), the terminal fossils are scattered throughout the phylogeny, which may account for these differences.

Whether or not analyses that use node calibrations versus analyses that use fossils as terminal tips result in different dates is largely going to be a function of what prior node calibrations are input into the analysis. Ronquist et al. (2012) showed that when fossils are used as terminal tips, divergence date estimations are less sensitive to prior assumptions than in more traditional node-calibration methods. In this study, we also found that when fossils are used as terminal tips, the divergence date estimations are less sensitive to prior distributions: when the prior distribution log of the mean was doubled (analysis ii.a), the resulting node age estimations were older compared with analysis (ii), more closely mimicking the results from when terminal fossils were used in analysis ((i) and (v)). Although a researcher theoretically could adjust their prior distribution values by making an educated guess about how much morphological evolution has occurred in the fossil taxa, there is not a rigorous way to do this. As recent studies have pointed out, the choice of proper prior node calibrations is a difficult issue (Pyron 2011; Heath 2012; Parham et al. 2012; Ronquist et al. 2012). With treating fossils as terminal taxa, on the other hand, all of the assumptions are explicit and justifiable, cutting out the need for devising a prior constraint on particular nodes and thereby, this subjectivity is removed.

Ronquist et al. (2012) also showed that age estimations are more precise when fossils are used as terminal tips. However, in the current study, when fossils were treated as terminal tips, the error bars (95% Bayesian CI) for the node age estimations did not become obviously more precise compared with when fossils were used for constraining nodes as calibration points (compare error bars in Fig. 2 with Fig. 3). This may be due to our technique where the fossil tip date was treated as a range. However, in analysis (i.a), where the range of the fossil tip date was reduced to span only 1 myr, we found that the CI interval was not greatly reduced: the average difference in CI between analysis (i) and analysis (i.a) was 3 Ma, with a range spanning 10 to −5 Ma; the negative values indicate instances where the 95% CI was smaller in the original analysis (Table 1). This suggests that incorporating uncertainty into the fossil tip date does not inflate the 95% CI and that this approach should be

utilized because this uncertainty in the fossil age is real. Because of the findings outlined above, and also because treating fossils as terminal taxa allow a researcher to make the most use of the available data, we believe this method to be better than more traditional methods when it is possible to do so. In addition, while our combined analysis (v) also uses fossils as calibration points, we believe analysis (v) to be the most accurate because it is making the most use of our current knowledge.

Although incorporation of fossils as terminal taxa eliminates the subjectivity involved in deciding on priors for nodal ages, as is required in previous methods, this method also allows for a better assessment of biogeographical conclusions. One of the goals of this study was to examine archaeid diversification in relation to continental breakup, particularly regarding the biogeography patterns and the timing of the diversification event between the northern and southern fauna. It is impossible to examine the diversification between the extant and fossil taxa without incorporating the fossil taxa into the phylogeny, particularly because the fossil taxa have a different distribution than the extant taxa. This study found the extant archaeids to be monophyletic, as also found by Wood et al. (2012). There are several morphological synapomorphies that are characteristic of the extant archaeids and argue strongly for their monophyly (Wood et al. 2012). Incorporation of fossils as terminal tips into biogeographic and temporal analyses (i) and (v) is consistent with the vicariance hypothesis that the extant archaeids diverged from the northern lineages when Pangaea split into Gondwana and Laurasia 180 Ma (Smith et al. 2004). The mean divergence time of the split between the extant and fossil archaeids (node 13) is 178 Ma (95% CI = 236–126) for analysis (i) and 175 Ma (95% CI = 226–128) for analysis (v). Furthermore, all the likely ancestor range reconstructions at this node result in NH areas (Eurasia and Southeast Asia) splitting with SH areas (Australia and Madagascar) (Figs. 4–6, Table 2, node 13). Using this evidence, we conclude that the split between the northern and southern archaeid fauna was likely due to the vicariance event caused by the breakup of Pangaea into Laurasia and Gondwana, rather than due to dispersal or to pan-continental diversification that predated Pangaean breakup, accompanied by extinction (i.e., the "ousted relicts" theory of Eskov and Golovatch [1986]).

In contrast, in the temporal analyses where fossils are treated as calibration points (analyses ii–iv) to constrain nodes, the results are not as clear. Based on the phylogenetic study of Wood et al. (2012), we know that the archaeid fossils diverged somewhere along the branch between nodes 9 and 15 (see arrow in Fig. 3). In analysis (ii) (analysis (iv) gives similar results), the estimated divergence dates of nodes 9 and 15 are 140 Ma (95% CI = 112–162) and 168 Ma (95% CI = 162–186), respectively. These estimations reveal that the northern archaeid clade split with the southern clade sometime between 140 and 168 Ma based on the mean of nodes 9 and 15 (112 and 186 Ma based on the 95% CI). Awkwardly though, in analyses (ii) and (iv), node 15 was constrained with a calibration point based on the oldest archaeid fossil. In analysis (iii), which contains all the fossil calibrations except the constraint at node 15, the northern archaeid clade split with the southern clade sometime between 138 and 171 based on the mean of nodes 9 and 15 (the 95% CI of nodes 9 and 15 spans 91–227 Ma). The time intervals for analyses 'ii–iv' are somewhat congruent with a vicariance scenario of 180 Ma, given that the oldest estimated mean is around 170 Ma based on node 15, with the 95% CI going back to 186 Ma. However, compared with the analyses that use fossils as terminal tips, because the estimated divergence dates span 2 nodes, it is more difficult to pinpoint this divergence event. Within the date range spanned by nodes 9 and 15, 180 Ma, which dates the event where Pangaea separated into northern and southern elements, falls much closer to the upper bound of the range, rather than very close to the mean, as it did in analyses where fossils are treated as terminal tips. The fact that there is overlap between the estimated divergence dates between the 2 different approaches (either treating fossils either as terminal tips or as calibration points) indicates that we have made reasonable choices for the prior distribution used to constrain node; however, we could have poorly chosen our priors and we would have no way of knowing this without the comparison to the analysis with terminal fossils.

By incorporating the fossil taxa directly into the phylogeny, we are better able to pinpoint the timing of the diversification between the northern and southern fauna. But most importantly, inclusion of fossils as terminal tips allows us to avoid subjective guessing of where the fossils diverged between 2 nodes, and avoid the situation where one of the nodes of interest is the same node that is being constrained with a calibration point. Finally, when fossil lineages have a different distribution than the extant taxa, it is absolutely crucial to include fossils as terminals in order to examine biogeographic patterns between extant and extinct lineages. In analyses where archaeid fossils were treated as node calibrations (analyses ii–iv), it is impossible to perform ancestral range reconstructions between living and extinct lineages on the resulting BEAST chronogram because the fossils are not included in these analyses. Instead, we would be restricted to parsimony ancestral reconstructions on the undated phylogeny that includes both fossils and extant taxa; however, then we would be throwing out information on branch lengths.

Extant Archaeid Biogeography

For all further discussion of biogeography we refer to the topology from only the analyses that incorporate fossils as terminal tips. In particular, we refer to the combined analysis (v), because this analysis makes the most use of the available data, and for simplicity, we discuss only the results from the LAGRANGE analysis of the single BEAST chronogram (Fig. 4). Regarding the

diversification events among the extant archaeids, the split (node 9) between the Australian clade, *Austrarchaea*, and the African genera (comprised of Madagascan and South African genera *Eriauchenius*, *Afrarchaea*, and the "Gracilicollis group") occurred 161 Ma (95% CI = 108–221). Ancestral range reconstructions at this node suggest the most likely split to be between Australian and African areas (Madagascar and South Africa; node 9, Table 2). The diversification event between the Australian and the African archaeid fauna is consistent with the vicariance event where rifting began with Madagascar + India separating from Australia and other parts of Gondwana starting 165 Ma (Rabinowitz et al. 1983; Scotese 2004; Smith et al. 2004) with complete isolation of Madagascar and India by 140 Ma (Seward et al. 2004). However, it is important to note that node 6 is not well supported in this study and these conclusions may be altered in trees lacking node 6.

A previous study, which examined timing of divergence in Australian archaeids by applying an arthropod substitution rate to the molecular data, suggested slightly different divergence dates. Rix and Harvey (2012) suggested that major Australian lineages diverged in the early Tertiary (69–34 Ma) prior to the separation of Australia and Antarctica around 35 Ma (Li and Powell 2001; Crisp et al. 2004). Rix and Harvey (2012) also found that divergence between the Australian lineages and the Madagascan taxon occurred 70–115 Ma. Although the current study found the split between the Australian and Madagascan taxa (node 9) to be much older, these differences are likely because the divergence time estimations from Rix and Harvey (2012) were based on a substitution rate instead of using the fossil record for calibration.

Regarding the South African archaeid genus *Afrarchaea*, the timing of the diversification event between *Afrarchaea* and the "Gracilicollis group" from Madagascar (node 4) occurred 116 Ma (95% CI of 68–177), which could be congruent with the separation of Africa from Madagascar + India 165 Ma. Yet, given the range of the 95% confidence interval, this is more likely explained by a single dispersal from Madagascar to South Africa after these landmasses were separated. Dispersal from Madagascar to Africa has also been found for chameleons (Raxworthy et al. 2002) and rodents (Jansa et al. 1999), but is contrary to the general pattern found in Madagascar biota, where typically a lineage disperses to Madagascar from Africa (Yoder and Nowak 2006). However, node 4 is not well supported in this study and these conclusions may be altered in trees lacking node 4.

If archaeid diversification relates to the breakup of Pangaea into northern and southern regions and possibly to the splitting of eastern and western Gondwana (with a more recent dispersal to Africa), the implication is that archaeids must have gone extinct in many areas that were previously occupied. Given the extended duration in time of the fossils, from the Jurassic to the Eocene, and in their distribution, from Baltic and Burmese amber and from Inner Mongolia, it is apparent that archaeids must have once occupied a large range over a long period of time in the NH where they are now extinct. In the SH, extant archaeids are only known from Madagascar, Australia, and South Africa, yet at one time these areas were all joined along with other Gondwanan areas. Given the ancient origin of archaeids, this could imply that archaeids may have also gone extinct in Gondwanan areas such as Africa (with a possible later re-colonization to southern Africa from Madagascar), South America, New Zealand, and New Caledonia. Ancient climate reconstructions suggest that Pangaea and Gondwana had a broad range of climates, with equatorial tropical areas and more southern, cool, temperate areas (Rees et al. 2002). Although multiple independent extinctions could explain archaeid distribution patterns, an alternative explanation is that archaeids may always have occupied only the tropical areas of Pangaea (and later northern Gondwana), and never occurred in the southern temperate areas. If this is the case, then the lack of archaeids in areas such as New Zealand, New Caledonia, and southern South America may be original and attributable to unsuitable climate in southern Pangaea. Today, archaeids seem limited to habitats that are warm and moist year round, such as Afro-montane and coastal areas in eastern South Africa, the eastern rainforests of Madagascar, the northeastern rainforests in Australia, and coastal or mountain area in other parts of Australia that have microclimates ensuring year-round moisture. Several archaeid species occur in the temperate western forests of Madagascar, with one species even found in the southern spiny dry forests, but these few species seem to be the exception to a general trend.

Deep Divergence within the Araneomorphae and Palpimanoidea

This study suggests that the deep diversification events within the araneomorph spiders were ancient, with the root of our tree, representing the diversification of the Araneomorphae, occurring in the Devonian, based on the mean age estimation = 351 Ma, although with large uncertainty (node 36, 95% CI = 270–441) that spans the Silurian to the Permian. This finding is consistent with those of Ayoub et al. (2007) who found that the diversification of the Araneomorphae was late Devonian to mid-Carboniferous, and Dimitrov et al. (2012) who found dates from mid-Carboniferous to early Permian. Furthermore, while we do not recover the classic Haplogynae (Platnick et al. 1991; Ramírez 2000) as monophyletic with our restricted sampling, the diversification events suggested for Haplogynae taxa occurred throughout the Carboniferous, as also suggested by Ayoub et al. (2007). In this study, the estimated age of the most recent common ancestor (MCRA) of the major clade containing both the Palpimanoidea and the Entelegynae (the majority of familiar spiders) occurs in the Permian (node 31; however, the 95% CI spans the Triassic to

the Carboniferous), with Entelegynae diversification starting in the Triassic-Jurassic (node 30). This is consistent with the Dimitrov et al. (2012) study that found the MCRA of the clade containing both the Entelegynae and a palpimanid to be mid-Permian to late Triassic, and with Entelegynae diversifying in the late-Triassic. Although Ayoub et al. (2007) did not include any Palpimanoidea members in their study, their estimation of Entelegynae diversification, represented by the "RTA-clade" and the Orbiculariae (the orb-weavers and their relatives), occurred in the Triassic, whereas our estimation of the diversification event between the orb-weavers and the "RTA-clade" was more recent, in the Jurassic (node 29). Age estimations from our study, as well as those from Ayoub et al. (2007) and Dimitrov et al. (2012), are considerably older than those based on the fossil record (Penney et al. 2003, 2012), which is expected because the fossil record represents a minimum age. These findings suggest that diversification within major Araneomorphae clades was ancient, occurring in the Devonian and Carboniferous.

This study also finds Palpimanoidea to be a very ancient group, with diversification of major lineages occurring in the Permian and Triassic, prior to Pangaea breakup. The fossil record suggests that Palpimanoidea was once more widespread (with archaeids once occurring in the NH) and also had families and genera that are known only as fossils that are now extinct, such as *Sinaranea* (family unknown) from Jurassic formations in Inner Mongolia (Selden et al. 2008a), Spatiatoridae (Petrunkevitch 1942) from Tertiary Baltic amber (Penney and Selden 2006), and Lagonomegopidae (Eskov and Wunderlich 1995) and Grandoculidae (Penney 2011) from Cretaceous amber. In addition, huttoniid fossils have been described from juveniles in Cretaceous Canadian amber (Penney and Selden 2006), which were used as a calibration point in this study. Many of the known palpimanoid fossil specimens are poorly preserved or are juveniles that are placed in the Palpimanoidea based on the presence of spatulate hairs on the legs (highly modified in the Lagonomegopidae), whereas many other palpimanoid characters, such as peg teeth and cheliceral gland mound, are often unavailable or obscured, making phylogenetic and taxonomic placement difficult. Because of this, these poorly preserved fossil lineages were not included in the phylogenetic data set of Wood et al. (2012), and thus not included in the current study. Regardless, the range and diversity of fossil taxa that are very likely Palpimanoidea from the NH suggest that this superfamily may have been a more abundant, diverse, and dominant member of the ancient spider fauna.

Regarding the present distribution of mecysmaucheniids, which belong to the Palpimanoidea, these spiders live in the cold, temperate *Nothofagus* forests of New Zealand and southern South America and they seem to be more abundant and active during the colder times of the year. Their present distribution and tolerance for cold habitats, coupled with the fact that the estimated age of the family precedes the timing of Pangaea breakup for the most part (node 16: mean = 225, 95% CI = 117–308), suggests that mecysmaucheniids may have always occupied only the southern, cool, temperate regions of Pangaea (Rees et al. 2002) and later Gondwana, and never occurred in the more tropical northern areas, which may have been occupied by the remaining Palpimanoidea.

Members of the Palpimanoidea tend to be araneophages, meaning they are specialized to prey on other spiders, with some members adopting highly specialized feeding strategies (Wood et al. 2012). Araneophagy has been well documented in the archaeids (Millot 1948; Legendre 1961; Wood 2008; Wood et al. 2012) and in the palpimanids (Cerveira and Jackson 2005; Pekar et al. 2011), whereas the documentation of prey choice in other palpimanoid taxa is scant, but trends toward araneophagy (Wood et al. 2012). Prey choice records of archaeids (Wood et al. 2012) and palpimanids (Cerveira and Jackson 2005) and the few known records for mecysmaucheniids (Vellard 1957; Wood et al. 2012) suggest that Palpimanoidea seem to prey mostly on the Entelegynae. In this study, Palpimanoidea and the Entelegynae are sister taxa that diversified from a common ancestor in the Permian (node 31). It is possible that Palpimanoidea diversification and evolution of their specialized predatory behaviors may have been congruent with Entelegynae diversification.

Conclusions

Fossils clarify biogeography patterns especially, as in our case, when the fossil distribution differs from that of the extant distribution. In this study, we included fossils as node calibration points, and also as terminal tips with a uniform distribution that spans the uncertainty of the fossil age, a technique pioneered here. Using this technique, we found evidence that archaeid distribution patterns are consistent with the breakup of Pangaea into Gondwana and Laurasia. It is important to note that the Jurassic age of some archaeid fossils (Selden et al. 2008a) coupled with the monophyly of the extant southern lineages are facts suggestive of vicarance, in and of themselves, without having to rely on sophisticated statistical methods, although these support our conclusion. Often, phylogenetic estimates of divergence times turn out to be far too recent to be a result of Gondwanan vicariance, meaning dispersal must play a major role in distributional patterns. Instead, here we reveal an example in which biogeographic distributions are plausibly linked to Gondwanan vicariance.

Supplementary Material

Supplementary material, including data files and/or online-only appendices, can be found in the Dryad data repository at http://datadryad.org, 10.5061/dryad.7231d.

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