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Evolution of Archaeid and Mecysmaucheniid Spiders (Arachnida, Araneae)

By

Hannah Marie Wood

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of the

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Committee in charge:

Professor Rosemary Gillespie, Chair
Professor Charles Griswold
Professor Rauri Bowie

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ABSTRACT

Evolution of Archaeid and Mecysmaucheniid Spiders (Arachnida, Araneae)

by

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Doctor of Philosophy in Environmental Science, Policy and Management

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Professor Rosemary Gillespie, Chair

The limits of the superfamily Palpimanoidea, as well as the phylogenetic placement of archaeid and mecysmaucheniid spiders within the Araneomorphae, are unresolved. Furthermore, the relationships between the extant and extinct archaeid taxa is also debated and unresolved. This study focuses on these issues by creating a phylogeny from molecular and morphological data and addresses three features of archaeid and mecysmaucheniid evolution: (1) inclusion of several lineages of fossil archaeids clarifies relationships between extant and extinct archaeids and helps explain the disjunct distribution whereby fossils are known only from the northern hemisphere while extant taxa are restricted to the southern hemisphere; (2) the placement of archaeids and mecysmaucheniids within the Araneomorphae; (3) the limits of the superfamily Palpimanoidea and its placement within the Araneomorphae. In addition, the timing of deep diversification within the Araneomorphae is estimated by enforcing a molecular clock that includes the archaeid fossil taxa as noncontemporaneous tips. These temporal estimations are used to examine biogeographic patterns of congruence with continental break-up. Total evidence analysis supports the monophyly of a redefined Palpimanoidea, which includes the archaeids and mecysmaucheniids. This study finds Palpimanoidea to be sister to the Entelegynae and to be an ancient group, with diversification occurring in the Permian. Furthermore, the split between the northern and southern archaeid fauna and the diversification of the southern archaeid clades was likely due to the vicariant events caused by the break-up of Pangaea and Gondwana.

Further study of archaeid spiders offers the possibility to better understand speciation patterns in a group of taxa that have low dispersal abilities and that likely have been on Madagascar since Pangean times. To examine speciation patterns in a lineage that likely did not disperse to Madagascar, the current study sets out to (1) create a phylogeny of archaeid spiders that thoroughly samples Madagascan lineages; (2) calibrate this phylogeny using fossil and geological data and determine the timing of splitting events between the different Gondwana fragments; (3) examine lineage through time plots to determine diversification patterns. In addition, the “neck” trait is treated as a continuous character and its evolution is examined. This study shows that archaeid biogeography patterns are likely explained by vicariance due to Gondwanan break up. The lineage through time plots reveal that the Madagascan archaeids have not experienced increases or decreases in the rate of diversification, meaning a constant rate of lineage accumulation cannot be rejected. Furthermore, the evolution of the “neck” best fits the Brownian motion model, implying that evolution of “neck” length is a product of genetic drift.

For archaeid lineages that have been on Madagascar since pre-isolation times gradual accumulation appears to be the rule.

Next, the current study focuses on the trap-jaw in mecysmaucheniid spiders in order to address how it has become modified over the evolutionary history of the lineage. Evolution, function, and morphology of the trap-jaw are examined among different lineages of mecysmaucheniids to assess the extent of conservatism versus plasticity in the trait. This study involves molecular phylogenetic analyses, detailed morphological analysis of jaw structure, and high-speed video recording to assess the variability and evolution of the trap-jaw. Results indicate that there is a large degree of variation in jaw function spanning two orders of magnitude. Within mecysmaucheniids, rapid-inertia-based mechanisms have evolved in parallel 3-4 times. Examination of trap-jaw morphology reveals that each rapid-inertia-based mechanism is unique with different morphologies. The trap-jaw movements in some mecysmaucheniid lineages may be among the fastest animal movements known, with the fastest species attaining jaw-closing speeds of greater than 25 meters/second in less than one tenth of a millisecond.

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CHAPTER I

Inclusion of Fossils Clarifies Biogeographic History: Placement of Archaeid Spiders with Insight into Evolution of the "Neck" and Diversification of the Palpimanoidea

Introduction

Evolutionary biologists seek to understand broad evolutionary patterns by examining phylogenetic relationships among organisms, yet, the vast majority of all organisms that have ever existed have gone extinct (Raup, 1993), which makes conclusions drawn from the vast majority of studies that focus on contemporary taxa incomplete. Including fossils in phylogenetic studies is also important for understanding biogeography patterns, particularly, as in the case of this study, when fossil distributions differ from those of contemporary taxa. Taxa with disjunctive Gondwanan distributions are often explained by vicariance due to continental break-up. However, there are several examples where the incorporation of fossils into phylogenetic studies has instead explained biogeographic disjunctions as being due to migration across landbridges, and then subsequent extinction in intermediate areas, such as in the angiosperm clade Malpighiaceae (Davis *et al.*, 2002) and in cornelian cherries (Xiang *et al.*, 2005). Alternative to mobilistic biogeography and dispersal is the "ousted relicts" theory which proposes that austral disjunctions, with extant taxa living in Gondwanan areas, result from extinction in Northern Hemisphere areas from a previously pancontinental distribution (Eskov & Golovatch, 1986). There are many examples of groups that have living taxa in Gondwanan areas with fossil taxa known from northern areas (Eskov, 1987; 1992). However, these distribution patterns may in fact turn out to be a result of Gondwanan vicariance if it can be shown that northern and southern clades are distinct lineages and that the timing of diversification is congruent with Pangean break-up into Gondwana and Laurasia. In this study we attempt to explain a disjunct biogeographic pattern found in archaeid spiders where extant members occur only in the Southern Hemisphere, but have an excellent Northern Hemisphere fossil record.

Archaeid spiders are cursorial hunters unique in their extreme modification of the cephalic area and chelicerae (jaws) giving them the appearance of a "neck" and "head" (Fig. 1E, G, H). Whereas most spiders are predatory generalists, archaeids are highly specialized and will only prey on other spiders (Millot, 1948; Legendre, 1961). The highly modified cephalic area in archaeids is used to employ a novel prey capture strategy that is unique among spiders (see Fig.1 in Wood *et al.*, 2007). Furthermore, extant archaeids have a highly restricted, seemingly Gondwanan distribution in the Southern Hemisphere, being found only in Madagascar, Australia, and South Africa. Yet, archaeids were first described from fossils from the Northern Hemisphere. Their grotesque appearance, unique predatory behaviors, 'living fossil' status, and endemism in different parts of the southern hemisphere make them a charismatic group that is well known to arachnologists (Griswold, 2003). The relationships between the extant and extinct archaeid taxa as well as the phylogenetic placement of the entire family within the derived, higher spiders (the Araneomorphae) is debated and unresolved (Griswold *et al.*, 2005). This study focuses on addressing these issues by creating a phylogeny from molecular and

morphological data for a diverse array of fossil and extant archaeids, with extensive outgroup sampling that includes a diverse array of taxa representing the major groups of Araneomorphae spiders. Furthermore, it recently has become possible to include fossils into divergence time estimation as non-contemporaneous tips rather than as calibration points (Pyron, 2011), and this analysis is also performed here.

The family Archaeidae was first described from three Baltic amber fossils in 1854 (Koch & Berendt) dated to be of mid-Eocene age (Penney *et al.*, 2011). It was not until 1881 that the first living archaeid was found in Madagascar (Cambridge, 1881). Later, many more extant species were discovered from Madagascar, South Africa and Australia. There have since been additional fossil species and genera described from Baltic and Burmese amber (Penney, 2003; Wunderlich, 2004; 2008), and even compression fossils from Inner Mongolian rocks of Jurassic age (Selden *et al.*, 2008). This study focuses specifically on this apparent shift in distribution, from Northern Hemisphere extinct lineages to Southern Hemisphere extant lineages and seeks to understand the lack of overlap between extant and extinct faunas by examining the fossil material from a phylogenetic context. The fossil record suggests that the spider order (Araneae) diversified about 390 my ago (Penney & Selden, 2007) and that archaeid spiders may have originated before the breakup of Pangaea, which occurred ca. 180 mya (Smith *et al.*, 2004). An archaeid phylogeny that includes fossils may determine whether the distribution of extant and fossil archaeids is due to continental break-up (vicariance), dispersal, or alternatively due to relictualism, i.e. "ousted relicts."

The phylogenetic placement of archaeids within the Araneomorphae spiders is also unresolved (Griswold *et al.*, 2005). The suborder Araneomorphae 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, 2011). Within the Araneomorphae, families are divided into two genitalic types, the basal haplogynes (or "simple" genitalia, with a common entrance for copulation and oviposition) and the more derived, monophyletic, entelegynes (or "complex" genitalia, with separate entrances for copulation and oviposition). Placement of archaeids, which have "simple" haplogyne genitalia, within the Araneomorphae is confounded by the issue as to whether archaeids are primitively haplogyne and fall outside the Entelegynae ("complex" genitalia clade), or whether they are Entelygynae that have secondarily reverted back to the ancestral condition of "simple" genitalia.

Furthermore, the historical classifications of archaeid spiders and their closest relatives are influenced by the idea that lineages that have evolved an elevated cephalic area (the "neck" and "head") are more closely related (Forster & Platnick, 1984). The evolution of a "neck" is an unusual trait that is very rare and uncharacteristic of the typical spider body plan (Fig.1A), yet, whereas this trait is taken to the extreme in archaeids, this trait also occurs in two other spider families, Mecysmaucheniidae and Pararchaeidae (Fig.1B, F). There are also other spider families that may be intermediate for this trait, such as Holarchaeidae, or that have other modifications to the cephalic area, such as elevated eyes. Based on the trait of having a "neck" as well as several other morphological characters, Forster & Platnick (1984) suggested that archaeids belong to the superfamily Palpimanoidea along with nine other families, an expansion of the "traditional" Palpimanoidea, which contained only three families, Huttoniidae, Palpimanidae and Stenochilidae. Relationships among archaeid genera and species are generally also based on this trait (Legendre, 1970; Platnick, 1991), although Wood *et al*. (2007) established that within the Madagascan species the level of elevation in the cephalic area has evolved in parallel.

Subsequent to Forster & Platnick's expansion of Palpimanoidea, several studies have demonstrated that Palpimanoidea is paraphyletic; however, these studies did not fully address the placement of ousted members or the placement of archaeids. Using morphological characters, Schütt (2000; 2002) was the first to show that Palpimanoidea was not monophyletic, although this work did not adequately sample throughout the Araneomorphae in order to place archaeids. Additionally, Rix *et al.* (2008), using molecular data, also broke apart Forster & Platnick's Palpimanoidea, yet archaeids were not included in this study, leaving their placement within the Araneomorphae unclear. Another phylogenetic study, which relied on morphological data and included taxa from throughout the Araneomorphae, was ambiguous in their findings regarding archaeid placement: in the parsimony analysis with characters held under equal weights, archaeids and their Palpimanoidea relatives fell within the Entelygynae ("complex" genitalia) and the Palpimanoidea hypothesis was not refuted; whereas under the implied weights analysis, Palpimanoidae was split up and archaeids fell outside the Entelygynae (Griswold *et al.*, 2005).

To date, there has not been a study which samples the Araneomorphae and Palpimanoidea broadly enough to adequately place archaeids, and which includes both molecular and morphological data as well as fossil archaeids. In this study we do just that resulting in a total evidence phylogeny that includes the majority of the families of Forster & Platnick's expanded Palpimanoidea as well as additional families representing major clades within the Araneomorphae. This study addresses three features of archaeid evolution: (1) inclusion of several lineages of fossil archaeids will clarify relationships between extant and extinct archaeids and help understand the disjunct, enigmatic distribution whereby fossils are known only from the northern hemisphere while extant taxa are restricted to the southern hemisphere; (2) the placement of archaeids within the Araneomorphae; (3) the limits of the superfamily Palpimanoidea and its placement within the Araneomorphae. In addition, we estimate the timing of deep diversification within the Araneomorphae by enforcing a molecular clock that is calibrated with other non-archaeid fossils and that includes the archaeid fossil taxa as noncontemporaneous tips. These temporal estimations are then used to examine biogeographic patterns of congruence with continental break-up among archaeids and their close relatives. This phylogeny will also allow for a more informed view of the evolutionary history of a novel morphological trait, the modified and elevated cephalic area or "neck," across the Araneomorphae. To date, this is the most comprehensive study ever performed that deals with phylogenetic relationships among archaeids and their relatives.

Materials and Methods

Taxon sampling

To examine relationships among extant and fossil archaeids we included 10 species from Madagascar, Australia and South Africa, representing the three known extant genera: *Eriauchenius* (Cambridge, 1881), *Austrarchaea*, *Afrarchaea* (Forster & Platnick, 1984), as well as the monophyletic "Gracilicollis Group" from Madagascar (Wood *et al.*, 2007; Wood, 2008) that is currently placed in *Eriauchenius* (Table 1). Five fossil archaeid taxa were also included in this study. These five fossils are made up of 1 taxon from Burmese amber, 3 taxa from Baltic amber, and one compression fossil from Inner Mongolian rocks. The included fossil taxa represent 5 of the 11 fossil archaeid genera (Dunlop *et al.*, 2011). See Selden *et al.* (2008) for a discussion of archaeid fossils. The remaining six archaeid fossil genera were omitted from the study subsequent to examination for the following reasons: the genus *Eoarchaea* (Forster & Platnick, 1984) has been erected from juvenile specimens and no adult specimens are known;

two *Saxonarchaea* (Wunderlich, 2004) specimens were examined and the inclusions were obstructed, preventing examination of important morphological traits; *Filiauchenius* (Wunderlich, 2008) is know from one specimen that is highly obstructed by cloudy, discolored amber; *Eomysmauchenius* (Wunderlich, 2008) is known from only one specimen that is highly distorted; *Lacunauchenius speciousus* (Wunderlich, 2008) is known from one specimen that is distorted and it was very difficult to determine whether many of the viewed morphological traits were real or artifacts of preservation (see discussion for more detail on this enigmatic taxon); *Jurarchaea* (Eskov, 1987) is too poorly preserved to be identified as an archaeid (Wunderlich, 2004; Selden *et al.*, 2008).

The remaining five fossil taxa used for this study are all adults, with the exception of *Myrmecarchaea* sp. (Wunderlich, 2004), which consists of a few specimens that all appear to be juveniles. *Myrmecarchaea* was included in this study because the morphology was preserved well enough to score for somatic characters even though genitalic data were lacking. Specimens representing both adult male and females were present only in the fossil *Archaea paradoxa* (Koch & Berendt, 1854) whereas in all other fossils one sex was missing. Thus, because it was not possible to score fossil taxa for internal or microscopic characters, and due to lack of genetic data for fossil taxa, the character sets for the fossil taxa are highly incomplete. However, archaeids possess a number of somatic features that are easy to see with a dissecting microscope and through the use of Computed Tomography scans, and for this reason it was still possible to score the fossil taxa for many characters. Studies have shown that taxa missing partial data are still useful for interpreting homology among characters, and that they do not necessarily create inaccuracies in the phylogeny, and that while inclusion of taxa with partial data matrices may reduce resolution, the inclusion of such taxa may also improve accuracy (Wiens, 2003b; a; Driskell *et al.*, 2004; Philippe *et al.*, 2004; Santini & Tyler, 2004).

In order to understand the placement of archaeids within the Araneomorphae, we included an additional 22 non-archaeid taxa representing 18 families, with the most basal Araneomorphae family Hypochilidae as the outgroup (Table 1). These additional taxa represent the major clades within the Araneomorphae (Griswold *et al.*, 2005): we intend to avoid biasing the outcome by restricting possibilities, and therefore give archaeids several different places to fall within the Araneomorphae. Furthermore, all family members of Forster & Platnick's (1984) Palpimanoidea were included in the study with the exception of the Micropholcommatidae and Malkaridae. It has previously been shown that these families group with members from the superfamily Araneoidea (the orb-weavers and their relatives) (Schütt, 2000; 2002; Rix *et al.*, 2008) rather than with the Palpimanoidea.

When possible we used non-chimeric taxa, but for some species this was not possible because we were limited to assembling terminals from a variety of sources. Of the few taxa that are chimeras, there is no question about the monophyly of the family they are representing, for example, the specimens representing the families Pararchaeidae, Gnaphosidae and Lycosidae are assembled from two different genera, yet the classification of these families is not controversial (Pararchaeidae: Rix, 2006; Gnaphosidae: Platnick, 1990; Lycosidae: Griswold, 1993). Including archaeids, there are a total of 37 ingroup taxa and data for all molecular and morphological vouchers are presented in Tables 1 and 2. We were able to obtain data from four molecular markers (for only the extant taxa) and for 126 morphological characters across a wide range of taxa spanning the Araneomorphae.

Morphological character acquisition

Many of the 126 morphological characters (Appendix 2) were formulated specifically for this study and since the focus of this study is the placement of archaeid spiders, many of these new characters deal with archaeid traits, for example, spines on the carapace, scopulae presence, peg-teeth shape. The remaining characters are based mostly on Griswold *et al*. (2005) and are characters commonly used in spider systematics. The 126 characters deal with genitalia, spinnerets, and somatic traits; the morphological matrix is presented in Appendix 3. For some taxa, the morphological character states were scored using data from other studies (Forster & Platnick, 1984; Griswold *et al.*, 2005) as well as from SEM images acquired from other arachnology labs as part of the Arachnology Tree of Life project (PIs Wheeler *et al*.)

Morphological data was gathered using a Leo 1450VP scanning electron microscope (for only the extant taxa) and a Leica MZ12.5 stereomicroscope (for both the extant and fossil taxa). Vouchers used for morphological character acquisition are presented in Table 1. When possible, one voucher of each sex was selected per taxon and used for scoring the majority of the characters. Regarding fossil data, over 75 archaeid amber fossil specimens were borrowed from museums and from these, vouchers were selected. Additional specimens were occasionally needed for scoring a fossil taxon when a body part was obstructed or distorted (also listed in Table 1). Three fossil taxa were additionally examined by Computed Tomography scanning, which was done at the High Resolution X-ray CT Facility at UT, Austin. There were a total of 4 scans performed representing 3 taxa: a male and female *Archaea paradoxa* and a female *Baltarchaea* sp. were scanned; although the taxon *Launauchenius speciosus* was scanned it was not used for this phylogenetic study (see discussion). From these scans, 3D digital reconstructions were created which could be rotated and sliced through and examined to score characters (Fig.1E). Characters were scored for the compression fossil *Patarchaea muralis* by examining the detailed published images (Selden *et al.*, 2008).

DNA sequence collection and alignment

The majority of the molecular data used in this study were gathered using the methods listed below. Molecular data for some taxa were also acquired from GenBank using additional studies (Wheeler & Hayashi, 1998; Starrett & Waters, 2007; Binford *et al.*, 2008; Rix *et al.*, 2008; Spagna & Gillespie, 2008; Álvarez-Padilla *et al.*, 2009; Arnedo *et al.*, 2009; Blackledge *et al.*, 2009; Duncan *et al.*, 2010; Miller *et al.*, 2010). An additional 8 unpublished sequences were acquired from the Arachnology Tree of Life project (AToL). Some of the sequences taken from GenBank and AToL were not as complete as the sequences generated in this study, and furthermore, some specimens sequenced for this study were difficult to amplify and/or sequence for some markers, even though new primers were designed. For these two reasons, a few taxa are incomplete at some regions or markers, but the majority of the taxa are complete for all four markers (see Table 2).

Prior to extraction, field collected specimens were placed in 95% EtOH and stored in a freezer (-20°C). 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, and the ribosomal nuclear genes 28S and 18S. The four fragments were extracted, amplified, and sequenced using standard protocols (Wood *et al.*, 2007). Amplified PCR product was sequenced in the Evolutionary Genetics Lab at the Museum of Vertebrate Zoology at the University of California, Berkeley. Also, cleaned PCR product was sent to the UC Berkeley DNA Sequencing Facility.

The quality of forward and reverse sequences was confirmed using Sequencher version 4.7 (Gene Codes Co., Ann Arbor, MI) by assembling forward and reverse sequences into aligned contigs. Consensus sequences were exported from each high quality contig. Non-protein coding genes were aligned using the online interface (http://align.genome.jp/mafft/) for Mafft (Katoh *et al.*, 2002) using the E-INS-i strategy, which operates best on sequences with multiple conserved domains and long gaps. The gap open penalty was set to the default of 1.5 and the offset value at the default of 0.14. Alignments were visually inspected using MacClade v4.08 (Maddison & Maddison, 2005) and no egregious errors were found. Protein coding genes were manually aligned, translated into amino acids and checked for stop codons using MacClade. The four gene alignments were then combined with the morphological data to form a concatenated data set using Mesquite v2.74 (Maddison & Maddison, 2010).

Phylogenetic Analysis

Phylogenetic analyses were carried out using parsimony and Bayesian methods. Using these methods, analyses were performed on each of the 4 individual genetic markers, the morphological data set, the 4 concatenated genetic markers, and the concatenated molecular and morphological total evidence (TE) data set. To test how the alignment may have affected the results, additional parsimony and Bayesian analyses were run with gapped characters removed from the TE concatenated data set, the concatenated genetic markers, and the single marker data sets for 28S and 18S. Furthermore, to examine how incomplete taxa affect the phylogenetic results the fossil taxa were removed and additional analyses were performed on the TE data set and on the data set that contained only morphological characters. All analyses were rooted with the most basal Araneomorphae family Hypochilidae (*Hypochilus pococki*).

Parsimony searches were performed in PAUP* version 4.0b10 (Swofford, 2003) using the random stepwise addition option of the heuristic search for 1000 replicates with tree bisection-reconnection (TBR) branch swapping, collapse of zero-length branches, and equal weighting of all characters. To measure the robustness of branching patterns of the parsimony trees, bootstrap analyses (Felsenstein, 1985; Hillis & Bull, 1993) were executed for molecular data by using the random stepwise addition of the heuristic search for 1000 replicates. Bremer support values were also assessed using TreeRot v3 (Sorenson & Franzosa, 2007) for the morphology data set.

Bayesian analyses were implemented in MrBayes version 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Using the Akaike information criterion (AIC; Akaike, 1973), the best fit substitution model was estimated for the genetic data using MrModeltest version 2.2 (Nylander, 2004) for 28S, 18S, and each of the three codon positions in the protein coding H3 and COI genes. The final concatenated TE data set had a total of 9 partitions made up of the 3 codon positions for the 2 protein coding genes (6 partitions), the 2 ribosomal nuclear markers and the morphological data. For the morphological partition, the standard discrete Markov model (Mkv) was used following Lewis (2001) with rates set to equal. Bayesian analyses were performed using four chains, the analysis was run twice simultaneously, and the starting trees were randomly generated. All analyses were run for 10 million generations, with sampling every 1000^{th} generation, except for the 4-gene-marker analysis with gaps removed and the analysis of only 28S with gaps removed (both run for 20 million generations), and the 4-gene-marker analysis (run for 40 million generations), since these analyses took longer to converge.

Additional Bayesian analyses of the TE data set were also performed to further explore the data. In order to examine how the priors were biasing the results the branch length prior was changed from the default value to the extreme value of 1, which is contrary to expectations when dealing with very divergent taxa, such as in our study (Yang & Rannala, 2005). We also performed an analysis of the TE data where all partitions that were GTR+I+G were instead set to only GTR+G. This was done because it has been shown that I+G do not properly mix in analyses (Brian Moore, personal communication).

All Bayesian 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 & Drummond, 2007). The burn-in value was visualized and determined by summarizing posterior distributions of scalar values, which identified the first 25% of the initial trees to be discarded, resulting in a final consensus tree with node support expressed as posterior probabilities. Morphological characters were mapped on the tree for visualization using WinClada version 2.0 (Nixon, 1999), optimized using the "Fast" command.

Molecular dating

Our interest is in determining whether the age of the split between extant and fossil archaeids is congruent with continental patterns (e.g. splitting of Pangaea into Laurasia and Gondwana, dated around 180 mya (Smith *et al.*, 2004)). We are also interested in estimating the age of diversification events within the extant archaeids, the superfamily Palpimanoidea, and the deep nodes in Araneomorphae divergence. We estimated the mean node ages and their 95% highest posterior density interval (HPD) using a relaxed molecular clock model implemented in BEAST (Drummond & Rambaut, 2007). The fossil taxa were included in the analysis as tips rather than as calibration points and 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 Mkv model (Lewis, 2001). In Pyron (2011), fossil ages were entered as a non-contemporaneous tip date 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 that spanned the entire estimated age range of the fossil. For each fossil the geological stage and reference is 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 & Ren, 2006), 161-176 Ma (based on www.geosociety.org/science/timescale/).

Three additional fossils were used as calibration points in the molecular clock analysis and the age of the root node was also constrained. The three fossil calibration points were treated as lognormal distributions with a hard lower bound and a soft 95% CI upper bound, described here:

1. (node 24) fossil *Mesozygiella dunlopi* (Penney & 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, soft 95% CI upper = 142.5 Ma.

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 & MacPhee, 1996). Parameters: median = 22.4 Ma, hard lower = 15 Ma, soft 95% CI upper = 42.6 Ma.

3. (node 29) fossil *Nephila jurassica* (Selden *et al.*, 2011) from the family Tetragnathidae 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/). Parameters: median = 168.4 Ma, hard lower = 161 Ma, soft 95% CI upper = 193.5 Ma.

4. The age of the root node for the Araneomorphae was constrained to be from 392-161 Ma: the maximum age was based on the oldest known spider fossil *Attercopus fimbriunguis* (Selden *et al.*, 1991; Penney *et al.*, 2003; Penney & Selden, 2007) and the minimum age was based on the oldest fossil spider 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% CI upper and lower bounds with a median of 276.5 Ma, stdev of 70.

The molecular clock model was set to relaxed, uncorrelated lognormal and the tree prior was set to speciation, yule process. Using the same partitions as the Bayesian phylogenetic analysis, five MCMC Bayesian analyses were run in BEAST for 20 million generations, sampling the chain every 1,000 generations, resulting in five files of 20,000 trees. Log files were visualized in Tracer v.1.4 to examine that the effective sample size (ESS) of the combined log files reached 200 for most parameters (Drummond *et al.*, 2006). The burn-in was set to 25% for each independent run, resulting in a combined file of 75,000 trees. The final chronogram and node ages were visualized in FigTree v.1.3.1 (Rambaut, 2010).

Palpimanoidea biogeography analysis

The purpose of this analysis is to examine ancestral ranges of archaeid spiders and their relatives within the Palpimanoidea. Since the archaeid fossils occur in geographic areas different than the extant archaeids it is crucial that they are included in the ancestral reconstructions. Reconstructions of Palpimanoidea ancestral distributions were performed using the BEAST chronogram, and in order to account for uncertainty in branch length, analyses were also performed on 1000 randomly sampled dated phylogenies that were taken from the BEAST output distribution of phylogenies. The non-Palpimanoidea taxa were pruned from the BEAST phylogenies. Clades within the Palpimanoidea have fairly restricted distributions with the exception of the spider family Palpimanidae, which is widespread, although it is not known to occur in Australia, New Zealand or North America. Biographic regions were based on Cox's (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; Eurasian; Madagascar. Ancestor reconstructions are examined using likelihood methods, implemented in LAGRANGE C++ ver.0.1 (Ree *et al.*, 2005; Ree & Smith, 2008) using the basic settings. Implementation of the LAGRANGE analyses run on the 1000 randomly drawn phylogenies from the BEAST output occurred using the statistical program R (R Development Core Team, 2008).

Results

Phylogenetic results

Our alignment resulted in a concatenated data set with a final length of 5185 characters, consisting of 658 base pairs (bp) for COI, 328 bp for H3, 2,454 bp for 18S, 1,745 bp for 28S, and 126 morphological characters. In archaeid taxa the 18S and 28S markers had several areas with large insertions, the largest being 213 bp. The concatenated data set with gapped characters removed had 4,207 bp. In the analyses with gapped-characters removed there were not any topological conflicts when compared to the analyses with gaps retained and we therefore conclude that the alignment did not influence the topology of the tree. In the TE parsimony analysis, removal of gapped characters increased the resolution of the phylogeny. Additionally, the removal of the fossil taxa did not alter the phylogenetic relationships among extant taxa. Regarding the additional Bayesian analyses performed on the TE data set, when the branch length prior was changed the results did not change, suggesting that the prior is not biasing the results. Also the results did not change in the analysis where all partitions set to GTR+I+G were changed to GTR+G, suggesting that the analysis is not have mixing problems between I+G. In all analyses (with the exception of the analysis of only the morphological data) archaeid taxa and *Colopea* sp. have relatively long branch lengths, which may be due to an increased rate of molecular evolution.

There were only minor differences between the parsimony and Bayesian analyses, with the parsimony analyses often having less topological resolution. Because of this we present and discuss only the results from the Bayesian analyses. The Bayesian results from the TE analysis, the concatenated 4 molecular marker analysis, and the morphological analysis are presented in Figs. 2-4. The phylogenies that were recovered from the analysis of the individual morphological and molecular markers were sometimes topologically incongruent with the TE analysis (Figs. 4-8). The morphological characters were mapped onto the Bayesian TE phylogeny and are shown in Figs. 9-10.

Total evidence (TE) analyses – We used the combined TE analysis as the best estimate of the phylogenetic relationships because this analysis incorporates multiple lines of evidence (Fig. 2). The Bayesian TE analysis recovered a monophyletic clade containing all archaeid taxa, and a monophyletic clade of the extant archaeids, with the fossil archaeids falling outside. This analysis also recovered a monophyletic Palpimanoidea clade, to which the archaeids belong, which is sister to the monophyletic Entelegynae ("complex" genitalia) clade. In this analysis, the remaining taxa, which are the more basal Araneomorphae, fall outside the Palpimanoidea + Entelegynae clade.

Analyses of only the morphological data – As in the TE analyses, the analyses of only the morphological data recovered a monophyletic archaeid clade and a clade containing only the extant archaeids (Fig. 4). Also the analyses recovered a monophyletic Palpimanoidea. Unlike the TE analyses, in the analyses of only the morphological data, Palpimanoidea is nested within the Entelygynae clade.

Analyses of only the molecular data set – The analyses of the 4 molecular marker concatenated data set recovered a monophyletic clade for the archaeid taxa (fossils are not included in the molecular data) (Fig. 3). The molecular data recovered a paraphyletic Palpimanoidea.

Molecular dating results

Visualization of the log files from the BEAST analyses in Tracer v1.4 confirmed that the effective sample sizes were sufficient for the majority of the parameters and for the age estimations of all nodes. The burn-in of 25% was conservative. There were moderate amounts of rate heterogeneity, meaning that the data are not clock-like: the coefficient of variation is 1.24 and the ucld.stdev is 1.10. There was evidence for autocorrelation, rate covariance = 0.143.

The results of age estimations for major clades of interest are presented in Table 3 and the resulting chronogram is presented in Fig. 11. Mean values, although with broad confidence intervals, show that archaeids originated 239 Ma in the Triassic (95% CI = 185-298), with the extant lineages splitting with the fossil lineages 183 Ma (95% CI = 133-237). Palpimanoidea and the major clade containing the Entelegynae spiders (the majority of familiar spiders) originated 288 Ma in the Permian (95% CI = 221-361). Palpimanoidea then diversified within the past 270 Ma (95% CI = 206-338) and the Entelegynae diversified 210 Ma (95% CI =167-265). Deeper diversification events within the Araneomorphae spiders occur in the Palaeozoic.

Biogeography analysis

Results from the Lagrange biogeography analysis on the BEAST chronogram is presented in Fig. 12 and Table 4. Results from the analysis on the randomly sampled 1000 dated phylogenies taken from the BEAST distribution of phylogenies were examined and do not differ from the analysis performed on the single BEAST chronogram. Lagrange estimated the global rate of dispersal and extinction to be 0.000445 and 0.000184 per million years, respectively, for the single chronogram. The mean global rate of dispersal and extinction for the 1000 randomly sampled phylogenies is 0.000469 and 0.000430. 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. Because the results from the 1000 dated phylogenies and the BEAST chronogram do not differ, we discuss only the results from the single BEAST chronogram.

The DEC model employed by Lagrange allows only one of the daughter species to inherit a range of a single area and does not include a mechanism that allows the vicariance scenario where both daughter species inherit ranges of two or more areas (Ree *et al.*, 2005), and because of this, at node 13 we summed the probabilities of the most likely ancestral splits. Node 13 of the BEAST chronogram analysis deals with the split between the extant Southern Hemisphere archaeid taxa and the extinct Northern Hemisphere archaeid taxa. The two most likely splits at this node are 1) Eurasia splits with Australia + Madagascar and 2) Eurasia splits with Australia + Madagascar + Africa, but there are other less likely splits, such as Southeast Asia + Eurasia splits with Australia. Because of this assumption of the DEC model, at node 13 there will never be the result where Southeast Asia + Eurasia splits with Australia + Madagascar + Africa, and instead, when interpreting Lagrange results, dispersal or range expansion must be employed to explain on descendent branches how lineages came to either Madagascar or Australia. Since 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 Northern Hemisphere areas splitting with one or more Southern Hemisphere areas, which equals 0.87 and which accounts for all the likely scenarios at this node. Results for nodes 16 and 22 are also summarized to highlight the general biogeography patterns. At node 16 all the likely splits

involve New Zealand splitting from multiple areas and at node 22 all the likely splits involve either New Zealand or South America splitting from multiple areas.

To summarize, the general biogeography patterns that emerge are that the more recent divergences are restricted to one or two areas and the ancestral nodes are widespread or restricted to many areas, a pattern suggestive of vicariance. The basal nodes within the Palpimanoidea are widespread or ambiguous and several nodes that are higher up (nodes 9, 13, 16, and 19) suggest vicariance events. Southeast Asian, Australia and Eurasian areas were important in archaeid distribution patterns and likely served as their origin.

Discussion

The TE Bayesian analysis recovers a phylogeny with a strongly supported topology (Fig. 2) and because the TE phylogeny was generated from multiple lines of evidence we consider this phylogeny to be the best current hypothesis of evolutionary relationships for these taxa. The phylogenies that were derived from the analysis of the individual morphological and molecular markers were sometimes topologically incongruent with the TE analyses (Figs. 4-8), possibly due to spiders being a very ancient group and their diversification could have been rapid, and also possibly confounded by the effect of homoplasy. In this study, even though the number of molecular characters greatly outnumbered the number of morphological characters, the phylogenetic signal from the morphological data contributed to the results, which can be seen by comparing the topology from the phylogenies derived from the morphological, molecular and total evidence data.

When possible, it is important to include fossils into the phylogenetic data matrix, helpful for studying character evolution, for estimating timing of diversification events, and for examining biogeographic patterns especially, in our case, when the fossil distribution is different from that of the extant distribution. The fossil taxa in this study were missing more than 95% of the data, yet they could still be phylogenetically placed using morphological characters. In this study we included fossils as calibration points and also as tips with a uniform distribution that spans the uncertainty of the fossil age. Doing so may allow for a better estimation of the age of geological formations using phylogenetic methods.

Redefined Palpimanoidea

TE and morphology only analyses supported the monophyly of a redefined Palpimanoidea. According to these results, Palpimanoidea should be delimited to consist of the following families: Palpimanidae, Stenochilidae, Huttoniidae, Mecysmaucheniidae and Archaeidae. This study does not address the placement of the Malkaridae, although Schütt (2000; 2002) found them to group within the Araneoidea. Our study is in agreement with the findings of Schütt and Rix *et al.* (2008) that Palpimanoidea, as defined by Forster & Platnick (1984), should be broken up based on genitalic systems, where families with "complex" (entelygyne) genitalia were monophyletic and those with "simple" (haplogyne) genitalia fell outside. For a discussion of the morphological characters important for understanding evolution of the Palpimanoidea see Appendix 4.

Deep divergence within the Araneomorphae and age and diversification of Palpimanoidea

This study suggests that the deep diversification events within the Araneomorphae 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 = 367 mya,

although with a large confidence internal (node 36, 95% CI = 282-460). This finding is consistent with Ayoub *et al.* (2007) who found that the diversification of the Araneomorphae was late Devonian to mid-Carboniferous. Furthermore, while we do not recover a monophyletic Haplogynae clade, the diversification events involving Haplogynae taxa occurred throughout the Carboniferous, as also suggested by Ayoub *et al*. (2007). Palpimanoidea and the major clade containing the Entelegynae (the majority of familiar spiders) originated 288 Ma in the Permian (node 31, 95% CI = 221-361), with the Entelegynae diversifying 210 mya in the Triassic (node 30, 95% CI = 167-266). Although Ayoub *et al.* (2007) did not include Palpimanoidea members in their study, their estimation of Entelegynae diversification, represented by the "RTA-clade" and the Orbicularia (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, mean = 171 mya, 95% CI = 161-187). Age estimations from our study, as well as those from Ayoub *et al.* (2007), are considerably older than those based on the fossil record (Penney *et al.*, 2003), which is expected since 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 occurring in the Permian (node 22, mean = 270 mya, 95% CI = 206-338), and falling as sister to the Entelegynae rather than nested within. The fossil record suggests that Palpimanoidea was once more widespread (with archaeid fossils occurring in the Northern Hemisphere) and possibly more diversified than today, having 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.*, 2008), Spatiatoridae (Petrunkevitch, 1942) from Tertiary Baltic amber (Penney & Selden, 2006), and Lagonomegopidae (Eskov & Wunderlich, 1995) and Grandoculidae (Penney, 2011) from Cretaceous amber. In addition, Huttoniidae fossil taxa have been described from juveniles in Cretaceous Canadian amber (Penney & Selden, 2006). The majority of the fossil specimens listed above are poorly preserved 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 Palpimanoidea characters, such as peg teeth, gland mound, and genitalia, are often unavailable or obscured, making phylogenetic and taxonomic placement difficult (also see discussion of *Lacunauchenius* below). For this reason these fossil lineages were not included in this study. Regardless, the range and diversity of Palpimanoidea fossil taxa from the Northern Hemisphere suggests that this superfamily at one time may have been a more abundant, diverse and dominant member of the ancient spider fauna.

Some members of the Palpimanoidea are known to be araneophages, meaning they are specialized to prey on other spiders, obligate in archaeids: a behavior that seemingly never evolved (or that was lost) in the mecysmaucheniids, although some mecysmaucheniid species may have this behavior (pers. obv.). Araneophagy has been mostly observed in the archaeids (Millot, 1948; Legendre, 1961; pers. obv.) and in the palpimanids (Cerveira & Jackson, 2005; Pekar *et al.*, 2011; pers. obv.). The predatory behaviors of huttoniids and stenochilids are unknown, but they have similar modifications on their first pair of legs (thickened legs with spatulate hairs) as the palpimanids. The first pair of legs is heavily utilized by palpimanids during predation in order to invade spider retreats and to touch the spider prey (Cerveira & Jackson, 2005; Pekar *et al.*, 2011; pers. obv.). Stenochilids and huttoniids have been observed to readily eat spider prey in captivity (pers. obv., although with a small sample size). Archaeids (pers. obv.) and palpimanids (Cerveira & Jackson, 2005) seem to prey mostly on the Entelgynae

spiders. In this study Palpimanoidea and the Entelgynae are sister taxa that diversified from a common ancestor in the Permian (node 31) and since Palpimanoidea may be ancestrally araneophagic, it is possible that Palpimanoidea diversification and evolution of their specialized predatory behaviors may have been congruent with Entelegynae diversification. This highlights the need for more detailed knowledge of the predatory behaviors within the Palpimanoidea.

Families within the Palpimanoidea tend to have highly restricted distributions, with the exception of the Palpimanidae, which are widespread but do not occur in North America, Australia or New Zealand (Fig.12): extant archaeids occur only in South Africa, Madagascar and Australia; mecysmaucheniids occur only in New Zealand and southern South America; huttoniids occur only in New Zealand; and stenochilids occur mostly in Southeast Asia although they also occur in Australia (R. Raven, personal communication), spanning India to the north-east of Australia. According to the dated phylogeny (Fig. 11) the families within Palpimanoidea were mostly already diversified prior to the breakup of Pangaea. Regarding the present distribution of mecysmaucheniids, 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 (pers. obv.). Their present distribution, tolerance for cold habitats, phylogenetic placement as the most basal Palpimanoidea, and the fact that the estimated age of the family precedes the timing of Pangaea breakup, suggest that mecysmaucheniids were an early diversification in the Palpimanoidea and they may have only occupied 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.

Although major clades within Palpimanoidea were already diversified prior to Pangaea breakup, there may be diversification events within and between these families that are a result of the breakup of Pangaea. Palpimanidae (represented by *Palpimanus* sp.) is a fairly widespread family that is sister to the Huttoniidae (represented by *Huttonia* sp.) and huttoniids are found only in New Zealand. According to the dated phylogeny the diversification between these families occurred a mean of 177 mya, although with a very broad 95% CI of 56-290, which suggests three possibilities: (1) these two families may have diversified prior to the break-up of Pangea and that Huttoniidae diversification occurred prior to the vicariant Gondwana break-up event whereby New Zealand broke off from Australia 80 mya (Scotese *et al.*, 1988), which suggests that huttoniids were once more widespread and have gone extinct everywhere except New Zealand where they are ousted relicts; (2) alternatively, since 80 my falls within the 95% confidence intervals of the dated node regarding the split between huttoniids and palpimanids, this phylogenetic split may represent an ancient vicariant event; (3) huttoniids were a result of a more recent dispersal event to New Zealand, although palpimanids and huttoniids do not occur in Australia. The range of the estimated age of the palpimanid-huttoniid diversification event is broad, making it difficult to draw conclusions, but even given this broad range the dispersal scenario (3) where huttoniids invaded New Zealand after it was already an isolated land mass seems unlikely since the 95% CI is still mostly older than the age of New Zealand isolation. In addition, there are huttoniid fossils described from Cretaceous Canadian amber, which is suggestive of the "New Zealand ousted relicts" theory (scenario 1) that was purported by Penney & Selden (2006). But these fossil specimens are all small juveniles less than 2mm in length and are very poorly preserved, making it risky to infer taxonomic and biogeographic conclusions from these specimens and until more better preserved adult fossils are discovered caution should be exercised.

Another diversification event that may relate to New Zealand separation from Gondwana is regarding the monophyletic, endemic New Zealand mecysmaucheniid genera (node 19, *Aotearoa* and *Zearchaea*). The remaining mecysmaucheniid genera are from southern South America. It is unclear whether the South American clades are monophyletic or paraphyletic with respect to the New Zealand clades because the placement of *Mesarchaea* is weakly supported (Fig. 2). On the dated phylogeny the mean age of diversification between the New Zealand and South American genera occurs 75 mya (node 19, 95% CI = 20-138). Since the confidence intervals surrounding this age are broad, it is difficult to determine whether the mecysmaucheniid distribution is due to vicariance or dispersal.

The presence in New Zealand of the huttoniids and the mecysmaucheniid genera *Aotearoa* and *Zearchaea*, all monophyletic groups that are endemic to the island, taken together with the evidence from the dated phylogeny, argues against the hypothesis that New Zealand was completely submerged underwater as it moved away from Gondwana and only resurfaced in the Oligocene, 26 mya (Cooper & Cooper, 1995; Trewick *et al.*, 2007). The diversification age estimations for the huttonids and New Zealand mecysmaucheniids have broad confidence intervals, yet even taking this into consideration, the 95% CI range in age estimations of these diversification events in general are older than the age of New Zealand's resurfacing 26 mya. While geological evidence suggests that the majority of New Zealand may have been submerged as it moved away from Australia, Antarctica and South America, there is no direct geological evidence that New Zealand was completely submerged and it is impossible to discount that small pockets of land remained emergent that may have been able to support tiny arthropods (Boyer & Giribet, 2009), although it appears that dispersal seems to be the general pattern (Waters & Craw, 2006).

Extant and fossil archaeid relationships and biogeography

One of the goals of this study was to examine archaeid diversification in relation to continental breakup. There is strong morphological support for monophyly of the extant archaeids with respect to the fossil archaeids. There are several important morphological synapomorphies that are characteristic of the extant archaeids. For a complete discussion of the characters uniting the extant archaeids and the family Archaeidae, see Appendix 5 and 6. The biogeographic and temporal analyses support the argument that the extant archaeids diverged from the northern lineages when Pangea split into Gondwana and Laurasia 180 mya (Smith *et al.*, 2004). On the dated phylogeny the mean divergence time of the split between the extant and fossil archaeids (node 13) is 183 mya (95% CI = 237-133). Also, all the likely ancestor range reconstructions at this node result in Northern Hemisphere areas (Eurasia) splitting with Southern Hemisphere areas (Australia and Madagascar) (Table 4, node 13). Using this evidence we conclude that the split between the northern and southern archaeid fauna was likely due to the vicariant event caused by the break-up of Pangaea into Laurasia and Gondwana.

Regarding the diversification events among the extant archaeids, the split (node 9) between the Australia clade, *Austrarchaea*, and the African genera (comprised of Malagasy and South African genera *Eriauchenius*, *Afrarchaea* and the "Gracilicollis group") occurred 166 mya (95% CI = 113-225). Ancestral range reconstructions at this node suggests the most likely split to be between Australia and Madagascar and the second most likely split to be between Australia and Madagascar + South Africa (node 9, Table 4). Although the clade containing the African fauna is not supported in the Bayesian and BEAST analyses (pp = 0.5 and 0.58, respectively), Bayesian analyses of preliminary molecular data that samples the family more thoroughly, by

including many more archaeid species and populations, consistently recovers with strong support (pp = 1) a monophyletic Africa + Madagascar group that is sister to the Australian *Austrarchaea* (H. Wood *et al*., in prep). It seems highly likely that the diversification event between the Australian and the African archaeid fauna is consistent with the vicariance event where rifting began among Africa, Madagascar + India, and between Australia and other parts of Gondwana starting 165 mya (Rabinowitz *et al.*, 1983; Scotese, 2004; Smith *et al.*, 2004) with complete isolation of Madagascar and India by 140 mya (Seward *et al.*, 2004).

Within the African clades, the timing of the diversification event between *Afrarchaea* from South Africa and the "Gracilicollis group" from Madagascar (node 4) occurred 123 mya, which could be congruent with the separation of Africa from Madagascar + India 165 mya given the 95% CI of 67-179 mya. Yet, since 165 mya is at the far end of the CI range, it is also likely that this diversification event was the result of a single dispersal from Madagascar to South Africa after these land masses 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 & Nowak, 2006). Given the above evidence, at this time we cannot rule out either a dispersal or vicariance scenario between the South African and Malagasy fauna, although dispersal seems more likely.

If these scenarios for archaeid diversification are true, then this implies 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 Northern Hemisphere where they are now extinct. In the Southern Hemisphere, 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 origination of archaeids, this implies that archaeids may have also gone extinct in Gondwanan areas like Africa (with a possible re-colonization to southern Africa from Madagascar), South America, New Zealand and New Caledonia. Although, a simpler explanation is that archaeids may have only occupied the more northern tropical areas of Pangaea (and later Gondwana), and never occurred in the more southern, cool, temperate areas (Rees *et al.*, 2002). If this is the case, then rather than extinction as the explanation, the lack of archaeids in New Zealand, New Caledonia, and southern South America may be because the climate in southern Pangaea was not suitable for archaeids. Today, archaeids seem limited to habitats that are moist year round, such as Afro-montane areas in South Africa, the eastern rainforests of Madagascar, the northeastern rainforests in Australia, and coastal or mountain area in other parts of Australia that have mini-microclimates ensuring yearly moisture. Several archaeid species are known to occur in the temperate western forests of Madagascar, with even one species being known from the southern spiny dry forests, but these few species are the exception to a general trend.

Evolution of the modified carapace in the Araneomorphae

A leading idea in the historical classifications of archaeid spiders and their closest relatives is that lineages with similarly modified cephalic areas (the "neck" and "head") are more closely related (Forster & Platnick, 1984). Forster & Platnick suggested that archaeids belong to the superfamily Palpimanoidea along with nine other families, an expansion of the "traditional" Palpimanoidea, which prior to 1984 contained only three families (Huttoniidae, Palpimanidae,

Stenochilidae). Also proposed was that relationships among archaeid genera could be based mainly on the amount of elevation in the carapace. However, recent research, which focused only on the Malagasy archaeid "Gracilicollis group," has shown that the length of the carapace may not be reliable for reconstructing phylogenetic relationships due to parallelism (Wood *et al.*, 2007). The only spider families that have a highly modified carapace forming a "neck" are Archaeidae (Fig.1E, G-H), Mecysmaucheniidae (Fig.1F) and Pararcheidae (Fig.1B), although there are other spider families that are intermediate, like Holarchaeidae. In typical spiders the carapace forms a convex plate that sits above the jaw and leg bases (see Fig.1A), whereas in the spiders mentioned above that have the "neck" trait, the carapace and jaw bases are lifted up, the jaws are elongated, and the carapace forms a circle (a foramen) enclosing the base of the jaws and that the plane of this circular opening is anterior. In this situation, the muscles that attach the jaw bases to the carapace, which in other spiders run vertically (Palmgren, 1980), have changed orientation and run horizontally (Petrunkevitch, 1939; Legendre, 1965). This unique orientation of the muscles resulting from the evolution of the modified carapace, along with the anterior orientation of the carapace foramen, and the great degree of membraneous cuticle around the jaw bases seems to have allowed archaeids, mecysmaucheniids and pararchaeids to have a much greater range of mobility in their jaws compared to typical spiders. This allows for the jaws to be held horizontally, or 90° away from their body.

Regarding the evolution of this trait within the Araneomorphae, when this trait is mapped onto the Bayesian TE analysis the "neck" has evolved independently at least three times, in the pararchaeids and twice in the Palpimanoidea, in both the archaeids and mecysmaucheniids. Prior to this study it was believed that mecysmaucheniids and archaeids were sister taxa based on the modified carapace as well as a few other traits, yet we find instead that stenochilids, which do not have an elevated "neck," may be the sister family to the archaeids.

The elevated carapace, or "neck," appears to be an ecological trait and does not show sexual dimorphism. The evolution of the "neck," by changing the orientation of the jaw muscles, seems to have allowed spiders with this trait to have highly specialized and unique jaw movements that may have allowed these spiders to diversify by targeting previously unavailable prey and thereby occupying previously unavailable niches. Among the archaeids, mecysmaucheniids and pararchaeids, the jaws operate in two very different ways during predatory attacks: in archaeids the jaws movement allows them to attack spider prey at a distance (Legendre, 1961); in pararchaeids (Rix, 2006) and mecysmaucheniids (unpublished data) the jaws operate using a trap-jaw mechanism, a trait that has evolved independently in each family. Along with the independent evolution of the trap-jaw, these two spider families have also independently evolved long "trigger-hairs," similar to those in trap-jaw ants (Gronenberg *et al.*, 1993), that upon stimulation cause the jaws to close (H. Wood, unpublished data). Yet the trap-jaw mechanism in these two families is different (H. Wood, unpublished data), which exemplifies that these two families arrived at a similar endpoint, but through convergence.

The archaeids, which are spider-specialists, not unique among Palpimanoidea, utilize a very different predatory strategy, attacking at a distance, something that has allowed them to successfully capture prey that has the potential to be injurious. Archaeids have much longer "necks" and jaws than the short, robust "necks" and jaws of the trap-jaw spiders, pararchaeids and mecysmaucheniids. Upon close proximity to their prey, archaeids reach their long jaws out and stab other spiders with both fangs at the tip, then they remove and lower only one jaw and leave the other jaw extended, holding the prey far away from the archaeid's body with the struggling prey impaled on the fang at the tip of the jaw (see Fig.1 in Wood *et al.*, 2007). This

behavior is especially eloquent in the African and Malagasy archaeids. Given that the fossil archaeids have the same overall morphology as the extant species, although with shorter "necks" and jaws and with the jaws at a slightly different orientation when at rest, extinct archaeids likely utilized similar predatory behaviors.

Examining the evolution of the "neck" within the Palpimanoidea may be useful for understanding how this trait evolved in both archaeids and mecysmaucheniids. While within Palpimanoidea only mecysmaucheniids and archaeids have the grossly elevated "neck," stenochilids and palpimanids also have a modification to their carapace: there is a sclerotized bar or rod that runs between the mouthparts and jaw bases, which together with the carapace, forms a circle surrounding the base of the jaws (arrow in Fig.1C). This modification is not found in other spiders and could be the initial stage of evolution of the foramen surrounding the jaw bases and the "neck." The sclerotized rod is fused with both sides of the carapace in adult specimens, but in juvenile specimens this rod is not completely formed and is made up of a few pieces. This suggests that the final sclerotized rod seen in adults is derived from sclerites that occur around the base of the legs and mouthparts (intercoxal sclerites) rather than as an outgrowth of the carapace. Huttoniids, on the other hand, do not have any modification between their jaw bases and mouthparts other than having a wide space (a diastema, character 72), which could also be an example of an intermediate initial state towards the evolution of the "neck." These two states offer two possible explanations for how, but not why, the evolution of the "neck" and the associated foramen surrounding the jaw bases occurred: (1) sclerites close to the mouthparts began to get successively larger until they fused with the carapace, which later evolved into the greatly elevated and rigid "neck" and the seams that showed this fusion were lost; (2) alternatively, a wide space evolved between the jaw bases and the mouthparts and the carapace began to successively wrap around to fill this area in until both edges of the carapace met and fused, forming a rigid circle around the jaw bases. Developmentally, in archaeids and mecysmaucheniids the "neck" is derived from the carapace, which wraps further and further around the jaw bases as juvenile spiders progress through their molt (H. Wood, pers. obv.). It is not until the final molt into adulthood that the two edges of the carapace meet and fuse together, completely encircling the jaw bases. The development of the "neck" as juvenile mecysmaucheniids and archaeids progress through their molts argues for explanation (2), yet it is intriguing that palpimanids and stenochilids have evolved a bar that encircles the jaw bases, suggesting the entire superfamily Palpimanoidea may have been predisposed to evolving a foramen encircling the jaw bases, which may have led to the evolution of a "neck."

There are other spider families with modifications causing elevations in the carapace, such as the raised carapace in micropholcommatid spiders, which does not include the raised jaw bases, and also, modifications to the carapace are sometimes sexually dimorphic in nature, such as the raised eyes or raised processes on the carapace of male linyphiids (sheet-weaver spiders). Furthermore there are spider families that have evolved greatly elongated jaws, yet have not evolved extreme modifications to the carapace, such as in the tetragnathid spiders (long-jawed orb-weavers), although in the tetragnathid genus *Dolichognatha* not only are the jaws greatly elongated, but the carapace is somewhat elevated as well. There is lots of variation in carapace shape among spiders and these modifications likely affect many aspects of a spider's lifestyle, such as sexual and predatory behavior, ecology, and prey choice.

Placement of the fossil Lacunauchenius speciousus

The Burmese amber fossil (Cretaceous age, Penney, 2003) *Lacunauchenius speciousus* (Wunderlich, 2008) is an enigmatic species with an elevated and modified carapace, and is known from only one male specimen. This fossil was ultimately removed from this study because it is poorly preserved in cloudy amber making it difficult to distinguish whether assigned character states were real or instead artifacts of preservation. This specimen likely belongs to the Palpimanoidea based on presence of peg teeth that also occur on the fang retromargin, having both tubercles and scales for the carapace texture, having a foramen surrounding the jaw bases, a raised carapace and a brush of hairs on the third metatarsus. This specimen has a grossly elevated carapace similar to the archaeids and mecysmaucheniids. This specimen has several traits that are archaeid synapomorphies, having anterior median eyes that are on a ridge (character 5) and the presence of a bend in femur IV (character 33), yet, the legs and carapace of this specimen are distorted, so the presence of these traits may be due in fact to poor preservation. On the other hand, this specimen also has greatly elongated hairs on the inner margins of the jaws, very similar to those that serve as "trigger hairs" in the trap-jaw mecysmaucheniids. Since these long hairs are only known from the trap-jaw spider families the presence of these hairs argues that this specimen may be a trap-jaw spider, possibly related to the mecysmaucheniids. Yet, because the specimen is poorly preserved and because it is a fossil, it could not be scored for additional mecysmaucheniid traits, such as the shape of the sclerite at the base of the jaws (character 17) and the shape of the tarsal organ (character 31 and 32), a microscopic sensory organ which can only be viewed using a scanning electron microscope. Furthermore, the posterior row spinnerets are not reduced as is found in the mecysmaucheniids (character 79), and the abdomen does not have characteristic folds found in the archaeids (character 83). This enigmatic fossil is currently considered a monotypic archaeid genus (Wunderlich, 2008), but it is also possible it could be a new Palpimanoidea family, or a new genus of mecysmaucheniid. Caution should be used regarding the phylogenetic placement of this taxon until more fossil specimens are discovered.

Conclusion

In summary, the superfamily Palpimanoidea likely diversified a very long time ago. The present distribution of extant members of Palpimanoidea is not the same as what it once was, with the present distribution of extant families probably arising through some vicariance or dispersal events and also extinction events. While at one time members of Palpimanoidea may have been much more diverse and dominant than they are today, there are many extant clades that are still very successful and that have diversified greatly and are abundant in certain regions of the world like Africa, Madagascar, New Zealand and southern South America. It appears that the extant Palpimanoidea clades are highly specialized in diet and predatory behaviors, making them very successful and formidable predators.

CHAPTER II

Speciation on Madagascar: Island or Continent? Depends When You Arrive

Introduction

Madagascar is often referred to by biologists and geologists as an island-continent because it shows characteristics of both an island and a continent without fitting unambiguously into either (Wit, 2003). Madagascar is known for its high endemism and its in situ radiations of species, with many groups undergoing remarkable diversifications, such as lemurs (Yoder, 2003), songbirds (Cibois *et al.*, 2001), satyrine butterflies (Torres *et al.*, 2001), dung beetles (Wirta *et al.*, 2008) and ranid frogs (Bossuyt & Milinkovitch, 2000). This speciation pattern is typical of islands, where organisms arrive via dispersal, and due to isolation and resulting open ecological space, these groups undergo adaptive radiation. As a consequence, the biota exhibits extensive species richness and endemism, often accompanied by some island species adopting unusual ecologies and niches uncharacteristic of their mainland ancestors (Gillespie & Roderick, 2002; Leigh *et al.*, 2007). Dispersal to Madagascar, often from Africa, appears to be the predominant pattern, at least in the majority of taxa studied thus far (Yoder & Nowak, 2006).

The role played by vicariance in the assemblage of Madagascar's biodiversity is still debated. With the advent of improved molecular techniques that facilitated examination of the timing of lineage diversification, many supposedly Gondwanan groups have been suggested instead to be products of more recent dispersals (Queiroz, 2005; Upchurch, 2008), including *Nothofagus* (Cook & Crisp, 2005; Knapp *et al.*, 2005), chameleons (Raxworthy *et al.*, 2002), and Melastomataceae (Renner, 2004). Further, the majority of studies on Madagascan taxa have recovered diversification events that are too recent to be explained by vicariance, such as primates (Yoder *et al.*, 1996), carnivores (Yoder *et al.*, 2003), dung beetles (Wirta *et al.*, 2008), frogs (Vences *et al.*, 2003) and colubrid snakes (Nagy *et al.*, 2003). Although, there have been several studies that support Gondwanan vicariance in Madagascan groups, like the boid snakes, podocnemid turtles, iguanid lizards (Noonan & Chippindale, 2006), and rainbowfish (Sparks & Smith, 2004), although the rainbow study was not time calibrated. Even so, both of these studies invoke Late Cretaceous landbridges. These landbridges were also hypothesized to explain the cosmopolitanism of Cretaceous Gondwanan vertebrate communities (Krause *et al.*, 1997; Sampson *et al.*, 1998; Buckley *et al.*, 2000; Krause, 2003). The Kerguelen Plateau and Gunnerus Ridge landbridges are hypothesized to have formed a connection between India, when still connected to Madagascar, and Antarctica when still connected to other Gondwanan landmasses like Australia, as late as 80 mya (Hay *et al.*, 1999; Case, 2002). Yet, to date, there is no known study that has shown a vicariance event in Madagascar dated around 165-140 mya, covering the range of time from when rifting began among Africa, Madagascar + India, and between Australia and other parts of Gondwana starting 165 mya (Rabinowitz *et al.*, 1983; Scotese, 2004; Smith *et al.*, 2004) with complete isolation of Madagascar and India by 140 mya (Seward *et al.*, 2004).

Archaeid spiders, in contrast, are a group of ancient spiders shown to have existed since Pangean times (Wood *et al*., in prep.). Archaeid spiders have distinct Northern Hemisphere lineages, now extinct and known mostly from amber fossils, the oldest being of Jurassic age

(Selden *et al.*, 2008), whereas the Southern Hemisphere lineage is extant, with monophyletic groups occurring only on Australia, South Africa and Madagascar (Wood *et al*., in prep.). A previous molecular clock study that included fossil archaeids as terminal tips (Wood *et al*. in prep.) showed that the split between the northern and southern faunas likely relates to Pangaea breaking into Gondwana and Laurasia 180 mya, and the split between the Australian and Madagascan clades could be due to breakup of Gondwana starting 165 mya (Scotese *et al.*, 1988; Smith *et al.*, 2004). Thus, further study of archaeid spiders offer the possibility to better understand speciation patterns in a group of taxa that have low dispersal abilities and that likely have been on Madagascar since Pangean times. Archaeids, an icon of Madagascan spiders (Griswold, 2003), are morphologically and behaviorally bizarre due to their highly modified carapace and jaws giving them the appearance of a "neck" and "head" (Wood *et al.*, 2007; Wood, 2008). By all outward appearances Madagascan archaeids appear to be an adaptive radiation, with 27 species occurring on Madagascar, living in sympatry, and with extensive variation in the "neck" length, a trait that directly relates to feeding ecology (Legendre, 1961; Wood et al., in prep.). To examine speciation patterns in a lineage that likely did not disperse to Madagascar, the current study sets out to (1) calibrate the phylogeny using fossil and geological data and hence determine the time of splitting events between the different Gondwana fragments; (2) examine lineage through time plots to determine whether there were any changes in rate of diversification. In addition, to examine whether the "neck" trait relates to speciation patterns, e.g. adaptive radiation, we treated the "neck" as a continuous character and statistically tested how well it fits various models of trait evolution. Specifically, our interest is in determining whether lineages that exist on Madagascar due to ancient Gondwanan vicariance show different diversification patterns than the lineages that have more recently dispersed to Madagascar and undergone radiation.

Materials and Methods

Taxon sampling

To examine relationships among extant archaeids we included 78 ingroup taxa representing 44 species from Madagascar, Australia and South Africa, comprising the three known extant genera: *Eriauchenius* (Cambridge, 1881), *Austrarchaea*, and *Afrarchaea* (Forster & Platnick, 1984), as well as the monophyletic "Gracilicollis Group" from Madagascar (Wood *et al.*, 2007; Wood, 2008) that is currently considered part of *Eriauchenius*. From Madagascar all known archaeid species as well as several undescribed species are included in this study and for many species there are specimens from different populations. Archaeids belong to the superfamily Palpimanoidea: the outgroup taxa include 11 terminals representing the remaining four Palpimanoidea families, the family Austrochilidae, and the tree is rooted with the Haplogynae family Segestriidae.

DNA sequence collection and alignment

Molecular data for the taxon *Hickmania troglodytes* (family Austrochilidae) were acquired from GenBank (Miller *et al.*, 2010). The molecular data for the remaining specimens were gathered following the methods described below. Some specimens sequenced for this study were difficult to amplify and/or sequence at some markers, even though new primers were designed. For these two reasons, a few taxa are incomplete at some regions or markers, but the majority of the taxa are complete for all four markers.

Regarding the specimens sequenced for this study, prior to extraction, field collected specimens were placed in 95% EtOH and stored in a freezer (-20°C). 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, and the ribosomal nuclear genes 28S and 18S. The four fragments were extracted, PCR-amplified, and sequenced using standard protocols (Wood *et al.*, 2007). Cleaned PCR product was also sequenced in the Evolutionary Genetics Lab at the Museum of Vertebrate Zoology at the University of California, Berkeley. Also, cleaned PCR product was sent to the UC Berkeley DNA Sequencing Facility.

The quality of forward and reverse sequences was confirmed using Sequencher version 4.7 (Gene Codes Co., Ann Arbor, MI) by assembling forward and reverse sequences into aligned contigs. Consensus sequences were exported from each high quality contig. Non-protein coding genes were aligned using the online interface (http://align.genome.jp/mafft/) for Mafft (Katoh *et al.*, 2002) using the L-INS-i strategy, which operates best on sequences with conserved domains and long gaps. The gap open penalty was set to the default of 1.5 and the offset value was left at the default of 0.123. Alignments were visually inspected using MacClade v4.08 (Maddison & Maddison, 2005) and no egregious errors were found. Protein coding genes were manually aligned, translated into amino acids and checked for stop codons using MacClade. The four gene alignments were then combined with the morphological data to form a concatenated data set using Mesquite v2.74 (Maddison & Maddison, 2010).

Phylogenetic Analysis

Phylogenetic analyses were carried out using Bayesian methods. Analyses were performed on each of the 4 individual molecular markers and the data set containing the 4 concatenated markers. Bayesian analyses were implemented in MrBayes version 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Using the Akaike information criterion (AIC; Akaike, 1973), the best fit substitution model was estimated for the molecular data using MrModeltest version 2.2 (Nylander, 2004) for 28S, 18S, and each of the three codon positions in the protein coding H3 and COI genes. The final concatenated TE data set had a total of 8 partitions made up of the 3 codon positions for the 2 protein coding genes (6 partitions) and the 2 ribosomal nuclear markers. Bayesian analyses were performed using four chains, the analysis was run twice simultaneously, and the starting trees were randomly generated. All analyses were run for 10 million generations, with sampling every 1000^{th} generation, except for the analysis of only H3 (run for 20 million generations), since this analysis took longer to converge. All Bayesian 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 & Drummond, 2007). The burn-in value was visualized and determined by summarizing posterior distributions of scalar values, which identified the first 25% of the initial trees to be discarded, resulting in a final consensus tree with node support expressed as posterior probabilities.

Molecular dating

Our interest is in determining whether the age of the split between the Australian and African and Malagasy archaeid lineages is congruent with: (1) the initial breakup of Gondwana starting 165 mya (Rabinowitz *et al.*, 1983; Scotese, 2004; Smith *et al.*, 2004) with complete isolation of Madagascar + India by 140 mya (Seward *et al.*, 2004); (2) the Late Cretaceous landbridge hypothesis (Hay *et al.*, 1999; Case, 2002); or (3) a more recent dispersal event. The

more extensive sampling is expected to corroborate a previous study where the diversification between Australian archaeids and Malagasy archaeids was found to occur 166 mya (95% CI = 113-225) (Wood *et al*., in prep.). This study used fossil archaeid taxa as non-contemporaneous tips to calibrate the molecular clock. Here, we use a different suite of taxa that contains a greater number of archaeid lineages and a combination of fossil data as well as geological events as calibration points. Mean node ages and their 95% highest posterior density interval (HPD) were estimated using a relaxed molecular clock model implemented in BEAST (Drummond & Rambaut, 2007). The taxa, molecular markers and partitions used for the Bayesian phylogenetic analysis were also used for the BEAST analysis.

The oldest known archaeid fossil was used to constrain archaeids and their sister family Stenochilidae (Wood *et al.*, in prep.), treated as a lognormal distribution. Wood *et al*. (in prep.) included this fossil in a phylogenetic analysis and confirmed it to be a basal archaeid spider. In addition we included several internal calibration points based on the geological formations of Nosy Be, an island off the coast of Madagascar, the Montagne d'Ambre massif, and the Australian Black Mountain Corridor. These geological calibration points were treated as normal distributions in BEAST. The constraints placed on the nodes are described here; node numbers follow Fig. 15:

1. (node 1) The origin of Nosy Be is dated around 7-10 mya (Emerick & Duncan, 1982) and was used to constrain the node for the species *"Eriauchenius" gracilicollis*, which occurs on Nosy Be, with its sister species *"E." lavatenda*: mean = 7, stdev = 2, soft 5% CI = 3.7, soft 95% CI = 10.3.

2. (nodes 2 & 3) The origin of the Montagne d'Ambre massif commenced ca. 10 mya (Emerick & Duncan, 1982; Wells, 2003) and was used to constrain the nodes for the species *"Eriauchenius" amber*, which occurs on the massif, and *"Eriauchenius"* sp.nov. C, with their closest relative. This was also used to constrain *"E."* sp.nov. A from its closest relatives: mean = 9, stdev = 1.5, soft 5% CI = 6.5, soft 95% CI = 11.5.

3. (node 4) The Black Mountain Corridor is a well studied biogeographic barrier that restricts the movement of rain forest species in the Australian wet tropics and is estimated to be 4.7-9.2 mya (Edwards & Melville, 2010). This calibration point was used to constrain *Austrarchaea* species on either side of the barrier: mean = 7, stdev = 1.5, soft 5% CI = 4.5, soft 95% CI = 9.5.

4. (node 12, Fig.13) The oldest known archaeid fossil *Patarchaea muralis* (Selden *et al.*, 2008) was used as a calibration points constraining the node for the common ancestor of the archaeids and the closely related family Stenochilidae, set to the following parameters: Middle Jurassic (Chen *et al.*, 2004; Gao & Ren, 2006), dated at 161-176 Ma (based on www.geosociety.org/science/timescale/) treated as lognormal distributions with a hard lower bound and a soft 95% CI upper bound, median = 168.4 Ma, hard lower = 161 Ma, soft 95% CI upper = 193.5 Ma.

The molecular clock model was set to relaxed, uncorrelated lognormal and the tree prior was set to speciation, birth-death process. Using the same partitions as the Bayesian phylogenetic analysis, four MCMC Bayesian analyses were run in BEAST for 10 million generations, sampling the chain every 1,000 generations, resulting in two files of 10,000 trees. Log files were visualized in Tracer v.1.4 to examine that the effective sample size (ESS) of the combined log files reached 200 for most parameters (Drummond *et al.*, 2006). The burn-in was set to 25% for each independent run, resulting in a combined file of 30,000 trees. The final chronogram and node ages were visualized in FigTree v.1.3.1 (Rambaut, 2010).

Testing patterns of lineage diversification

If archaeids underwent a rapid radiation in Madagascar then we would expect to see a pattern of early rapid diversification that slowed down as niches became filled (Schluter, 2000; Gavrilets & Losos, 2009). Rate of lineage diversification was tested using Pybus and Harvey's (2000) MCCR test that examines whether lineage diversification starts out rapid and slows over time. This model was applied using the BEAST chronogram for the combined South African and Malagasy archaeids, for only the Malagasy genera, and for only the South African genus. This test was implemented in R (R-Development-Core-Team., 2008) using the Laser package (Rabosky, 2006).

Evolution of the "neck" trait

In order to understand the mode of character evolution in the continuous morphological trait, the "neck," the likelihood fit of the Brownian motion model (BM) was compared to alternative models. The other models examined were Pagel's (1999) "lambda," "kappa," and "delta," and the Ornstein-Uhlenbeck (OU) model (Butler & King, 2004). The likelihood fit of these models was directly compared using the AICc score. Analysis was implemented in the statistical program R (R-Development-Core-Team., 2008) using the Geiger package (Harmon *et al.*, 2008).

For the first analysis non-archaeid taxa and duplicate archaeid species were pruned from the resulting BEAST chronogram, resulting in an ultrametric tree with one terminal for each archaeid species. Next, the South African and Australian archaeid species were pruned from the BEAST chronogram so that "neck" evolution could be assessed for only the Malagasy species. For each archaeid species the CH/CC ratio was measured: CH/CC = carapace height to carapace constriction (see Fig.2 of Wood *et al.*, 2007). One specimen per species was measured; within archaeid spiders the interspecific variation in "neck" shape is greater than the intraspecific variation (Wood *et al.*, 2007).

Results

Our alignment resulted in a concatenated data set with a final length of 5409 characters, consisting of 658 base pairs (bp) for COI, 328 bp for H3, 2,555 bp for 18S, and 1,868 bp for 28S. In archaeid taxa the 18S and 28S markers had several areas with large insertions, the largest being 213 bp. The result from the four-marker concatenated analysis is presented in Figs. 13 and 14. The phylogenies that were recovered from the analysis of the individual molecular markers were sometimes topologically incongruent with the concatenated analysis, but in general show similar topologies and for this reason only the phylogeny resulting from the concatenated analysis is discussed.

The concatenated analysis recovered a monophyletic clade containing all archaeid taxa. This analysis also recovered all genera and the "Gracilicollis group" as monophyletic, suggesting the "Gracilicollis group" should be raised to genus status. *Austrarchaea* is sister to the African + Madagascan clades. The African *Afrarchaea* is sister to the newly delimited Malagasy *Eriauchenius* and these two genera are sister to the "Gracilicollis group." Within Madagascar, based on our present sampling there are likely six new undescribed species of archaeids. The genus *Afrarchaea* is confined to South Africa and the delimited *Eriauchenius* and "Gracilicollis group" are confined to Madagascar. Previous work put some Malagasy species in *Afrarchaea* based on the presence of a short "neck," and also some African species in *Eriauchenius* based on the presence of a long "neck." Instead our study shows that the length of the "neck" has many

instances of parallelism and should not be used to diagnose genera, (see also Wood *et al.*, 2007), that all species that live in South Africa belong to the monophyletic, endemic genus *Afrarchaea*, and that all species in Madagascar belong to one of two monophyletic, endemic genera found there.

Visualization of the log files from the BEAST analyses in Tracer v1.4 confirmed that the effective sample sizes were sufficient for the majority of the parameters and for the age estimation of all nodes. The burn-in of 25% was conservative. There are low amounts of rate heterogeneity, meaning that the data cannot reject a molecular clock: the coefficient of variation is 1.02 and the ucld.stdev is 1.04. There was limited evidence for autocorrelation, rate covariance = 0.041.

The resulting chronogram with outgroups pruned is presented in Fig. 15. Mean values show that archaeid origination, diversifying from the stenochilids (Fig. 13), occurred 175 mya in the Jurassic (95% CI = 163-195). The Australian archaeids split with the Madagascar archaeids 132 mya in the Jurassic (node 11, 95% CI = 97-167). On Madagascar, the diversification event that gave rise to the two Malagasy genera occurred 99 mya (node 10, 95% CI = 67-134), with diversification of *"Gracilicollis Group"* occurring 65 mya (node 5, 95% CI = 39-98) and diversification of *Eriauchenius* occurring 59 mya (node 7, 95% CI = 36-85). Then, 84 mya a dispersal event occurred from Madagascar to Africa (node 9, 95% CI = 54-116) giving rise to *Afrarchaea*, which began to diversify 36 mya (node 6, 95% CI = 18-63).

The lineage through time plots revealed that for the Madagascan archaeids and the combined Malagasy and African archaeids lineages are accumulating at a constant rate (Fig. 16). In contrast, the lineage through time plot for just the South African *Afrarchaea* shows a slight early burst in diversification that slows over time. The results of the MCCR test (Table 5) suggest that for the Madagascan and South African clades the constant diversification rate model cannot be rejected. The Brownian motion (BM) model best explains the evolution of the "neck" in archaeid spiders (Table 6) when compared to the alternative models.

Discussion and conclusion

Wood *et al.* (in prep.) found that the ancient split between the Australian and the Africa + Madagascar clades occurred 166 mya (95% CI = 113-225), whereas the present study found this diversification event to be younger with a mean of 132 mya (node 11, 95% CI = 97-167). The previous study (Wood *et al*., in prep.) contained a different suite of taxa and also used fossils at both calibration points and terminal points, whereas the current study samples archaeid species more thoroughly and uses both fossil and geological data to calibrate the clock. Both of these studies are still within the range of Gondwanan breakup starting 165 mya (Rabinowitz *et al.*, 1983; Scotese *et al.*, 1988; Smith *et al.*, 2004) and complete isolation of Madagascar + India from the remaining Gondwanan areas by 140 mya (Seward *et al.*, 2004). The South African archaeids are a result of a colonization event from Madagascar that occurred 84 mya (node 9, 95% CI = 53-116), well after Madagascar and Africa were separated, with diversification of *Afrarchaea* occurring in the Eocene, likely congruent with aridification and geological uplift. The timing of diversification between Madagascar and Australian lineages supports the Gondwanan breakup models of Scotese (1988) and Smith *et al.* (2004), and do not support the Late Cretaceous landbridge hypothesis of Hay *et al*. (1999) and Case (2002). This study and Wood *et al*. (in prep.) are the first known to show, using a molecular clock, vicariance in Madagascar that resulted when Gondwana first began to break up without needing to invoke late Cretaceous landbridges. The Gunnerus Ridge and Kerguelen Plateau were hypothesized to allow

migration to occur between Madagascar + India and Antarctica in the late Cretaceous (Hay *et al.*, 1999; Case, 2002). These landbridges have since been falsified as possible migratory routes because the Gunnerus Ridge and Kerguelen Plateau have both been shown to be separated from Madagascar + India by vast marine expanses (Ali & Aitchison, 2008; 2009; Ali & Krause, 2011).

The lineage through time plots reveal that the Madagascan archaeids have not experienced an initial increased rate of diversification with a later slowing down that would be characteristic of an adaptive radiation. The MCCR test shows that the null hypothesis of a constant rate of lineage accumulation cannot be rejected. Furthermore, the evolution of the "neck" best fits the Brownian motion model, implying that evolution of "neck" length is a product of genetic drift. However, the "neck" could still be an adaptive trait even though it is evolving under the BM model.

Thus, Madagascan archaeids are not undergoing radiation. Instead the remarkable diversity and morphological variation that has evolved in these spiders is a result of gradual accumulation since Madagascar first became isolated. In Madagascar, whether a lineage displays island-like diversification or continent-like accumulation likely depends on how long that lineage has been there. For groups that evolved long after Madagascar's isolation and then later dispersed there, Madagascar's long isolation, meaning it lacked those floras and faunas that had since evolved in the world around it, could have allowed lineages that dispersed there to radiate and diversify in signature island-like ways. Yet, for those lineages, like archaeids that have been on Madagascar since pre-isolation times, gradual accumulation may be the rule, with no opportunity to move into empty niche space.

CHAPTER III

Evolution of Rapid-Inertia-Based Jaw Movements in Trap-Jaw Spiders

Introduction

Trap-jaw mechanisms are innovations that provide extremely rapid jaw closing speeds, overcoming the limitation of the maximal contraction speeds of muscles that restrict speed of movement (Bárány, 1967; Asmussen & Marechal, 1989; Josephson, 1993; James *et al.*, 2007). These extreme high-speed mechanisms have been described for several ant genera (Gronenberg, 1996) but, prior to this research, were only known in the arachnids from a natural history observation that the small Australasian spider family Pararchaeidae (Forster & Platnick, 1984) cock their jaws open and then snap them closed to capture prey (Rix, 2006). Recent work has shown that Mecysmaucheniidae (Simon, 1985) spiders have a similar behavior (Wood *et al*., in prep.). Mecysmaucheniids are cryptic spiders that rely on hunting rather than building a web to capture prey and are known for their bizarre morphology due to a highly modified and unusually shaped frontal area (the carapace or cephalic area). The current study focuses on the evolution of the trap-jaw in mecysmaucheniid spiders to address how it has become modified over the evolutionary history of the lineage.

Mecysmaucheniids were placed in the superfamily Palpimanoidea by Forster & Platnick (1984) along with the pararchaeids and several other families based on several morphological characters. Forster & Platnick (1984) considered mecysmaucheniids to be sister to the Archaeidae (Koch & Berendt, 1854), which together were sister to the pararchaeids based on the shared trait of a highly modified carapace that completely encircles the jaw bases, making these three spider families appear to have a "neck." However, Rix (2008) found pararchaeids and mecysmaucheniids to be distantly related. The recent analysis of Wood *et al*. (in prep.) also found pararchaeids and mecysmaucheniids to be unrelated and found mecysmaucheniids to be true Palpimanoidea, which was delimited to contain five families: Palpimanidea, Stenochilidae, Huttoniidae, Archaeidae and Mecysmaucheniidae, a limitation previously suggested by Schütt (2002). Unlike the suggestion of Forster & Platnick (1984), Archaeidae and Mecyamaucheniidae are not sister groups: Archaeidae are sister to Stenochilidae, and these in turn sister to Huttoniidae plus Palpimanidae, with Mecysmaucheniidae being the sister group to the remaining four families Wood *et al*. (in prep.). These findings mean that the similarity between pararchaeids and mecysmaucheniids may be due to convergent evolution, with both families independently evolving a "neck" or highly modified carapace, "trigger-hairs," and trap-jaw behaviors and jaw movements. Wood *et al*. (in prep.) reported that the jaw morphology and mechanism of the trap-jaw is very different between these two families, highlighting that they arrived at the same endpoint through convergence.

Given the similar morphologies of the Pararchaeidae and Mecysmaucheniidae, yet rather distant relationships, the current study set out to examine the evolution of jaw morphology and associated behavior both between the families and within the family Mecysmaucheniidae to assess the extent of conservatism versus plasticity in the trait. The study involves molecular phylogenetic analyses, detailed morphological analysis of jaw structure, and high-speed video

recording to assess the variability. Here, we report for the first time a phylogeny of mecysmaucheniid spiders and also the jaw closing speeds among various lineages of trap-jaw spiders. We find that there is considerable variation in jaw morphology and function found within the mecysmaucheniids, with the fastest species being two orders of magnitude faster than the slowest species. Trap-jaw movements in some lineages of mecysmaucheniid spiders are among the fastest animal movements known, operating within the same order of magnitude as the trap-jaw ants and mantis shrimp strike (Gronenberg *et al.*, 1993; Patek *et al.*, 2004). Whereas all mecysmaucheniids spiders have trap-jaw morphological modifications and behaviors in place (e.g. presence of "trigger-hairs", a highly modified carapace that has changed the orientation of the jaw muscles compared to typical spiders, and the behavior of holding the jaws open prior to a strike in response to prey movement), only some species within this family have evolved a specific trap-jaw mechanism where there is a specific catch/release mechanism for storing kinetic energy.

Materials and Methods

Taxon sampling

To examine relationships among mecysmaucheniid spiders we included 44 ingroup taxa representing 28 species from New Zealand and Chile, comprising the seven known genera, all described by Forster & Platnick (1984) except when stated otherwise: *Aotearoa*, *Chilarchaea*, *Mecysmauchenioides*, *Mecysmauchenius* (Simon, 1884), *Mesarchaea*, *Semysmauchenius*, and *Zearchaea* (Wilton, 1946). The outgroup taxa include four terminals representing the Palpimanoidea families Stenochilidae (sister group to Arachaeidae, Wood et al., in prep), Huttoniidae and Palpimanidae. Six additional outgroups were included, made up of one terminal each representing the families Austrochilidae, Desidae, Eresidae, Mimetidae, and Segestriidae, and the tree is rooted with the most basal Araneomorphae family Hypochilidae. There are a total of 54 taxa, made up of 44 ingroup mecysmaucheniids and 10 outgroup lineages.

DNA sequence collection and alignment

Molecular data for five of the ten outgroups was acquired from GenBank. The molecular data for the remaining specimens were gathered following the methods below. Some specimens sequenced for this study were difficult to amplify and/or sequence at some markers, even though new primers were designed. For these two reasons, a few taxa are incomplete at some regions or markers, but the majority of the taxa are complete for all four markers.

Regarding the specimens sequenced for this study, prior to extraction, field collected specimens were placed in 95% EtOH and stored in a freezer (-20°C). 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, and the ribosomal nuclear genes 28S and 18S. The four fragments were extracted, amplified, and sequenced using standard protocols (Wood *et al.*, 2007). Amplified PCR product was sequenced in the Evolutionary Genetics Lab at the Museum of Vertebrate Zoology at the University of California, Berkeley. Cleaned PCR product was also sent to the UC Berkeley DNA Sequencing Facility.

The quality of forward and reverse sequences was confirmed using Sequencher version 4.7 (Gene Codes Co., Ann Arbor, MI) by assembling forward and reverse sequences into aligned contigs. Consensus sequences were exported from each high quality contig. Non-protein coding genes were aligned using the online interface (http://align.genome.jp/mafft/) for Mafft (Katoh *et al.*, 2002) using the L-INS-i strategy, which operates best on sequences with conserved domains

and long gaps. The gap open penalty was set to the default of 1.5 and the offset value was left at the default of 0.123. Alignments were visually inspected using MacClade v4.08 (Maddison & Maddison, 2005) and no egregious errors were found. Protein coding genes were manually aligned, translated into amino acids and checked for stop codons using MacClade. The four gene alignments were then combined with the morphological data to form a concatenated data set using Mesquite v2.74 (Maddison & Maddison, 2010).

Phylogenetic Analysis

Phylogenetic analyses were carried out using Bayesian methods. Analyses were performed on each of the 4 individual genetic markers and the data set containing the 4 concatenated markers. Bayesian analyses were implemented in MrBayes version 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Using the Akaike information criterion (AIC; Akaike, 1973), the best fit substitution model was estimated for the genetic data using MrModeltest version 2.2 (Nylander, 2004) for 28S, 18S, and each of the three codon positions in the protein coding H3 and COI genes. The final concatenated TE data set had a total of 8 partitions made up of the 3 codon positions for the 2 protein coding genes (6 partitions) and the 2 ribosomal nuclear markers. Bayesian analyses were performed using four chains, the analysis was run twice simultaneously, and the starting trees were randomly generated. All analyses were run for 10 million generations, with sampling every 1000th generation, except for the analysis of only H3 (run for 20 million generations), since this analysis took longer to converge. All Bayesian 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 & Drummond, 2007). The burn-in value was visualized and determined by summarizing posterior distributions of scalar values, which identified the first 25% of the initial trees to be discarded, resulting in a final consensus tree with node support expressed as posterior probabilities.

High-speed video

Using a Photron SA3 high-speed video camera a diverse array of mecysmaucheniid species were selected to record jaw closure. In addition, the jaw closures of the species *Pararchaea alba*, a Pararchaeidae spider from New Zealand, was also video recorded. Depending on the speed of the jaw closure, different species were recorded at a rate of 1,000 to 40,000 frames per second. Digital video recordings were made with the specimen in a small glass tube while an eyelash, affixed to a needle, was used to stimulate the specimen and elicit a trap-jaw response. Once the response was recorded, the high-speed videos were analyzed frame-by-frame starting at the moment the open jaws first began to close and ending when both jaws were touching. Using a digital protractor (Screen Protractor 4.0 from Iconico) the angle between the jaws was measured at each frame as the jaws progressed from open to closed. After video recordings were completed the specimens were preserved in 75-95% ETOH and the length of the jaws from anterior tip to base was measured using a Leica M205 FA microscope and associated Leica Application Suite software. Furthermore, jaw morphology was examined for all specimens using a Leica MZ12.5 stereomicroscope. For each specimen the jaw was measured five times and the average was used for the kinematic calculations. Using data for jaw length, time (based on the camera frame rate per second), and the change in jaw angle from one frame to the next, the linear velocity of the jaw tip and the angular velocity were calculated frame-by-frame for the entire jaw closure.

Results

Our alignment resulted in a concatenated data set with a final length of 4,277 characters, consisting of 658 base pairs (bp) for COI, 328 bp for H3, 1,809 bp for 18S, and 1,482 bp for 28S. The result from the four-marker concatenated analysis is presented in Fig. 17. The phylogenies that were recovered from the analysis of the individual molecular markers were sometimes topologically incongruent with the concatenated analysis, but overall show similar topologies and for this reason only the phylogeny resulting from the concatenated analysis is discussed.

The concatenated analysis recovered a monophyletic clade containing all mecysmaucheniid taxa. This analysis also recovered the two New Zealand genera *Aotearoa* and *Zearchaea* as monophyletic. There is also a monophyletic group recovered that contains the southern South American genera: *Chilarchaea*, *Mecysmauchenius*, *Mecysmauchenioides*, and *Semysmauchenius*. The placement of the monotypic genus *Mesarchaea* from southern Chile is ambiguous because the branch support uniting it with the New Zealand genera is low (posterior probability = 0.60).

179 high-speed video recordings were made of jaw closing behavior of 10 different species of mecysmaucheniid spiders and one pararchaeid spider. Some of these videos were unusable because the specimen was out of focus or the orientation of the specimen prevented measuring the angle of the jaws, so only a subset of these videos was used for the frame-by-frame analysis. Table 7 presents for 11 species the maximum recorded jaw closing velocity, the maximum recorded total time for jaw closure, and the average maximum velocities and times recorded for that lineage. Since some of these closing velocities are faster than the speeds allowed by muscles, a mechanism for storing kinetic energy to produce these extremely rapid jaw movements must have evolved at least three times within the mecysmaucheniids.

Discussion

There are many morphological characters uniting the mecysmaucheniid spiders (for characters, see Wood *et al*., in prep.), including having a smooth foramen seam where the carapace wraps around the jaw bases, the interjaw sclerite modified into a rod that interacts with the jaws, the exposed tarsal organ has a greatly elongated sensilla, the presence of trigger-hairs that are organized in one row, a prolateral row of spines on the female palps, and a characteristic groove on the male palpal tegulum. Our study supports previous work (Wood *et al*., in prep.) from combined morphological and molecular data that indicates the monophyly of the family. Regarding relationships among genera, we found the New Zealand genera *Aotearoa* and *Zearchaea* to form a clade (also found by Wood *et al*., in prep.). Regarding South American fauna, this is also monophyletic with the exception of *Mesarchaea*. The placement of this South American monotypic genus *Mesarchaea* is found to be basal, but ambiguous (also found by Wood *et al*., in prep.) because the branch support values uniting it with the New Zealand genera are weak (posterior probability = 0.6). *Mesarchaea* has four pairs of spines on its carapace similar in number and position to the New Zealand genera (character 1 and 2, Wood *et al*., in prep). Yet, *Mesarchaea* has three pairs of eyes due to loss of the anterior median eyes, similar to the South American mecysmaucheniids, whereas the New Zealand genera have all four pairs (character 3, Wood *et al*., in prep.). The female of this monotypic genus is unknown and the morphology of the female genitalia will likely help clarify placement of *Mesarchaea*. The genus *Mecysmauchenius* is paraphyletic, suggesting that the "BigGroup," currently considered *Mecysmauchenius* should be considered a new genus, and also that *Mecysmauchenioides*, which nests inside *Mecysmauchenius*, should be considered *Mecysmauchenius*. Our conclusions differ

from those of previous work by Forster & Platnick (1984). They suggested that neither the New Zealand nor South American faunas were monophyletic, with the New Zealand genera *Aotearoa* and *Zearchaea* each related to different South American genera. There are currently 25 described species in the family, but we estimate that there are an additional 20 undescribed species, mostly from New Zealand.

Results of the video analysis indicate that within this family there is a large degree of variation in jaw function spanning two orders of magnitude (Fig. 18). Additionally, there is also considerable variation in jaw morphology, particularly in the "inter-jaw pivot," a piece that occurs between the jaw bases, probably a modification of the intercheliceral sclerite (postchilum), exhibits a variety of shapes and sizes among different species. Minor changes in the shape of this structure are likely responsible for the evolution of rapid trap-jaw mechanisms (Fig. 19). While all spiders within this family have trap-jaw morphological modifications and behaviors in place (e.g. presence of "trigger-hairs", a highly modified carapace that has changed the orientation of the jaw muscles compared to typical spiders, and the behavior of holding the jaws open prior to a strike in response to prey movement), only some lineages within this family have evolved a specific rapid-inertia-based trap-jaw mechanism. For this reason, among trap-jaw spider species we distinguish between muscular-based jaw movements and those that are rapid-inertia-based, where a specific catch/release mechanism for storing kinetic energy has evolved. In the muscular-based lineages the basic trap-jaw spider body-plan is in place (as discussed above), but the "inter-jaw pivot" does not contribute to jaw closure and does not appear to interact with the jaw bases. Among lineages that have evolved a rapid-inertia-based mechanism the jaws accelerate rapidly and only stop when they smash together or into the prey. In comparison, in the muscular-based lineages the jaws accelerate, reach a maximum velocity and then decelerate (see Fig. 18). The pararchaeid spiders, represented by the species *Pararchaea alba*, which are distantly related to the mecysmaucheniids, appear not to have evolved a rapid-inertia-based trap-jaw mechanism (Table 7).

Within Mecysmaucheniidae, rapid-inertia-based mechanisms have evolved in parallel 3-4 times (see Fig. 17). Examination of trap-jaw morphology reveals that each inertia-based mechanism is unique with different morphologies (Fig. 19). Based on this it is likely that rapid-inertia-based mechanisms have evolved independently rather than being repeatedly lost. Within *Zearchaea*, the fastest species known thus far, the muscles that in typical spiders operate to close the jaws have evolved to become thick tendon-like structures that likely have elastic properties (Fig. 19C). When muscles crank the jaws open these thick tendons likely store energy. In *Zearchaea* the "inter-jaw pivot" is likely used to lock the jaws open by interacting with the jaw bases and an additional sclerite close to the jaw bases: this additional sclerite does not occur in other mecysmaucheniids. When the latch is removed, then the jaws are flung forward. In *Chilarchaea quellon* the "inter-jaw pivot" likely serves as a rod that once the jaws are opened obstructs the jaws from closing (Fig. 19B). As muscles begin to pull the jaws closed energy is stored in the "inter-jaw pivot" until finally the muscles apply enough force to cause the jaws to pop around the "inter-jaw pivot." In the species *Semysmauchenius* sp. B the mechanism is unknown, but the shape of the "inter-jaw pivot" is different than in *Chilarchaea*. Furthermore, unlike in *Chilarchaea*, *Semysmauchenius* sp. B jaws could not be manually locked into place in recently preserved specimens. It appears that "BigGroup" lineages have not evolved a rapid-inertia-based mechanism and likely rely on a muscular-based mechanism. Regardless, in this group there still seems to be a modification of the "inter-jaw pivot," which is uniquely shaped and seems to interact with the jaw bases by locking them open. All of these different

mechanisms need to be more thoroughly examined though to fully understand their function. Based on morphology, we also predict that there are still several more species that may have evolved a rapid-inertia-based mechanism but high-speed video recordings of these lineages are needed to confirm this (Fig. 17).

Trap-jaw spiders are millimeter sized, ranging in carapace length from approximately1-4 mm, with the smallest species having the fastest jaw closures. The trap-jaw movements in some of these lineages are among the fastest animal movements known, with the fastest species attaining jaw-closing speeds of greater than 25 meters/second in less than one tenth of a millisecond. It remains to be seen what these spiders are using this mechanism to achieve, whether for capturing extremely fast prey or for generating strong forces to puncture prey, something that may be difficult if you are a millimeter sized hunter. Based on field and lab observations, it is possible that the fastest high-speed trap-jaw mechanisms allow lineages of these spiders to exploit an ecological niche by preying on extremely fast springtails (H. Wood, pers. obs.). Springtails have an escape jump that occurs in a few milliseconds (Christian, 1979; Brackenbury & Hunt, 1993), the same order of magnitude as the jaw closure of *Chilarchaea quellon*, *Semysmauchenius* sp.B and *Zearchaea* sp.E (Table 7). Captive *Chilarchaea* and *Zearchaea* appear to only eat springtails and will reject all other prey items, whereas *Semysmauchenius* sp.B seems to readily eat other types of prey (H. Wood, pers. obs.). Even more enigmatic is knowing why the muscular-based trap-jaw lineages still retain the trap-jaw behaviors (holding jaws open prior to the strike), rather than reverting to the more typical predatory behaviors and jaw movements of hunter spiders. It remains to be examined whether holding the jaws open until triggered in muscular-based lineages (without a rapid-inertia-based mechanism) is faster than opening and closing the jaws in typical hunter spiders. Captive muscular-based lineages seem to eat various types of prey, so they do not seem to be targeting rapidly moving prey. The trap-jaw movements in mecysmaucheniid lineages seem to have evolved to be fast, faster, and may be among the fastest animal movements known, with the fastest species attaining jaw-closing speeds of greater than 25 meters/second in less than one tenth of a millisecond.

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TABLE 1: List of vouchers used for gathering morphological data for phylogenetic analysis. Morphological data also came from other sources for some taxa. Unless otherwise specified the voucher number is from the California Academy of Sciences Entomology Dept (CASENT); AToL = Arachnology Tree of Life Project; F&P = Forster & Platnick, 1984; Atlas = Griswold *et al*., 2005.

Family	Species	Morphology voucher number	Additional sources
Hypochilidae	*Hypochilus pococki*	9034568	Atlas
Filistatidae	*Kukulcania hibernalis*	9025730, 9034584	Atlas
Austrochilidae	*Hickmania troglodytes*	9034570	Atlas
Dysderidae	*Dysdera crocata*	9034577	AToL
Sicariidae	*Loxosceles rufescens*		AToL
Sicariidae	*Loxosceles deserta*	9034578, 9034579	
Eresidae	*Stegodyphus* sp.	9005868	AToL
Oecobiidae	*Uroctea* sp.	9021405, 9021406	AToL
Araneiidae	*Araneus diadematus*	9034573	AToL
Mimetidae	*Mimetus hesperus*	9034580, 9034581	AToL; Atlas; F&P
Holarchaeidae	*Holarchaea* sp.	9023856, 9023852	AToL
Pararchaeidae	Pararchaeidae spp.	9023530 -bartlefre., 9028408 - NZ	AToL
Desidae	*Badumna longinqua*	9021775, 9021779	AToL
Gnaphosidae	*Gnaphosa sericata*	9034582	AToL
Lycosidae	*Schizocosa ocreata*	9034571, 9034572	AToL
Palpimanidae	*Palpimanus* sp.	9034583	AToL
Huttoniidae	*Huttonia* sp.	9021410, 9028078	
Stenochillidae	*Colopea* sp.	9035143, 9028424	
Mecysmaucheniidae	*Aotearoa magna*	9028269	F&P
Mecysmaucheniidae	*Zearchea* sp.	9028245, 9028257, 9028253, 9028275	
Mecysmaucheniidae	*Mesarchaea bellavista*	9019105	F&P
Mecysmaucheniidae	*Mecysmauchenius segmentatus*	MACN10284	
Mecysmaucheniidae	*Chilarchaea quellon*	9028089, 9028091, 9034556, 9034519	
Archaeidae	*"Eriauchenius" lavatenda*	9018944, 9007247	
Archaeidae	*"Eriauchenius" jeanneli*	9028293, 9015372	
Archaeidae	*"Eriauchenius" legendrei*	9018992, 9012347	
Archaeidae	*Eriauchenius workmani*	9012335, 9028369	
Archaeidae	*Eriauchenius bourgini*	9028315, 9001207	
Archaeidae	*Afrarchaea "*pilgrim's rest"	9028270	
Archaeidae	*Afrarchaea woodae*	9018956, 9018994	
Archaeidae	*Austrarchaea nodosa*	9028426, S30820	
Archaeidae	*Austrarchaea daviesae*	9034523	
Archaeidae	*Austrarchaea mainae*	9028430, 9028361	
Archaeidae	*Archaea paradoxa*	MBA1669, 7565 (Hwood_049)	CT X-ray scans
Archaeidae	*Myrmecarchaea* sp.	S3999, S3907, 1132 (Hwood_033)	
Archaeidae	*Baltarchaea conica*	2171 (Hwood_037)	CT X-ray scans
Archaeidae	*Afrarchaea grimaldii*	AMNH Bu-256	
Archaeidae	*Patarchaea muralis*	examined published images	Selden *et al*., 2008

TABLE 2. List of vouchers used for gathering molecular data for phylogenetic analysis. Molecular data also came from other sources than the present study for some taxa. Unless otherwise specified the voucher number is from the California Academy of Sciences Entomology Dept (CASENT); AToL = Arachnology Tree of Life Project.

Family	species	DNA source - voucher code	DNA sequence	GenBank Accession No.
Hypochilidae	*Hypochilus pococki*	GenBank - Starretts & Waters, 2007; Wheeler & Hayashi, 1998;	COI, 28S, 18S	EF537064.1, AF062977.1, AF062951.1
Filistatidae	*Kukulcania hibernalis*	present study - 9034219	COI, 28S, 18S, H3	-
Austrochilidae	*Hickmania troglodytes*	GenBank - Miller *et al*., 2010	COI, 28S, 18S, H3	FJ948985.1, FJ948945.1, [FJ948862.1, FJ948903.1], FJ949025.1
Dysderidae	*Dysdera erythrina*	GenBank - Arnedo *et al*., 2009	COI, 28S, H3	GQ285643.1, GQ285619.1, GQ285625.1
Dysderidae	*Dysdera erythrina*	AToL ARAMA000013	18S	AToL
Sicariidae	*Loxosceles* sp.	GenBank - Duncan *et al*., 2010	COI	GQ279221.1
Sicariidae	*Loxosceles rufescens*	GenBank - Binford *et al*., 2008	28S	EU817780.1
Sicariidae	*Loxosceles rufescens*	AToL ARAPS000001	18S	AToL
Sicariidae	*Loxosceles* sp.	AToL ARASP000030	H3	AToL
Eresidae	*Stegodyphus* sp.	present study - 9028232	COI, 28S, 18S, H3	-
Oecobiidae	*Uroctea durandi*	GenBank - Miller *et al*., 2010	COI, 28S, 18S, H3	FJ949021.1, FJ948980.1, [FJ948939.1, FJ948897.1], FJ949058.1
Araneiidae	*Araneus marmoreus*	GenBank - Alvarez-Padilla *et al*., 2009	COI, 28S, 18S, H3	EU003278.1, EU003397.1, EU003342.1, EU003312.1
Mimetidae	*Mimetus* sp.	GenBank - Blackledge *et al*., 2009	COI, 28S, 18S, H3	FJ607574.1, FJ607538.1, FJ607500.1, FJ607612.1
Holarchaeidae	*Holarchaea* sp.	AToL ARACG000249	COI, 18S, H3	AToL
Holarchaeidae	*Holarchaea* sp.	GenBank - Rix *et al*., 2008	28S	EU302963.1
Pararchaeidae	Pararchaeidae sp.	AToL ARACG000286	COI, H3	AToL, AToL
Pararchaeidae	*Nanarchaea binnaburra*	GenBank - Rix *et al*., 2008	28S, 18S	EU302964.1, EU302916.1
Desidae	*Badumna longinqua*	GenBank - Miller *et al*., 2010	COI, 28S, 18S, H3	DQ628610.1, DQ628665.1, [DQ628738.1, DQ628701.1], DQ628637.1
Gnaphosidae	*Zelotes* sp.	GenBank - Spagna & Gillespie, 2008	COI, 28S, 18S	DQ628624.1, DQ628686.1, [DQ628759.1, DQ628722.1],
Gnaphosidae	*Zelotes* sp.	AToL ARAMR000525	H3	AToL

TABLE 2 cont.

Family	species	DNA source - voucher code	DNA sequence	GenBank Accession No.
Lycosidae	*Alopecosa kochi*	GenBank - Spagna & Gillespie, 2008	COI, 28S, 18S, H3	DQ628607.1, DQ628662.1, [DQ628735.1, DQ628698.1], DQ628635.1
Palpimanidae	*Palpimanus* sp.	present study - 9024279	COI, 28S, 18S, H3	-
Huttoniidae	*Huttonia* sp.	present study - 9024279	COI, 28S, 18S, H3	-
Stenochillidae	*Colopea* sp.	present study - 9028424	COI, 28S, 18S, H3	-
Mecysmaucheniidae	*Aotearoa magna*	present study - 9028246	COI, 28S, 18S, H3	-
Mecysmaucheniidae	*Zearchea* sp.	present study - 9028243	COI, 28S, 18S, H3	-
Mecysmaucheniidae	*Mesarchaea bellavista*	present study - 9027870	28S, 18S	-
Mecysmaucheniidae	*Mesarchaea bellavista*	present study - 9019105	COI	-
Mecysmaucheniidae	*Mecysmauchenius segmentatus*	present study - 9028435	COI, 28S, 18S, H3	-
Mecysmaucheniidae	*Chilarchaea quellon*	present study - 9028089	COI, 28S, 18S, H3	-
Archaeidae	*"Eriauchenius" lavatenda*	present study - 9018981	COI, 28S, 18S, H3	-
Archaeidae	*"Eriauchenius" jeanneli*	present study - 9028293	COI, 28S, 18S, H3	-
Archaeidae	*"Eriauchenius" legendrei*	present study - 9018992	COI, 28S, 18S, H3	-
Archaeidae	*Eriauchenius workmani*	present study - 9018984	COI, 28S, 18S, H3	-
Archaeidae	*Eriauchenius bourgini*	present study - 9028315	COI, 18S, H3	-
Archaeidae	*Afrarchaea"* pilgrim's rest"	present study - 9018959	COI, 28S, 18S, H3	-
Archaeidae	*Afrarchaea woodae*	present study - 9018957	COI, 28S, 18S, H3	-
Archaeidae	*Austrarchaea nodosa*	present study - 9028388	COI, 28S, 18S	-
Archaeidae	*Austrarchaea daviesae*	present study - 9023672	COI, 28S, 18S, H3	-
Archaeidae	*Austrarchaea mainae*	present study - 9028389	COI, 28S, 18S	-

TABLE 3. Estimates of divergence times in millions of years for nodes in Fig. 11.

Node	Stem node	Crown node	Mean	95% HPD
1			57	[108, 18]
2			82	[134, 34]
3			49	[99, 8]
4			123	[179, 67]
5			72	[125, 21]
6			142	[201, 89]
7			49	[91, 12]
8			76	[127, 28]
9		Southern Hemis. Archaeidae	166	[225, 113]
10			99	[173, 50]
11			112	[177, 61]
12			145	[201, 91]
13	Southern Hemis. Archaeidae		183	[237, 133]
14		Archaeidae	214	[261, 173]
15	Archaeidae; Stenochilidae		240	[298, 185]
16			177	[290, 56]
17			265	[331, 204]
18			58	[116, 9]
19			75	[138, 20]
20			52	[111, 7]
21		Mecysmaucheniidae	103	[180, 33]
22	Mecysmaucheniidae	Palpimanoidea	270	[338, 205]
23			137	[227, 39]
24			123	[134, 116]
25		Araneoidea	146	[168, 122]
26			111	[157, 53]
27			28	[49, 16]
28		RTA-clade	88	[153, 31]
29	Araneoidea; RTA-clade		171	[187, 161]
30		Entelegynae	210	[265, 167]
31	Palpimanoidea; Entelegynae		288	[361, 221]
32			312	[391, 239]
33			331	[414, 254]
34			196	[354, 25]
35			353	[440, 269]
36		Araneomorphae	369	[460, 282]

Table 4. Ancestral area reconstructions using maximum likelihood: only splits within 2 log-likelihood values are shown. Area reconstructions are for two descendent daughter branches. Node numbers correspond with Fig. 11 and 12. Asterisk (*) refers to the preferred area reconstruction depicted in Fig. 12. At several nodes the results have been summarized.

Node	Area reconstruction	Rel. prob.	Node	Area reconstruction	Rel. prob.
1	Mad | Mad	1.00	15	Au | Au	0.32
2	Mad | Mad	0.99		* Au | Au + Eu	0.12
3	AF | AF	0.97		SeA | SeA	0.12
4	AF | Mad	0.86	16	* NZ | SeA + AF + SA + Eu + Mad	0.19
5	Mad | Mad	1.00		NZ | SeA + SA + Eu + Mad	0.06
6	* Mad | Mad	0.48		NZ | SeA + AF + SA + Eu	0.06
	Mad | AF + Mad	0.47		NZ | SeA + AF + SA + Mad	0.06
7	Au | Au	1.00		NZ | AF + SA + Eu + Mad	0.06
8	Au | Au	0.99		NZ | SeA + AF + Eu + Mad	0.06
9	* Au | Mad	0.51		Summary:	
	Au | AF + Mad	0.30		NZ | various area combinations	0.50
	Au | AF	0.08	17	Summary:	
10	Eu | Eu	1.00		various area combinations	
11	Eu | Eu	0.99		no clear patterns	
12	Eu | SeA	0.92	18	NZ | NZ	0.99
13	* Eu | Au + Mad	0.27	19	NZ | SA	0.97
	Eu | AF + Au + Mad	0.15	20	SA | SA	1.00
	SeA + Eu | Au	0.12	21	SA + NZ | SA	0.62
	Eu | Au	0.10	22	Summary:	
	SeA + Eu | Mad	0.07		SA | various area combinations	0.58
	SeA | AF + Au + Mad	0.06		NZ | various area combinations	0.20
	Eu | AF + Au	0.06		* SA + NZ | various area combinations	0.78
	SeA | Au + Mad	0.04			
	Summary:			KEY:	
	* Northern Hemis. | Southern Hemis	0.87		SeA: Southeast Asia	
14	* Eu | Au + Eu	0.33		AF: Africa	
	Eu | Au + Eu + Mad	0.13		SA: South America	
	Eu | SeA + Eu	0.09		Au: Australia	
	Eu | AF + Au + Eu + Mad	0.07		NZ: New Zealand	
	Eu | Eu	0.05		Eu: Eurasia	
	Eu | SeA + Au + Eu	0.05		Mad: Madagascar	

Table 5. MCCR results

Clade	Richness	Sampled	Gamma	P-value
All African archaeids	40	38	-0.61	0.19
Madagascar	27	27	-0.40	0.25
South Africa	13	11	-1.31	0.07

Table 6. "Neck" evolution, lowest AICc score is set to zero.

Clade	BM	lambda	delta	kappa	OU
All Archaeids	**0**	2.2	0.54	2.2	1.7
Madagascar	**0**	2.4	0.87	2.4	1.8

Table 7. For each species the maximum linear velocity (mm/s) and the minimum time (s) for the jaws to close. The average max. velocity and average time for N number of high-speed videos. < and > symbols represent videos where the frame rate of the camera wasn't adequate to fully capture jaw movement thereby underestimating the actual velocity. ** This species is not included in the phylogeny (Fig. 1) and is a juvenile. * For this species the reported velocities are not maximums but rather the average velocity taken from the start to finish of the jaw movement.

Species	Max. Velocity (mm/s)	Min. Time (s)	N	Average max. velocity (mm/s)	Average min. time (s)
Zearchaea sp. E	> 27, 817	< 0.0001	3	> 19,987	< 0.00013
Semysmauchenius sp. B	14,392	0.0003	12	10,127	0.00043
Chilarchaea quellon	> 3,740	< 0.0002	1	-	-
"BigGroup" sp. C	582	0.004	3	351	0.005
"BigGroup" sp. B	377	0.007	7	284	0.011
"BigGroup" sp. E**	285	0.0055	3	201	0.008
Mecysmauchenius sp. E	89.6	0.017	3	63.7	0.022
Mecysmauchenius segmentatus	144	0.018	4	124	0.019
Mecysmauchenioides sp. B	139	0.015	2	96.5	0.017
Semysmauchenius sp. A*	31.7	0.013	2	38.1	0.01
Pararchaea alba	170	0.0064	4	137	0.01

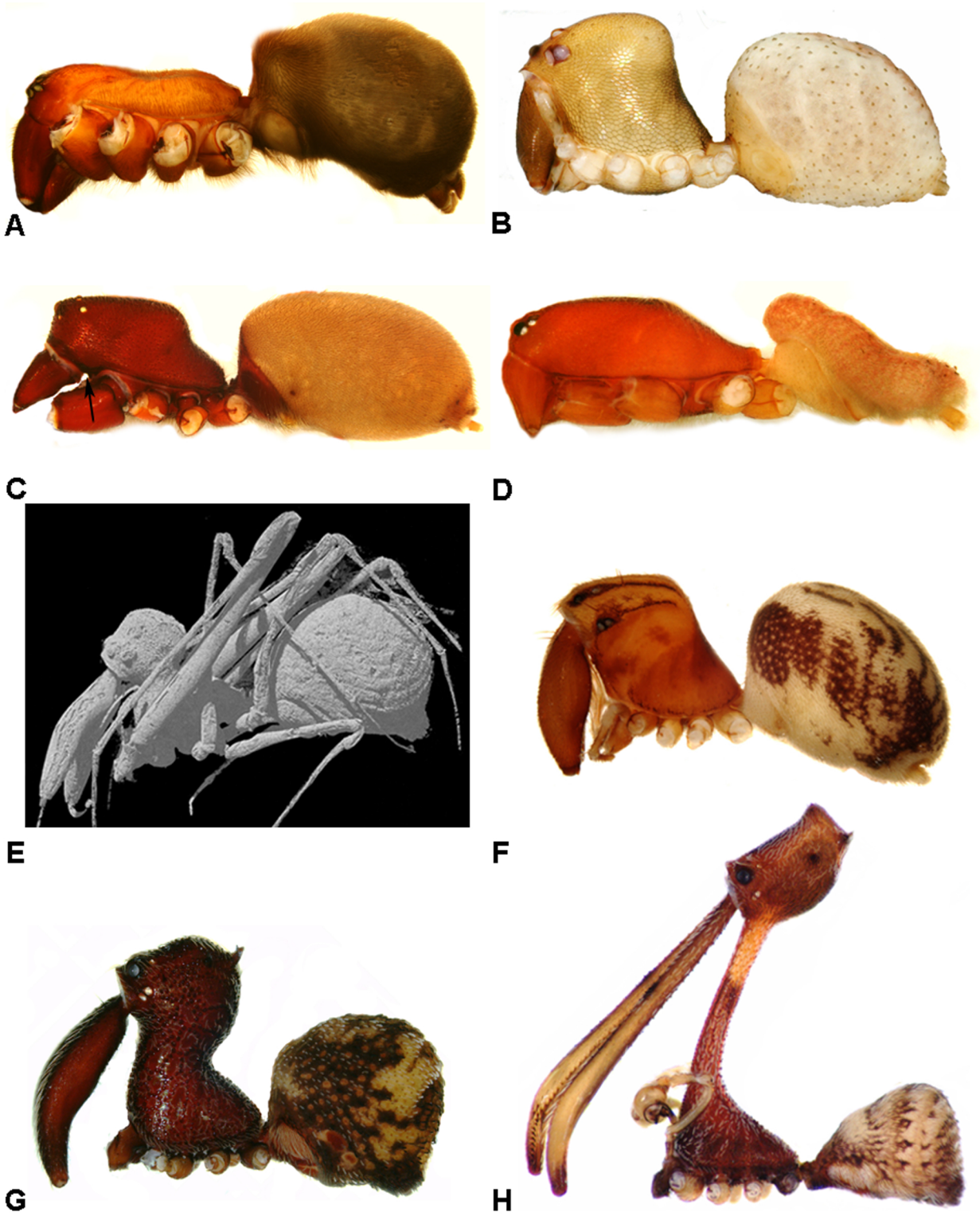
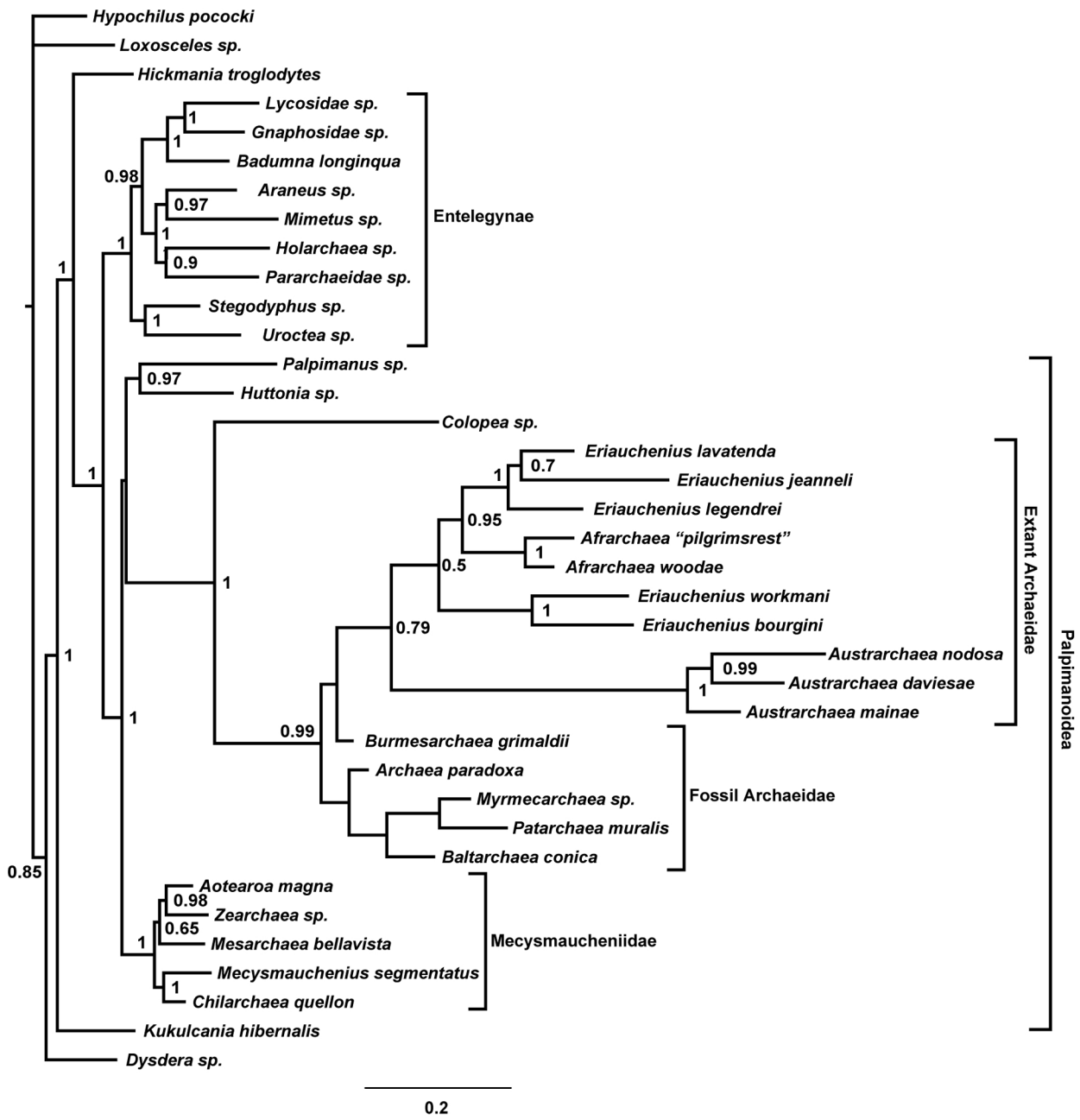


Figure 1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Hickmania troglodytes
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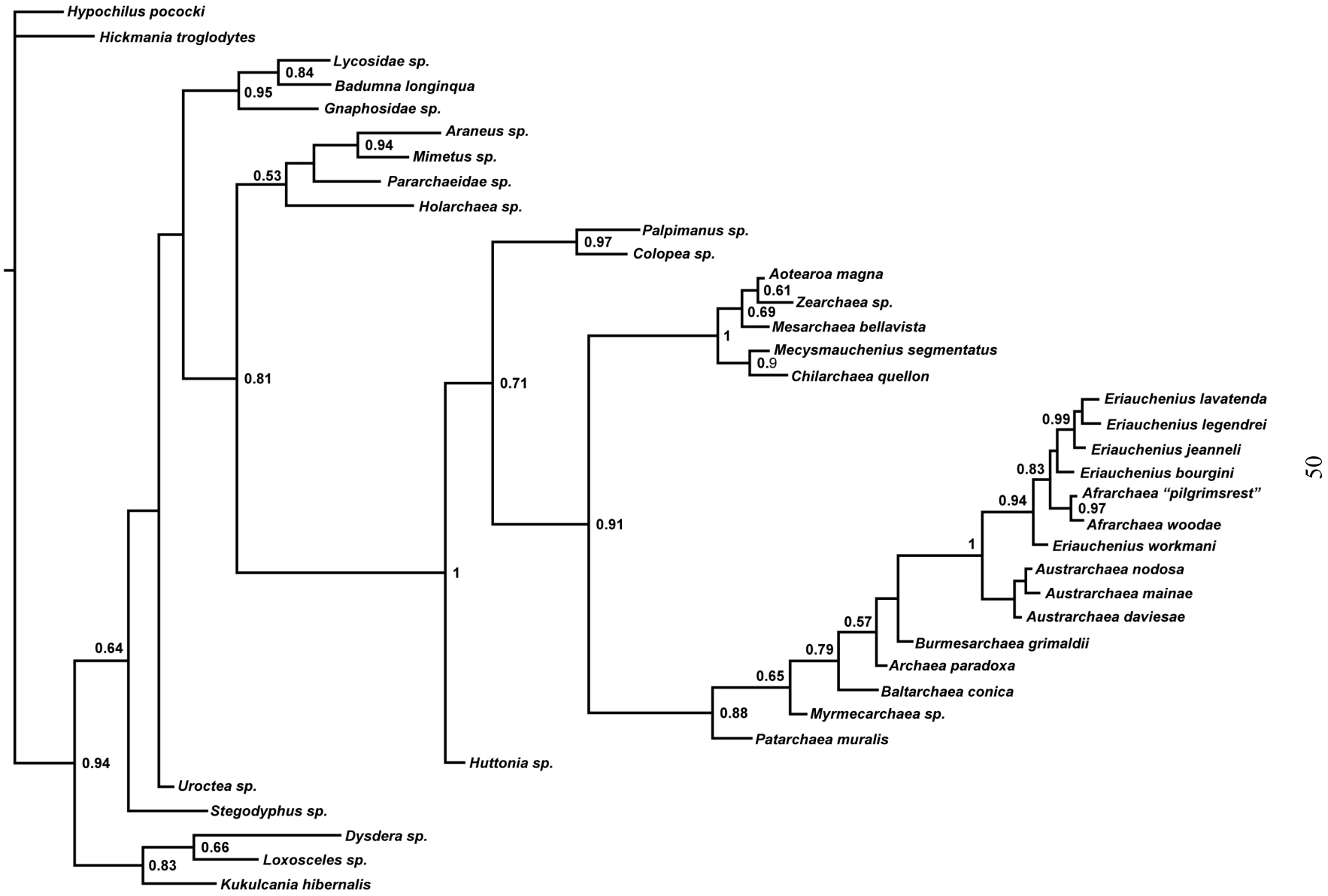
Gnaphosidae sp.
Badumna longinqua
Araneus sp.
Mimetus sp.
Holarchaea sp.
Pararchaeidae sp.
Stegodyphus sp.
Uroctea sp.
Entelegynae
Palpimanus sp.
Huttonia sp.
Colopea sp.
Eriauchenius lavatenda
Eriauchenius jeanneli
Eriauchenius legendrei
Afrarchaea "pilgrimsrest"
Afrarchaea woodae
Eriauchenius workmani
Eriauchenius bourgini
Austrarchaea nodosa
Austrarchaea daviesae
Austrarchaea mainae
Extant Archaeidae
Burmesarchaea grimaldii
Archaea paradoxa
Myrmecarchaea sp.
Patarchaea muralis
Baltarchaea conica
Fossil Archaeidae
Aotearoa magna
Zearchaea sp.
Mesarchaea bellavista
Mecysmauchenius segmentatus
Chilarchaea quellon
Mecysmaucheniidae
Kukulcania hibernalis
Dysdera sp.
Palpimanoidea
0.2

Figure 2


Hypochilus pococki
Loxosceles sp.
Hickmania troglodytes
Lycosidae sp.
Gnaphosidae sp.
Badumna longinqua
Araneus sp.
Mimetus sp.
Stegodyphus sp.
Uroctea sp.
Holarchaea sp.
Pararchaeidae sp.
Colopea sp.
Eriauchenius lavatenda
Eriauchenius jeanneli
Eriauchenius legendrei
Afrarchaea "pilgrimsrest"
Afrarchaea woodae
Eriauchenius workmani
Eriauchenius bourgini
Austrarchaea nodosa
Austrarchaea daviesae
Austrarchaea mainae
Palpimanus sp.
Huttonia sp.
Aotearoa magna
Zearchaea sp.
Mesarchaea bellavista
Mecysmauchenius segmentatus
Chilarchaea quellon
Kukulcania hibernalis
Dysdera sp.
0.2

Figure 3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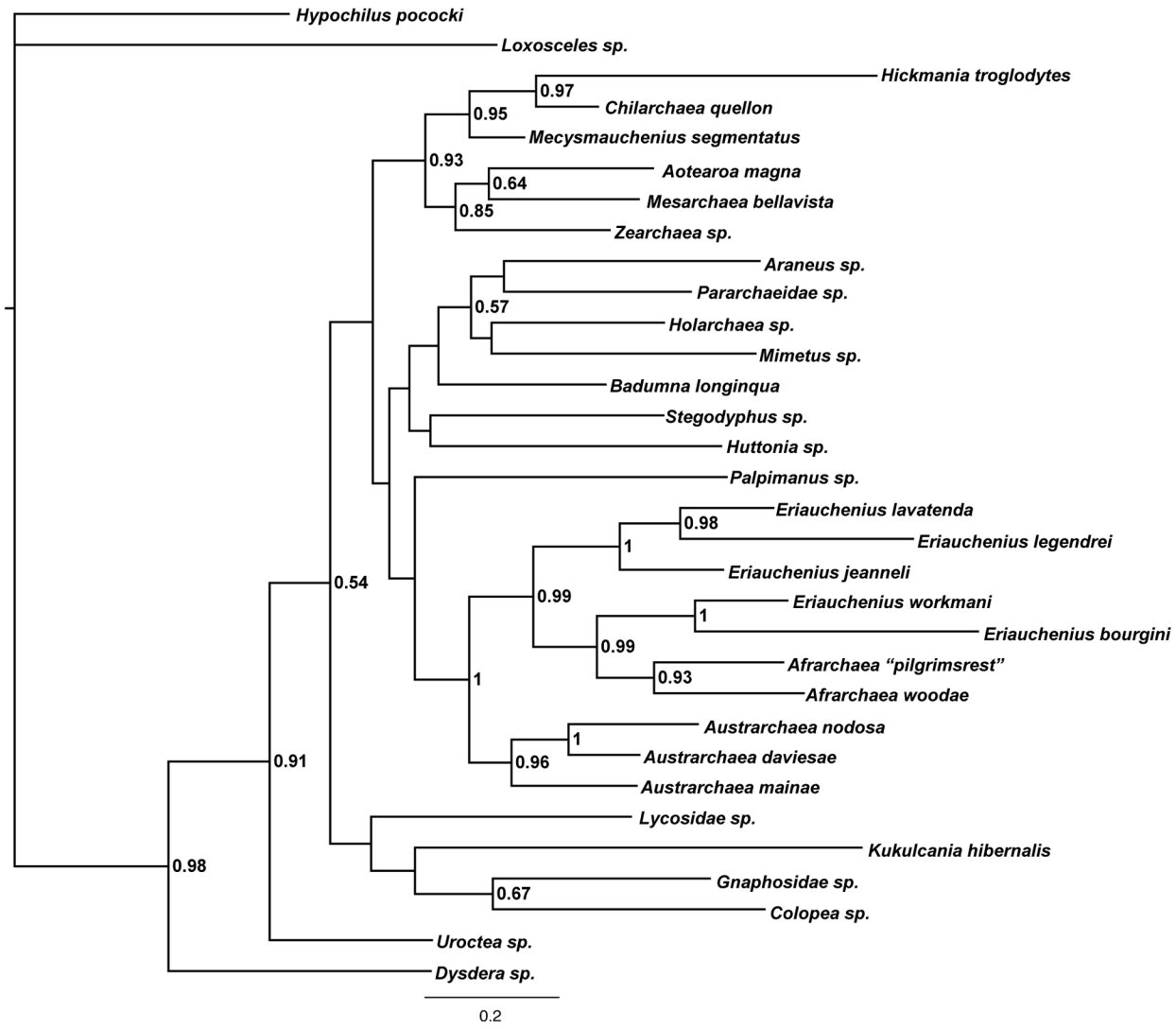
Hickmania troglodytes
Lycosidae sp.
0.84
Badumna longinqua
0.95
Gnaphosidae sp.
Araneus sp.
0.94
Mimetus sp.
0.53
Pararchaeidae sp.
Holarchaea sp.
Palpimanus sp.
0.97
Colopea sp.
Aotearoa magna
0.61
Zearchaea sp.
0.69
Mesarchaea bellavista
1
Mecysmauchenius segmentatus
0.9
Chilarchaea quellon
0.81
0.71
Eriauchenius lavatenda
0.99
Eriauchenius legendrei
Eriauchenius jeanneli
0.83
Eriauchenius bourgini
Afrarchaea "pilgrimsrest"
0.94
0.97
Afrarchaea woodae
0.91
Eriauchenius workmani
1
Austrarchaea nodosa
Austrarchaea mainae
Austrarchaea daviesae
0.57
Burmesarchaea grimaldii
0.64
0.79
Archaea paradoxa
0.65
Baltarchaea conica
0.88
Myrmecarchaea sp.
Patarchaea muralis
1
Huttonia sp.
0.94
Uroctea sp.
Stegodyphus sp.
Dysdera sp.
0.66
Loxosceles sp.
0.83
Kukulcania hibernalis
0.2

Figure 4


Hypochilus pococki
Loxosceles sp.
Hickmania troglodytes
0.97
Chilarchaea quellon
0.95
Mecysmauchenius segmentatus
0.93
Aotearoa magna
0.64
Mesarchaea bellavista
0.85
Zearchaea sp.
Araneus sp.
Pararchaeidae sp.
0.57
Holarchaea sp.
Mimetus sp.
Badumna longinqua
Stegodyphus sp.
Huttonia sp.
Palpimanus sp.
Eriauchenius lavatenda
0.98
Eriauchenius legendrei
1
Eriauchenius jeanneli
0.54
0.99
Eriauchenius workmani
1
Eriauchenius bourgini
0.99
Afrarchaea "pilgrimsrest"
0.93
Afrarchaea woodae
1
Austrarchaea nodosa
1
Austrarchaea daviesae
0.91
0.96
Austrarchaea mainae
Lycosidae sp.
Kukulcania hibernalis
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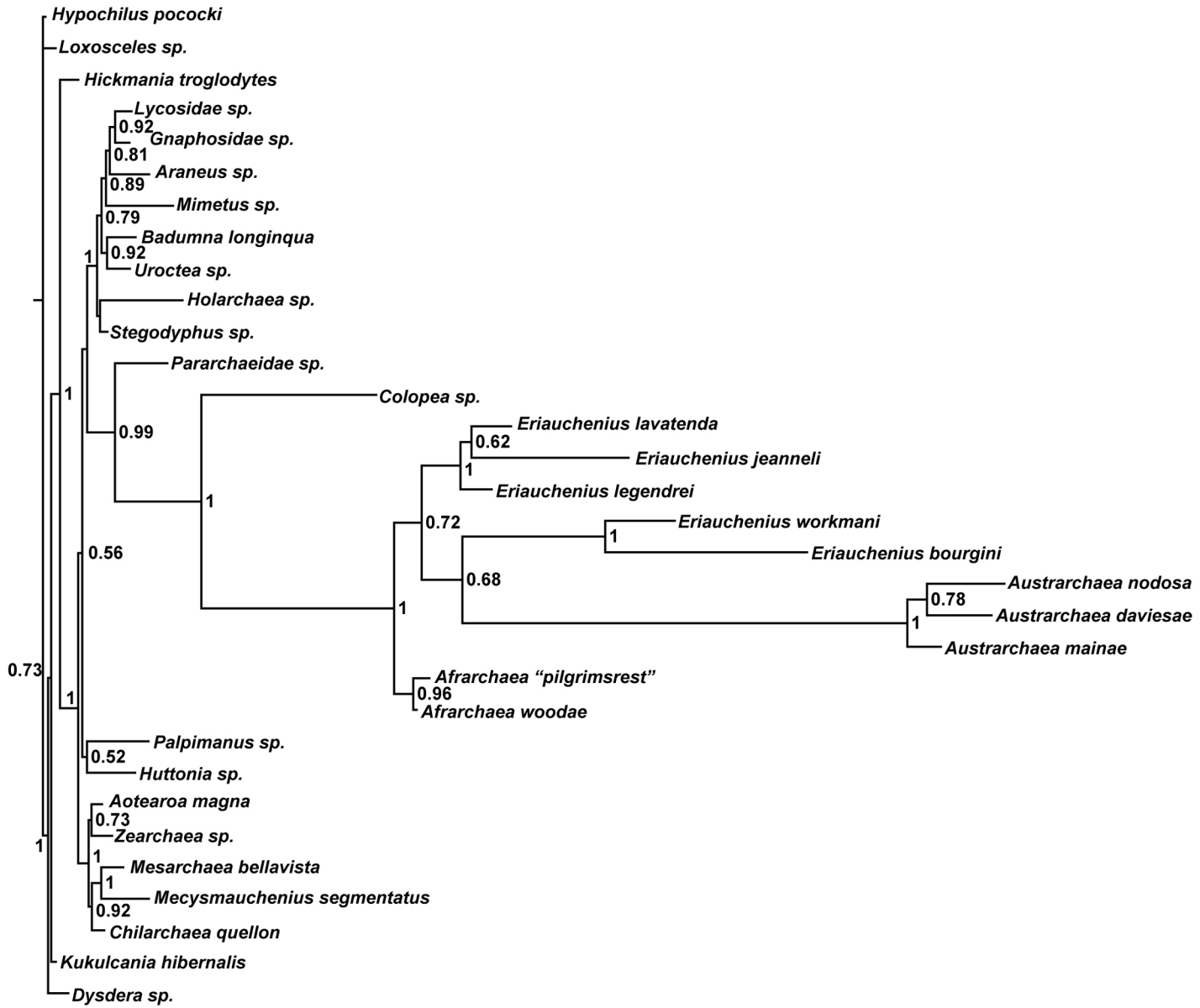
Gnaphosidae sp.
0.67
Colopea sp.
Uroctea sp.
Dysdera sp.
0.2

Figure 5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Hickmania troglodytes
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0.92
Gnaphosidae sp.
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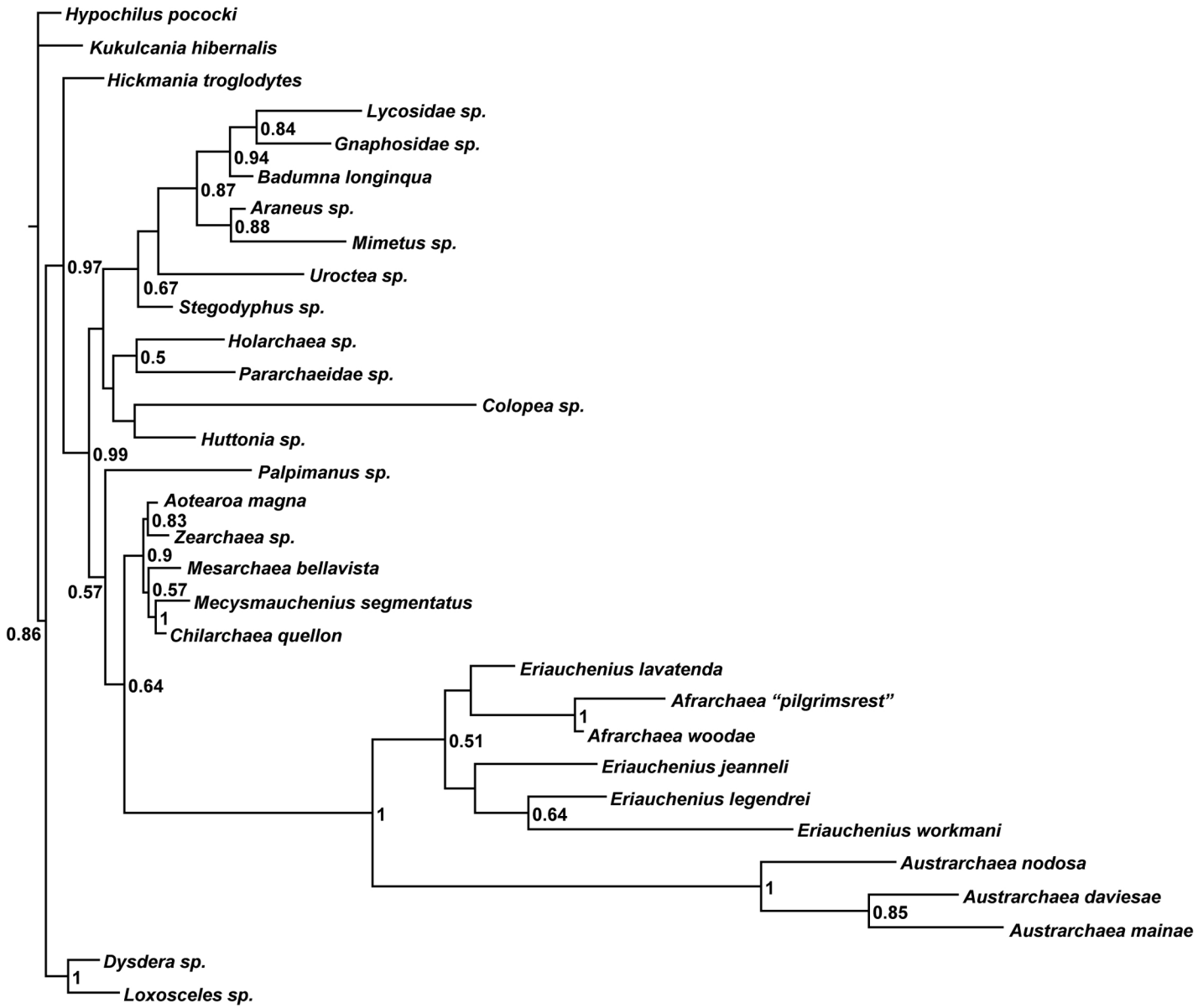
Araneus sp.
0.89
Mimetus sp.
0.79
Badumna longinqua
0.92
Uroctea sp.
1
Holarchaea sp.
Stegodyphus sp.
Pararchaeidae sp.
1
Colopea sp.
0.99
Eriauchenius lavatenda
0.62
Eriauchenius jeanneli
1
Eriauchenius legendrei
1
0.72
Eriauchenius workmani
1
Eriauchenius bourgini
0.56
0.68
Austrarchaea nodosa
0.78
1
Austrarchaea daviesae
1
Austrarchaea mainae
0.73
Afrarchaea "pilgrimsrest"
1
0.96
Afrarchaea woodae
Palpimanus sp.
0.52
Huttonia sp.
1
Aotearoa magna
0.73
Zearchaea sp.
1
Mesarchaea bellavista
1
Mecysmauchenius segmentatus
0.92
Chilarchaea quellon
Kukulcania hibernalis
Dysdera sp.
0.2

Figure 6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Kukulcania hibernalis
Hickmania troglodytes
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Gnaphosidae sp.
0.94
Badumna longinqua
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Araneus sp.
0.88
Mimetus sp.
0.97
Uroctea sp.
0.67
Stegodyphus sp.
Holarchaea sp.
0.5
Pararchaeidae sp.
Colopea sp.
Huttonia sp.
0.99
Palpimanus sp.
Aotearoa magna
0.83
Zearchaea sp.
0.9
Mesarchaea bellavista
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0.57
Mecysmauchenius segmentatus
1
Chilarchaea quellon
0.86
Eriauchenius lavatenda
Afrarchaea "pilgrimsrest"
1
Afrarchaea woodae
0.64
0.51
Eriauchenius jeanneli
Eriauchenius legendrei
1
0.64
Eriauchenius workmani
Austrarchaea nodosa
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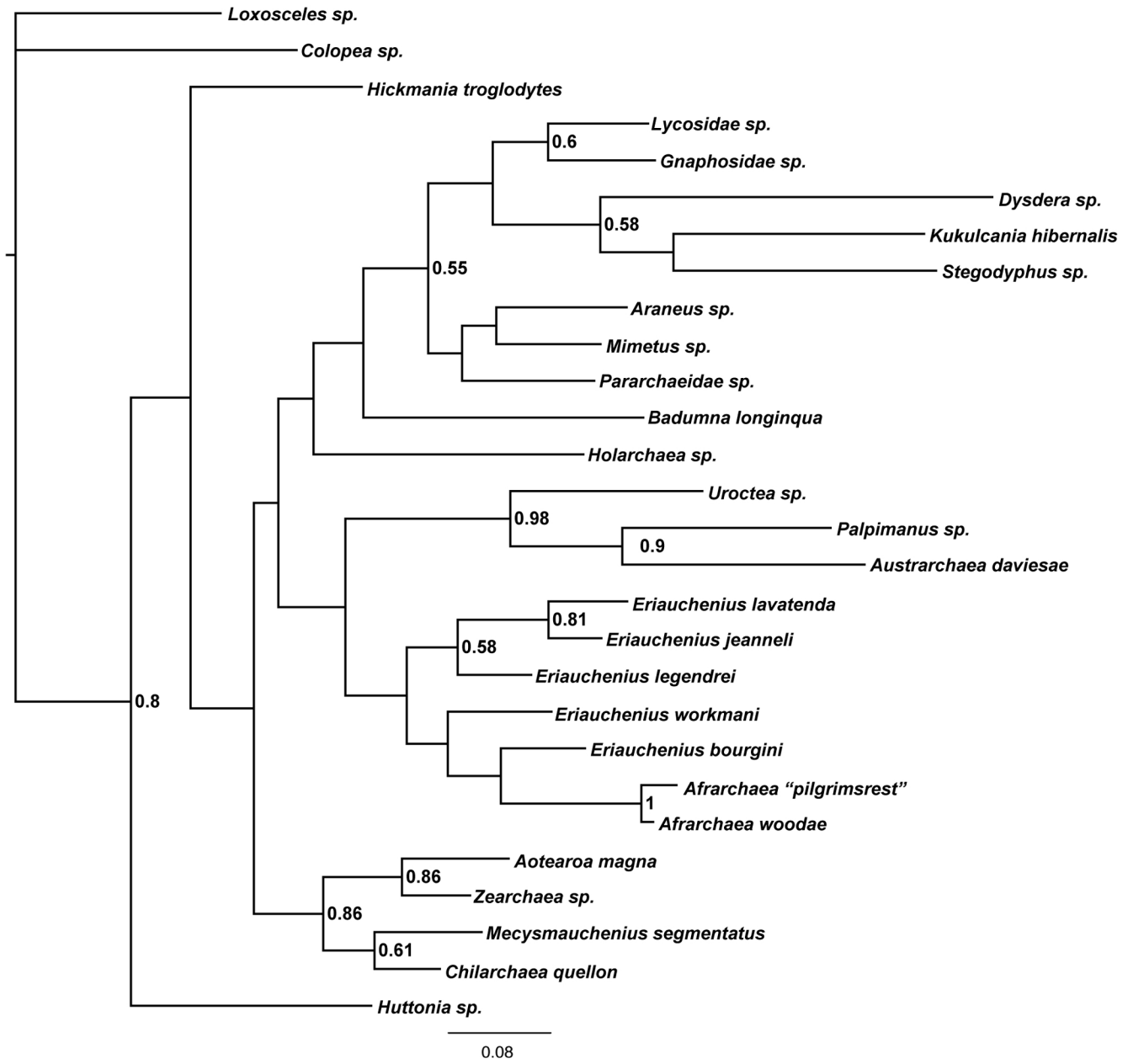
Austrarchaea mainae
Dysdera sp.
1
Loxosceles sp.
0.3

Figure 7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Colopea sp.
Hickmania troglodytes
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Gnaphosidae sp.
Dysdera sp.
0.58
Kukulcania hibernalis
Stegodyphus sp.
0.55
Araneus sp.
Mimetus sp.
Pararchaeidae sp.
Badumna longinqua
Holarchaea sp.
Uroctea sp.
0.98
Palpimanus sp.
0.9
Austrarchaea daviesae
Eriauchenius lavatenda
0.81
Eriauchenius jeanneli
0.58
Eriauchenius legendrei
Eriauchenius workmani
Eriauchenius bourgini
Afrarchaea "pilgrimsrest"
1
Afrarchaea woodae
0.8
Aotearoa magna
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Mecysmauchenius segmentatus
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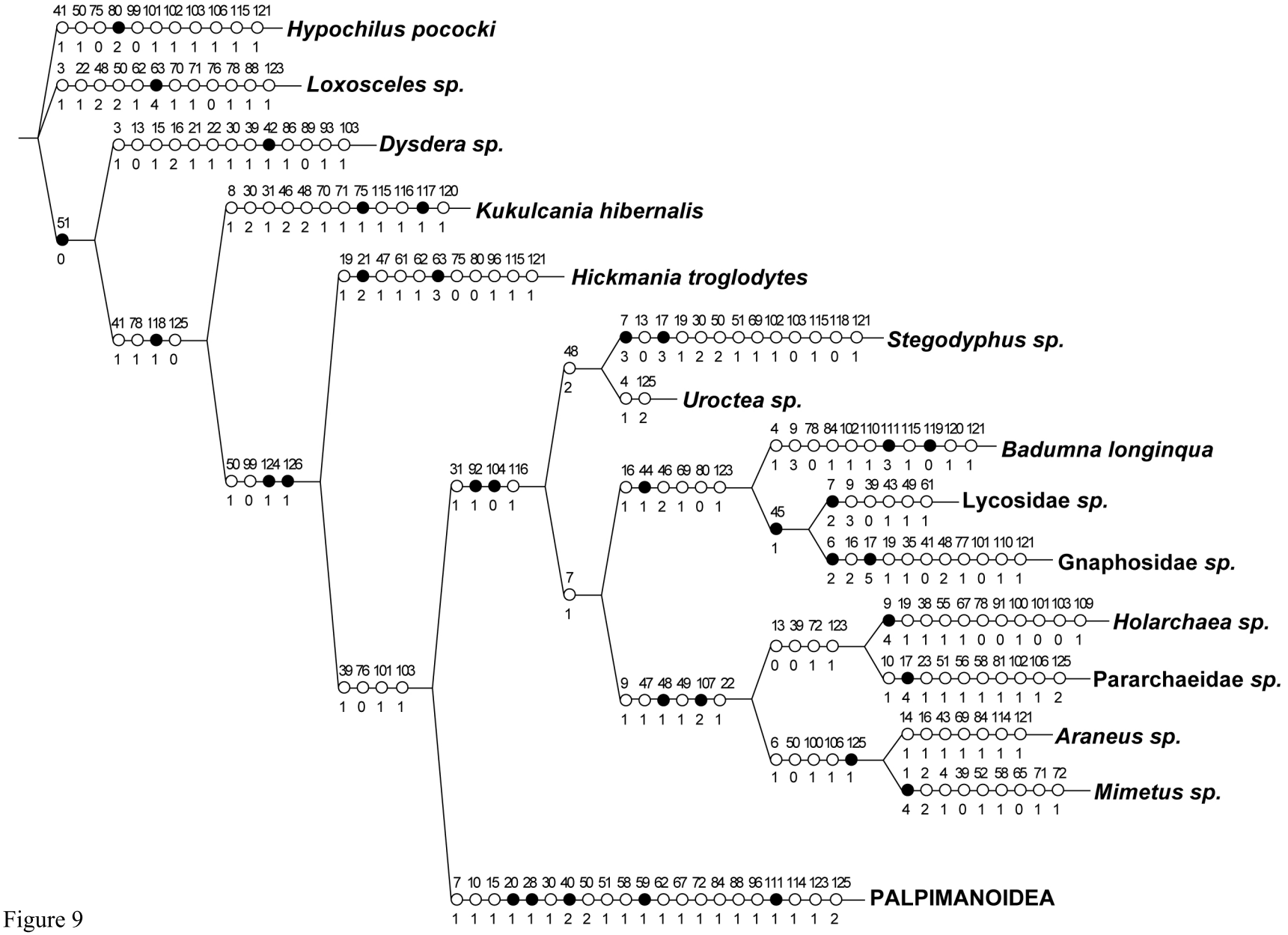
Chilarchaea quellon
Huttonia sp.
0.08

Figure 8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Loxosceles sp.
1 1 2 2 1 4 1 1 0 1 1 1
3 13 15 16 21 22 30 39 42 86 89 93 103
Dysdera sp.
1 0 1 2 1 1 1 1 1 1 0 1 1
8 30 31 46 48 70 71 75 115 116 117 120
Kukulcania hibernalis
1 2 1 2 2 1 1 1 1 1 1 1
51
0
19 21 47 61 62 63 75 80 96 115 121
Hickmania troglodytes
1 2 1 1 1 3 0 0 1 1 1
41 78 118 125
1 1 1 0
7 13 17 19 30 50 51 69 102 103 115 118 121
Stegodyphus sp.
3 0 3 1 2 2 1 1 1 0 1 0 1
48
2
4 125
Uroctea sp.
1 2
4 9 78 84 102 110 111 115 119 120 121
Badumna longinqua
1 3 0 1 1 1 3 1 0 1 1
50 99 124 126
1 0 1 1
31 92 104 116
1 1 0 1
16 44 46 69 80 123
1 1 2 1 0 1
7 9 39 43 49 61
Lycosidae sp.
2 3 0 1 1 1
45
1
6 16 17 19 35 41 48 77 101 110 121
Gnaphosidae sp.
2 2 5 1 1 0 2 1 0 1 1
7
1
9 19 38 55 67 78 91 100 101 103 109
Holarchaea sp.
4 1 1 1 1 0 0 1 0 0 1
13 39 72 123
0 0 1 1
10 17 23 51 56 58 81 102 106 125
Pararchaeidae sp.
1 4 1 1 1 1 1 1 1 2
39 76 101 103
1 0 1 1
9 47 48 49 107 22
1 1 1 1 2 1
14 16 43 69 84 114 121
Araneus sp.
1 1 1 1 1 1 1
6 50 100 106 125
1 0 1 1 1
1 2 4 39 52 58 65 71 72
Mimetus sp.
4 2 1 0 1 1 0 1 1
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PALPIMANOIDEA
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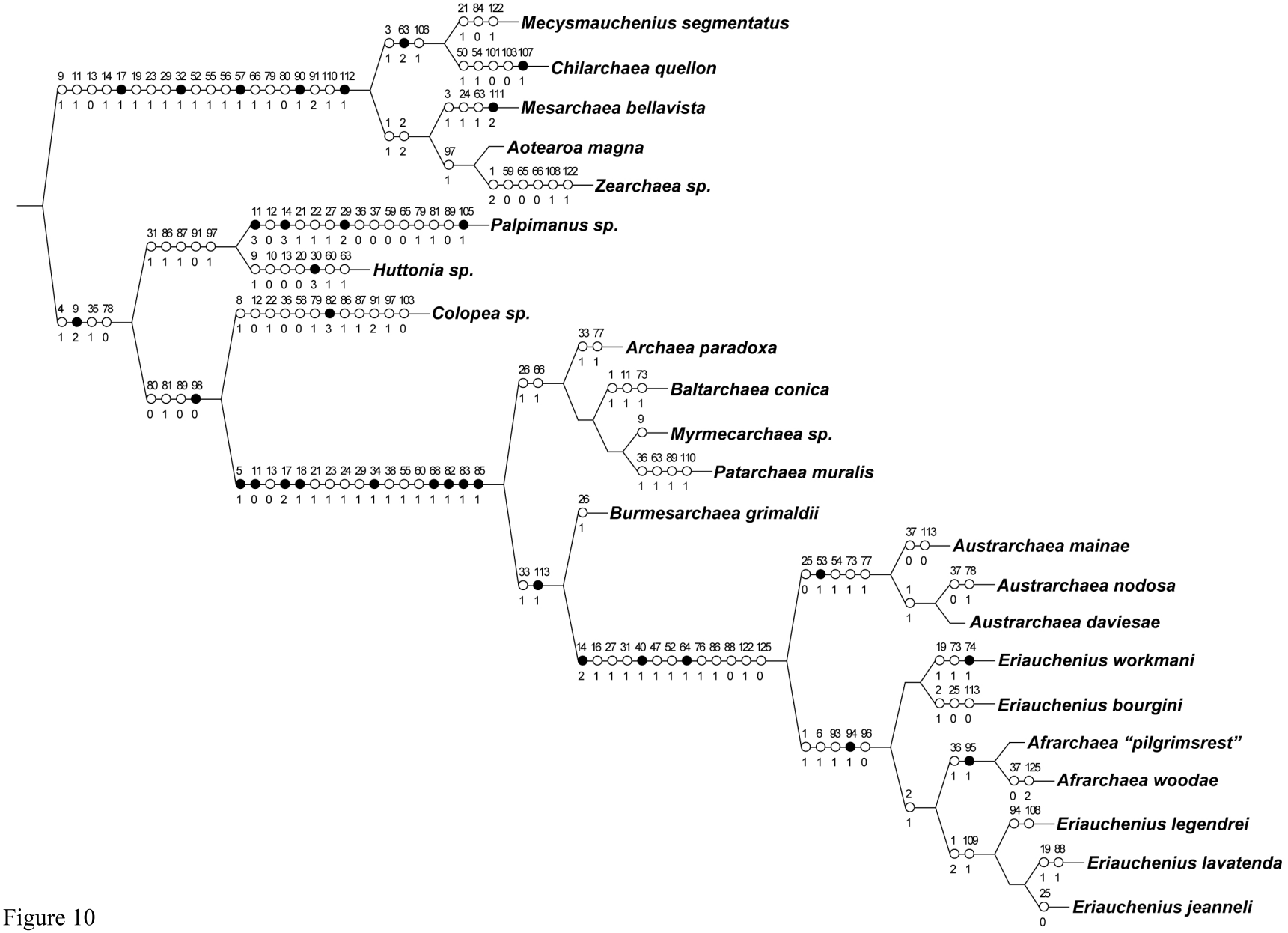
Figure 9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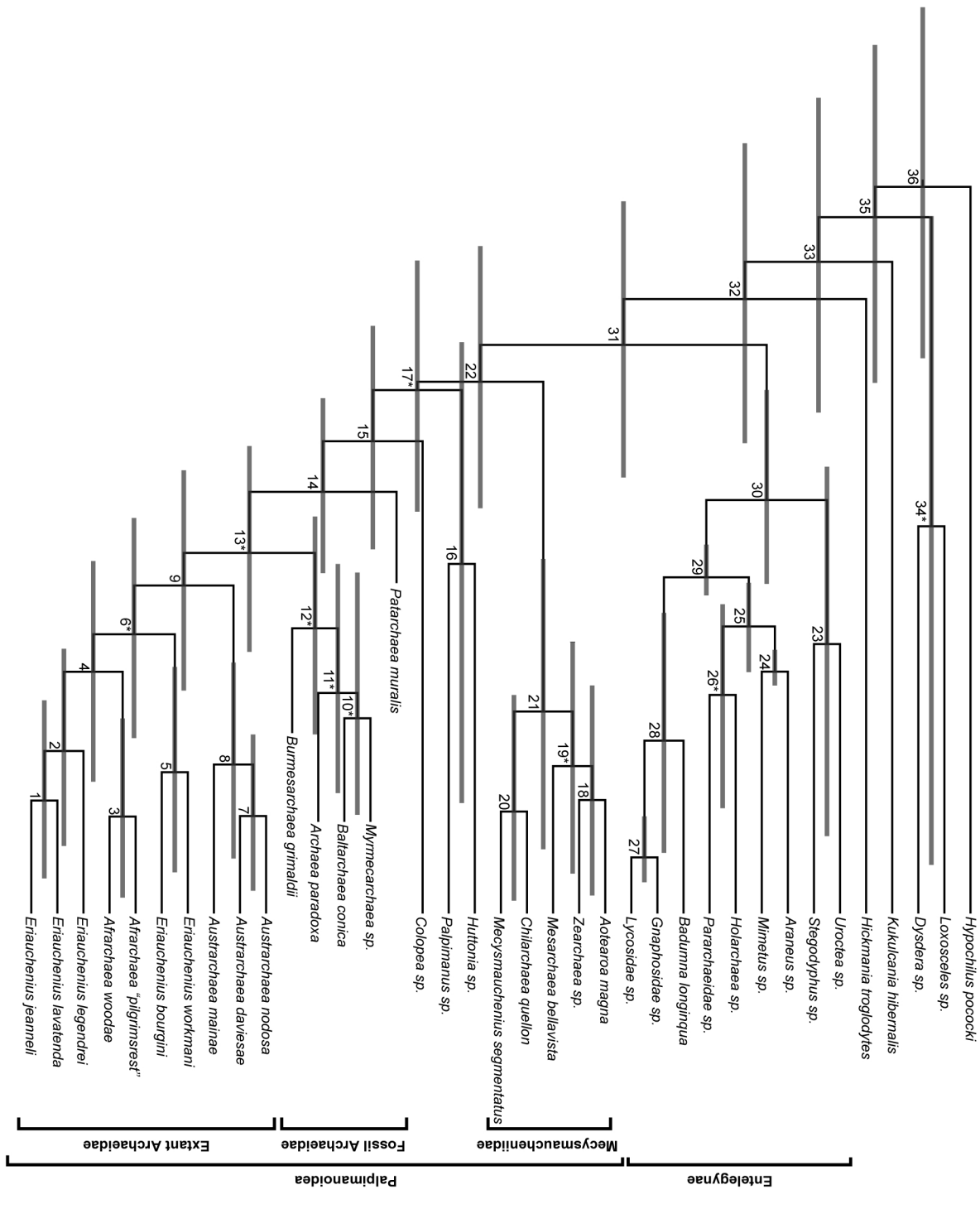
Chilarchaea quellon
Mesarchaea bellavista
Aotearoa magna
Zearchaea sp.
Palpimanus sp.
Huttonia sp.
Colopea sp.
Archaea paradoxa
Baltarchaea conica
Myrmecarchaea sp.
Patarchaea muralis
Burmesarchaea grimaldii
Austrarchaea mainae
Austrarchaea nodosa
Austrarchaea daviesae
Eriauchenius workmani
Eriauchenius bourgini
Afrarchaea "pilgrimsrest"
Afrarchaea woodae
Eriauchenius legendrei
Eriauchenius lavatenda
Eriauchenius jeanneli

Figure 10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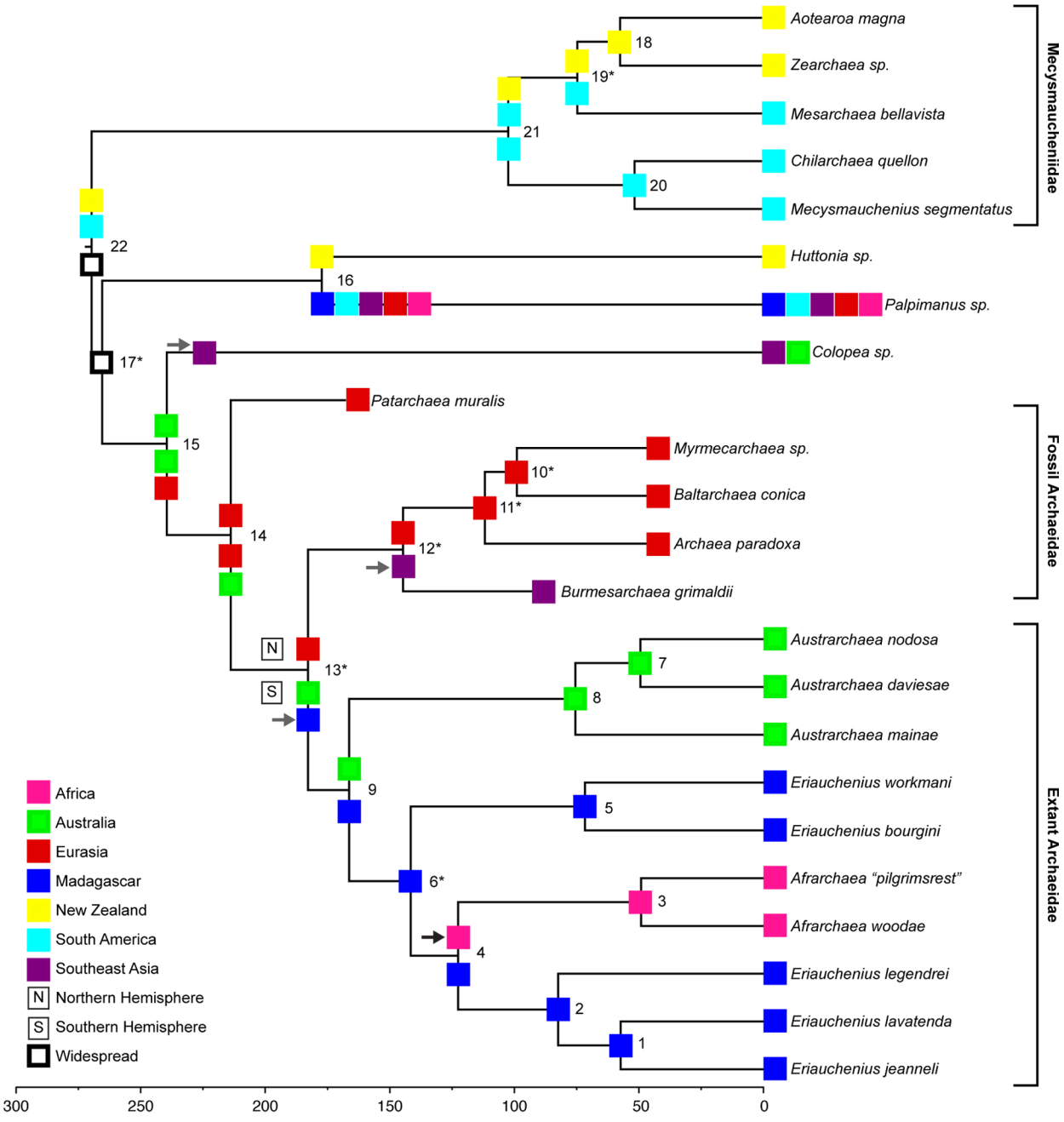
Mimetus sp.
Holarchaea sp.
Pararchaeidae sp.
Baduma longinqua
Gnaphosidae sp.
Lycosidae sp.
Aotearoa magna
Zearchaea sp.
Mesarchaea bellavista
Chilarchaea quellon
Mecysmaucheniidae
Mecysmaucheniinae
Mecysmaucheniini
Mecysmaucheniini segmentatus
Huttonia sp.
Palpimanus sp.
Colopea sp.
Patarchaea muralis
Myrmecarchaea sp.
Baltarchaea conica
Archaea paradoxa
Burmesarchaea grimaldii
Austrarchaea nodosa
Austrarchaea daviesae
Austrarchaea mainae
Eriauchenius workmani
Eriauchenius bourgini
Afrarchaea "pilgrimsrest"
Afrarchaea woodae
Eriauchenius legendrei
Eriauchenius lavatenda
Eriauchenius jeanneli
Entelegynae
Mecysmaucheniidae
Palpimanoidea
Fossil Archaeidae
Extant Archaeidae
400
350
300
250
200
150
100
50
0

Figure 11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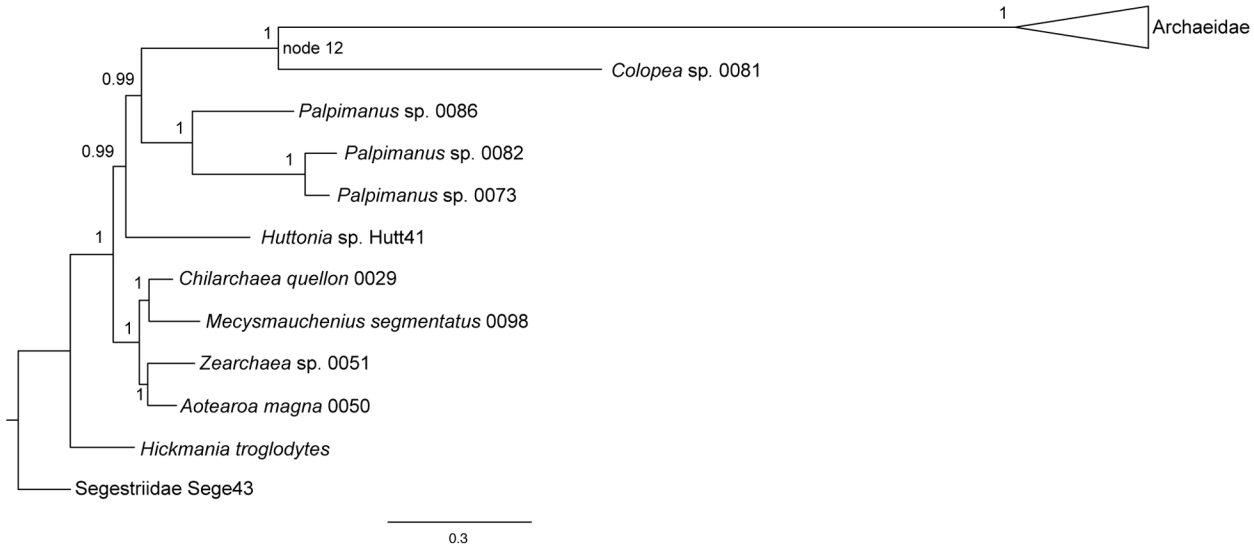
Huttonia sp.
Palpimanus sp.
Colopea sp.
Patarchaea muralis
Myrmecarchaea sp.
Baltarchaea conica
Archaea paradoxa
Burmesarchaea grimaldii
Austrarchaea nodosa
Austrarchaea daviesae
Austrarchaea mainae
Eriauchenius workmani
Eriauchenius bourgini
Afrarchaea "pilgrimsrest"
Afrarchaea woodae
Eriauchenius legendrei
Eriauchenius lavatenda
Eriauchenius jeanneli
Mecysmaucheniidae
Fossil Archaeidae
Extant Archaeidae
18
19*
21
20
22
16
17*
15
14
10*
11*
12*
N
13*
S
7
8
9
5
6*
3
4
2
1
Africa
Australia
Eurasia
Madagascar
New Zealand
South America
Southeast Asia
Northern Hemisphere
Southern Hemisphere
Widespread
300
250
200
150
100
50
0

Figure 12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1
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1
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1
Palpimanus sp. 0082
Palpimanus sp. 0073
1
Huttonia sp. Hutt41
1
Chilarchaea quellon 0029
1
Mecysmauchenius segmentatus 0098
Zearchaea sp. 0051
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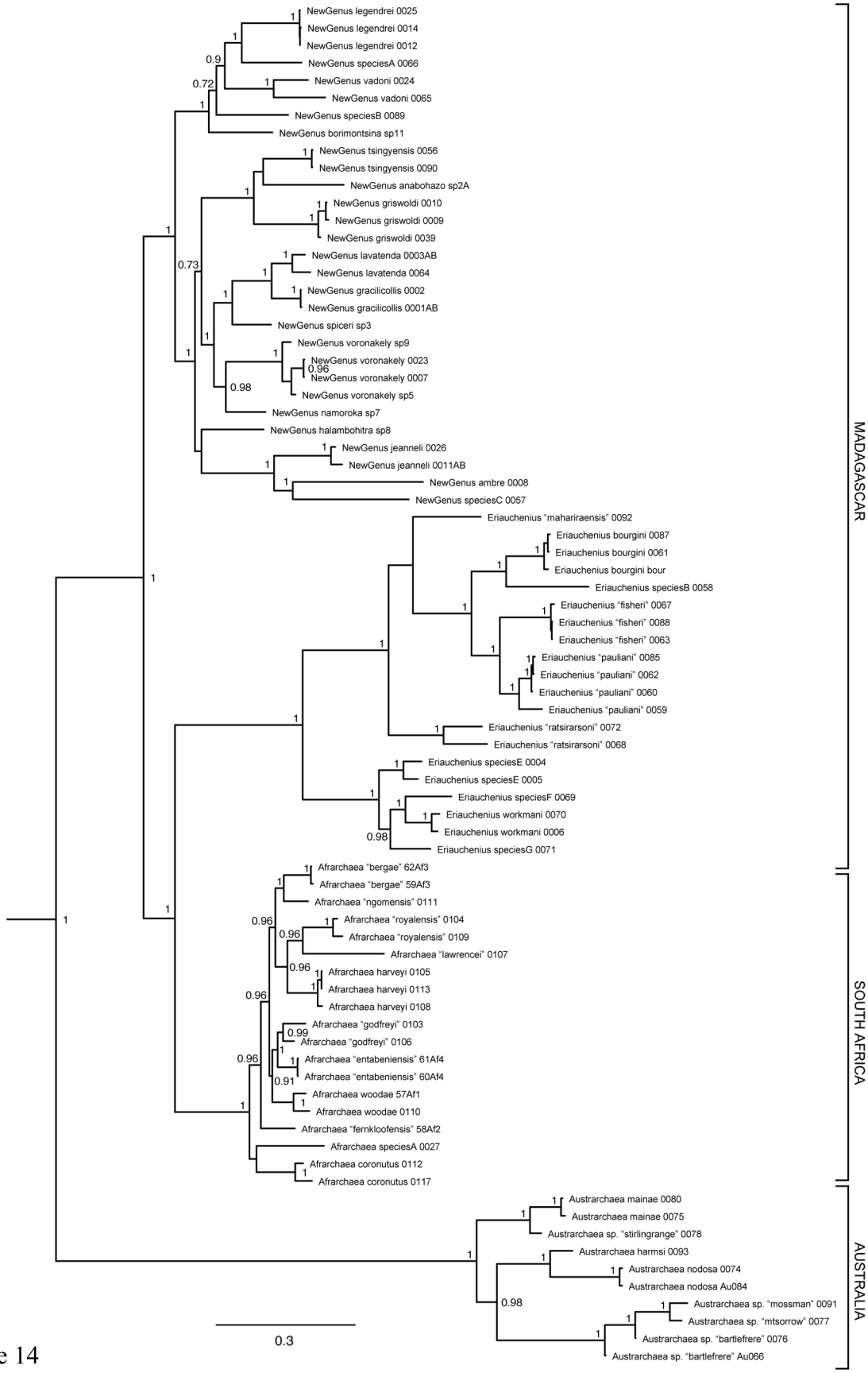
Aotearoa magna 0050
Hickmania troglodytes
Segestriidae Sege43
0.3

Figure 13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NewGenus tsingyensis 0056
NewGenus tsingyensis 0090
NewGenus anabohazo sp2A
NewGenus griswoldi 0010
NewGenus griswoldi 0009
NewGenus griswoldi 0039
NewGenus lavatenda 0003AB
NewGenus lavatenda 0064
NewGenus gracilicollis 0002
NewGenus gracilicollis 0001AB
NewGenus spiceri sp3
NewGenus voronakely sp9
NewGenus voronakely 0023
NewGenus voronakely 0007
NewGenus voronakely sp5
NewGenus namoroka sp7
NewGenus halambohitra sp8
NewGenus jeanneli 0026
NewGenus jeanneli 0011AB
NewGenus ambre 0008
NewGenus speciesC 0057
Eriauchenius "mahariraensis" 0092
Eriauchenius bourgini 0087
Eriauchenius bourgini 0061
Eriauchenius bourgini bour
Eriauchenius speciesB 0058
Eriauchenius "fisheri" 0067
Eriauchenius "fisheri" 0088
Eriauchenius "fisheri" 0063
Eriauchenius "pauliani" 0085
Eriauchenius "pauliani" 0062
Eriauchenius "pauliani" 0060
Eriauchenius "pauliani" 0059
Eriauchenius "ratsirarsoni" 0072
Eriauchenius "ratsirarsoni" 0068
Eriauchenius speciesE 0004
Eriauchenius speciesE 0005
Eriauchenius speciesF 0069
Eriauchenius workmani 0070
Eriauchenius workmani 0006
Eriauchenius speciesG 0071
Afrarchaea "bergae" 62Af3
Afrarchaea "bergae" 59Af3
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Afrarchaea "royalensis" 0104
Afrarchaea "royalensis" 0109
Afrarchaea "lawrencei" 0107
Afrarchaea harveyi 0105
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Afrarchaea harveyi 0108
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Afrarchaea "entabeniensis" 61Af4
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Afrarchaea woodae 0110
Afrarchaea "fernkloofensis" 58Af2
Afrarchaea speciesA 0027
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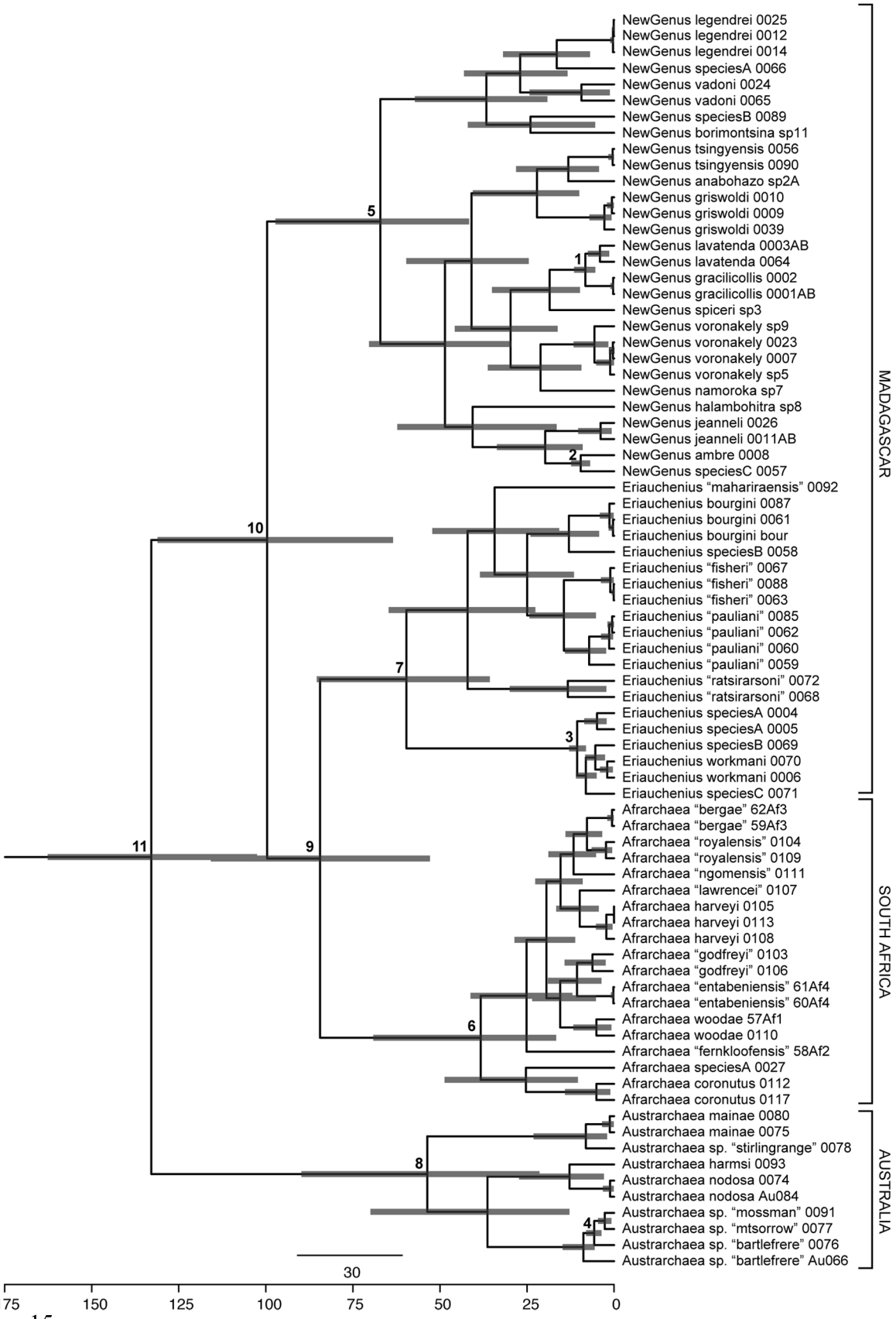
0.3
MADAGASCAR
SOUTH AFRICA
AUSTRALIA

Figure 14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NewGenus borimontsina sp11
NewGenus tsingyensis 0056
NewGenus tsingyensis 0090
NewGenus anabohazo sp2A
NewGenus griswoldi 0010
NewGenus griswoldi 0009
NewGenus griswoldi 0039
NewGenus lavatenda 0003AB
NewGenus lavatenda 0064
NewGenus gracilicollis 0002
NewGenus gracilicollis 0001AB
NewGenus spiceri sp3
NewGenus voronakely sp9
NewGenus voronakely 0023
NewGenus voronakely 0007
NewGenus voronakely sp5
NewGenus namoroka sp7
NewGenus halambohitra sp8
NewGenus jeanneli 0026
NewGenus jeanneli 0011AB
NewGenus ambre 0008
NewGenus speciesC 0057
Eriauchenius "mahariraensis" 0092
Eriauchenius bourgini 0087
Eriauchenius bourgini 0061
Eriauchenius bourgini bour
Eriauchenius speciesB 0058
Eriauchenius "fisheri" 0067
Eriauchenius "fisheri" 0088
Eriauchenius "fisheri" 0063
Eriauchenius "pauliani" 0085
Eriauchenius "pauliani" 0062
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Eriauchenius speciesB 0069
Eriauchenius workmani 0070
Eriauchenius workmani 0006
Eriauchenius speciesC 0071
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Afrarchaea "bergae" 59Af3
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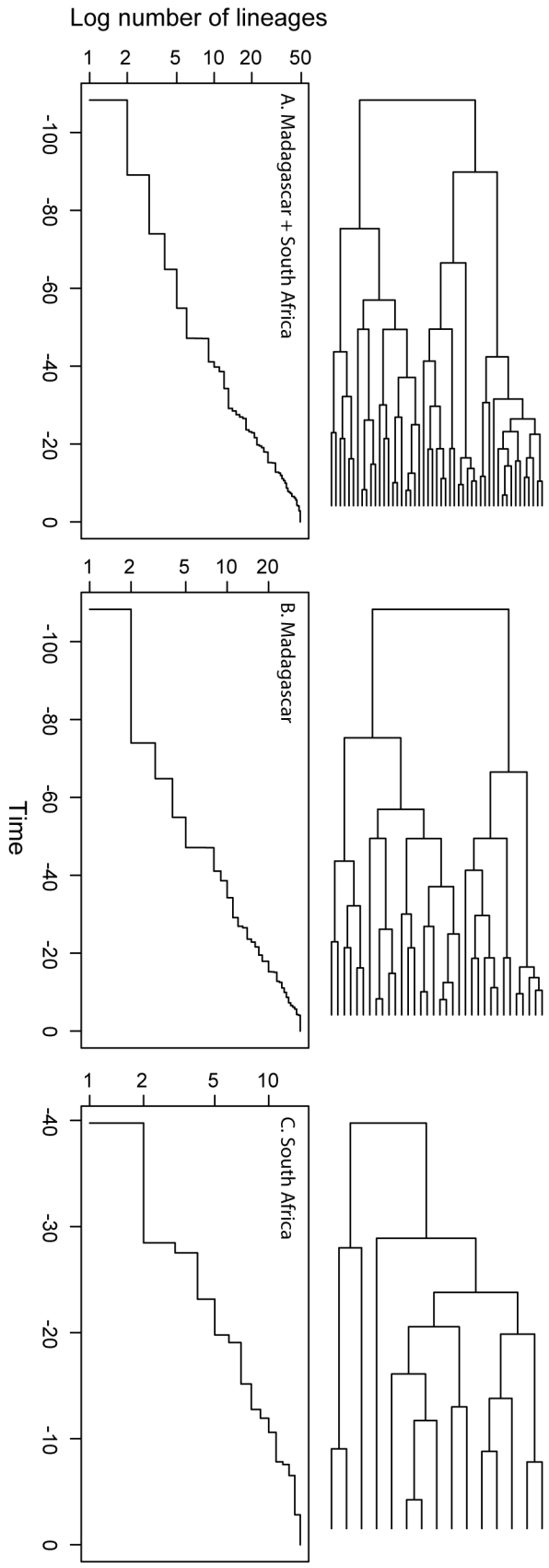
Afrarchaea harveyi 0105
Afrarchaea harveyi 0113
Afrarchaea harveyi 0108
Afrarchaea "godfreyi" 0103
Afrarchaea "godfreyi" 0106
Afrarchaea "entabeniensis" 61Af4
Afrarchaea "entabeniensis" 60Af4
Afrarchaea woodae 57Af1
Afrarchaea woodae 0110
Afrarchaea "fernkloofensis" 58Af2
Afrarchaea speciesA 0027
Afrarchaea coronutus 0112
Afrarchaea coronutus 0117
Austrarchaea mainae 0080
Austrarchaea mainae 0075
Austrarchaea sp. "stirlingrange" 0078
Austrarchaea harmsi 0093
Austrarchaea nodosa 0074
Austrarchaea nodosa Au084
Austrarchaea sp. "mossman" 0091
Austrarchaea sp. "mtsorrow" 0077
Austrarchaea sp. "bartlefrere" 0076
Austrarchaea sp. "bartlefrere" Au066
MADAGASCAR
SOUTH AFRICA
AUSTRALIA
1
2
3
4
5
6
7
8
9
10
11
30
175
150
125
100
75
50
25
0

Figure 15

Figure 16


Log number of lineages
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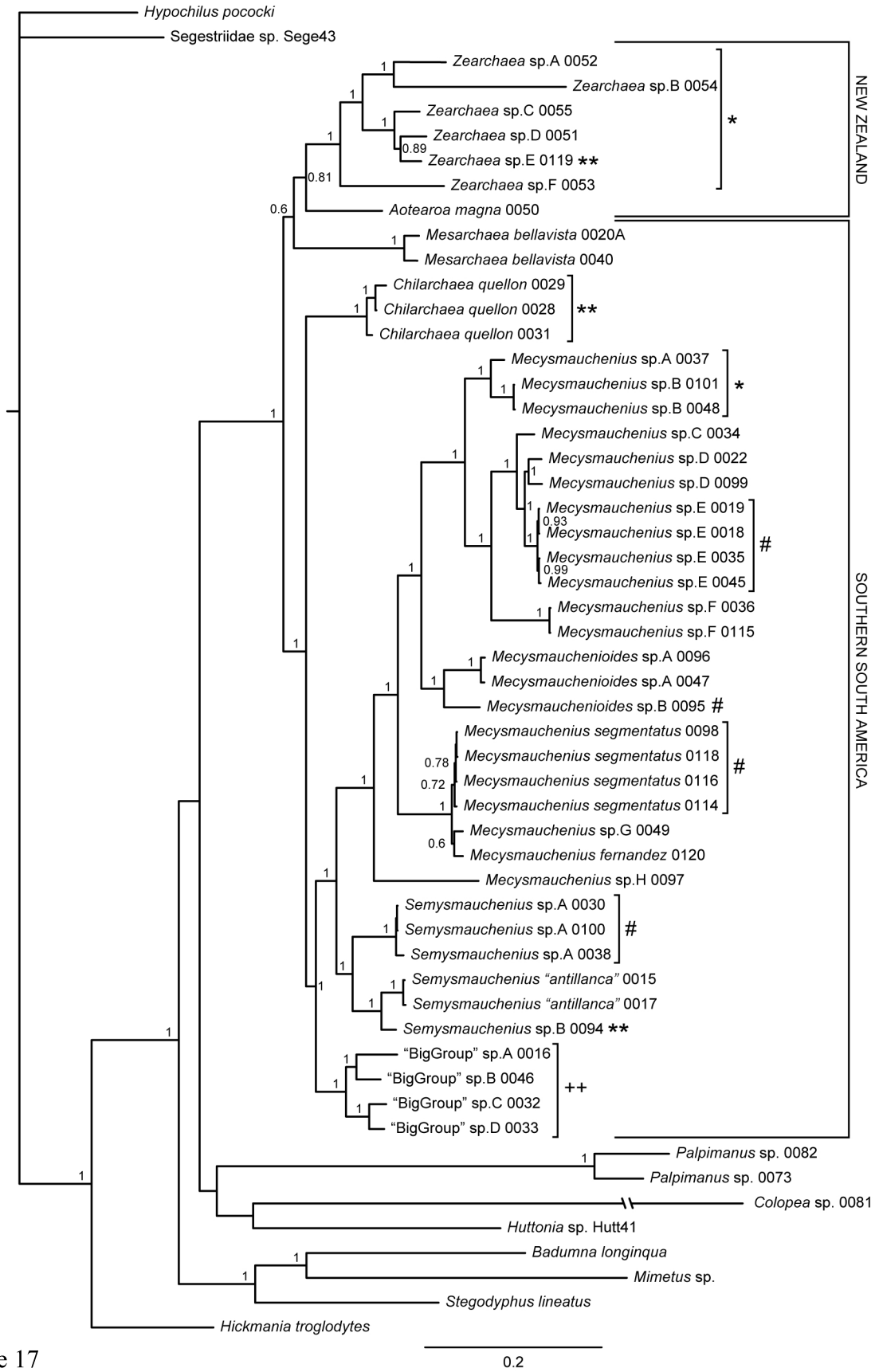
A. Madagascar + South Africa
-100 -80 -60 -40 -20 0
1 2 5 10 20
B. Madagascar
Time
-100 -80 -60 -40 -20 0
1 2 5 10
C. South Africa
-40 -30 -20 -10 0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Segestriidae sp. Sege43
Zearchaea sp.A 0052
Zearchaea sp.B 0054
Zearchaea sp.C 0055
Zearchaea sp.D 0051
Zearchaea sp.E 0119 **
Zearchaea sp.F 0053
Aotearoa magna 0050
Mesarchaea bellavista 0020A
Mesarchaea bellavista 0040
Chilarchaea quellon 0029
Chilarchaea quellon 0028
Chilarchaea quellon 0031
Mecysmauchenius sp.A 0037
Mecysmauchenius sp.B 0101
Mecysmauchenius sp.B 0048
Mecysmauchenius sp.C 0034
Mecysmauchenius sp.D 0022
Mecysmauchenius sp.D 0099
Mecysmauchenius sp.E 0019
Mecysmauchenius sp.E 0018
Mecysmauchenius sp.E 0035
Mecysmauchenius sp.E 0045
Mecysmauchenius sp.F 0036
Mecysmauchenius sp.F 0115
Mecysmauchenioides sp.A 0096
Mecysmauchenioides sp.A 0047
Mecysmauchenioides sp.B 0095 #
Mecysmauchenius segmentatus 0098
Mecysmauchenius segmentatus 0118
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Mecysmauchenius segmentatus 0114
Mecysmauchenius sp.G 0049
Mecysmauchenius fernandez 0120
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Semysmauchenius sp.A 0100
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Semysmauchenius "antillanca" 0017
Semysmauchenius sp.B 0094 **
"BigGroup" sp.A 0016
"BigGroup" sp.B 0046
"BigGroup" sp.C 0032
"BigGroup" sp.D 0033
Palpimanus sp. 0082
Palpimanus sp. 0073
Colopea sp. 0081
Huttonia sp. Hutt41
Badumna longinqua
Mimetus sp.
Stegodyphus lineatus
Hickmania troglodytes
NEW ZEALAND
SOUTHERN SOUTH AMERICA
0.2

Figure 17

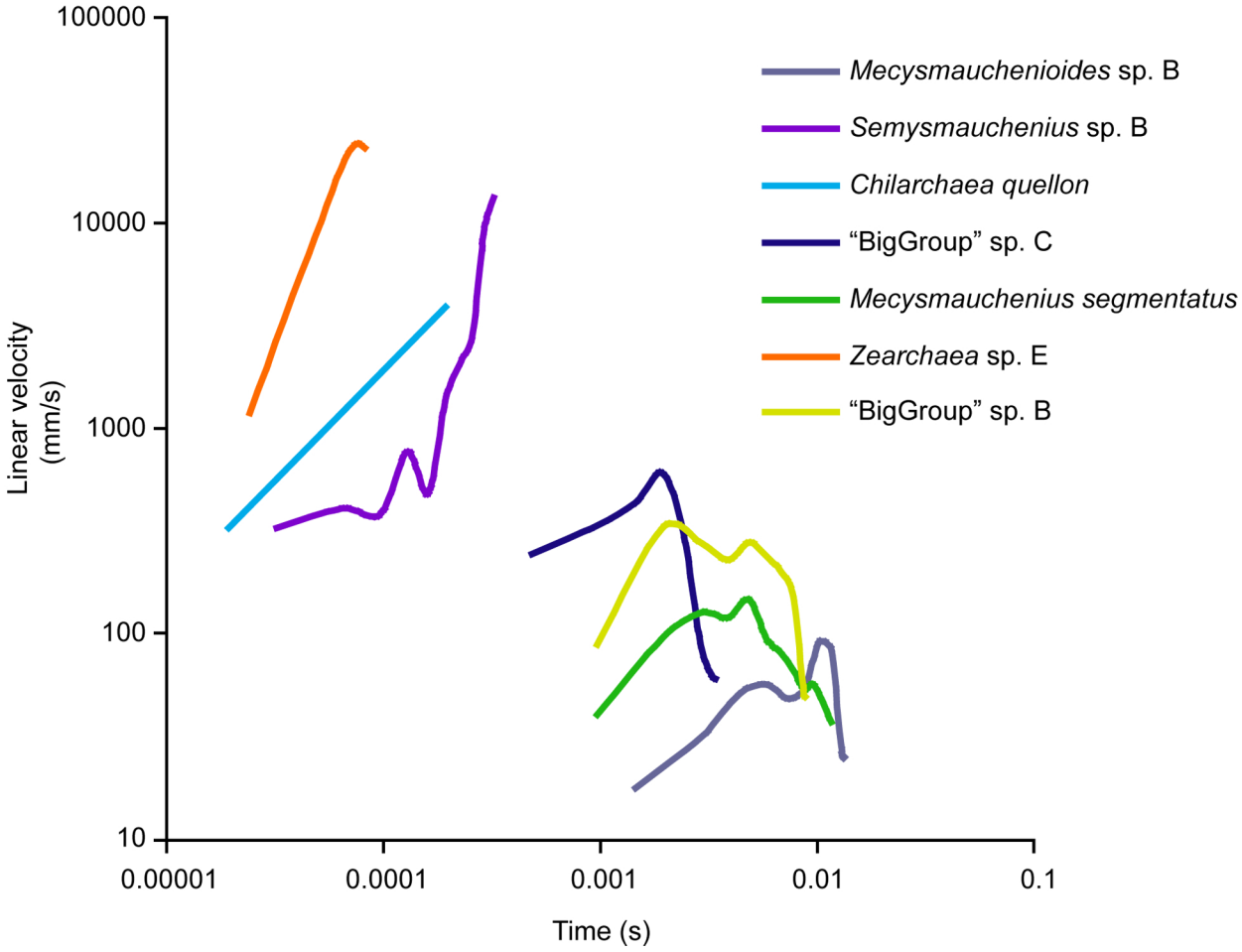
100000
10000
1000
100
10
Linear velocity (mm/s)
0.00001
0.0001
0.001
0.01
0.1
Time (s)
Mecysmauchenioides sp. B
Semysmauchenius sp. B
Chilarchaea quellon
"BigGroup" sp. C
Mecysmauchenius segmentatus
Zearchaea sp. E
"BigGroup" sp. B

Figure 18

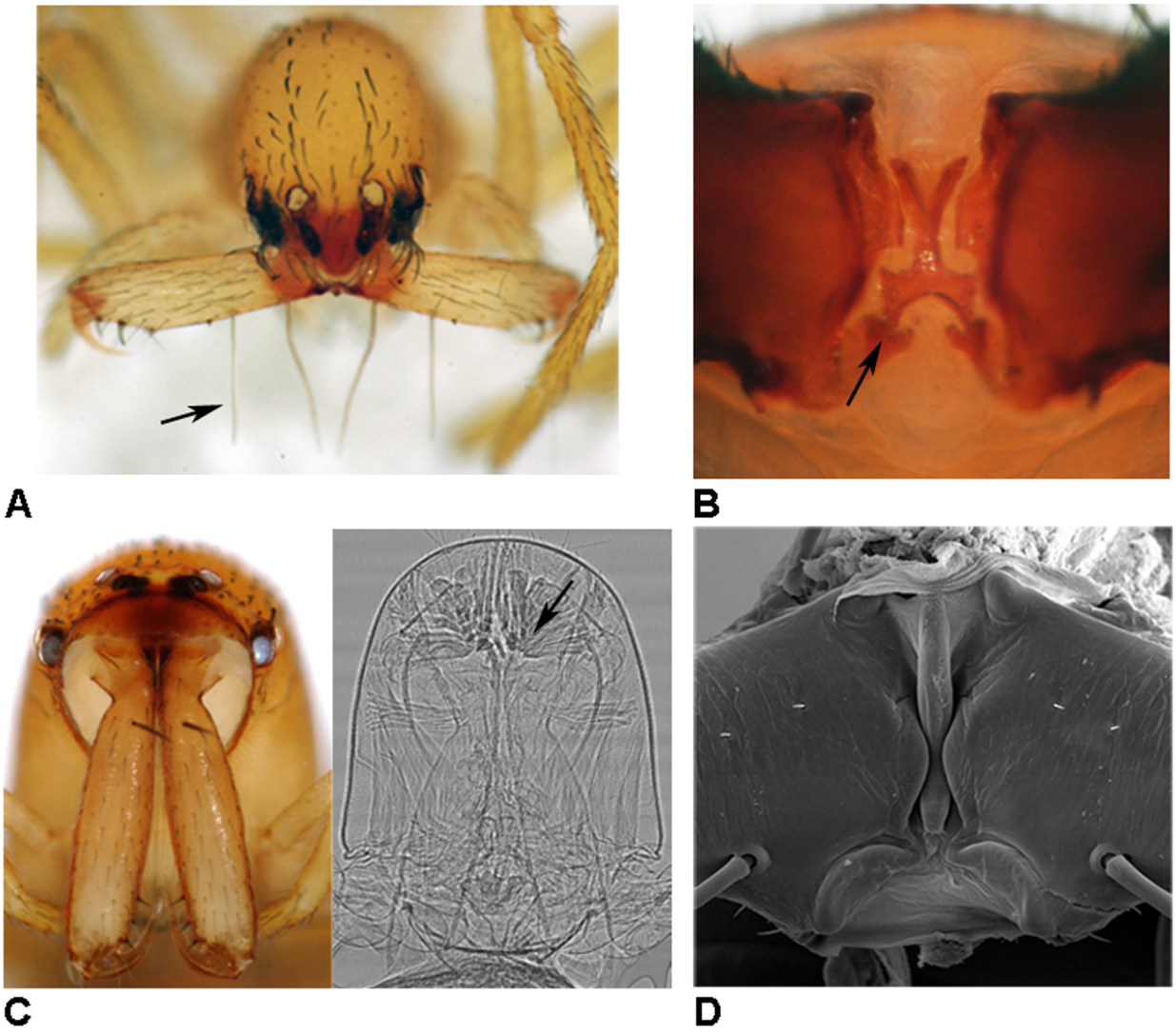

Figure 19

Appendix 1: Figure Legends

Figure 1. Lateral view, legs removed, images not to scale. A. *Hickmania troglodytes*, family Austrochilidae, typical spider body plan without distorted carapace; B. Pararchaeidae trap-jaw spider; C. *Palpimanus* sp., family Palpimanidae, arrow showing the sclerotized piece between the chelicerae and mouthparts; D. *Colopea* sp., family Stenochilidae; E. CT scan of archaeid fossil spider *Archaea paradoxa*; F. *Aotearoa magna*, a trap-jaw Mecysmaucheniidae; G. archaeid *Afrarchaea woodae*, a species with a short neck; H. archaeid "*Eriauchenius" gracilicollis*, the species with the longest neck.

Figure 2. Total evidence phylogram from Bayesian analysis of combined molecular and morphological data. Numbers at nodes represent posterior probabilities and only values greater than 0.50 are reported.

Figure 3. Phylogram from Bayesian analysis of concatenated molecular data. Numbers at nodes represent posterior probabilities.

Figure 4. Phylogram from Bayesian analysis of morphological data. Numbers at nodes represent posterior probabilities and only values greater than 0.50 are reported.

Figure 5. Single marker phylogram from Bayesian analysis of the molecular marker COI. Numbers at nodes represent posterior probabilities and only values greater than 0.50 are reported.

Figure 6. Single marker phylogram from Bayesian analysis of the molecular marker 18S. Numbers at nodes represent posterior probabilities and only values greater than 0.50 are reported.

Figure 7. Single marker phylogram from Bayesian analysis of the molecular marker 28S. Numbers at nodes represent posterior probabilities and only values greater than 0.50 are reported.

Figure 8. Single marker phylogram from Bayesian analysis of the molecular marker H3. Numbers at nodes represent posterior probabilities and only values greater than 0.50 are reported.

Figure 9. Morphological characters mapped onto the Bayesian total evidence phylogeny, using fast optimization in WinClada. Numbers above each circle are the character number (Appendix 1) and numbers below the circle are the character state. Black circles represent character states that are non-homoplasious synapomorphies.

Figure 10. Morphological characters mapped onto the Bayesian total evidence phylogeny for the Palpimanoidea taxa. Numbers above the circle are the character number and numbers below the circle are the character state. Black circles represent character states that are non-homoplasious synapomorphies. Branches without synapomorphies are considered collapsed.

Figure 11. Dated phylogeny with branch lengths drawn to reflect BEAST divergence age estimations. Error bars reflect the 95% highest posterior density interval (HPD). Numbers next to nodes refer to Tables 3 and 4 and an asterisk (*) next to the number signifies the posterior probability at that branch is less than 0.70. Scale = millions of years before present.

Figure 12. Ultrametric phylogeny with branch lengths drawn to reflect BEAST divergence age estimations used for biogeography analysis. 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 4. Arrows represent a range expansion or dispersal. The black arrow represents a dispersal event from one area to another when those two areas were isolated from each other. Grey arrows represent a dispersal or range expansion event that occurred during a geological time when the two areas were a contiguous part of Pangaea. Numbers next to nodes follow Tables 3 and 4 and an asterisk (*) next to the number signifies the posterior probability at that branch is less than 0.70.

Figure 13. Phylogeny from Bayesian analysis of concatenated molecular data for only the outgroup taxa. Numbers at nodes represent posterior probabilities.

Figure 14. Phylogeny from Bayesian analysis of concatenated molecular data for the archaeid spiders. Numbers at nodes represent posterior probabilities and only values greater than 0.70 are reported. Species names in parentheses are identified based on locality; the type specimens still need to be examined.

Figure 15. Dated phylogeny with branch lengths drawn to reflect BEAST divergence age estimation. Error bars reflect the 95% highest posterior density interval (HPD). Numbers next to node follow the discussion in the text. Scale at bottom = millions of years before present.

Figure 16. Lineage through time plots for A. the combined Madagascan and South African genera; B. only the Madagascan genera; C. only the South African genus. X-axis is millions of years before present.

Figure 17. Phylogeny from Bayesian analysis of concatenated molecular data. Numbers at nodes represent posterior probabilities and only values greater than 0.60 are reported. ** marks lineages that have evolved a rapid-inertia-based trap-jaw mechanism. * marks lineages which, based on morphology, we predict may have evolved a rapid-inertia-based mechanism. # marks lineages that have muscular-based trap-jaw movements. ++ marks the “BigGroup” that seems to have muscular-based jaw movements but the “inter-jaw pivot” still interacts with the jaw bases.

Figure 18. Logarithmically scaled graph showing linear velocity versus time of the jaw movements for a high-speed video recording selected for the lineages shown. Ripples in the graph lines likely are due to measurement error. Note peak finishing velocity in lineages with a rapid-inertia-based trap-jaw mechanism and decrease in velocity in lineages that have muscular-based trap-jaw movements.

Figure 19. A. Dorsal view of *Chilarchaea quellon* carapace and jaws, preserved specimen with jaws manually locked open, arrow to trigger hair. B. The “inter-jaw pivot” in the “BigGroup”

that is positioned between the jaw bases, arrow marking a portion of the pivot that seems to interact with the jaw base. C. Anterior view of *Zearchaea* sp., image on left is in same orientation as image on right, which is an X-ray image showing internal structures, arrow marks the location where a thick bundle of tendon-like structures likely used to store energy attaches to the jaw base. D. Scanning electron micrograph of the jaw bases of *Chilarchaea quellon* that are locked open by the "inter-jaw pivot," two trigger-hair bases are visible in the image.

Appendix 2: Morphological characters

There are a total of 126 morphological characters used in the phylogenetic analysis. Inapplicable characters are coded (–) and data missing for characters are coded (?). Characters that are new or newly interpreted are discussed in detail; others are referenced to their original sources.

SOMATIC CHARACTERS

1. Organized pairs of spines on carapace: absent, no carapace spines (0); two pairs (1); three pairs (2); four pairs (3); greater than four pairs, or in triplets (4). Mecysmaucheniids and archaeids have pairs of spines on their carapace that are very consistent in their placement and number. These also occur in *Mimetus* although these are more numerous and may be in triplets.
2. Spine next to lateral eyes: absent, no spines (0); one pair (1); two pairs (2). This character occurs in mecysmaucheniids, archaeids and *Mimetus*.
3. Anterior median eyes (AME): present (0); absent (1).
4. AME larger than all other eyes: no, AME equal to or smaller than (0); yes (1).
5. AME on tubercle: no (0); yes (1). The AME in archaeids are on a large tubercle.
6. Relative distance between median eyes: distance between AME less than distance between posterior median eyes (PME) (0); distance between PME less than distance between AME (1); AME-AME and PME-PME equal (2).
7. Tapetum: primitive (0); canoe shaped (1); grate shaped (2); absent (3). (Griswold *et al*., 2005 character 47).
8. PME shape: round (0); elongated (1).
9. Carapace texture: smooth (0); scales (1); tuberculate (2); fingerprint (3); pitted (4).
10. Foramen around cheliceral bases: absent (0); present (1). In pararchaeids, archaeids, mecysmaucheniids, *Palpimanus*, and *Colopea* the jaw bases are surrounded by sclerotized cuticle.
11. Foramen seam posterior to chelicerae: rebordered (0); smooth (1); seam not completely fused (2); thickened (3). This character is only applicable for taxa scored as present for character 10 and deals with the nature of the foramen seam.
12. Foramen formed around cheliceral bases: formed from intercoxal sclerites (0); formed from carapace (1). This character is only applicable for taxa scored as present for character 10 and records whether the foramen is formed from an extension of the carapace or from intercoxal sclerites.
13. Fovea: absent (0); present (1).
14. Posterior sternum tubercle: absent, posterior of sternum flat or evenly convex (0); mound (1); tubercle (2); 2 tubercles (3). In mecysmaucheniids and *Araneus* there is a mound at the posterior edge of the sternum. In extant archaeids there is a single tubercle and in *Palpimanus* there are two.
15. Sternum border: absent (0); present (1). In several of the taxa in this study the edge of the sternum has a different texture and thickness than the rest of the sternum.
16. Chilum: absent (0); divided, bilateral (1); single, median (2). (Griswold *et al.*, 2005 character 46)
17. Shape of sclerite between cheliceral bases: reduced rod (0); thick rod that interacts with cheliceral bases to produce a trap-jaw mechanism (1); triangular (2); tear-drop shaped (3); fused to cheliceral bases to produce trap-jaw mechanism (4); two tear-drop shapes pointing toward each other (5). The shape of the sclerite between the jaw bases is variable among spider families.

In pararcheids and mecysmaucheniids this sclerite interacts with the jaw bases to produce a trap-jaw mechanism, but the mechanism is different in each family.
18. Additional rectangular sclerite beneath cheliceral base sclerite: absent (0); present (1). In archaeids and *Zearchaea* there is a triangular sclerite between the jaw bases, character 17, state 2. In archaeids there an additional rectangular sclerite beneath the triangular sclerite.
19. Clypeal hood: absent (0); present (1). (Griswold *et al.*, 2005 character 30).
20. Lateral labral spurs, two protrusions posterior to labral tongue: absent (0); present (1). Noted by Platnick & Forster (1984) as "lateral protuberances found on the labrum." This was scored as present in archaeids and mecysmaucheniids, but also in *Palpimanus* and *Colopea* where the lateral spurs are small and collapsed in SEM preparations. Our expanded interpretation differs from that of Platnick *et al.* (1991) character 49, where lateral labral protuberances were scored only for archaeids and mecysmaucheniids. See Fig. 93 of Miller, Griswold & Yin (2009) for images of the labral tongue and spurs.
21. Labium distal edge: straight to rounded (0); with narrow v-shaped notch (1); with shallow wide notch (2). Archaeids, *Mecysmauchenis*, *Palpimanus*, and *Dysdera* have a very narrow notch at the distal edge of the labium.
22. Posterior dorsal edge of pedicle with two elongations greatly extending into abdomen: absent (0); present (1). The posterior part of the pedicle (lorum 2) has two elongations that extend into the abdomen (Wilson, 1965). These elongations of the pedicle are pronounced in *Dysdera* and *Loxosceles*, and are extreme in *Palpimanus* and *Colopea*.
23. Pars cephalica shape: unelevated (0); elevated (1). (Platnick *et al*. 1991 character 21; Griswold *et al.* 2005 character 31).
24. Raised cephalic area shape: tubular (0); constricted to form "neck" (1). Only applicable if character 23 is scored as present. This is present in archaeids and *Mesarchaea*: the most distal portion of the elevated cephalic area is wider than the stalk, creating a neck-like appearance.
25. Posterior edge of raised cephalic area shape is: flat (0); rounded out (1). Only applicable if character 24 is scored as present. This character refers to the posterior part of the cephalic area that is distal to the constriction, which is rounded out in *Mesarchaea* and some archaeids.
26. Endite length: less than half the carapace length (0); at least half the carapace length (1). Fossil archaeids have very long endites whereas extant archaeids that have shorter endites. Correlated with elongate endites are cheliceral stridulatory ridges being more basal than in extant archaeids. These features are correlated because in taxa with elongated endites the pedipalps and chelicerae are at different orientations and the pedipalps come in contact with the stridulatory ridges on the chelicerae.
27. Shape of posterior edge of carapace: gradually tapering off (0); flattened (1). In archaeids and *Palpimanus* the posterior edge of the carapace is truncated. This is best seen in the lateral view. In most spiders the carapace gradually tapers off.

LEG CHARACTERS
28. Dorsal basal portion of tarsus 1: similar to rest of segment (0); with basal area of membranous or folded cuticle (1). Some modification of metatarsal cuticle appears to be present in all Palpimanoidea spiders. This interpretation differs from that of Platnick *et al.* 1991 character 50, which considered only the membranous ring encircling tarsus 1 as a synapomorphy for archaeids and mecysmaucheniids.
29. Type of modification on tarsus 1: large membranous bulge (0); membranous ring around tarsus (1); cuticular foldings (2). Modifications occur at the same place on the tarsus in

Palpimanoidea and are coded as homologous. In *Colopea* and *Huttonia* there is a membranous tubercle that collapses when the leg is critically point dried. In *Palpimanus* there are foldings in the cuticle. In archaeids and mecysmaucheniids there is a membranous ring encircling the tarsus, previously noted by Forster and Platnick (1984).
30. Leg 3 metatarsus apical ventral setae: similar to other segment setae (0); distinct brush of setae different to setae on remainder of leg (1); comb of one row of setae (2); spines (3). Considered a preening comb (character 19) in Griswold *et al.* (2005), here we expand the definition to include a brush of setae as well as a comb. Only *Huttonia* has a comb (state 2), while *Kukulcania* and *Stegodyphus* have spines and archaeids, mecysmaucheniids, *Dysdera*, *Palpimanus*, and *Colopea* have a brush of setae.
31.Tarsal organ: exposed (0); capsulate (1). (Platnick *et al*. 1991 character 65; Griswold *et al.* 2005 character 2).
32. Shape of exposed tarsal organ: flat plate (0); with greatly elongated sensilla (1). Mecysmaucheniids have a uniquely shaped tarsal organ with long sensilla.
33. Femur 4 shape: straight (0); with bend (1). The bent fumur 4 is present in most archaeid taxa with the exception of some fossil archaeids.
34. Dorsal surface of femora: smooth (0); with prominent bump (1). This bump is present in all archaeids.
35. Scopulae on leg 1: absent (0); present (1).
36. Scopulae leg 1 position: large prolateral group (0); prolateral row (1); one prolateral and one retrolateral row (2).
37. Scopulae on leg 2: absent (0); present (1).
38. Patella and tibia juncture on leg 4: straight (0); bent, patella-tibia joint hyperextended (1). In archaeids the patella-tibia joint is hyperextended in leg 4.
39. Relative length of patella and tarsus 1: patella shorter than tarsus (0); patella longer than or equal to tarsus (1).
40. Relative shape and size of the superior tarsal claws (STC) 1 and 4: the same (0); STC 1 with many long teeth, like a comb; STC 4 with fewer teeth that are short and more widely spaced (1); STC 1 smaller than STC 4 (2). In *Palpimanus*, *Huttonia*, *Colopea*, and mecysmaucheniids STC 1 are noticeably smaller than STC 4. In mecysmaucheniids and archaeids STC 1 are shaped differently than STC 4.
41. Tarsal claws: two (0); three (1). (Griswold *et al.* 2005 character 12)
42. Claw tufts: absent (0); present (1). (Griswold *et al.* 2005 character 13)
43. Trochanter distal margin: entire (0); deeply notched (1). (Griswold *et al.* 2005 character 11)
44. Tarsal trichobothria: absent (0); present (1). (Griswold *et al.* 2005 character 3)
45. Tarsal trichobothria rows: one row (0); two or more rows (1). (Griswold *et al.* 2005 character 4)
46. Metatarsal trichobothria: one (0); two (1); three or more (2). (Griswold *et al.* 2005 character 5)
47. Serrate accessory claw setae: absent (0); present (1). (Griswold *et al.* 2005 character 14)
48. Leg cuticle texture: fingerprint (0); squamate (1); smooth (2). (Griswold *et al.* 2005 character 10)
49. Leg hair type: plumose (0); serrate (1). (Griswold *et al.* 2005 character 17)
50. Trichobothrial base hood and texture: hood absent (0); smooth or same as leg texture (1); with transverse ridges (2). (Griswold *et al.* 2005 character 8)

51. Reduced leg spination: no (0); yes, with spines absent or limited to a few scattered examples (1). (Griswold *et al.* 2005 character 21)

CHELICERAE CHARACTERS

52. Chelicerae anterior surface: smooth (0); with spine or protuberance (1). *Mimetus*, mecysmaucheniids and the extant archaeids have spines or protuberances on the anterior of the chelicerae.
53. Cheliceral modification in females: spine (0); bump (1).
54. Cheliceral modification in males: same as female (0); a brush of setae (1). In some taxa that have an anterior cheliceral modification, the males, unlike females, have a brush of setae. This is the case for *Austrarchaea* and *Chilarchaea*.
55. Basal edge of chelicerae: parallel (0); splayed out (1). In *Holarchaea*, mecysmaucheniids and archaeids the basal edge of the chelicerae fans outward making the muscle attachment sites larger.
56. Cheliceral trigger hairs: absent (0); present (1). These are long modified setae with a modified base that are only found in the trap-jaw spiders Pararchaeidae and Mecysmaucheniidae. Stimulation of these setae causes the chelicerae to snap closed.
57. Trigger hairs distribution on chelicerae: scattered throughout the interior lateral side (0); in one evenly spaced row (1). In *Pararchaea*, unlike the mecysmaucheniids, the trigger hairs are scattered throughout the interior lateral side of the chelicerae.
58. Peg teeth: absent (0); present (1). (Platnick *et al.* 1991 character 19)
59. Peg teeth distribution on chelicerae: limited only to promargins (0); with some peg teeth on retromargin (1). In some of the taxa with peg teeth these may occur posterior to the area where the fang closes (the retromargin).
60. Two peg teeth in first row: absent (0); present (1). In archaeids and *Huttonia* there is an additional row of two peg teeth.
61. Thickened setae at fang base: absent, setae uniform (0); present, with a larger seta at fang base (1). (Griswold *et al.* 2005 character 34)
62. Stridulatory striae on chelicerae: absent, surface smooth (0); present (1). (Griswold *et al.* 2005 character 45)
63. Texture of stridulatory striae (in males): uniform and densly spaced fingerprint ridges (0); widely spaced uniform ridges (1); widely spaced heterogeneous ridges (2); rounded bumps (3); uneven small ridges (4).
64. Shape of chelicerae distad of stridulatory ridges: straight (0); curved toward posterior (1). The distal portion of the chelicerae are curved to posterior only in extant archaeids.
65. Peg teeth shape: straight, tapering, smooth (0); straight, blunt, textured (1); curved, tapering, textured.
66. Promarginal row of peg teeth: uniform lengths (0); with different lengths (1).
67. Gland mound: absent (0); present (1). Like Griswold *et al*. (2005) character 42, we scored *Mimetus* as absent for this trait. We also differed from this and previous assessments in scoring our pararchaeid exemplar as absent for this trait. The voucher specimen for the morphological data was a *Pararchaea* from Mount Bartle Frere in Australia: in this specimen there was a ridged spur adjacent to the keel (see Fig 227 and 230 of Forster & Platnick, 1984), but there was no associated gland mound with pores.
68. Cuticle adjacent to cheliceral gland mound: flat (0); with deep groove (1). In archaeids there is a deep groove immediately adjacent to the gland mound.

69. Cheliceral boss: absent (0); present (1). (Griswold *et al.* 2005 character 43)
70. Cheliceral chela: absent (0); present (1). (Griswold *et al.* 2005 character 40)
71. Cheliceral basal fusion: free (0); fused (1). (Griswold *et al.* 2005 character 38)
72. Cheliceral diastema: absent (0); present (1). We scored this character as present for *Palpimanus* and *Colopea* because these taxa have a sclerotized piece or pieces between the endites and the chelicerae, see character 10.

ABDOMEN CHARACTERS
73. Abdomen shape: smoothly curved (0); with tubercles (1). Several archaeid taxa have tubercles on the abdomen.
74. Abdomen tubercles placement: in pairs (0); singular (1).
75. Posterior respitory system: pair of normal booklungs (0); pair of reduced booklungs (1); pair of tracheae or modifications thereof (2). Following Platnick *et al*. 1991 character 16, which doesn't differentiate between lateral and median tracheae, archaeids are scored as state 2. Kukulcania is scored as having reduced booklungs, state 1, following Griswold *et al*, 2005.
76. Posterior spiracle: single (0); double (1). (Griswold *et al.* 2005 character 60)
77. Dorsal abdominal sclerite on male: absent (0); present (1). This is seen in some archaeids and our gnaphosid exemplar.
78. Epiandrous spigots: absent (0); present (1). (Griswold *et al.* 2005 character 66)
79. Posterior spinnerets: medians developed, laterals about as large as anterior laterals (0); very reduced (1). The posterior spinnerets are very reduced in *Palpimanus*, *Colopea* and the mecysmaucheniids, with the spigots either arising directly from the abdominal cuticle or from highly reduced spinnerets.
80. Spigot base texture: fingerprint (0); smooth (1); scaley (2). Modified from Griswold *et al*. 2005 character 69.
81. Sclerotization around anterior of abdomen: absent (0); present (1).
82. Modification of sclerotization around anterior of abdomen in females: dorsal and ventral sclerites separate (1); dorsal and ventral sclerites fused (2); only ventral plate present, dorsal plate absent (3).
83. Abdomen with folds: absent (0); present (1). This character is present in all archaeids and is discussed by Forster & Platnick (1984). This trait is especially apparent in the fossil taxa, but is also apparent in living taxa, particularly specimens with shrunken abdomens.
84. Abdomen cuticle highly wrinkled when critically point dried: absent (0); present (1). This feature is imaged in Forster & Platnick (1984, fig 41) but not discussed. In several taxa in this study the abdomen is peculiarly wrinkled when prepared for SEM imaging by critical point drying.
85. Spinnerets projected on conical tubercle: absent (0); present (1). The spinnerets arise from a conical tubercle in archaeids.

FEMALE PEDIPALP CHARACTERS
86. Brush of hairs on female palpal tarsus (also on male cymbium): absent (0); present (1). We score this as present if there is a brush on the male cymbium.
87. Placement of palpal brush on tarsus: on prolateral side (0); on retrolateral side (1).
88. Picks on palpal femur: absent (0); at least one cusp present (1). These picks likely come in contact with the stridulatory file on the chelicerae.
89. Prolateral spines on female palp tarsus: absent (0); present (1).

90. Placement of female palp spines: scattered (0); one row (1). In mecysmaucheniids the tarsal spines on the palp are in one row.
91. Female palp claw: absent (0); present (1); very reduced, e.g., only a nubbin (2). Modified from Platnick *et al*. 1991 character 37.

FEMALE GENITALIC CHARACTERS
92.Female genitalia: haplogyne (0); entelegyne (1).
93. Female sclerotized genital plate (FSGP): absent (0); present (1). See Wood, 2008 pg. 259 for description of this character.
94. FSGP with wings: absent (0); present (1). See Wood, 2008 pg. 259 for description of this character.
95. FSGP with keel: absent (0); present (1). The FSGP in *Afrarchaea* has a keel, see Fig. 58 in Forster & Platnick, 1984.
96. Membranous sacs (receptaculae) originating from bursa: absent (0); present (1). *Hickmania* and all Palpimanoidea families are scored present for this character, although this character is absent in the African and Malagasy archaeids, see Figs. 66-69, 210-211, 295-299 of Forster & Platnick, 1984.
97. Distribution of bursal membranous sacs: dispersed evenly all over bursa (0); clustered and originating from one or two openings on the bursa (1). In *Austrarchaea* and some mecysmaucheniids the genitalic membranous sacs are dispersed over the bursa. In the remaining Palpimanoidea these sacs are clustered. Although this character isn't broken down further, it is important to note that only in the New Zealand mecysmaucheniids (*Aotearoa* and *Zearchaea*) does this cluster join to the center of the bursa, whereas in other palpimanoids, e.g., *Huttonia*, *Colopea*, and *Palpimanus*, these clusters originate from the lateral sides of the bursa.
98. Membraneous sac shape: large sacs sessile, not on stalks (0); sacs on long stalks (1). Compare Figs. 210-211 with Figs. 66-69 in Forster & Platnick, 1984. Only in the *Austrarchaea* and *Colopea* are the genitalic membranous sacs sessile.

MALE GENITALIC CHARACTERS
99. Fusion of tegulum and subtegulum,: absent, tegulum and subtegulum free (0); fused, bulb piriform (1). (Griswold *et al.* 2005 character 114)
100. Pedipalp rotated with cymbium prolateral and bulb retrolateral: absent (0); present (1). See Griswold *et al.* (1998) character 2 for a discussion of this character.
101. Conductor: absent (0); present (1). (Griswold *et al.* 2005 character 118)
102. Conductor shape: conductor separate from embolus (0); conductor embraces embolus (1). (Griswold *et al.* 2005 character 120)
103. Median apophysis: absent (0); present (1). (Griswold *et al*. 2005 character 123)
104. Palpal tarsus M30 muscle: absent (0); present (1). (Griswold *et al.* 2005 character 129)
105. Palpal tarsus M29 muscle: absent (0); present (1). (Griswold *et al.* 2005 character 128)
106. Paracymbium: absent (0); present (1). The paracymbium in this study was treated as any type of apophysis on the retrolateral side of the cymbium. (Griswold *et al.* 2005 character 112)
107. Shape of paracymbium: protrusion with thick spine or setae (0); cluster of long setae not on protrusion (1); long curved apophysis (2). The taxa in this study have different types of paracymbium.
108. Retrolateral apophysis on femur: absent (0); present (1).
109. Retrolateral apophysis on patella: absent (0); present (1).

110. Retrolateral apophysis on tibia (RTA): absent (0); present (1). (Griswold *et al.* 2005 character 105)
111. Shape of RTA: protrusion at distal edge (0); protrusion with thick seta (1); many thick setae not on protrusion (2); complex, 2 to 4 processes (3).
112. Palpal tegulum: entire, surface smooth (0); with sulcus (1). Mecysmaucheniid spiders have a characteristic sulcus that divides the tegulum. This trait was also observed in *Austrarchaea* by Forster & Platnick (1984). In this study *Austrarchaea* was coded as absent for this character because the tegular shapes and the placement of the sulcus is different between mecysmaucheniids and archaeids.
113. Shape of bulb apex: various (0); with a dark ridged spiral forming a conductor (1). Most archaeids have a dark ridged spiral at the apex of the bulb, which has been scored as the "conductor" (Griswold *et al.* 2005 fig. 168D).
114. Palpal bulb expands distally: no (0); yes (1). In all spiders in this study the palp bulb expands basally, close to the attachment to the cymbium. Yet, only in some taxa does the bulb also expand distally, with membranous tissue ballooning out at the apex of the bulb. This is a character unique to the Palpimanoidea, although *Araneus* was also coded as present for this character since distal parts of the araneid bulb have moveable joints.

SPINNERET CHARACTERS
115. Cribellum: absent (0); present (1). (Griswold *et al.* 2005 character 71).
116. Cribellum organization: entire (0); divided (1). (Griswold *et al.* 2005 character 72).
117. Cribellate spigots: strobilate (0); claviform (1). (Griswold *et al.* 2005 character 74).
118. Posterior median spinnerets (PMS) paracribellar spigots in females: absent (0); present (1). (Griswold *et al.* 2005 character 88).
119. PMS paracribellar gland spigots in male: absent (0); present (1). (Griswold *et al.* 2005 character 89).
120. Posterior lateral spinnerets (PLS) paracribellar in females: absent (0); present (1). (Griswold *et al.* 2005 character 99).
121. PLS modified spigot: absent (0); present (1). (Griswold *et al.* 2005 character 96).
122. ALS major ampullate gland spigot (MAP) field separated by furrow: absent (0); present (1). This character was difficult to score because it seems to be continuous. (Griswold *et al.* 2005 character 77).
123. ALS segment number: three (0); two (1). (Griswold *et al.* 2005 character 75).
124. Tartipores: absent (0); present (1). (Platnick *et al.* 1991 character 63).
125. PMS minor ampullate gland spigot (mAP) postion: median to anterior (0); posterior (1); absent (2). (Griswold *et al.* 2005 character 83).
126. Cylindrical gland spigots: absent (0); present (1). (Platnick *et al.* 1991 character 23).

Appendix 3. Morphological character matrix. Terminals scored with more than one state are coded as: a=(0&1); b=(1&2).

	1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4 5 5 5 5 5 5 5 5 5 5 6 6 6 6 6 6 6 6 6 6 7
Character	1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0
Hypochilus pococki	0 0 0 0 0 0 0 0 0 0 - - 1 0 0 0 0 0 0 0 0 0 0 - - 0 0 0 - 0 0 0 0 0 0 - - 0 0 0 1 0 0 0 - 0 0 0 0 1 1 0 - - 0 0 - 0 - - 0 0 - 0 - - 0 0 0 0
Hickmania troglodytes	0 0 0 0 0 0 0 0 0 0 - - 1 0 0 0 0 0 1 0 2 0 0 - - 0 0 0 - 0 0 0 0 0 0 - - 0 0 0 1 0 0 0 - 0 1 0 0 1 0 0 - - 0 0 - 0 - - 1 1 3 0 - - 0 0 0 0
Lycosidae *sp*	0 0 0 0 0 0 2 0 3 0 - - 1 0 0 1 0 0 0 0 0 0 0 - - 0 0 0 - 0 1 - 0 0 0 - - 0 0 0 1 0 1 1 1 2 0 0 1 1 0 0 - - 0 0 - 0 - - 1 0 - 0 - - 0 0 1 0
Araneus sp	0 0 0 0 0 1 1 0 1 0 - - 1 1 0 1 0 0 0 0 0 0 0 - - 0 0 0 - 0 1 - 0 0 0 - - 0 1 0 1 0 1 0 - 0 1 1 1 0 0 0 - - 0 0 - 0 - - 0 0 - 0 - - 0 0 1 0
Badumna longinqua	0 0 0 1 0 0 1 0 3 0 - - 1 0 0 1 0 0 0 0 0 0 0 - - 0 0 0 - 0 1 - 0 0 0 - - 0 1 0 1 0 0 1 0 2 0 0 0 1 0 0 - - 0 0 - 0 - - 0 0 - 0 - - 0 0 1 0
Dysdera sp	0 0 1 - - - 0 0 0 0 - - 0 0 1 2 0 0 0 0 1 1 0 - - 0 0 0 - 1 0 0 0 0 0 - - 0 1 0 0 1 0 0 - 0 0 0 0 0 0 0 - - 0 0 - 0 - - 0 0 - 0 - - 0 0 0 0
Holarchaea sp	0 0 0 0 0 0 ? 0 4 0 - - 0 0 0 0 - 0 1 0 0 0 0 - - 0 0 0 - 0 1 - 0 0 0 - - 1 0 0 1 0 0 0 - 0 1 1 a 1 0 0 - - 1 0 - 0 - - 0 0 - 0 - - 1 0 0 0
Kukulcania hibernalis	0 0 0 0 0 0 0 1 0 0 - - 1 0 0 0 0 0 0 0 0 0 0 - - 0 0 0 - 2 1 - 0 0 0 - - 0 0 0 1 0 0 0 - 2 0 2 0 0 0 0 - - 0 0 - 0 - - 0 0 - 0 - - 0 0 0 1
Loxosceles sp	0 0 1 - - - 0 0 0 0 - - 1 0 0 0 0 0 0 0 0 1 0 - - 0 0 0 - 0 0 0 0 0 0 - - 0 0 0 0 0 0 0 - 0 0 2 a 2 1 0 - - 0 0 - 0 - - 0 1 4 0 - - 0 0 0 1
Mimetus sp	4 2 0 1 0 1 1 0 1 0 - - 1 0 0 0 0 0 0 0 0 0 0 - - 0 0 0 - 0 1 - 0 0 0 - - 0 0 0 1 0 0 0 - 0 1 1 1 0 0 1 0 0 0 0 - 1 0 0 0 0 - 0 0 0 0 0 0 0
Pararchaeidae *sp*	0 0 0 0 0 0 1 0 1 1 2 1 0 0 0 0 4 0 0 0 0 0 1 0 - 0 0 0 - 0 1 - 0 0 0 - - 0 0 0 1 0 0 0 - 0 1 1 1 1 1 0 - - 0 1 0 1 0 0 0 0 - 0 1 0 0 0 0 0
Stegodyphus sp	0 0 0 0 0 0 3 0 0 0 - - 0 0 0 0 3 0 1 0 0 0 0 - - 0 0 0 - 2 1 - 0 0 0 - - 0 1 0 1 0 0 0 - 0 0 2 0 2 1 0 - - 0 0 - 0 - - 0 0 - 0 - - 0 0 1 0
Uroctea sp	0 0 0 1 0 0 0 0 0 0 - - 1 0 0 0 0 0 0 0 0 0 0 - - 0 0 0 - 0 1 - 0 0 0 - - 0 1 0 1 0 0 0 - 0 0 2 0 1 0 0 - - 0 0 - 0 - - 0 0 - 0 - - 0 0 0 0
Gnaphosidae *sp*	0 0 0 0 0 2 1 0 0 0 - - 1 0 0 2 5 0 1 0 0 0 0 - - 0 0 0 - 0 1 - 0 0 1 2 1 0 1 0 0 0 0 1 1 2 0 2 0 1 0 0 - - 0 0 - 0 - - 0 0 - 0 - - 0 0 1 0
Palpimanus sp	0 0 0 1 0 0 1 0 2 1 3 0 1 3 1 0 0 0 0 1 1 1 0 - - 0 1 1 2 1 1 - 0 0 1 0 0 0 1 2 a a 0 0 - 0 0 0 0 2 1 0 - - 0 0 - 1 0 0 0 1 0 0 0 - 1 0 0 0
Colopea sp	0 0 0 1 0 0 1 1 2 1 2 0 1 0 1 0 0 0 0 1 0 1 0 - - 0 0 1 0 1 0 0 0 0 1 0 1 0 1 2 a 0 0 0 - 0 0 0 0 2 1 0 - - 0 0 - 0 - - 0 1 0 0 - - 1 0 0 0
Huttonia sp	0 0 0 1 0 0 1 0 1 0 - - 0 0 1 0 0 0 0 0 0 0 0 - - 0 0 1 0 3 1 - 0 0 1 2 1 0 1 b 1 0 0 0 - 0 0 a 0 2 1 0 - - 0 0 - 1 1 1 0 1 1 0 1 0 1 0 0 0
Aotearoa magna	1 2 0 0 0 0 1 0 1 1 1 1 0 1 1 0 1 0 1 1 ? 0 1 0 - 0 0 1 1 1 0 1 0 0 0 - - 0 1 b 1 0 0 0 - 0 ? ? 0 ? 1 1 0 0 1 1 1 1 1 0 0 1 0 0 1 1 1 0 0 0
Mesarchaea bellavista	1 2 1 - - - 1 0 b 1 1 1 0 1 1 0 1 0 1 1 0 0 1 1 1 0 0 1 1 1 0 1 0 0 0 - - 0 1 b 1 0 0 0 - 0 ? ? 0 ? 1 1 0 0 1 1 1 1 1 0 0 1 1 0 1 1 1 0 0 0
Mecysmauchenius segmentatus	0 0 1 - - - 1 0 1 1 1 1 0 1 1 0 1 0 1 1 1 0 1 0 - 0 0 1 1 1 0 1 0 0 0 - - 0 1 b 1 0 0 0 - 0 0 a 0 2 1 1 0 0 1 1 1 1 1 0 0 1 2 0 1 1 1 0 0 0
Chilarchaea quellon	0 0 1 - - - 1 0 1 1 1 1 0 1 1 0 1 0 1 1 0 0 1 0 - 0 0 1 1 1 0 1 0 0 0 - - 0 1 b 1 0 0 0 - 0 0 a 0 1 1 1 0 1 1 1 1 1 1 0 0 1 2 0 b - 1 0 0 0
Zearchaea sp	2 2 0 0 0 0 1 0 1 1 1 1 0 1 1 0 b 0 1 1 0 0 1 0 - 0 0 1 1 1 0 1 0 0 0 - - 0 1 b 1 0 0 0 - 0 0 a 0 2 1 1 0 0 1 1 1 1 0 0 0 1 0 0 0 0 1 0 0 0
Eriauchenius lavatenda	2 1 0 1 1 1 1 0 2 1 0 1 0 2 1 1 2 1 1 1 1 0 1 1 1 0 1 1 1 1 1 - 1 1 1 2 1 1 1 1 1 0 0 0 - 0 1 a 0 2 1 1 0 0 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Eriauchenius jeanneli	2 1 0 1 1 1 1 0 2 1 0 1 0 2 1 1 2 1 0 1 1 0 1 1 0 0 1 1 1 1 1 - 1 1 1 2 1 1 1 1 1 0 0 0 - 0 ? ? ? ? 1 1 0 0 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Eriauchenius legendrei	2 1 0 1 1 1 1 0 2 1 0 1 0 2 1 1 2 1 0 1 1 0 1 1 1 0 1 1 1 1 1 - 1 1 1 2 ? 1 1 1 1 0 0 0 - 0 ? ? ? ? 1 1 0 0 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Eriauchenius workmani	1 0 0 1 1 1 1 0 2 1 0 1 0 2 1 1 2 1 1 1 1 0 1 1 1 0 1 1 1 1 1 - 1 1 1 2 1 1 1 1 1 0 0 0 - 0 1 a 0 2 1 1 0 0 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Eriauchenius bourgini	1 1 0 1 1 1 1 0 2 1 0 1 0 2 1 1 2 1 0 1 1 0 1 1 0 0 1 1 1 1 1 - 1 1 1 2 1 1 1 1 1 0 0 0 - 0 ? ? ? ? 1 1 0 0 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Afrarchaea "pilgrimsrest"	1 1 0 1 1 1 1 0 2 1 0 1 0 2 1 1 2 1 0 1 1 0 1 1 1 0 1 1 1 1 1 - 1 1 1 1 1 1 1 1 1 0 0 0 - 0 ? ? ? ? 1 1 0 0 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Afrarchaea woodae	1 1 0 1 1 1 1 0 2 1 0 1 0 2 1 1 2 1 0 1 1 0 1 1 1 0 1 1 1 1 1 - 1 1 1 1 0 1 1 1 1 0 0 0 - 0 1 a 0 2 1 1 0 0 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Austrarchaea nodosa	1 0 0 1 1 0 1 0 2 1 0 1 0 2 1 1 2 1 0 1 1 0 1 1 0 0 1 1 1 1 1 - 1 1 1 2 0 1 1 1 1 0 0 0 - 0 1 a 0 2 1 1 1 1 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Austrarchaea daviesae	1 0 0 1 1 0 1 0 2 1 0 1 0 2 1 1 2 1 0 1 1 0 1 1 0 0 1 1 1 1 1 - 1 1 1 2 1 1 1 1 1 0 0 0 - 0 ? ? ? ? 1 1 1 1 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Austrarchaea mainae	0 0 0 1 1 0 1 0 2 1 0 1 0 2 1 1 2 1 0 1 1 0 1 1 0 0 1 1 1 1 1 - 1 1 1 2 0 1 1 1 1 0 0 0 - 0 ? ? ? ? 1 1 1 1 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Archaea paradoxa	0 0 0 1 1 0 ? 0 2 1 0 1 0 0 1 ? 2 1 0 1 1 ? 1 1 1 1 0 1 1 1 ? ? 1 1 1 ? ? 1 1 ? 1 0 0 0 - 0 ? ? ? ? 1 0 - - 1 0 - 1 1 1 ? 1 0 0 1 1 1 1 0 0
Burmesarchaea grimaldii	0 0 0 1 1 0 ? 0 2 1 0 1 0 0 1 ? ? ? 0 1 1 ? 1 1 1 1 0 ? ? ? ? ? 1 ? ? ? ? 1 1 ? 1 0 0 0 - 0 ? ? ? ? 1 0 - - 1 0 - 1 1 ? ? 1 ? 0 1 0 ? ? 0 0
Myrmecarchaea sp	0 0 0 1 1 0 ? 0 1 1 ? 1 0 0 ? ? ? ? 0 1 ? ? 1 1 1 1 0 ? ? ? ? ? 0 1 1 ? ? 1 1 ? ? ? 0 ? ? ? ? ? ? ? 1 0 - - ? 0 - 1 ? ? ? ? ? 0 1 1 ? ? 0 0
Baltarchaea conica	1 0 0 1 1 0 ? 0 2 1 1 1 0 0 ? ? 2 ? 0 1 1 ? 1 1 1 1 0 ? ? ? ? ? 0 1 ? ? ? 1 1 ? ? ? 0 ? ? ? ? ? ? ? 1 0 - - 1 0 - 1 ? ? ? 1 0 0 1 ? ? ? 0 0
Patarchaea muralis	? ? ? ? ? ? ? ? ? 1 ? ? ? ? ? ? ? ? ? ? ? ? 1 1 ? 1 ? ? ? ? ? ? 0 ? 1 1 ? ? 1 ? 1 0 ? ? ? ? ? ? ? ? 1 0 - - 1 0 - 1 1 ? ? 1 1 0 1 ? 1 ? 0 0

Appendix 3 cont.

Character	7 7 7 7 7 7 7 7 8 8 8 8 8 8 8 8 8 9 9 9 9 9 9 9 9 9 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 1 1 1 1 1 1 1 1 0 1 2 3 4 5 6
Hypochilus pococki	0 0 0 - 0 1 0 0 0 2 0 - 0 0 0 0 - 0 1 0 1 0 0 - - 0 - - 0 0 1 1 1 ? ? 1 0 0 0 0 - 0 0 0 1 0 0 0 - 0 1 0 0 0 - 0
Hickmania troglodytes	0 0 0 - 0 1 0 1 0 0 0 - 0 0 0 0 - 0 1 0 1 0 0 - - 1 0 1 0 0 0 - 0 ? ? 0 - 0 0 0 - 0 0 0 1 0 0 1 1 0 1 0 0 1 0 1
Lycosidae *sp*	0 0 0 - 2 0 0 ? 0 0 0 - 0 0 0 0 - 0 1 0 1 1 0 - - 0 - - 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 0 0 0 - - - - - 0 0 1 1 0 1
Araneus sp	0 0 0 - 2 0 0 1 0 1 0 - 0 1 0 0 - 0 1 0 1 1 0 - - 0 - - 0 1 1 0 1 0 0 1 2 0 0 0 - 0 0 1 0 - - - - - 1 1 0 1 1 1
Badumna longinqua	0 0 0 - 2 0 0 0 0 0 0 - 0 1 0 0 - 0 1 0 1 1 0 - - 0 - - 0 0 1 1 1 ? ? 0 - 0 0 1 3 0 0 0 1 1 0 1 0 1 1 0 1 1 0 1
Dysdera sp	0 0 0 - 2 1 0 0 0 1 0 - 0 0 0 1 0 0 0 - 1 0 1 0 0 0 - - 1 0 0 - 1 ? ? 0 - 0 0 0 - 0 0 0 0 - - - - - 0 0 0 0 2 0
Holarchaea sp	0 1 0 - 2 0 0 0 0 1 0 - 0 0 0 0 - 0 1 0 0 1 0 - - 0 - - 0 1 0 - 0 ? ? 0 - 0 1 0 - 0 0 0 0 - - - - - 0 1 1 1 0 1
Kukulcania hibernalis	1 0 0 - 1 1 0 1 0 1 0 - 0 0 0 0 - 0 1 0 1 0 0 - - 0 - - 1 0 0 - 0 1 ? 0 - 0 0 0 - 0 0 0 1 1 1 1 1 1 0 0 0 0 0 0
Loxosceles sp	1 0 0 - 2 0 0 1 0 1 0 - 0 0 0 0 - 1 1 0 1 0 0 - - 0 - - 1 0 0 - 0 ? ? 0 - 0 0 0 - 0 0 0 0 - - - - - 0 0 1 0 2 0
Mimetus sp	1 1 0 - 2 0 0 1 0 1 0 - 0 0 0 0 - 0 1 0 1 1 0 - - 0 - - 0 1 1 0 1 ? ? 1 2 0 0 0 - 0 0 0 0 - - - - - 0 1 0 1 1 1
Pararchaeidae *sp*	0 1 0 - 2 0 0 1 0 1 1 2 0 0 0 0 - 0 1 0 1 1 0 - - 0 - - 0 0 1 1 1 ? ? 1 2 0 0 0 - 0 0 0 0 - - - - - 0 1 1 1 2 1
Stegodyphus sp	0 0 0 - 2 0 0 1 0 1 0 - 0 0 0 0 - 0 1 0 1 1 0 - - 0 - - 0 0 1 1 0 ? ? 0 - 0 0 0 - 0 0 0 1 1 0 0 - 0 1 0 0 1 0 1
Uroctea sp	0 0 0 - 2 0 0 1 0 1 0 - 0 0 0 0 - 0 1 0 1 1 0 - - 0 - - 0 0 1 0 1 0 0 0 - 0 0 0 - 0 0 0 0 - - - - - 0 0 0 1 2 1
Gnaphosidae *sp*	0 0 0 - 2 0 1 1 0 a 0 - 0 0 0 0 - 0 1 0 1 1 0 - - 0 - - 0 0 0 - 1 ? ? 0 - 0 0 1 0 0 0 0 0 - - - - - 1 0 1 1 0 1
Palpimanus sp	0 1 0 - 2 0 0 0 1 1 1 2 0 1 0 1 1 1 0 - 0 0 0 - - 1 1 1 ? 0 ? ? ? ? 1 1 0 - 0 0 0 - 0 0 1 0 - - - - - 0 0 1 1 2 1
Colopea sp	0 1 0 - 2 0 0 0 1 0 1 3 0 1 0 1 1 1 0 - 2 0 0 - - 1 1 0 0 0 1 0 0 ? ? 0 - 0 0 0 - 0 0 1 0 - - - - - 0 0 1 1 2 1
Huttonia sp	0 1 0 - 2 0 0 0 0 1 0 - 0 1 0 1 1 1 1 0 0 0 0 - - 1 1 1 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 0 1 0 - - - - - 0 0 1 1 2 1
Aotearoa magna	0 1 0 - 2 0 0 ? 1 ? 0 - 0 ? 0 0 - 1 1 1 ? 0 0 - - 1 1 1 0 0 1 0 1 ? ? 0 - 0 0 1 1 1 0 1 0 - - - - - ? ? 1 ? ? ?
Mesarchaea bellavista	0 1 0 - 2 0 0 1 1 ? 0 - 0 ? 0 0 - 1 ? ? ? 0 ? ? ? ? ? ? 0 0 1 0 ? ? ? 0 - 0 0 1 2 1 0 1 0 - - - - - ? ? 1 ? ? ?
Mecysmauchenius segmentatus	0 1 0 - 2 0 0 1 1 0 0 - 0 0 0 0 - 1 1 1 2 0 0 - - 1 0 1 0 0 1 0 ? 1 ? 1 0 0 0 1 1 1 0 1 0 - - - - - 0 1 1 1 2 1
Chilarchaea quellon	0 1 0 - 2 0 0 1 1 0 0 - 0 1 0 0 - 1 1 - 2 0 0 - - 1 0 1 0 0 0 - 0 ? ? 1 1 0 0 1 1 1 0 1 0 - - - - - 0 0 1 1 2 1
Zearchaea sp	0 1 0 - 2 0 0 1 1 0 0 - 0 1 0 0 - 1 1 1 2 0 0 - - 1 1 1 0 0 1 0 1 ? ? 0 - 1 0 1 1 1 0 1 0 - - - - - 0 1 1 1 2 1
Eriauchenius lavatenda	0 1 0 - 2 1 0 0 0 0 1 1 1 1 1 1 1 0 1 0 - 1 0 1 1 0 0 - - 0 0 1 0 1 ? ? 0 - 0 1 0 - 0 1 1 0 - - - - - 0 1 1 1 0 1
Eriauchenius jeanneli	0 1 0 - 2 1 0 0 0 ? 1 1 1 ? 1 1 0 0 0 - 1 0 1 1 0 0 - - 0 0 1 0 1 ? ? 0 - 0 1 0 - 0 1 1 0 - - - - - ? ? 1 ? ? ?
Eriauchenius legendrei	0 1 0 - 2 1 0 0 0 ? 1 1 1 ? 1 1 0 0 0 - 1 0 1 0 0 0 - - 0 0 1 0 1 ? ? 0 - 1 1 0 - 0 1 1 0 - - - - - ? ? 1 ? ? ?
Eriauchenius workmani	0 1 1 1 2 1 0 0 0 0 1 1 1 1 1 1 1 0 0 0 - 1 0 1 1 0 0 - - 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 1 1 0 - - - - - 0 1 1 1 0 1
Eriauchenius bourgini	0 1 0 - 2 1 0 0 0 ? 1 1 1 ? 1 1 0 0 0 - 1 0 1 1 0 0 - - 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 0 1 0 - - - - - ? ? 1 ? ? ?
Afrarchaea "pilgrimsrest"	0 1 0 - 2 1 0 0 0 ? 1 1 1 ? 1 1 0 0 0 - 1 0 1 1 1 0 - - 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 1 1 0 - - - - - ? ? 1 ? ? ?
Afrarchaea woodae	0 1 0 - 2 1 0 0 0 0 1 1 1 1 1 1 1 0 0 0 - 1 0 1 1 1 0 - - 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 1 1 0 - - - - - 0 1 1 1 2 1
Austrarchaea nodosa	0 1 1 0 2 1 1 1 0 0 1 1 1 1 1 1 1 0 0 0 - 1 0 0 - - 1 0 0 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 1 1 0 - - - - - 0 1 1 1 0 1
Austrarchaea daviesae	0 1 1 0 2 1 1 ? 0 ? 1 1 1 ? 1 1 0 0 0 - 1 0 0 - - 1 0 0 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 1 1 0 - - - - - ? ? 1 ? ? ?
Austrarchaea mainae	0 1 1 0 2 1 1 ? 0 ? 1 1 1 ? 1 1 0 0 0 - 1 0 0 - - 1 0 0 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 0 1 0 - - - - - ? ? 1 ? ? ?
Archaea paradoxa	0 1 0 - ? ? 1 ? 0 ? 1 1 1 ? 1 0 - 1 0 - ? 0 ? ? ? ? ? ? 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 0 1 0 - - - - - ? ? ? ? ? ?
Burmesarchaea grimaldii	0 1 0 - ? ? ? ? 0 ? ? ? 1 ? 1 0 - ? ? ? ? ? ? ? ? ? ? 0 0 1 0 ? ? ? 0 - 0 0 0 - 0 1 ? 0 - - - - - ? ? ? ? ? ?
Myrmecarchaea sp	0 1 0 - ? ? ? ? 0 ? ? ? 1 ? 1 ? 0 - - - - - ? ? ? ? ? ?
Baltarchaea conica	0 1 1 a ? ? ? ? 0 ? ? ? 1 ? 1 ? ? ? ? ? ? 0 ? 0 - - - - - ? ? ? ? ? ?
Patarchaea muralis	0 1 ? ? ? ? ? ? ? ? ? ? ? ? ? 0 - ? 1 0 ? ? ? ? ? ? ? ? 0 ? ? ? ? ? ? ? 0 - ? ? 1 1 ? ? ? 0 - - - - - ? ? ? ? ? ?

Appendix 4: Palpimanoidea characters

Rather than discussing all 126 characters in detail, we discuss only the morphological characters that are useful and important for understanding evolution of the Palpimanoidea (Figs. 9-10); other characters are optimized on the TE Bayesian tree. With the exception of huttoniids, all members of Palpimanoidea have a sclerotized foramen encircling the base of the jaws (character 10), which may take the form of a narrow rod that runs between the chelicerae and mouthparts (labrum, endites and labium), as in palpimanids and stenochilids, or as a modification of the carapace, as in archaeids and mecysmaucheniids. This trait is also found in Pararchaeidae. The sternum has a border (character 15), which also independently occurs in *Dysdera* sp. The labrum, a mouthpart structure, has two spurs (character 20), which are lost in huttoniids, and that are greatly reduced, as in stenochilids, or very prominent, as in archaeids and mecysmaucheniids. Within Palpimanoidea, all members have a modification on the dorsal, basal side of tarsus 1 (character 28), which can be a membraneous bulge or ring, or cuticular foldings. There is a brush of hairs on metatarsus III (character 30), which is a comb in *Huttonia* sp. and which also occurs in *Dysdera* sp. In Palpimanoidea, with the exception of archaeids, claw I is smaller than claw IV (character 40). With the exception of *Chilarchaea* all Palpimanoidea taxa have transverse ridges on the trichobothria hood (character 50), and these ridges also occur in *Loxosceles* and *Stegodyphus*. There is also a reduction in leg spination (character 51), a trait that also appears in several other taxa in this study. There are modified hairs on the chelicerae (character 58), termed "peg-teeth", which are lost in stenochilids and which have evolved independently in mimetids and pararchaeids. Within the Palpimanoidea, peg-teeth also occur on the retrolateral margin of the chelicerae, close to the location where the fang closes (character 59), whereas the peg-teeth in non-Palpimanoidea taxa occur only on the promargin. The presence of cheliceral stridulatory ridges (character 62) occurs in all Palpimanoidea, and also is found in *Loxosceles* and *Hickmania*. A gland mound is present on the jaws in all Palpimanoidea (character 67), which has also evolved independently in holarchaeids. Within Palpimanoidea as well as some Araneoidea taxa there is a cheliceral diastema (character 72), and this was also scored as present in *Palpimanus* and *Colopea* because of the presence of a sclerotized rod running between the chelicerae and mouthparts. An interesting character involves the wrinkle pattern observed in the abdomen cuticle after being critically point dried (character 84). In Palpimanoidea taxa, although with some taxa scored as "unknown" and with the exception of *Mecysmauchenius,* the cuticle has a distinctive pattern (compare Figs. 44, 100, 316 and 331 with Figs. 226 and 365 of Platnick & Forster, 1984); this is also observed in *Badumna* and *Araneus*. Another characteristic of Palpimanoidea, with the exception of most extant archaeids, is the presence of picks on the palpal femur (character 88), which also occur in *Loxosceles* sp. *Hickmania troglodytes* and the Palpimanoidea taxa (with the exception of the African/Madagascar archaeids) have large membraneous sacs originating from the bursa, or sperm storage organ, in the female genitalia (character 96). Since this trait doesn't appear in the Entelygynae clade, this feature either evolved twice independently or evolved once and was then lost in the Entelegynae. An important morphological discovery is the finding that the distal membraneous section of the male palpal bulb expands (character 114) in all Palpimanoidea. The male palp serves as secondary genitalia in spiders; in Entelegynae basal parts of the bulb expand during copulation. Distal expansion of the palp bulb may be exclusive to the Palpimanoidea and was even observed in a fossilized *Archaea paradoxa* specimen. This character was also scored as present in *Araneus* sp. even

though the expansion involves movable "joints" within sclerotized structures rather than an entire ballooning out of the distal palpal membranes, which occurs in Palpimanoidea.

There are several other notable characters that are worth mentioning. Palpimanoidea taxa have either tuberculate (or bumpy) or scaly cuticle (character 9) on the carapace. The transition from tuberculate to scale or vice versa has occurred several times within the Palpimanoidea. A character uniting the non-mecysmaucheniid Palpimanoidea is that the anterior median eyes (AME) are larger than the other eyes (character 4), a trait that has independently evolved in several non-Palpimanoidea taxa. Another character uniting non-mecysmaucheniid Palpimanoidea is the presence of modified spatulate hairs, termed scopulae, that are found on the inside surface of leg I and sometimes leg II (character 35). This character is also occurs in Gnaphosidae. With the exception of archaeids and huttoniids, the posterior row of spinnerets are greatly reduced (character 79). *Palpimanus, Colopea,* and archaeids are heavily sclerotized around the anterior portion of the abdomen, while this doesn't occur in *Huttonia* and the mecysmaucheniids (character 81). The presence of a brush of hairs on the palp tarsus (character 86) occurs in several members of the Palpimanoidea, as well as independently in *Dysdera* sp.

Appendix 5: Archaeidae characters

Some characters that are shared by all archaeids, extant and fossil, include: the anterior median eyes are on a ridge (character 5); the seam that fuses the edges of the carapace to form a foramen around the base of the jaws is rebordered or thickened, absent in *Baltarchaea conica* (character 11); the sclerite between the chelicerae bases is triangular (character 17), and beneath this there is an additional long, narrow sclerite (character 18); the labium has a narrow v-shaped notch at the distal edge (character 21 – also occurs in other taxa); the cephalic area is raised at least the length of the carapace (character 23 – also occurs other taxa); there is a constriction in the "neck" (character 24 – also occurs in *Mesarchaea*); there is a membraneous ring around the basal portion of the tarsi (character 29 – also occurs in mecysmaucheniids); femur IV has a distinctive bend (character 33, missing in some fossil archaeids); femora I-IV have a small, dorsal bump (character 34); the patella-tibia joint of leg IV is hyperextended (character 38 – also found in *Holarchaea*); there is a constriction immediately preceeding the cheliceral bases (character 55 – also found in mecysmaucheniids and *Holarchaea*); there are only two peg teeth in the first row (character 60 – also occurs in *Huttonia*); there is a deep depression adjacent to the cheliceral gland mound (character 68); in females the dorsal and ventral sclerites that surround the anterior of abdomen are separate (character 82); there are folds in the abdomen (character 83), which are less obvious in the extant archaeids, but still visible, especially in a hungry individual; the spinnerets arise from a conical projection (character 85).

Appendix 6: Extant archaeid characters

Some of the following characters were not scored for the fossil archaeids because these features were too small to observe in amber specimens. For this reason, some of these characters may turn out to be true for both the extant and fossil archaeids. All extant archaeids have a tubercle on the posterior edge of their sternum (character 14). The chilum is divided (character 16), although this character isn't scored for fossil archaeids. The posterior edge of the carapace is flattened in extant archaeids rather than tapering off (character 27 – also occurs in *Palpimanus*). The tarsal organ is capsulate (character 31 – not scored for fossil archaeids). The superior tarsal claws 1 are shaped differently than the superior tarsal claws 4 in archaeids (character 40 – also found in mecysmaucheniids and not scored for fossil archaeids). The extant archaeids have serrate accessory claw setae (character 47), but again this trait isn't scored for fossil archaeids. Extant archaeids, unlike their extinct relatives, have a spine or protuberance on the anterior surface of their chelicerae (character 52). This character was also reported in the fossil *Burmesarchaea grimaldii* but our observations did not confirm this observation. The distal portion of the chelicerae are curved towards the posterior in extant archaeids (character 64). In extant archaeids the posterior respitory system consists of a pair of tracheae (character 76), unlike the single opening seen in most Araneomorphae. This character is scored as "unknown" in the fossil archaeids, and could be a trait characteristic of the entire family. Extant archaeids have a brush of hairs that occurs on the prolateral side of the pedipalp tarsi (character 86). This has been observed to interact with the stridulatory file on the chelicerae (Forster & Platnick, 1984; Wood, 2008) to produce courtship vibrations, and in the fossil archaeids stridulatory picks instead likely interact with the stridulatory file. Unlike the fossil archaeids, the extant members do not have picks on palpal femur (character 88 – although this is occurs in *Eriauchenius gracilicollis*, an extant species not included in this study). The major ampullate spigot (MAP) field on the ALS is separated by furrow in extant archaeids (character 122). This character is observed in other taxa in our study, and is also "unknown" in the fossil archaeids: this may be characteristic of the family. In most extant archaeids the minor ampullate gland spigot (mAP) on the PMS is median to anterior (character 125 – also occurs in other taxa). This character is also scored as "unknown" in the fossil archaeids. A final character worthy of discussion involves the length of the endites (the mouthparts), which are greatly extended in the fossil archaeids (character 26), whereas the extant archaeids have shorter endites comparable to those of other spiders.