Biogeography and Evolution of the Araneae: A Synthetic Approach

by

Erin Elizabeth Saupe
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Advisory Committee:

_____
Paul Selden - Chair

_____
Bruce Lieberman

_____
Ed Wiley

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The Thesis Committee for Erin Saupe certifies that this is the approved version of the following thesis:

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_____
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Abstract

Various methods are used to study the evolution and biogeography of the Araneae through time. Two new fossil spider species were described from Miocene Dominican amber and French Cretaceous amber. A preliminary biogeographic analysis was performed on the former in order to elucidate the biogeographic origins of the genus to which it belongs. Further, ecological niche modeling, a biogeographic technique used to delineate the set of tolerances and limits in multidimensional space that define where a species is potentially able to maintain populations, was undertaken on the brown recluse (*Loxosceles reclusa)* spider for extant distributions and potential future distributions given climate change. A methodological analysis addressing how error within species occurrence points influences model quality within ecological niche modeling was conducted. Results indicated that studies of lower spatial resolution are valid, if enough data are utilized; this has implications for using ecological niche modeling in the fossil record.

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Introduction

This thesis is a compilation of three separate, but related, projects detailing the biogeography and evolution of the Araneae. Biogeographic studies (and specifically paleobiogeographic studies) are vital because they can provide insight into the mechanisms promoting speciation, extinction, and the maintenance of stasis (i.e., macroevolutionary patterns and processes). Paleobiogeography can also elucidate the role that Earth history changes play in influencing evolution.

Various methods were used to study the evolution of the Araneae, including mBPA (Lieberman, 2000, also referred to as LBPA by Stigall, 2008), phylogenetics, and niche modeling techniques (this paper and forthcoming). A new species within the genus *Molinaranea* was described from Miocene Dominican amber; this is the first fossil within this extant genus and extends the geographical range of the lineage through time (since extent members are found only in southern South America and the fossil is from the Dominican Republic). We performed a phylogenetic and modified Brooks Parsimony analysis (mBPA) on the genus in order to further understand the geographic origins of the lineage and its implications for the colonization of the West Indies. The West Indies has been designated a Conservation International Biodiversity Hotspot, and there has been tremendous amounts of discussion on 1) how to preserve this diversity and 2) how this diversity arose and/or how organisms colonized the islands. Debate has particularly focused on whether colonization occurred via vicariance or dispersal, and if the latter, by what dispersal mechanism. The mBPA (Lieberman, 2000) analysis indicated the lineage arrived on Hispaniola via dispersal, which provides another piece of evidence within the larger

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colonization puzzle of the West Indies. Understanding how this biodiversity hotspot arose can help us protect these fragile regions.

A new species of spider within the family Mecysmaucheniidae is also described from French Cretaceous amber. This is the first fossil within the family Mecysmaucheniidae, thus extending the record of this group back ~90 million years. Extant mecysmaucheniids are found only in southern South America and New Zealand, whereas the fossil was discovered in French Cretaceous amber. This find is quite interesting biogeographically and suggests a re-analysis of the typical "Gondwanan" explanation for the distribution of this group (and its sister, the Archaeidae). Describing and documenting new fossil species is extremely important not only for understanding the evolution of the Araneae, but also for elucidating past diversity of life on Earth. Discovery of new fossil species provides further biogeographic data to use in phylogenetic biogeographic and niche modeling analyses. This data allows you to search for congruence within and among clades, which would provide information on how geologic events shaped evolution. 99.9 percent of all life on Earth is now extinct (Lieberman, 2000), and the fossil record is our only source on this past diversity.

Techniques like mBPA can be used in conjunction with ecological niche modeling to study paleobiogeographic relationships. Ecological niche modeling looks at the set of environmental conditions that potentially constrains the distribution of a species within space (i.e., its fundamental niche). Using niche modeling within a phylogenetic framework can provide insight into the relative importance of abiotic and biotic factors in constraining distributions and ultimately influencing evolution. Ecological niche modeling has been applied to the fossil record (e.g., Maguire &

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Stigall, 2008; Stigall Rode & Lieberman, 2005); however, in order to further test the validity of this method, we performed a methodological analysis addressing how spatial error within species occurrence points influences model quality. The fossil record places constraints on the resolution of paleo-ENM studies (Schindel, 1980; Sadler, 1981; Dingus & Sadler, 1982; Dingus, 1984; Lieberman, 2000), and many modern biologists are increasingly concerned with working only with fine-scale data and shy away from larger-scale studies with presence only data that are lower in geographic resolution. An analysis of the error within locality points and how this influences model quality has not been well studied, but needed to be addressed, especially when data from museum collections is utilized. I found that the number of data points was more significant in producing accurate niche models than the geographic resolution of individual points. This has implications for the use of ENM in the fossil record and suggests the models produced from this data are accurate and useful. In the future, further work using ENM will be performed in combination with mBPA analyses to address questions such as: what is driving the evolution of life through time, and is it primarily abiotically or biotically forced?

In addition to the above methodological study, I used ENM to characterize the niche of the brown recluse spider (*Loxosceles reclusa)*. The brown recluse is an infamous and medically important spider in North America; its bite can cause serious necrotic lesions, and it has become a feared (often unnecessarily) object in many North American homes. Given its notoriety, the species' geographic range was surprisingly unknown and had never been quantified (Vetter 2000; Vetter 2005; Swanson and Vetter 2005). Bite mis-diagnoses for several medical conditions, including fungal infections, *Herpes simplex*, MRSA, chemical burns, and syphilis

(Vetter 2000; Vetter et al. 2003, 2004; Swanson and Vetter 2005) are quite common, even in states without brown recluse populations. We found that the environmental conditions suitable to the brown recluse (its niche) are quite similar to its known distribution (i.e., the Midwest), and medical professionals should think twice about diagnosing brown recluse bites in areas outside its natural range.

I projected the niche of the brown recluse into the future given climate change scenarios (forthcoming). Since the brown recluse is such a high-profile species, testing hypotheses of distributional change provides valuable information to medical professionals and has greater potential to enhance public awareness of the impact of climate change on the Earth's biota. Furthermore, by identifying potential areas of range expansion, public health initiatives can be designed to assure effective response. Affected areas can be educated on proper protocol for dealing with populations of *L. reclusa* (e.g., always shake out clothes and shoes before donning) and potential bites (e.g., do not excise or heat the wound). This work also has implications for analyzing the effect of invasive species on biodiversity. Invasive species are a serious concern in the current biodiversity crisis, and there is evidence that species invasions in deep time (which occurred due to the collapse of climatic, geologic, or ecologic barriers) contributed to decreased speciation and biodiversity decline (e.g., the Late Devonian Biodiversity Crisis at the Frasnian-Famennian boundary, see Lieberman, 2000; Stigall Rode & Lieberman, 2005 and Stigall & Lieberman, 2006).

CHAPTER 1 | Quality does not always trump quantity: effects of sample size and spatial error of species presences in ecological niche modeling

Chapter Summary

We investigate, using the brown recluse spider (*Loxosceles reclusa*), how uncertainty in species occurrence data affects ecological niche modeling results. In doing so, we address the age-old problem of which is better: quality or quantity (of species occurrence points). We georeferenced and assigned error to species locality points using the latest techniques, including Biogeomancer and the MaNIS/HerpNet/ORNIS Georeferencing Calculator. Three error treatments of 1, 4.5, and 18 km were used in conjunction with two of the more popular presence-only ecological modeling methods: Maxent and GARP. We assessed model quality based on a number of measures, including sensitivity tests and partial AUC ratios. We found no significant difference between partial AUC ratios of differing spatial uncertainty, and all ratios were statistically significant above the line of null expectations (z-tests, P< 0.001). Overall, the lower spatial resolution data with a greater number of occurrence points produced the most reliable results, while the highest-resolution data with the fewest points produced narrower predicted distributions. Species occurrence data is increasingly being digitized and assigned geographic coordinates. While this facilitates sharing and utilization of data from natural history museum collections, much of the digital locality data lack attribute information, such as the error associated with each assigned coordinate. This is potentially problematic because different applications and questions require different levels of data precision. However, at least in terms of larger-scale ecological niche modeling studies, we found that museum locality data with typical error (e.g., up to 18 km) will produce predicted distributions comparable with a species known distribution; quantity *is* perhaps better than quality in many circumstances.

1.1 Introduction

Ecological niche modeling (ENM) is a rich area of study that has seen tremendous growth in past years. Species geographic occurrence points and predictor variables (usually climatic or environmental parameters) are used in correlative approaches to make inferences about the ecological requirements for a species, which can then be projected onto geography. These models can be used in many applications, such as examining future potential distributions of species under climate change scenarios

(Price, 2000; Peterson *et al.*, 2001; Pearson & Dawson, 2003; Araújo *et al.*, 2005; Thuiller *et al.*, 2005), predicting species invasions (Peterson & Vieglais, 2001; Papeş & Peterson, 2003; Peterson, 2003; Ficetola *et al.*, 2007), finding unknown species (Raxworthy *et al.*, 2003), determining areas in need of conservation (Pressey, 1994; Williams *et al.*, 1996), analyzing paleo-distributions and related questions (Peterson *et al.*, 2004; Stigall-Rode & Lieberman, 2005; Maguire & Stigall, 2009) and understanding the ecological requirements of species (Austin & Meyers, 1996; Costa *et al.*, 2002; Hirzel *et al.*, 2002). While there has been much research in the field of ENM, few have explored how model quality is affected by geographic spatial error in species occurrence points (Graham *et al.*, 2008; Fernandez *et al.*, 2009).

Museum collections are the primary source of species occurrence points used in presence-only ENM. There are over 2500 million geological, biological, and cultural specimens housed in museums around the world (Duckworth *et al.*, 1993), but only about one percent of these have been georeferenced (i.e., assigned geographic coordinates indicating location of collecting event, the data format used in ENM) (Guralnick *et al.*, 2006). Retrospective georeferencing, or assigning coordinates from historical descriptions (Guralnick *et al.*, 2007), can lead to errors or uncertainty in the locality data. Error is introduced from vague locality descriptions with large geographical extents (e.g., "Austin, Texas"), inaccuracy in georeferencing localities with offset distances (e.g., "1 mi south of Rolla, Missouri"), an unknown datum, and uncertainty in map scale used, to name a few (Wieczorek *et al.*, 2004; Graham *et al.*, 2008). Stockwell and Peterson (2002a) have estimated that the spatial resolution (or uncertainty) associated with museum data is generally 0.5 km and above. If a high degree of spatial accuracy in occurrence data is required, few data points may be

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available that meet this standard; conversely, lowering the spatial resolution affords a greater number of occurrences but decreases the accuracy. The question we address here is which is more important for accurate ENM: quality of species occurrence points or quantity of occurrence points?

In the past few years, programs have been developed to assign error to georeferenced locality points, such as BioGeomancer (Guralnick *et al.*, 2006) and the MaNIS/HerpNet/ORNIS Georeferencing Calculator (Wieczorek *et al.*, 2004). While error is now being quantified and accounted for, few have used this error as a filter to choose only those points that fit a certain or appropriate use and even fewer have examined the influence of locality error on model quality (Wieczorek *et al.*, 2004).

Most recently, Fernandez *et al.* (2009) addressed how model accuracy degrades under increasing locality data uncertainty. They simulated error within an original dataset by randomly replicating and moving each locality point to a new position within a specified buffer, testing four different sizes: of 5, 10, 25, and 50 km. Model quality was measured through Monte Carlo simulations and a similarity measure, as compared to predictions generated from unaltered data. They found that the modeling method (i.e., BIOCLIM, DOMAIN, Maxent and GARP) influenced model quality more so than the simulated error associated with the data points.

Similarly, but offering a different perspective on the issue, Graham *et al.* (2008) introduced error into georeferenced coordinates by drawing a number from a normal distribution with a mean of zero and a standard deviation of 5 km. They evaluated model quality based on a comparison of AUC scores and found that, overall, accurate

predictions were possible with introduced error in coordinates, although quality did decline.

At a much finer spatial scale, Engler *et al.* (2004) evaluated whether the grain (spatial resolution) or the quality of occurrence points is more important for model accuracy using two datasets of 45 and 77 occurrence points with a spatial resolution of 25 and 100 meters, respectively. Model quality was assessed using a variety of statistical analyses, including the Gini coefficient. They found that the quality of points (spatial resolution and location accuracy) is more important than the quantity of points, differing from the findings of the aforementioned studies. The authors claimed that the poor results obtained with the lower resolution data may have been a result of a) loss of information when environmental maps were aggregated, b) a greater measurement error than indicated, and c) the micro-habitat specificity of plants, their study organism.

Here, we use the brown recluse spider (*Loxosceles reclusa*) to investigate how uncertainty in species occurrence data affects model quality. In doing so, we address the age-old problem of which is better: quality or quantity (of species occurrence points).

We use two of the more popular modeling methods, GARP and Maxent. While Fernandez *et al.* (2009) and Graham *et al.* (2008) focused on the effects of simulated, degraded data, our study examines the trade-off between quantity and quality. Furthermore, we use the latest georeferencing tools to assign error to locality coordinates, a more realistic approach than artificially inserting error into a locality dataset. Like the present study, Engler *et al.* (2004) also assessed the trade-off

between quality and quantity of occurrence points, but our study differs from theirs in that it uses a mobile, widespread organism, different model development techniques, and a greater number of lower-resolution datasets.

1.2 Methods

1.2.1. Brown recluse distribution and data georeferencing

The brown recluse (also known as the fiddle-back spider, the brown spider, or the violin spider) is distributed throughout the central United States, from southern Illinois south to Texas and from eastern Tennessee west to Kansas and Oklahoma (Vetter, 2008). The species is infamous for its bite, which can cause necrotic lesions of medical concern (Da Silva *et al.*, 2004; Hogan *et al.*, 2004; Swanson & Vetter, 2005, 2006). The distribution of the brown recluse has been studied (Gertsch & Ennik, 1983; Swanson & Vetter, 2005; Vetter, 2008), and therefore a fairly accurate range map in which to test the models is available.

Occurrence points for *L. reclusa*, in the form of locality descriptions, were compiled from the American Museum of Natural History (AMNH), the Museum of Comparative Zoology (MCZ), and from individual researchers (see Acknowledgements).

Georeferencing was carried out using the point-radius method (after Wieczorek *et al.*, 2004), where each locality was treated as a circle with a point in the middle. The radius represents the maximum distance from the point within which the locality is expected to occur. All occurrence points were georeferenced, excluding the Mississippi dataset that had already been collected and assigned geographic

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coordinates with a GPS. The error associated with the GPS data points was calculated using the MaNIS/HerpNet/ORNIS Georeferencing Calculator (Wieczorek *et al.*, 2004). Georeferencing was primarily conducted using BioGeomancer (Guralnick *et al.*, 2006), since most localities simply referred to a town and state. The centre of the town was calculated manually using the underlying topographic map function, and the error was adjusted within BioGeomancer to include the full extent of the town (erring on the conservative side; i.e., associating the point with the most error possible within reason). When presented with a specific street address, the exact address was georeferenced, and the extent of the street was used to calculate error. Localities described with offset distances (e.g., "1 mi south of Rolla, Missouri") were georeferenced by measuring the extent and centre of the named place (usually a town) in Google Earth 5.0. These measurements were then imported into the MaNIS/HerpNet/ORNIS Georeferencing Calculator to find the geographic coordinates and error associated with them. Any obviously inaccurate and/or dubious locality information was not georeferenced.

1.2.2. Ecological niche modeling

1.2.2.1. Input data

Occurrence datasets

The locality data was divided into three sets for model building, based on georeferencing errors: ≤ 1 km, ≤ 4.5 km, and ≤ 18 km spatial error. Since there were only 36 spatially unique points within the 1 km dataset, it was not split for external testing. The 4.5 km dataset was randomly divided in two, and one portion was set aside for external testing of the model. The same points used in the 4.5 km resolution

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training dataset were included within the 18 km resolution training dataset, and the remaining lower resolution points were randomly assigned to either the 18 km training or testing dataset (i.e., the data were inclusive). The 4.5 km training dataset contained 88 spatially unique points, and the 18 km dataset was composed of 126 spatially unique points.

Environmental datasets

The predictor variables consisted of seven bioclimatic variables from WorldClim v. 1.4 (Hijmans *et al.*, 2005). We used three different resolutions: 30 arc-seconds, 2.5 arc-minutes, and 10 arc-minutes data, to match the 1 km, 4.5 km, and 18 km resolution occurrence datasets, respectively. Worldclim variables represent interpolations of average monthly climate data from weather stations on a 30 arc-second resolution grid from 1960–1990 (Hijmans *et al.*, 2005). We used the following variables: 1) annual mean temperature, 2) mean diurnal range, 3) maximum temperature of warmest month, 4) minimum temperature of coldest month, 5) annual precipitation, 6) precipitation of wettest month, and 7) precipitation of driest month to capture the climatic dimensions that are most likely to limit the distributional extent of the species. These seven variables have also been used in other studies and have produced viable ecological niche models (e.g., Neerinckx *et al.*, 2008; Peterson & Nyári, 2008).

The bioclimatic variables were clipped to the training region, which essentially included the area between the Rocky Mountains and the Appalachian Mountains, USA (i.e., the Midwest). This training region was used to build the ecological niche models and was chosen because it represents an area that is most likely ecologically

accessible to the brown recluse (i.e., within its "M" domain, *sensu* Soberón & Peterson, 2005).

1.2.2.2. Modeling algorithms

Of the more popular and widely used modeling methods, we chose two specifically designed for predicting species distributions when only presence data are available: GARP (Genetic Algorithm for Rule-Set Prediction, Stockwell & Peters, 1999) and Maxent (maximum entropy, Phillips *et al.*, 2004). Both of these techniques have been employed and validated in numerous studies (e.g., see Elith *et al.*, 2006 for a comprehensive comparison).

GARP

GARP is a machine-learning algorithm that utilizes known occurrence points and generated pseudo-absences. The algorithm relates these points to predictor (environmental) variables in an iterative, artificial-intelligence framework to create a set of rules describing ecological conditions potentially habitable to a species, which can then be projected onto geography (Stockwell & Peters, 1999).

GARP was run using the internal testing feature (i.e., 50 percent of the input data were used to evaluate model quality within GARP). We ran 100 models for each spatial resolution (see below), with a 0.01 convergence limit and max iterations of 1000. The 'best subsets' method (Anderson *et al.*, 2003) was used to retain 10 models based on two error statistics, omission (excluding known presence data), and commission (including areas without confirmed presence of species, but which are potentially habitable). A soft omission threshold was used so that 20 percent of

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models with the lowest omission error were retained; those models with intermediate levels of commission were then chosen from this subset. The 10 best models were summed in ArcMap 9.3 to create a model agreement map in GIS grid format.

Maxent

Maxent is also a machine-learning method for predicting species' distributions using organism occurrence data. Maxent estimates a probability distribution for species' occurrences by finding the distribution of maximum entropy (that which is closest to uniform), subject to constraints defined by the environmental parameters input into the model (Phillips *et al.*, 2004; Phillips *et al.*, 2006).

We primarily used the default features of Maxent v. 3.3.1. We also took advantage of the 'remove duplicate presences' function. Linear, quadratic, product, threshold, and hinge feature types were enabled. We converted the floating-point output models of Maxent into integer grids (retaining first 3 decimals), which are easier to manipulate in a GIS-framework, using the Raster Calculator in ArcMap 9.3.

Maxent and GARP models were trained in the Midwest region using all three spatial resolutions (1, 4.5, and 18 km), and each of the three resulting models was projected to the continental U.S., on the same three spatial resolutions. This resulted in a total of 6 training models and 18 projections.

1.3. Data analyses and model evaluation

1.3.1 Threshold-dependent tests: area predicted present, sensitivity, and expert opinion

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To facilitate comparison between predictions, we reclassified the model agreement (GARP) and continuous (Maxent) outputs to simple 0 and 1 values (i.e., 0 = unsuitable habitat, 1 = suitable habitat). All models were reclassified to presence/absence pixels within ArcMap 9.3 using threshold values that allowed a maximum of five percent omission error based on the presence data available. Obtaining binary models facilitated easy calculation of the area predicted as suitable for the species.

To calculate area predicted present in square kilometers, we defined the map projection of all predicted distributions as USA Contiguous Albers Equal Area Conic. The Zonal Statistics function of ArcMap 9.3 was used to find the number of pixels predicted present within each state, which was then converted to square kilometers.

It is important to note that the omission threshold was relaxed to 40 percent for the 1 km GARP projections. This was necessary because of lack of model agreement (and therefore predicted area) within the ten best GARP models.

Sensitivity tests

One of the tests used to assess prediction errors is sensitivity (Fielding & Bell, 1997), which measures model quality by examining the number of test occurrences predicted absent by the niche models. We calculated sensitivity of the models produced at two of the three spatial resolutions; the 1 km resolution model could not be tested for the reasoning cited above.

Expert opinion

Since the brown recluse's distribution has been studied and is of medical importance, experts have a fairly accurate knowledge of the current distribution of the species. The distribution maps from Rick Vetter (Vetter, 2005, 2008), who has studied *L. reclusa* for over 10 years, were consulted in order to further evaluate model quality. It is important to note that ecological niche models are often difficult to test and validate in this way (i.e., by comparison to the realized distribution of the species), because the actual distribution may not mirror the potential distribution of a species (the niche model). Historical and biological barriers may prevent a species from occupying all suitable habitat (Peterson, 2006).

All reported results are based on thresholded models, excluding the threshold-independent ROC analyses (see below).

1.3.2. Threshold-independent tests: Receiver operating characteristic analysis (ROC)

Model quality was evaluated in a variety of ways, including with receiver operating characteristic analysis (ROC) (Fielding & Bell, 1997). This statistic was originally used in medicine and has been accepted as a valid evaluator of model quality in ENM (Elith *et al.*, 2006). The area under the curve (AUC) in ROC analyses is a threshold-independent measure of model performance as compared to null expectations. Traditionally, the null expectation was the line linking the origin and upper right corner of a ROC graph (1,1), representing random models; however, we use the partial ROC concept of Peterson *et al.* (2008) where the null expectation is not fixed. In a partial ROC, several modifications to the original ROC are made (Peterson *et al.*, 2008): (1) the x-axis represents the proportion of area predicted present, (2) the AUC calculations are restricted to the domain in which predictions are being made,

and (3) a threshold applied on the y-axis excludes high omission error rates from AUC calculations. ROC results are expressed as ratios of the area under the partial curve to the area under the trapezoid defined by the random line and the interval on the x-axis corresponding to the threshold applied on the y-axis. In order to compare model ROC AUC ratios with null expectations, the dataset must be bootstrapped and a Z value (standard normal approximation) obtained. We used a Visual Basic routine developed by N. Barve (U. of Kansas; unpubl.) to calculate AUC ratios, performing 1000 iterations with the omission threshold set at five percent (Peterson *et al.*, 2008; threshold on y-axis). The 1 km model could not be tested with the partial ROC analysis because there were too few points to construct an external dataset for model validation.

1.4 Results

There was no significant difference between partial AUC ratios of differing spatial uncertainty, regardless of what algorithm was used in the model building process (Table 1). The AUC ratios for the 4.5 km Maxent and GARP models were 1.45 and 1.42, respectively, while AUC ratios for the 18 km Maxent and GARP models were 1.49 and 1.45, respectively. All ratios were statistically significant above the line of null expectations (z-tests, P< 0.001).

Table 1.1. Summary of statistics describing the results of the partial ROC analyses for GARP and Maxent, with an E = 5

4.5 km	Minimum AUC ratio	Maximum AUC ratio	Mean AUC ratio	Std Dev	# of replicates ≤1	P
GARP	1.121	1.517	1.422	0.058	0	1.180E-13
Maxent	1.241	1.679	1.449	0.145	0	9.382E-04
18 km						
GARP	1.353	1.542	1.451	0.045	0	5.220E-24
Maxent	1.224	1.709	1.478	0.070	0	3.890E-12

Maxent and GARP models omitted a similar number of external testing points, regardless of what error treatment was used. Six points were omitted from the 4.5 km Maxent model and 10 were not predicted present in the 4.5 km GARP model, while 16 test points were omitted from the 18 km Maxent model and 10 points were omitted from the 18 km GARP model.

The 1 km resolution data (i.e., quality of points, but not quantity) tended to produce narrower predicted distributions (with both GARP and Maxent) (Fig. 1.1A,D; Table 2). Furthermore, as mentioned, the 1 km GARP projections could not be thresholded at a 5 percent omission error because of lack of agreement in the 10 best models, indicating weak convergence of best models towards a comparable, similar outcome.
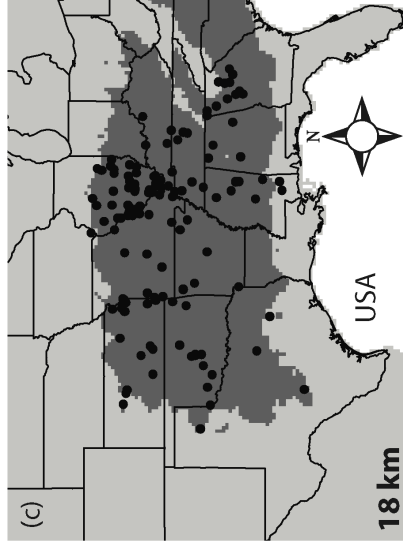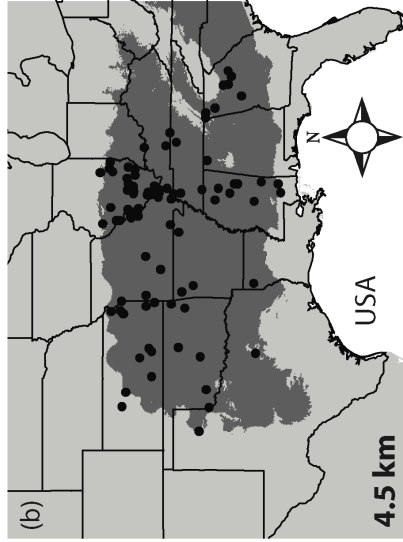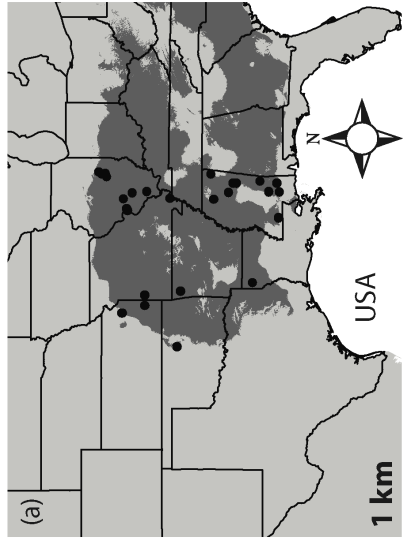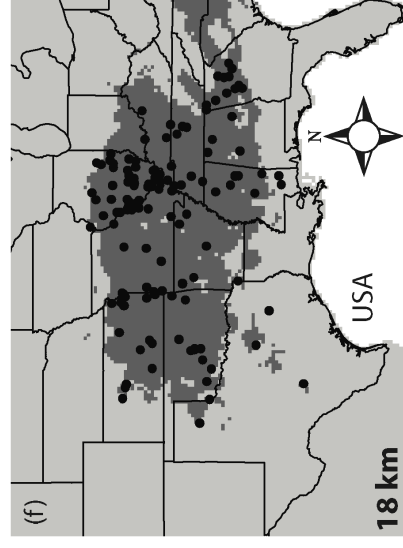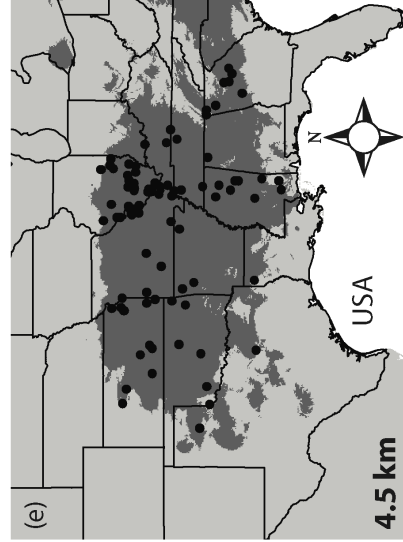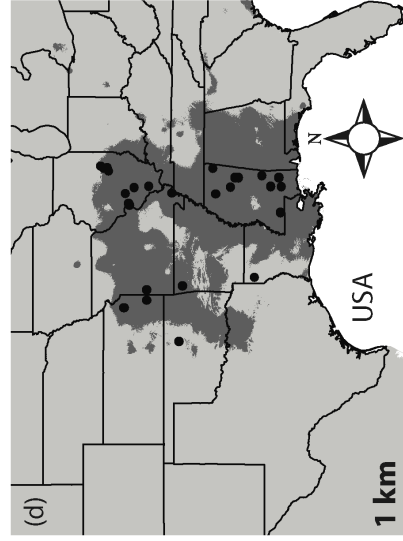
Fig. 1.1 A–F. Thresholded GARP and Maxent models for the three error treatments (training region depicted). The set of occurrence points used to train each model is depcited. Note how the 1 km Maxent and GARP models predict less suitable area than the lower-resolution (4.5 and 18 km) models.

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Models produced with the 4.5 and 18 km datasets (i.e., a greater quantity of low-resolution occurrence points) predicted a similar amount of suitable area, regardless of what algorithm was used (Fig. 1.1B,C, E, F; Table 2). Maxent predicted the most suitable habitat using the 4.5 km resolution data, whereas GARP predicted the largest suitable area with the 18 km resolution data.

Table 1.2. Amount of area (km^2) predicted present in select states for each uncertainty treatment (based on training data)

States	GARP		
	1 km	4.5 km	18 km
KS	23,959.6	119,647.3	133,352.6
OK	66,103.8	165,849.6	168,024.3
AK	120,600.0	137,046.0	137,353.2

	Maxent		
	1 km	4.5 km	18 km
KS	39,408.0	136,044.8	120,016.8
OK	57,041.2	158,958.3	154,021.6
AK	97,111.0	136,169.7	120,350.2

Altering the resolution at which the models were projected (as compared to that in which they were trained) had little effect, regardless of the algorithm used. For example, the three projections (i.e., 1 km, 4.5 km, and 18 km) produced from 18 km resolution data only differed at most by 0.1 percent of the area predicted present when using Maxent and by 0.94 percent of the area predicted present when using GARP.

In general, Maxent models predicted less suitable area and had less uniform coverage compared to those models produced with GARP. For example, the 18 km Maxent projection (derived from 18 km training data) estimated suitable habitat in 33 states (counting D.C.) with 13.68 percent of area predicted habitable. The 18 km GARP projection, on the other hand, only predicted suitable habitat in 25 states but predicted 15.89 percent of area as habitable (Fig. 2.2). This may be a reflection of the underlying mechanics of Maxent, as the algorithm tends to give very large probability distribution values for environmental conditions outside the range present in the study area (Phillips *et al.*, 2006). A separate Maxent output type ('clamping') identifies such areas; for example, a few small areas of California, Oregon and Washington were specified as suitable in the Maxent models but were also designated as 'clamped' regions.
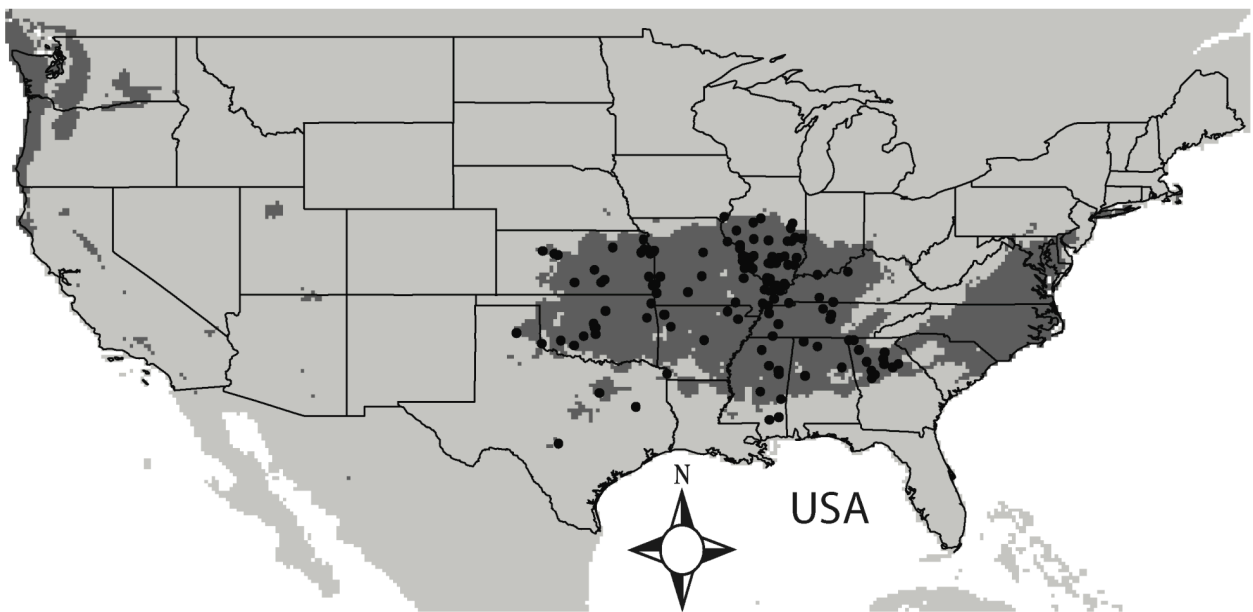
GARP
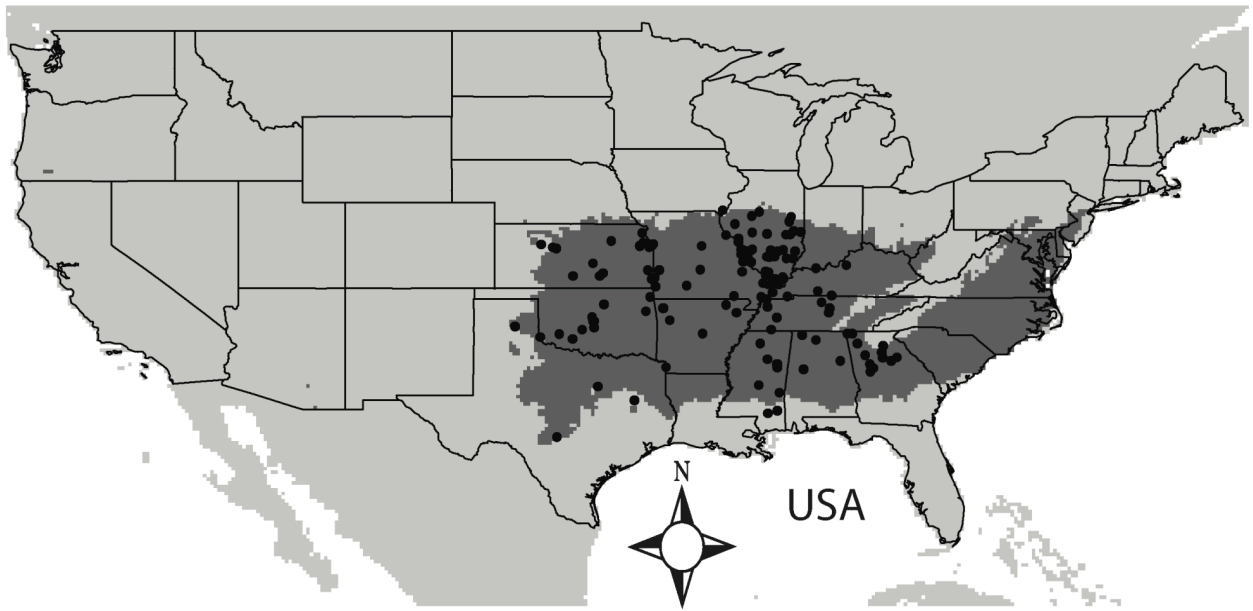
Maxent

Fig. 1.2. Thresholded GARP and Maxent 18 km projections; occurrence points used to train the models are included.

The 4.5 and 18 km resolution occurrence data produced models that fairly accurately mirror the distribution of the brown recluse, as our current knowledge stands (Fig. 1.2). The Maxent and GARP outputs do differ in some respects from the maps of Vetter (2005, 2008). The ecological niche models predicted suitable habitat on the east coast (e.g., MD, DE, NJ, VA, NC, and SC), when the eastern-most extent of the brown recluse's range is thought to be Kentucky, Tennessee, and the southwestern portion of Ohio (Vetter, 2005, 2008). This discrepancy either denotes a true error of commission (the area is *not* suitable to the species) *or* the models are correct, and the brown recluse is not found on the east coast because of potential barriers (i.e., biological or historical) or limited dispersal abilities. Possible omission errors include the southern portions of Louisiana and Mississippi, where the brown recluse is thought to reside, and parts of Texas (NB: recent study of the southern portion of the range of the brown recluse has suggested the species may not extend as far south as the map of Vetter (2008); see Vetter (2009) for details. Thus, the potential omission errors mentioned above may reflect the actual distribution of the brown recluse).

1.5 Discussion and conclusions

Natural history museum collections house a rich collection of data (Suarez & Tsutsui, 2004), but very little of it has been put into a format (i.e., assigned geographic coordinates) usable in modern analyses (e.g., ecological niche modeling). However, the field of biodiversity informatics and data sharing has seen promising advances in the past several years (Edwards, 2004), so the expectation is that data

with various degrees of accuracy will be increasingly available to researchers. We examined how error in point locality data, often introduced by retrospective georeferencing, influences ecological niche modeling, and we specifically analyzed how model quality was affected by the decision to use fewer, high-accuracy occurrence points versus a greater number of points with more uncertainty and error, a dilemma often encountered when working with museum data. Our study georeferenced and assigned error to museum data using the latest techniques; three error filters were used (1, 4.5, and 18 km), which are likely representative of the typical error found within museum locality data. Our study differs from most previous studies in that the error associated with each locality is accurately denoted, rather than artificially inserted into the dataset.

We found that the quality of our models increased when using a greater number of lower resolution points. Similarly, but without taking into account the resolution issue, Stockwell and Peterson (2002b) showed that increasing model accuracy was obtained with increased sample sizes. Our study shows that models produced with fewer, high-resolution points (quality vs. quantity) tended to distort and reduce the predicted distribution of the brown recluse. Furthermore, the GARP algorithm did not fare well with the 1 km, low sample size data: the projections experienced low model agreement probably due to over-fitting occurring in the training region. In this respect, Maxent performed better with fewer locality points. Our results indicate that the GARP and Maxent algorithms may be robust to at least some location error, a result also obtained by Fernandez *et al.* (2009) using artificially degraded data. Our study differs in that we matched georeferencing error with scale of climatic predictors used in ENM, instead of mixing different errors with a single resolution climatic

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dataset. A rising concern (as noted by Graham *et al.*, 2008) is that the niche models themselves may be imprecise if error does not affect model quality. We contend, as Graham *et al.* (2008) did, that this does not appear to be the case, as indicated by our accurate-appearing models and highly statistically significant partial AUC ratios.

Our results differ from Engler *et al.* (2004), who found that model quality decreased with decreasing spatial accuracy and from Graham *et al.* (2008), who found that although accurate models can be produced from datasets with introduced spatial error, the resulting models are of lower quality than those produced with non-degraded data. The latter study did not vary the number of input points (i.e., they did not look at the trade-off between quantity of occurrence points and quality), which may explain our differing results. The former study, which did analyze the trade-off between quantity of occurrence points and quality of points, used a non-mobile, habitat-specific plant (*Eryngium alpinum*) as their study organism. Degraded data may significantly alter model results depending upon the scale of the study and nature of the study organism. For example, locality error may alter model quality if the species is only found in certain microhabitats or if the study is smaller in scale (Meyer, 2007). Those researchers wishing to model species distributions (SDM) rather than model ecological niches (ENM) (for a discussion of the differences between the two, see Peterson, 2006) will require higher resolution points with less error. Larger-scale studies (e.g., continental or regional) do not necessitate as high of quality of points and some error can be tolerated and still provide usable results. The present study falls into the latter category, where increasing the number of locality points increased the spatial scale of the study and allowed for a more complete

characterization of the ecological niche (Peterson, 2006). More research is needed to assess when degraded locality data should or should not be used.

Our study has interesting implications for the use of ENM in the fossil record (Peterson *et al.*, 2004; Stigall-Rode & Lieberman, 2005; Maguire & Stigall, 2009). Most paleontological studies are performed at lower spatial resolutions (usually a necessity because of the limits of resolution in the fossil record; see Schindel, 1980; Sadler, 1981; Dingus & Sadler, 1982; Dingus, 1984; Lieberman, 2000) than studies on extant organisms. Our findings suggest the lower resolution paleontological data may not necessarily lower the model quality (as is typically perceived) if a sufficient number of occurrence points are utilized.

We find that museum locality data, although often imprecise, can be employed in ecological niche modeling to produce reliable results. Research in this area, however, is far from complete. Our study examined the effects of error up to 18 km; further research could investigate larger error treatments (i.e., when do the scales tip in favor of quality versus quantity and vice versa and in what situations/scales of study?). Additionally, we only examined two, presence-only model-building techniques, and it would be valuable to investigate whether other modeling algorithms handle error in a similar manner.

Our study highlights the importance of quantifying the error associated with locality data, which increases transparency and allows for the correct partitioning of data based upon the nature of a study. We demonstrate the need for adequate sampling of a species range, especially if the species is relatively widespread, and we emphasize that knowing the limits/error of data used in modeling species distributions

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is essential, especially when addressing important questions relating to conservation and the impacts of climate change on species.

1.6 Acknowledgements

CHAPTER 2 | First fossil *Molinaranea* Mello-Leitão 1940 (Araneae:

Araneidae), from middle Miocene Dominican amber, with a phylogenetic and

palaeobiogeographic analysis of the genus

Chapter Overview

The first fossil *Molinaranea* is described, from middle Miocene Dominican amber. This record extends the known range of the genus back 16 million years; it also extends the geographical range of the genus through time, with extant species known only from Chile, Argentina, the Falkland Islands, and Juan Fernandez Island. A parsimony-based phylogenetic analysis was performed, which indicates the fossil species, **M. mitnickii sp. nov.***,* is nested with *M. magellanica* Walckenaer, 1847 and *M. clymene* Nicolet, 1849. A modified Brooks Parsimony Analysis was conducted in order to examine the biogeography and origins of the fossil species in the Dominican Republic; the analysis suggests *Molinaranea mitnickii* arrived in Hispaniola from South America as a result of a chance dispersal event.

2.1 Introduction

Amber from the Dominican Republic has been known to the Western world since the second voyage of Christopher Columbus to the West Indies (Sanderson & Farr, 1960), but its inclusions were not examined for at least another four centuries. Since then, extensive study of Dominican amber inclusions has provided insight into the diversity of life and palaeoecology at, and spanning, the time of resin extrusion (e.g. Perez-Gelabert, 2008). The resin was probably deposited in a single sedimentary basin during the early to middle Miocene (16–19 Mya), although the exact age is still a matter of debate (Iturralde-Vinent, 2001; see Poinar & Poinar, 1999 for an alternative view). Much of the amber comes from the northern Dominican Republic in the La Toca Formation, a 300 m thick rock sequence characterized by siltstone and lignite lenses. Dominican amber was produced by the extinct tree *Hymenaea protera* Poinar, 1991, a member of the Fabaceae.

The first Dominican amber spider was described by Ono (1981) and placed in the family Thomisidae Sundevall, 1833. There are now around 170 fossil spider species described from Dominican amber, most of which were described by Wunderlich (1988). Wunderlich (1988) was the first to describe spiders from Dominican amber belonging to the family Araneidae Simon, 1895. The Araneidae are ecribellate, entelegyne spiders with eight eyes in two sub-equal rows (Jocqué & Dippenaar-Schoeman, 2007). Here we describe a new araneid species from Dominican amber. It represents the first fossil record of *Molinaranea* Mello-Leitão, 1940 and extends the known range of the genus back 16 million years. The presence of this genus in the Dominican Republic in the middle Miocene also extends the geographic range of *Molinaranea* through time; extant species are known only from Chile, Argentina, the Falkland Islands, and Juan Fernandez Island. A parsimony-based phylogenetic analysis was conducted on the seven extant taxa and the newly described fossil species, followed by a preliminary biogeographic analysis.

2.1.1. Fossil Record of Araneidae

The oldest described araneid comes from the Lower Cretaceous amber of Álava, Spain (Penney & Ortuño, 2006). Other fossil species have been described from upper Cretaceous (Turonian) New Jersey amber (Penney, 2004), the Jehol (Cretaceous) and Shanwang (Neogene) biotas of China (e.g. Chang, 2004 and Zhang *et al.*, 1994, respectively), Baltic amber (mid-Eocene to early Oligocene) (e.g. Petrunkevitch, 1942), the Messel Oil Shales of Germany (lower Eocene) (Wunderlich, 1986), Florissant Insect Beds (Tertiary) (e.g. Scudder, 1890), Quesnel Tertiary Beds in Canada (Scudder 1878), the Öhningen of Switzerland (Neogene) (Heer, 1865), and

Dominican and Mexican Chiapas amber (e.g. Wunderlich, 1988). An araneid reported from early Cretaceous Lebanese amber (upper Neocomian–basalAptian) (Wunderlich, 2004) is likely a misidentification according to Penney & Ortuño (2006), as is a juvenile described from Siberian amber (late Cretaceous) by Eskov & Wunderlich (1994). Orb-weavers have also been reported from Cretaceous Canadian amber (middle Campanian), but these have not been described or confirmed (McAlpine & Martin, 1969). The strictly fossil spider family Juraraneidae Eskov, 1984 described from a Jurassic non-amber fossil (which would pre-date all the above) has been suggested as being synonymous with Araneidae, although this has yet to be confirmed (Penney & Selden, 2006).

2.2 Material

The specimen was kindly donated to DP by Keith Luzzi, who obtained it during a visit to the La Toca region of the Dominican Republic. The amber had been cut and polished prior to being received by the authors. Further cutting and polishing was carried out in the laboratory of Dr Michael Engel (University of Kansas) in order to reveal morphological characters. Drawings were done under both incident and transmitted light with the aid of a camera lucida attached to a Leica MZ16 stereomicroscope. Drawings were then scanned and traced in Adobe Illustrator. Photographs were taken with a Leica DFC290 digital camera attached to a Leica M205C microscope. All measurements were taken with an ocular graticule and are in millimeters.

2.2.1. Preservation

The specimen is preserved in a piece of clear amber measuring 14 ×13 × 8 mm in size. The original piece had a small mycetophilid (fungus gnat) and mymarid wasp (Hymenoptera: Chalcidoidea: Mymaridae) (Michael Engel, pers. comm. 2008) as syninclusions that were later removed in order to observe the spider more clearly. The legs and antennae of a cockroach (Order Blattaria) (Vincent Perrichot, pers. comm. 2008) also co-occur with the spider. Small pieces of unidentified organic matter are present within the amber. A band of air bubbles spans diagonally across the spider. There are no fractures within the piece. During preparation, but before the authors received the specimen, the patella and distal portion of the femur of the left, first leg were ground away. The spider appears desiccated and almost flattened, and the right, fourth leg is detached and moved to the left side of the spider (Figs. 2.1A & 2.2A,C). The palps of the specimen are slightly twisted, which probably occurred when the spider was engulfed in resin. Careful observation revealed threads of silk wrapped around the spider's palps, legs, and body. Silk can also be seen emerging from the spinnerets. The tibiae of legs 1 and 2 are flattened and appear to widen distally; this is probably a result of desiccation prior to entombment in resin. Further, the macrosetae appear to arise from cuticular protrusions. While extant members of *Molinaranea* possess macrosetae that arise from strong bases, the particularly prominent, tubercle-like bases in *M. mitnickii* probably result from fossilization processes. Otherwise, the specimen is extremely well preserved. The holotype (along with the detached syninclusions) is deposited in the University of Kansas Natural History Museum, Division of Entomology.

2.2.2. Abbreviations

Leg formula (e.g. 1423) indicates the length of each leg relative to the other legs from longest to shortest (in the example, 1 is the longest, followed by leg 4). Anatomical abbreviations: A = terminal apophysis, ALE = anterior lateral eyes, AS = anterior spinneret, at = anal tubercle, bl = book lung, C = conductor, co = colulus, cx = coxa, cy = cymbium, E = embolus, en = endite, fe = femur, la = labium, ma = median apophysis, MS = median spinneret, mt = metatarsus, op = opisthosoma, pc = paracymbium, PLS = posterior lateral spinneret, ps = prosoma, pt = patella, sa = subterminal apophysis, sp = spiracle, sr = sternum, st = subtegulum, tf = thoracic furrow, ti = tibia, tr = trochanter, ts = tarsus. Institutional abbreviations: AMNH = American Museum of Natural History, MCZ = Museum of Comparative Zoology, Harvard University.

2.3 Systematic Paleontology

Order ARANEAE Clerck, 1757

Family ARANEIDAE Simon, 1895

Remarks: Scharff & Coddington (1997) found four synapomorphies that support the monophyly of Araneidae. Our specimen shows three of these: the mesal orientation of the cymbium, possession of a radix, and the wide separation of lateral eye groups from the medians. The fourth, a narrow posterior median eye tapetum, is not visible in the fossil specimen. A grooved booklung cover supports the monophyly of the Araneidae apart from *Chorizopes* Pickard-Cambridge, 1870 (Scharff & Coddington, 1997), and this character is also present in our specimen. Further, possession of a globose abdomen that overhangs the carapace, three tarsal claws, six simple

spinnerets, and numerous spines on the legs are all traits commonly found in both the Araneidae and our specimen.

Molinaranea Mello-Leitão, 1940

Type species: Molinaranea molinai Mello-Leitão, 1940

Diagnosis: See Levi (2001).

Distribution: Recent species are found in Chile, Argentina, the Falkland Islands, and Juan Fernandez Island. The fossil species is found in Dominican Republic amber (this paper).

Remarks: Molinaranea was created as a monotypic genus by Mello-Leitão in 1940; the gender is feminine. Levi (2001) used the paramedian apophysis to help distinguish between genera of Araneidae, a structure that is unfortunately not discernable in our specimen. A filiform (thread-like) embolus is visible adjacent to the conductor, however, and distinguishes our specimen from members of *Parawixia* Pickard-Cambridge, 1904 and *Ocrepeira* Marx, 1883, which have robust emboli. Furthermore, our specimen can be placed with confidence within *Molinaranea* for the following reasons: The median apophysis is prominent, forked, and projects away from the palpal bulb. While this morphology occurs in other genera, such as *Parawixia, Spilasma* Simon, 1897 and *Ocrepeira* (Levi, 1992, 1993, 1995), the details differ from those in our specimen. For example, our specimen and members of *Molinaranea* have prongs that do not re-curve as prominently as those in members of *Ocrepeira.* In those members of *Ocepeira* that do have median apophysis prongs, the prongs are usually of unequal thickness, differing from the quasi-equal prong widths

in *Molinaranea* and our specimen (Levi, 1993). Members of both *Ocrepeira* and *Parawixia* have median apophyses that typically thicken distally, whereas members of *Molinaranea* and our specimen thin distally (Levi, 1992, 1993). Members of these same genera also possess many processes, bumps and/or indentations on the median apophysis, unlike the smoother median apophyses present in *Molinaranea* and our specimen. Additionally, many *Parawixia* species with forked prongs on the median apophysis possess numerous (more than 3) tubercles on the opisthosoma (more than the two present in our specimen). In *Spilasma,* the median apophysis is commonly trifid distally, with relatively short prong lengths, unlike the bi-forked prongs in *Molinaranea.* Male members of *Spilasma* also possess a ventral, sclerotized area extending from the sides of the pedicel to the genital groove (Levi 1995), a feature lacking in our specimen.

Molinaranea mitnickii n. sp.

Figures 2.1– 2.3

Material examined: Holotype and only known specimen: Amber Fossil Collection, University of Kansas Natural History Museum KU-NHM-ENT, DR-018, adult male, Dominican amber, La Toca mines, northern Dominican Republic; coll. TerraTreasures.

Diagnosis: Molinaranea mitnickii can be distinguished from all other species by the median apophysis with long, thin/spindly, sub-equal prongs, resembling a lop-sided wishbone, with a proximal lobe/elbow. The ventral femora of legs 1 and 2 possess a row of strong macrosetae.

Etymology: The specific epithet is after Justin Mitnick, nephew of Keith Luzzi, the owner of TerraTreasures who found and donated the specimen for study.

Description: Body length 6.95. Carapace 2.82 long, 2.0 wide, ≥ 1.88 tall; pars cephalica only slightly elevated (approximately 0.42). Eyes small; ALE appear to be on small tubercles; numerous macrosetae in the ocular region. Details of chelicerae and fangs obscured; small. Sternum 1.41 long, 1.04 wide; relatively short and rounded; lateral margins project between coxae. Endites 0.38 long, longer than wide, sub-oval, tooth present. Labium 0.38, as wide as long, sub-oval to sub-circlular. Petiole attached 0.95 from anterior of opisthosoma immediately above book lungs; not sclerotized. Opisthosoma 4.13 long including spinnerets (Fig. 2.2D), 3.6 long without spinnerets, 2.23 at widest point, height uncertain due to flattened nature of specimen; likely elongate and sub-oval in life; dorsal surface bears abundant, long, scattered setae; concentrated setae on two anterior tubercles (Fig. 2.1B). PLS longer than MS and AS, PLS defined in two segments (Fig. 2.2E); AS 0.43 and PLS 0.51; colulus present, tongue-shaped with 9 setae. Spiracle situated 0.03 anterior to co and 0.13 to base of AS; anal tubercle 0.34.

   Leg formula 2143; leg 1 cx 0.52, tr 0.30, fe 3.16, pt 1.07, ti 4.13, mt 2.17, ts 0.63, total 11.98; leg 2 cx 0.50, tr 0.28, fe 3.44, pt 0.90, ti 4.13, mt 2.36, ts 0.64, total 12.25; leg 3 cx 0.42, tr 0.28, fe 2.36, pt 0.82, ti 1.25, mt 1.26, ts 0.48, total 6.87; leg 4 cx 0.45, tr 0.14, fe 2.43, pt 0.98, ti 2.10, mt 2.03, ts 0.46, total 8.59. Legs long; all legs possess strong macrosetae (Figs. 2.1 & 2.2A–B); macrosetae originate from strong cuticular bases; variable in length, longer macrosetae 0.7–0.8, shorter macrosetae 0.4–0.6; longer macrosetae appear to be concentrated on the lateral margins of tibiae

1and 2 and ventral surfaces of most leg segments, although this is variable; row of macrosetae on prolateral to ventral margin of tibia 1 and 2; row of 7–10 macrosetae on inferior surface of femora of legs 1 and 2; row of 3–4 macrosetae on superior surface of femora of legs 1 and 2; femora of leg 1 with lateral row of 7–8 macrosetae; scattered macrosetae, semi-aligned, on ventral femora of legs 3 and 4; tibia and femur of legs 1 and 2 thicker and more robust. Hook on distal margin of the first coxa; fourth coxa with at least one macroseta. Paired tarsal claws with teeth, unpaired claw simple.

Palps large (Figs. 2.1 & 2.2F); length of palpal bulb without median apophysis ≥ 1.09, width 0.79; median apophysis with bifurcation into long, thin spindly prongs (Figs. 2.2A,F & 2.3), resembling a wishbone; median apophysis 1.41 long; prongs on median apophysis equal, with re-curved, semi-pointed tip; median apophysis with proximal lobe or elbow; embolus distally filiform and situated between conductor and terminal apophysis (Fig. 2.3); conductor broader than terminal apophysis and attached in middle of bulb with a semi-pointed tip; subterminal apophysis present as a narrow band between embolus and terminal apophysis (Fig. 2.3); terminal apophysis lobate to truncate and narrow, larger than subterminal apophysis (Fig. 2.3); one macroseta on patella.

Female: Unknown.

Distribution and age: Dominican Republic amber; probably middle Miocene (16 –19 Mya) (see Iturralde-Vinent, 2001).

Remarks: The species can be distinguished from *M. vildav* Levi, 2001 by the presence of a proximal lobe or elbow below the radix of the median apophysis (Fig. 2.3) instead of above it, by the curved tip on the lower prong of the median apophysis, and by the prongs which appear more separated (like a wishbone) in *M. mitnickii* than in *M. vildav*. Further, *M. mitnickii* possesses a row of macrosetae on the ventral surfaces of femora 1 and 2, unlike in *M. vildav*. The length of the median apophysis prongs distinguishes *M. mitnickii* from *M. vildav, M. mammifera* Tullgren, 1902, and *M. clymene* Nicolet, 1849 (significantly shorter in *M. vildav, M. mammifera* and *M. clymene). M. mitnickii* lacks the short, wide median apophysis characteristic of *M. mammifera* and the tufts of setae on the abdomen that are present in *M. clymene* (Levi, 2001, figs. 27 & 30). Unfortunately, much of Levi's description and diagnostic characters are based on color pattern, which is usually not discernible in amber specimens.
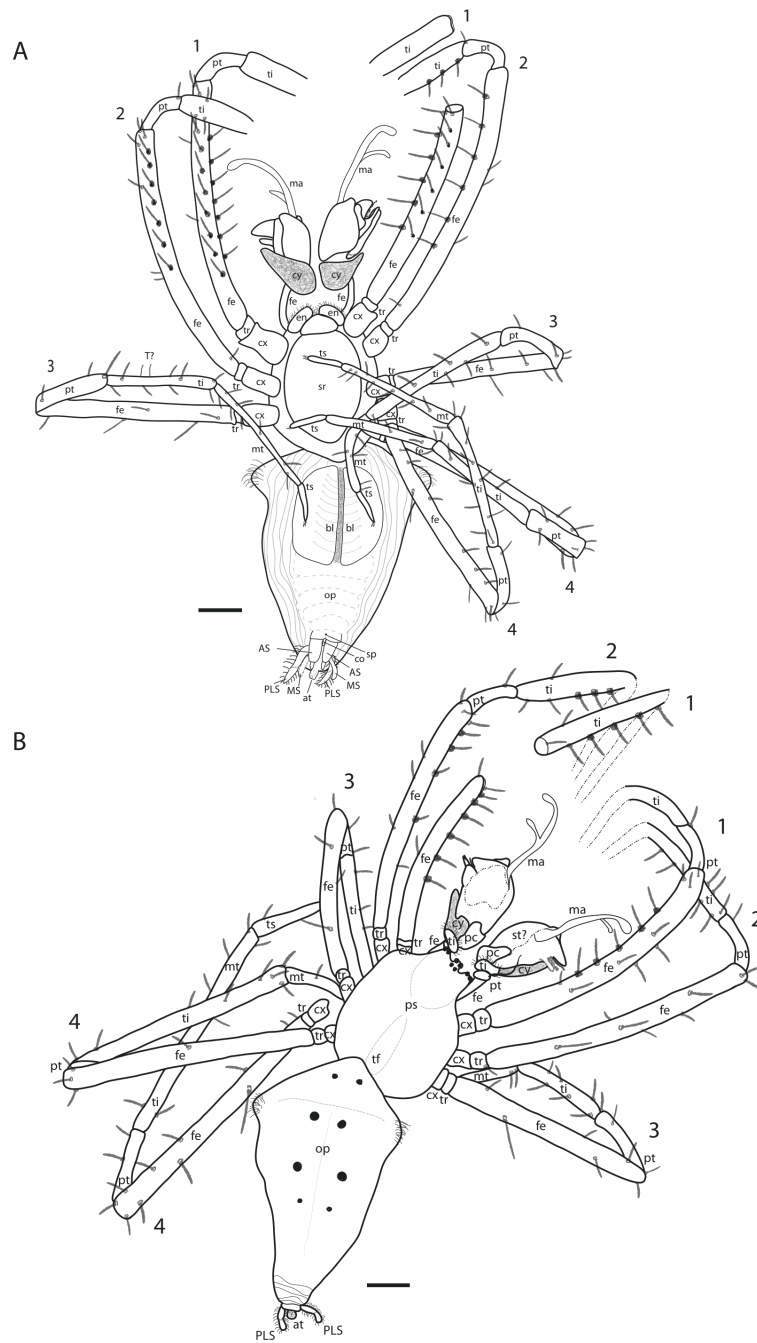
Fig. 2.1 A–B. Interpretive drawings of **_Molinaranea mitnickii_ n. sp.**, holotype KU-NHM-ENT, DR-018. **A.** ventral view. Note that legs 1 and 2 are not drawn past the patella; see Fig. 2.2B for details; **B.** dorsal view. Scale bar: 0.5 mm.
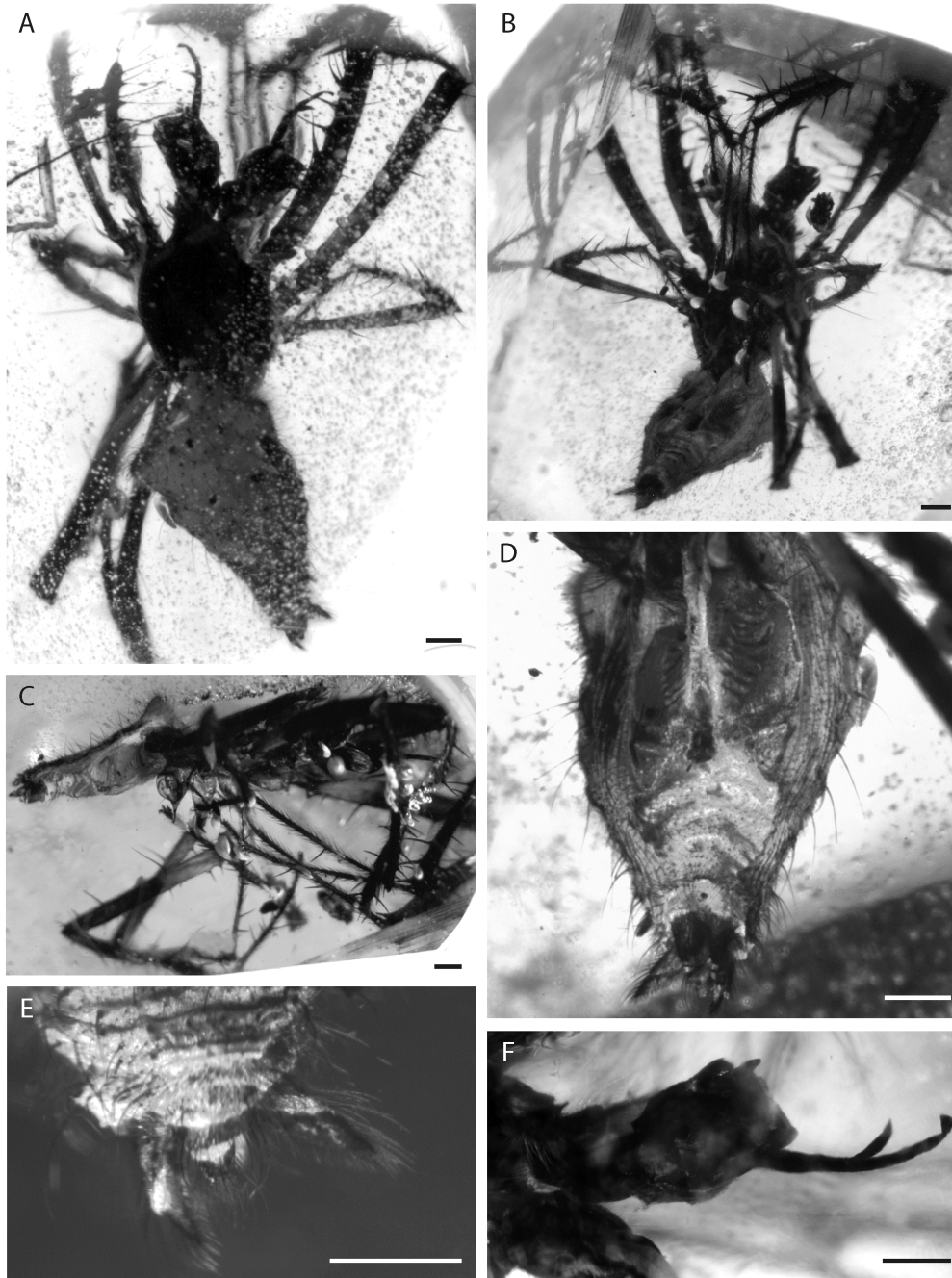
Fig. 2.2 A–F. *Molinaranea mitnickii* **sp. nov.**, holotype KU-NHM-ENT, DR-018. **A.** dorsal view; **B.** ventral view; **C.** lateral view; note how the specimen appears flattened; **D**. ventral view of opisthosoma; the opisthosoma appears desiccated; the spiracle is visible and situated anterior to the spinnerets; the booklungs are grooved; **E.** view of anal tubercle and posterior lateral spinnerets; **F.** lateral view of left palpus; the long, bifurcating median apophysis prongs are clearly visible; although the top prong may appear longer, this is not so. Scale bars = 0.5 mm.
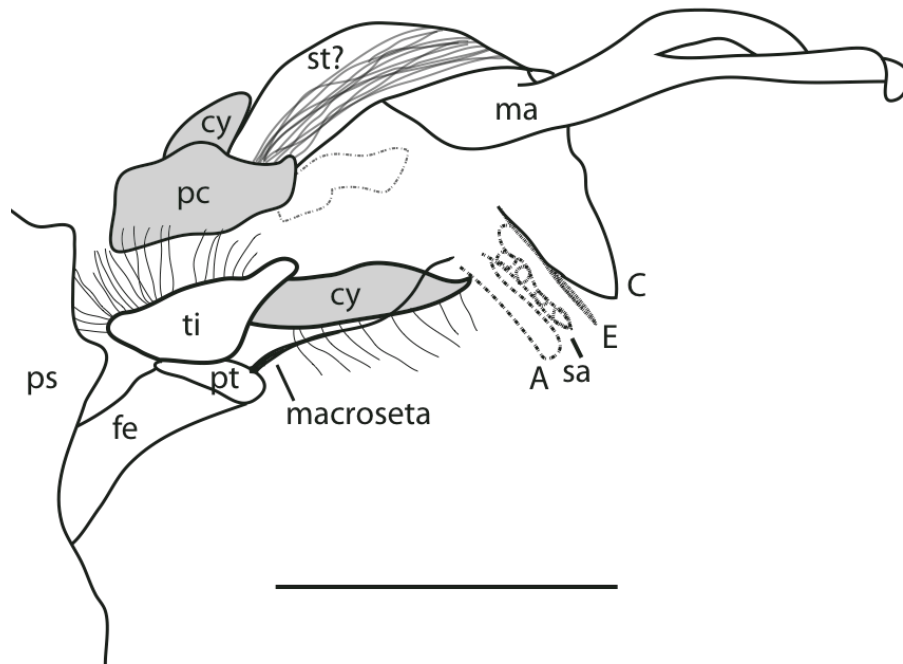
Fig. 2.3. Interpretive drawing of the lateral view of the right palpus. The cymbium is depicted as two segments because it is splayed behind the palpal bulb (but is one cohesive structure). The bump immediately behind the median apophysis is likely the tegulum. Setae on the tibial margin are not fully illustrated. Scale bar = 1 mm.

2.4 Phylogenetic Analysis

2.4.1. Taxa Analyzed

Molinaranea clymene Nicolet, 1849; ♂ from Chile, Osorno Prov., Puyehue, 500 m,

MCZ 76602 (coll. L.E. Peña, 26.I.1969); ♀ from Chile, Osorno Prov., Termas de

Puyehue, MCZ 76601 (coll. H. Levi, 10.III.1965).

Molinaranea fernandez Levi, 2001; ♀ (holotype) & ♂ (allotype) from Chile, Juan

Fernandez Island, Mas a Tierra, Valle Anson, Plazoleto de Yunque, 200–250 m,

AMNH (coll. B. Malkin, 1–28.IV.1962); ♂ & ♀ allotypes from Juan Fernandez

Islands, Mas a Tierra, Valle Anson, Plazoleto de Yunque, 200–250 m, Camote Side,

AMNH (coll. Borys Malkin, 1-28.IV.1962).

Molinaranea magellanica Walckenaer, 1847; ♂ from Chile, Osorno Prov., Puyehue,

500 m, MCZ 69796 (coll. L.E. Peña, 26.I.1969); ♂ from Chile, Llanquihue Prov.,

Correntoso, MCZ 79160 (coll. L. Peña, XII.1968); ♂ from Chile, Magallanes,

Laguna Amarga, Natales, MCZ 79161 (coll. L. Peña, 14–21.XII.1960); ♂ from

Chile, Llanquihue Prov., Chemisa, MCZ 79162 (coll. L. Peña, 13.XII.1968); ♀ from

Chile Cautín, Villarrica, MCZ 76600 (coll. H. Levi, 3.III.1965), and ♀ from Chile,

Concepcion Prov., Rio Andalien, AMNH (coll. German Munoz, 10.IV.1977).

Molinaranea mammifera Tullgren, 1902; ♂ from Chile, Osorno Prov., 7.7 km

north-east of Termas de Puyehue, Valdivian rainforest, AMNH (coll. A. Newton &

M. Thayer, 19–25.XII.1982); ♂ from Chile, Osorno Prov., Parque Nac., Puyehue, 4.1

km east of Anticura, 430 m, trap site 662, AMNH (coll. A. Newton & M. Thayer, 19–

26.XII.1982); ♀ from Chile, Conception Prov., Ramuntcho, MCZ 76599 (coll.

Cekalovic, 22.III.1975), and ♀ from Chile, Palena Prov., Chaiten, 0–100 m, AMNH

(coll. N.I. Platnick & R.T. Schuh, 4.XII.1981).

Molinaranea phaethontis Simon, 1896; ♂ from Chile, Santiago Prov., El-Manzano, AMNH (coll. L.E. Peña, 13.X.1982); 2 ♀♀ from Chile, Region de la Araucaría (IX), Melleco Prov., Malalcahuello, AMNH (coll. L.E. Peña, 9–15.XII.1985).

Molinaranea surculorum Simon, 1896; ♂ from Chile, region del Bío-Bío (VIII), Bío-Bío Prov., El Manzano, near Contulmo, AMNH (coll. L.E. Peña, 15.XII.1985); 2 ♂♂ & ♀ from Chile, Nuble Prov., Las Cabras, AMNH (coll. L. Umana, 26–28.XII.1986); ♂ from Chile, Valdivia, Santo Domingo, AMNH (coll. E. Krahmer, 19.IX.1976); ♂ from Chile, Region de Los Lagos (X), Valdivia Prov., Purolón, north-west of Panguipulli, AMNH (coll. L.E. Peña, 10.I.1985); ♂ from Chile, Osorno Prov. coast, Pucatrihue, MCZ 76598 (coll. L. Peña, I.III.1968); ♀ from Chile, Osorno Prov., Osorno Coast, MCZ 76597 (coll. L.E. Peña, I–III.1968), and ♀ from Chile, Valdivia, AMNH (coll. E. Krahmer, 5.XII.1976).

Molinaranea vildav Levi, 2001; ♂ & ♀ from Chile, Valdivia, AMNH (coll. E. Krahmer, 8.XII.1976); ♀ (holotype) from Chile, Valdivia Prov., Valdivia, AMNH (coll. E. Krahmer, 15/20.XI.1978).

Parawixia bistriata Rengger, 1836; ♂ & ♀ from Argentina, Tucuman, MCZ 78553 (coll. J.A. Kochalka, 30.XI.1986).

Parawixia rigida Pickard-Cambridge, 1889; ♀ from Costa Rica, Heredia, La Selva,

near Puerto Viejo, MCZ 81173 (coll. W.G. Eberhard, 31.I.1981); ♂ from Costa Rica,

Puntarenas, Osa Peninsula, Sirena, MCZ 81174 (coll. W.G. Eberhard, 31.I.1981).

Parawixia rimosa Keyserling, 1892; ♀ from Columbia, Huila, 19.3 kilometers east

of Sta. Leticia, MCZ 80109 (coll. W.G. Eberhard, 29.II.1976); ♂ from Columbia,

San Pedro, Sierra Nevada de Santa Marta, MCZ 80978 (coll. J. Kochalka, 3.IV.1975).

NB: additional members of *Parawixia, Ocrepeira,* and *Spilasma* were also examined

within the course of this study, primarily to delineate amongst palpal structures.

Table 2.1. Character Matrix

Taxon/Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
M. fernandez	1	1	0	0	0	0	1	0	0	1	1	0	1	0	1	0	0	1	1
M. magellanica	2	1	1	1	1	1	1	2	2	2	2	0	1	0&1	2	0	0	1	1
M. clymene	0	1	1	0&1	1	1	1	2	2	2	2	0	1	0&1	2	0	0	0	1
M. vildav	0	1	0	1	1	1	1	0	0	2	2	0	1	0	2	0	0	0	0
M. surculorum	1&3	0	0	0	1	1	1	1	1	2	2	0	1	0	0	0	0	0	1
M. phaethontis	1	1	1	1	0	1	0	1	1	2	2	0	1	0	1	0	0	0	1
M. mammifera	0	1	1	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	1
M. mitnickii	0	1	?	1	1	1	?	2	2	1	1	0	1	?	2	0	0	?	?
P. bistriata	3	0	1	0	0	1	1	2	2	2	2	1	0	0	1	0	0	0	0
P. rigida	0	0	1	0	0	1	1	2	2	2	2	0	0	0	1	1	1	1	0
P. rimosa	3	0	1	0	0	1	1	0	2	2	2	0	0	0	1	1	1	0	0

2.4.2. Methods

The data matrix (Table 1) was analyzed using PAUP v.4.0 (Swofford, 1998). Eleven species were included in this analysis. The genus *Parawixia* (Araneidae) was chosen as the outgroup, using *P. bistriata* Rengger, 1836, *P. rigida* Pickard-Cambridge, 1889, and *P. rimosa* Keyserling, 1891 as representative members, because Levi (2001) posited this genus is closely related to *Molinaranea*. This suggestion was based on five synapomorphies *Molinaranea* shares with *Parawixia, Ocrepeira,* and *Eriophora* Simon, 1864, including an unusually long scape and median apophysis, the attachment of the median apophysis above the radix, the proximal sculpturing of the median apophysis at its insertion above the radix, and a projection of the median apophysis away from the palpal bulb (NB: both *M. clymene* and *M. magellanica* were originally misclassified as *Parawixia*). The fifth synapomorphy Levi (2001) mentioned, distal branching of the median apophysis, is often absent in *Parawixia* (and other genera); we therefore included in our analysis two members of *Parawixia* that lack this feature, *P. bistriata* and *P. rimosa,* and one that possesses it, *P. rigida. Parawixia bistriata* is a common colonial orb weaver found throughout Brazil, Bolivia, Paraguay, and northeast Argentina and occupies the area between the Dominican Republic (amber fossil locality) and Chile (extant *Molinaranea* range). *Parawixia rigida* is found throughout Central America, and *P. rimosa* is found in Columbia, Ecuador, Peru and southern parts of Central America. It should be noted that Scharff and Coddington (1997) did not include *Molinaranea* and *Parawixia* in their phylogenetic analysis of the Araneidae, and therefore did not address or confirm the sister relationship of these two groups.

An exhaustive search was performed to determine the most parsimonious tree for the data matrix. All nineteen characters were treated as unordered and unweighted; multistate taxa were treated as polymorphisms. Bootstrap and Jackknife analyses were conducted using 1000 replications in a heuristic, step-wise search that sampled five random trees per replication. Groups were retained that were compatible with the 50% majority rule consensus tree. A test for Bremer support was also performed (Bremer, 1988). All data were compiled into Nexus files using Mesquite v. 2.5 (Maddison & Maddison, 2008) and MacClade v. 4.08 (Maddison & Maddison, 2005). Tree graphics were created using FigTree v.1.1.2 (Rambaut 2008) and Adobe Illustrator.

2.4.3. Characters

Males were the primary provider of character data because the fossil specimen is male. Female character data was used to bolster and support the positions of the extant taxa. Character one presents some difficulty since *P. bistriata* and *P. rimosa* do not have prongs and therefore cannot be coded for prong state. There are essentially two ways to deal with this situation: these taxa can be coded as a "?" or they can be coded as a multistate, where a particular state would indicate lack of prongs. Coding inexplicable characters as a "?" can lead to impossible ancestral states and unjustified trees and generally should be avoided (Waggoner, 1996; Lieberman, 1998). Further, coding inexplicable characters as a "?" is equivalent to ignoring data, as we know there are no prongs present in these species (Waggoner, 1996). Therefore, we chose to code this character as a multistate, with state three equal to "no prongs". We acknowledge that in doing so this can decrease character independence and increase

the weight of certain characters. We coded character 1 as a polymorphism for *M. surculorum* because we observed specimens that both lacked and possessed prongs (NB: if the species was coded as only possessing prongs, the topology of the tree would not change). Additionally, *M. clymene* was coded as having equal prongs in character one, although Levi (2001) suggests this species possesses a longer lower prong. Character 6 was coded as a polymorphism for *M. clymene* because Levi (2001) stated the species possesses macrosetae on the ventral side of the fourth coxae, but we did not observe this in the specimen studied. Levi (2001) noted *M. phaethontis* Simon, 1896 lacks ventral setae on all its femora; however, rows of macrosetae were present on the third and fourth femora of the specimen we studied. Levi (2001) also stated the ventral femora of *M. fernandez* Levi, 2001 are clothed in double rows of short macrosetae; we found only the third and fourth femora to have rows of macrosetae in this species (note: both Levi and ourselves studied male allotypes of *M. fernandez* from the AMNH). Further, Levi (1992) indicated *P. rimosa* has a row of ventral macrosetae on the second femur, while we observed rows of macrosetae on all ventral femora except the first. Characters are listed below:

2.4.3.1. Male Characters:

1. median apophysis prongs, assuming bi-pronged — (no prongs = 3 / shorter upper prong = 2 / longer upper prong = 1 / equal prongs = 0)

2. prongs on median apophysis — (present = 1 / short or reduced [$\leq \sim 0.08$] = 0)

3. male opisthosoma shape — (hump above spinnerets = 1 / lacks distinctive hump = 0). The hump was defined by the ability to draw an imaginary horizontal line

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from the anterior tubercles (in lateral view) of the opisthosoma to the posterior-most point of the abdomen that would intersect at a ~ 90 degree angle with a vertical line drawn from the spinnerets to the same posterior point on the opisthosoma.

4. macrosetae on ventral side of fourth coxa — (present = 1 / absent = 0)

5. anterior opisthosoma tubercles — (concentrated setae present = 1 / lacks concentrated setae = 0)

6. opisthosoma setae — (opisthosoma clothed in long [≥ 0.15 mm] setae, usually projecting outward from abdomen = 1 / possesses short or no setae on opisthosoma = 0)

7. eye area with black/brown pigment — (present = 1 / absent = 0)

8. macrosetae arrangement on ventral/ventro-lateral side of first femur — (strong row present = 2 / scattered or weak row [but more than three] or combination of state 2 and 0 = 1 / no row of spines = 0)

9. macrosetae arrangement on ventral/ventro-lateral side of second femur — (strong row present = 2 / scattered or weak row [but more than three] or combination of state 2 and 0 = 1 / no row of spines = 0)

10. macrosetae arrangement on ventral/ventro-lateral side of third femur — (strong row present = 2 / scattered or weak row [but more than three] or combination of state 2 and 0 = 1 / no row of spines = 0)

11. macrosetae arrangement on ventral/ventro-lateral side of fourth femur — (strong row present = 2 / scattered or weak row [but more than three] or combination of state 2 and 0 = 1 / no row of spines = 0)

12. strong row of macrosetae on dorsal side of fourth femur — (present = 1 / absent or otherwise = 0)

13. filiform(thread-shaped) embolus — (present = 1 / absent or otherwise = 0)

14. posterior macrosetae on sternum — (present = 1 / absent = 0)

15. median apophysis length from base to longest prong tip — (≥ 1.40 = 2 / 0.84–1.18 = 1 / ≤ 0.67 = 0).

16. tubercles on opisthosoma — (≥ 4 = 1 / 0–3 present = 0)

17. macrosetae on ventral, fourth trochanter — (present = 1 / absent = 0)

2.4.3.2. Female characters:

18. posterior median plate of epigynum (see Levi, 2001, fig. 6) — (plate T-shaped in ventral view = 1 / Y-shaped or otherwise = 0)

19. stem of posterior median plate of epigynum — (stem of plate about as thick as the two wide lateral arms/projections = 1 / no defined stem or lateral arms or stem not as thick as lateral arms = 0)

2.4.4. Results

The parsimony analysis yielded two most parsimonious trees (Fig. 2.4) of 41 steps, with a Consistency Index (CI) of 0.6944 (excluding uninformative characters)

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and a Retention Index (RI) of 0.6944 (excluding uninformative characters). Our strongest nodes were those uniting *M. fernandez* /*M. Mammifera, P. rigida/P. rimosa,* and the whole of *Molinaranea*, which had Bootstrap and Jackknife values (Fig. 2.4) of 76 & 71, 71 & 64, and 91 & 83, respectively. The node uniting *M. fernandez*/*M. mammifera* and *P. rigida/P. rimosa* had a Bremer value of 1 (Bremer, 1988). We performed the test of Hillis (1991) (the g_1 statistic) to determine if our results departed from those generated using random data, which they did at the 0.01 level (g_1 value of -0.733936).

2.4.5. Discussion

The analysis resulted in an unresolved clade that includes *M. mitnickii* (fossil taxon), *M. clymene,* and *M. magellanica*, within a larger grouping of *M. fernandez, M. mammifera,* and *M. vildav* (Fig. 2.4)*. Molinaranea surculorum* was the most basal taxon. Neither the fossil taxon, *M. mitnickii,* nor what appears to be the most widespread taxon, *M. magellanica,* placed basally.
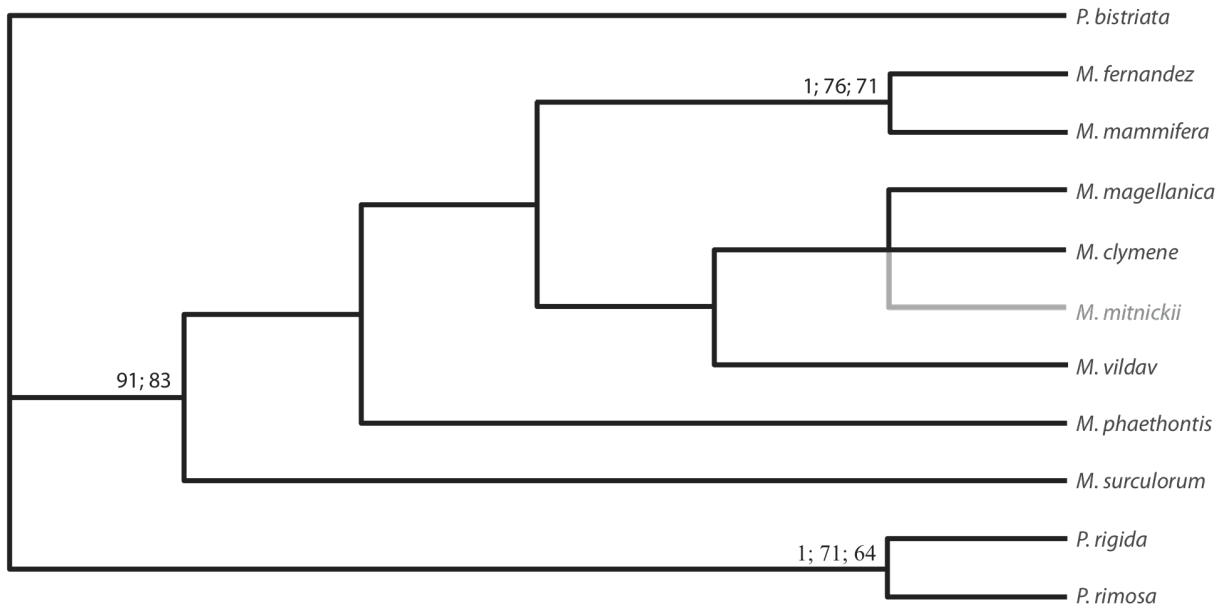
Fig. 2.4. Strict consensus cladogram resulting from the parsimony analysis. The fossil taxon, *M. mitnickii*, is depicted in light grey; note that it does not resolve basally but rather in the middle of the tree. The nodal values are from the statistical tests: the first is the Bremer Support value, the second is the Bootstrap value, and the third is the Jackknife value. Trees for the Bootstrap and Jackknife analyses were generated using 50% majority rule consensus.

2.5 Biogeographic Analysis

The genus *Molinaranea* has not been found in the fauna of the modern Dominican Republic or the surrounding areas. While this could reflect deficient knowledge of the spider diversity in the region, it is unlikely since members of *Molinaranea* are fairly large, conspicuous spiders and weavers of orb webs. The presence of *Molinaranea* in Dominican amber (middle Miocene in age) therefore presents an interesting palaeobiogeographical question, since extant members of the genus are currently found only in the southwestern portion of South America. There are three general explanations for the observed pattern: (1) the genus was originally endemic to the Dominican Republic region and dispersed to South America (with subsequent divergence), later becoming extinct in the Dominican Republic and surrounding region; (2) the genus was originally endemic to South America and dispersed to the

Dominican Republic where it speciated, later becoming extinct in the Dominican Republic and surrounding region; or (3) the genus was originally in South America and the Caribbean region (or was even more widespread), and divergence in the West Indies involved either vicariance or dispersal; members of the genus later became extinct throughout northern South America, the Caribbean, and any other areas. All three options must take into account the tectonic history of the region, which is a matter of contention among geologists (Dengo & Case, 1990; Donovan & Jackson, 1994; Hedges, 2001, 2006; Iturralde-Vinent & MacPhee, 1999; Iturralde-Vinent & Lidiak, 2006). According to Iturralde-Vinent (2006), only after the Middle Eocene was there a permanent landmass in the Caribbean that could provide a home for terrestrial biota. Donnelly (1992) and Hedges (1996c), however, while agreeing there was probably no continuous sequence of emerged land since the Cretaceous, speculated that some areas of Cuba, northern Hispaniola, and possibly Puerto Rico may have been exposed since the late Cretaceous. It should be noted, however, that strict continent-island vicariance *sensu* Rosen (1975, 1985) is problematic (see Iturralde-Vinent & MacPhee, 1999 for details).

We used our strict consensus tree to perform a preliminary biogeographic study using a modified Brooks Parsimony Analysis (Lieberman & Eldredge, 1996; Lieberman, 2000) to elucidate which of the above three hypotheses might be a viable explanation for the presence of *Molinaranea* in the Dominican Republic. Although the number of fossil taxa and areas involved limits this analysis, it is a first step towards understanding the biogeographic patterns implied by our phylogeny.

2.5.1. Methods

A detailed discussion of the methods involved in modified Brooks Parsimony is beyond the scope of this paper; see Lieberman & Eldredge (1996) and Lieberman (2000) for details. We created an area cladogram by replacing the taxa with the geographic area in which the taxa were found (Fig. 2.5). We used six areas: (1) Dominican Republic, (2) Juan Fernandez Island, (3) southwestern Chile and southwestern Argentina, (4) north/central South America, including Brazil, northeast Argentina, Paraguay, and Bolivia, (5) Central America, and (6) northwest South America, including Columbia, Ecuador, and Peru. Defining areas is problematic (see Lieberman, 2000 for a review on this topic); however, we defined our areas on both geological and biological grounds. The ancestral nodes of the area cladogram were then optimized using a modified Fitch parsimony algorithm (Fitch, 1971). The area cladogram was used to generate a geodispersal matrix, which provides insight into the relative time that barriers fell (allowing for expansion of taxa), and a vicariance matrix, which provides insight into the relative time that barriers formed (isolating taxa). Each matrix was analyzed in PAUP v.4.0 (Swofford, 1998) using an exhaustive search; characters were treated as ordered.
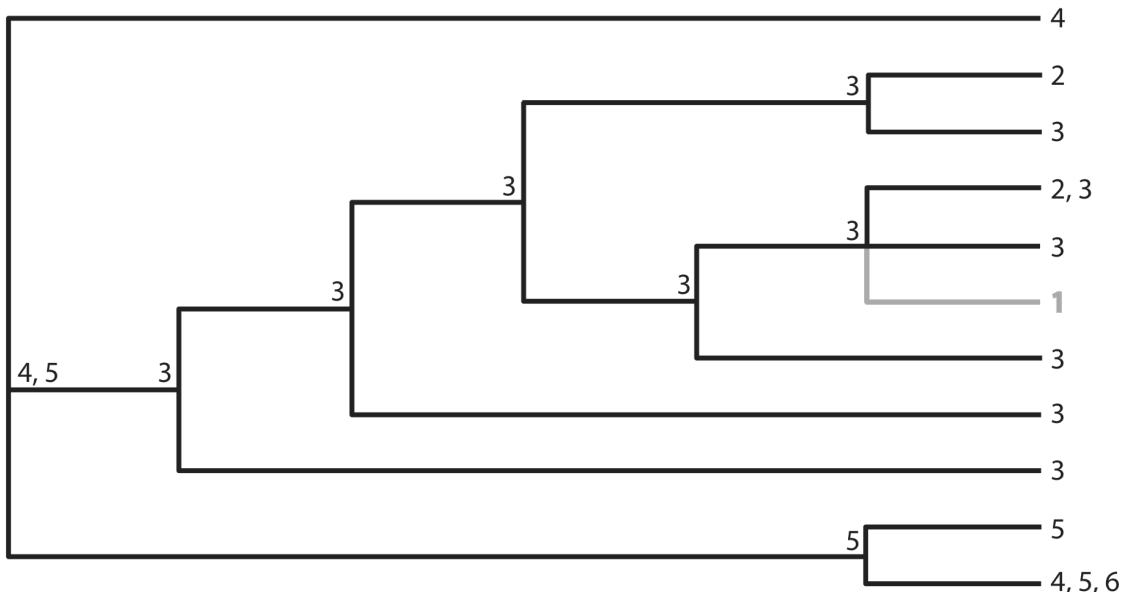
Fig. 2.5. Area cladogram obtained by replacing terminal taxa with the areas in which they are found. These are: (1) Dominican Republic, (2) Juan Fernandez Island, (3) southwest Chile & southwest Argentina, (4) north/central South America (includes Brazil, northeast Argentina, Paraguay, and Bolivia), (5) Central America, and (6) northwest South America (includes Columbia, Ecuador, and Peru). The numbers at the nodes are the optimized locations of the ancestral taxa. The fossil taxon, *M. mitnickii*, is depicted in gray.

2.5.2. Results

The vicariance analysis yielded a single most parsimonious tree of 15 steps, whereas the geodispersal analysis yielded three most parsimonious trees of 21 steps (Fig. 2.6). Only the Juan Fernandez Island/SW Chile & SW Argentina and north/central South America/Central America nodes were resolved in both analyses. When the relationships between the vicariance and geodispersal trees are correlated, such as with Juan Fernandez Island and SW Chile & SW Argentina, it suggests the processes affecting geodispersal and vicariance in these regions are similar and the regions are relatively close to each other (which they are). Coincident patterns often indicate that cyclical processes, such as rise and fall of sea level, played a role in alternating dispersal and vicariance between the two regions. The connection between

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north/central South America and Central America may on the one hand reflect larger-scale processes and patterns of geodispersal and vicariance, or, on the other hand, may simply be a result of sampling bias. The Dominican Republic probably placed basally due to the low diversity (i.e., one taxon) representing this region (see Lieberman, 2000).

Results from the modified Fitch parsimony algorithm (Fig. 2.5) suggests that the ancestor of the Dominican fossil dispersed into the Dominican Republic from the southwestern portion of South America. It must be noted that incomplete sampling due to extinction of taxa and lack of fossil traps in South and Central America (such as amber deposits) may have artificially biased our data by making the ancestral ranges appear more constrained than they really were. The ancestor of the Dominican fossil may have been more widespread in South America, making the mechanism of a dispersal event, for example from the northernmost region of South America, more realistic (i.e. the likelihood of a chance dispersal event having occurred, via any mechanism, from *southern* South America to the Caribbean is low). Unfortunately, the scarcity of fossil localities in Central and South America hinders our ability to observe what taxa were present where at different stages in Earth history. Members of this genus have not been found in other fossil deposits around the world, providing some indication the lineage was not globally distributed. Although our study was constrained by the limited number of fossil species and ranges and by the probable extinction that occurred within the lineage, we performed the analysis using the only data available; discovery of further fossil specimens or a modified phylogeny could verify or disprove our study. What is important is that our biogeographic analysis most strongly supports a dispersal event from South America to the Dominican

Republic (rather than having originated in the Dominican Republic - option 1. A vicariant origin is similarly not supported).

Fig. 2.6. The vicariance tree and strict consensus of three geodispersal trees. The nodal numbers are bootstrap and jackknife values, respectively. Trees for the bootstrap and jackknife analyses were generated using 50% majority rule consensus; no jackknife values were obtained for the vicariance tree. A test of Hillis (1991) was also performed, and the data departed from random at the 0.01 level (g1 value of -1.572235 and -0.734178 for the vicariance and geodispersal trees, respectively). Note that bootstrap values may have been artificially inflated by including autopomorphies within the analysis.

2.5.3 Discussion

Given that our data suggests a dispersal event (option 2), there are three tenable methods by which this chance dispersal could have occurred: (1) over-water dispersal *sensu* Hedges (1996a,b) and Hedges *et al*. (1992, 1994), (2) a GAARlandia (Greater Antilles + Aves ridge) landspan around 32 Mya *sensu* MacPhee & Iturralde-Vinent (1994, 1995), Iturralde-Vinent & MacPhee (1999), and Iturralde-Vinent (2006), and (3) ballooning. Here, we discuss each of these possibilities.

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(1) Over-water dispersal hypothesizes that organisms arrived in the West Indies by floating on flotsam directed by ocean currents, mostly from the northeastern coast of South America (the direction of current flow). This process was thought to have occurred throughout the Cenozoic. A study by Heatwole & Levins (1972) looked at organism transport on the Puerto Rican bank and found flotsam colonized by insects, pseudoscorpions, spiders, mites and worms 0.5–16 km out to sea. Vertebrates have also been documented to be capable of over-water travel on flotsam, especially after seasonal hurricanes (Censky, Hodge & Dudley, 1998). There has been much dispute regarding the over-water dispersal hypothesis (see MacPhee & Iturralde-Vinent, 2005 for criticisms), and the debate continues as to whether this is a viable mechanism for the colonization of the West Indies (especially for terrestrial vertebrates).

(2) The landspan hypothesis was championed by MacPhee & Iturralde-Vinent (1994, 1995) and Iturralde-Vinent & MacPhee (1999) and is based on the presumed presence of an exposed strip of land or series of islands (along the Aves ridge) running from the northern Greater Antilles to northwestern South America at about the time of the Eocene–Oligocene transition. MacPhee & Iturralde-Vinent (1994, 1995) used this theory to explain the origin of vertebrates in the West Indies, but this bridge may have aided invertebrate dispersal as well. As with the over-water dispersal hypothesis, there has been heated discussion as to whether the landspan hypothesis provides a viable mechanism for the colonization of the West Indies.

(3) Ballooning is the technique by which spiders extrude silken threads and are carried away on air currents. Spiders have been known to land on ships many miles out to sea (Darwin, 1839), and this dispersal ability may account for the presence of

at least some spider species in the West Indies. It is important to note, however, that Miocene amber contains both highly dispersive taxa (such as the Araneidae and Tetragnathidae) and also poorly dispersive taxa (Theraphosidae and Dipluridae). Penney (2008) suggested the presence of non-ballooning, poorly dispersive taxa in Miocene amber supports the GAARlandia landspan hypothesis (however this does not refute the hypothesis that poorly dispersive taxa could have floated over on flotsam from South America *sensu* Hedges, 1996,a,b).

The above processes all likely played a role in colonizing the West Indies, at least for arachnids. As referred to above, studies of various lineages differ on which of the dispersal and/or vicariance models is supported, and additional studies are needed in order to search for coincident patterns among different clades so as to tease apart the overall colonization pattern for the West Indies, if one is ever to emerge. Large-scale geological processes usually influence the Earth's biota in concert.

2.6 Extinction

The presence of *Molinaranea* in Miocene Dominican amber and its absence from the modern fauna of Hispaniola and elsewhere in the Caribbean region suggests the genus became extinct in the Dominican Republic, and presumably throughout much of its former range. A similar pattern can be seen in many other Dominican amber fossil arthropods. Riodinid butterflies provide a good example: two genera found in Dominican amber, *Voltinia* Stichel, 1910-11 and *Theope* Doubleday, 1847, no longer exist in the Greater Antilles, and only a single riodinid species lives there presently (Peñalver & Grimaldi, 2006). Ants offer another example: individuals of the genus

Leptomyrmex Mayr, 1862 are present in Dominican amber, but the only members alive today reside in Australia (Poinar, 1993).

Various models have been called upon in order to explain these extinction patterns in the West Indies. Peñalver & Grimaldi (2006) have cited insularization as the cause of the riodinid extinctions in the Greater Antilles (the authors suggest riodinid butterflies colonized the Greater Antilles when the landmasses were potentially closer to or actually fused with the mainland in the early Miocene or late Oligocene, but this is a tentative hypothesis and one that is complicated by the convoluted geology and tectonics of the region). Hall, Robbins & Harvey (2004) invoked Plio-Pleistocene cooling, habitat disruption, and xerophytization as possible extinction triggers for the riodinid butterflies and other arthropod groups, but Peñalver & Grimaldi (2006) argued that this model does not fit the riodinid example because a close living relative of the now extinct Dominican species resides in xerophytic environments in Mexico. Regardless, there seems to be consensus that the climate in the West Indies was considerably more arid during the Pleistocene, which may have had an influence on the biota (Bonatti & Gartner, 1973; Pregill & Olson, 1981; Schubert & Medina, 1982; Schubert, 1988).

The disjunct distribution between many Dominican fossil species and their extant relatives is mirrored in the rest of the world. Fossils have provided evidence (e.g. Eskov, 1987, 1992 for archaeid spiders; Wedmann & Makarkin, 2007 for mantidflies) that many lineages once thought to be Gondwanan in origin were present in the northern hemisphere and likely relics of a previously widespread distribution. The discovery of a fossil species of *Molinaranea* in the Dominican Republic (given

modern members are restricted to southern South American) provides another example of a lineage with a likely relict extant distribution.

Modern members of *Molinaranea* inhabit three areas within the temperate rainforest of southern Chile and Argentina: the Valdivian rainforest, the north Patagonian rainforest, and the Magellanic rainforest. All of these rainforests are characterized by evergreen broadleaf trees, evergreen conifers, and abundant epiphytes (Levi, 2001; Veblen & Alaback, 1996). Since modern members of the genus reside in what appears to be a relatively constrained niche space, one might be inclined to assume the habitat of the Dominican Republic in the middle Miocene was similar to that of southern Chile and surrounding regions. However, it is thought Dominican amber was probably deposited in a warm, humid tropical forest, unlike the modern temperate forest of southern Chile (Iturralde-Vinent, 2001).

Pleistocene glaciations significantly affected the climate and environment of southern South America, and during glacial maxima ice would have covered most of the forest that today supports *Molinaranea* (McCulloch *et al.* 2000; Hulton *et al.* 2002). This suggests members of *Molinaranea* occupied areas other than their current residence during the glaciations, perhaps tracking preferred habitat (unless they survived in mountainous refugia *sensu* Haffer, 1969 for Amazonian bird fauna). Since Hispaniola was a distinct island during the Pleistocene, members of *Molinaranea* may not have been able to escape changes in climate or track habitat as effectively as their South American counterparts; this, in part, could explain their absence from the modern West Indies.

2.7 Acknowledgements

CHAPTER 3 | First fossil Mecysmaucheniidae (Arthropoda: Chelicerata: Araneae), from Lower Cretaceous (uppermost Albian) amber of Charente-Maritime, France

Chapter Overview

The first known fossil mecysmaucheniid spider, *Archaemecys arcantiensis* **n. gen. n. sp.**, is described, from Lower Cretaceous (Upper Albian) amber of Charente-Maritime, France. This is the first fossil spider to be formally described from French Cretaceous amber and extends the geological record of Mecysmaucheniidae back into the Cretaceous, the family having previously been known only from the Recent. The fossil differs from other Mecysmaucheniidae in having four, rather than two spinnerets, so can be considered plesiomorphic with respect to modern members of the family in this character. The amber of the Archingeay–Les Nouillers area is uniquely considered to have largely preserved a litter fauna, and our specimen corroborates this hypothesis.

3.1 Introduction

Spiders (Araneae) are an extremely diverse order of arachnids, with 40,462 extant species in 3694 genera and 109 families (Platnick, 2008). They are characterized by numerous synapomorphies, including the presence of spinnerets on the abdomen for producing silk, naked fangs and associated venom glands (in most species), two body regions, eight legs, and pedipalps modified in the male for sperm transfer.

The Mecysmaucheniidae, a relatively small family within the Araneae, is composed of seven genera and 25 known species (Platnick, 2008). They are small, haplogyne, ecribellate spiders found in New Zealand and southern parts of South America (primarily Chile and Argentina) (Jocqué & Dippenaar-Schoeman, 2006). The type genus *Mecysmauchenius* was first described by Simon (1884) as a member of the Archaeidae Koch & Berendt, 1854. Mecysmaucheniids are distinguished from

other spiders by the presence of chelicerae originating from a foramen in the carapace and only two spinnerets (Forster & Platnick, 1984). Mecysmaucheniids belong to the superfamily Palpimanoidea, which has had a long and controversial history. Forster & Platnick (1984) enlarged the Palpimanoidea (originally it only included the Huttoniidae Simon, 1893, Palpimanidae Thorell, 1870 and Stenochilidae Thorell, 1873) to include the Archaeidae (and therefore the Mecysmaucheniidae), removing them from the araneoids. They also significantly enlarged the superfamily by including the Micropholcommatidae Hickman, 1944, Mimetidae Simon, 1881, Pararchaeidae Forster & Platnick, 1984 and Holarchaeidae Forster & Platnick, 1984 on the basis of two diagnostic characters: cheliceral peg teeth and a raised cheliceral gland. Although some accepted Forster & Platnick's revision (Coddington & Levi, 1991; Coddington *et al.*, 2004), others have contested the arrangement. According to Schütt (2000), Micropholcommatidae and Mimetidae should be placed within the Araneoidea, although the placement of the Archaeidae and Mecysmaucheniidae in Palpimanoidea was still dubious at best. Griswold *et al.* (2005) agreed with Schütt in that the Mimetidae should belong to the Araneoidea; however, they claimed that many of the palpimanoid familial placements are still debatable. Others have suggested that peg teeth are homoplasious (Coddington *et al.,* 2004; Schütt, 2000) and therefore should not serve as one of the diagnostic characters of the Palpimanoidea.

The archaeids were first described from Baltic amber fossils by Koch & Berendt (1854) and were considered an extinct group for some thirty years until extant species were found in Madagascar. The mecysmaucheniids were described soon after from specimens in Chile and were placed as a genus under the Archaeidae (Simon, 1884).

Mecysmaucheniids were considered a subfamily of the Archaeidae by Simon (1895), and some people continued to hold this view (see Wunderlich, 1986, 2004; Eskov, 1987, 1992). Lehtinen (1967) suggested the subfamily be raised to family level, which would include *Mecysmauchenius* Simon, 1884, *Pararchaea* Forster, 1955 and *Zearchaea* Wilton, 1946. Although Lehtinen's placement of the *Pararchaea* and *Zearchaea* was contested by Forster & Platnick (1984), these authors retained the Mecysmaucheniidae as a distinct family (see Forster & Platnick, 1984 for a detailed taxonomic history of the archaeids and related taxa).

There has been no formal description of a fossil mecysmaucheniid to date. Eskov (1987) tentatively assigned *Archaea conica* (see Koch & Berendt, 1854, fig. 10) to the subfamily Mecysmaucheniinae because of its short chelicerae and only slightly elevated cephalic region of the carapace, even though the Baltic amber type specimen had been lost. Eskov (1992) later created a new genus, *Baltarchaea,* for *A. Conica*; the species was listed under Mecysmaucheniidae in the table in Penney (2003b, Table 1). A description of a fossil mecysmaucheniid was said to be in preparation in Eskov & Golovatch (1986), but no such paper resulted, and the designation was likely changed to an archaeid (see Eskov, 1987).

Lacroix (1910) was the first to describe Cretaceous amber from France, but it was not until the 1970s that extensive study of the fossiliferous material in French ambers was undertaken (Perrichot *et al.,* 2007). The most fossiliferous French amber deposit from the Cretaceous is the Archingeay–Les Nouillers (herein referred to simply as Archingeay) locality (Perrichot *et al.,* 2007). The amber from Archingeay is late Albian in age and is unique in that a large percentage of the inclusions represent litter

fauna (Néraudeau *et al.,* 2002). It is thought that the resin was exuded from a member of the plant family Araucariaceae, and the abundant resin flowed directly onto the ground (Néraudeau *et al.,* 2002). The fossil assemblage of Archingeay is mainly composed of insects, but other arthropods are also present (Perrichot *et al.,* 2007; Néraudeau *et al.,* 2002). Nine percent of the total arthropod inclusions in Albian French amber are arachnids (Perrichot *et al.,* 2007). Hitherto, no spider fossils have been described from the Cretaceous of France, although they were referred to by Schlüter (1978) and Néraudeau *et al.* (2002), and members of the family Zodariidae were mentioned as being present by Perrichot (2004) and Perrichot *et al.* (2007).

Cretaceous spiders are relatively rare but have been described from Siberia (Eskov & Zonshtein, 1990; Eskov & Wunderlich, 1994), New Jersey (Penney, 2002; Penney, 2004a), the Isle of Wight (Selden, 2002), Lebanon (Penney & Selden, 2002; Penney, 2003a; Wunderlich & Milki, 2004), Canada (Penney, 2004c; Penney & Selden, 2006), Myanmar (Grimaldi *et al.,* 2002; Penney, 2003b, 2004b, 2005), Botswana (Rayner & Dippenaar-Schoeman, 1995), Brazil (Mesquita, 1996; Selden *et al.,* 2002; Selden *et al.,* 2006), Australia (Jell & Duncan, 1986) and Spain (Selden, 1989; Selden, 1990; Selden & Penney, 2003; Penney, 2006; Penney & Ortuño, 2006). Here, we provide the first description of a fossil mecysmaucheniid, from Cretaceous (Late Albian) French amber. Living mecysmaucheniids are litter-dwellers, like most of the fauna from Archingeay amber, but are confined to South America and New Zealand. The find of a mecysmaucheniid in Cretaceous Laurasia suggests a more widespread, or at least different, distribution for this family in the Mesozoic than today.

3.2 Methods

The specimen was cut, polished and encased in clear resin before the authors received it. Drawings were done under both incident and transmitted light with a camera lucida attached to a Leica MZ16 stereomicroscope. Drawings were scanned and re-traced using Adobe Illustrator. Photographs were taken with a Cannon Digital Rebel XTi attached to the microscope and manipulated in Adobe Photoshop. Fig. 3.1D was taken with a Leica DFC420 C camera attached to a Leica DM 2500 microscope; Leica Application Suite software was used to take a multifocus z-stack so as to achieve sharp focus throughout the image. Measurements were made using an ocular graticule.

Microtomography at the European Synchrotron Radiation Facility (ESRF) in Grenoble, France was attempted; however, the competing mediums within the amber piece (air, resin, arthropod cuticle, glue, and Canada balsam used for mounting) were problematical, and obtaining an image proved to be extremely difficult. In order to prepare the specimen for microtomography, it was removed from the clear, recent resin by gentle heating on a hot plate. Excess amber was cut away from the specimen so as to increase imaging ease; during this process, a small portion of the opisthosoma was unintentionally removed.

Fortuitously, removal of the specimen from the recent resin allowed for improved views of difficult to observe areas (i.e., we were able to observe cheliceral peg teeth). The specimen was mounted on a pin attached to a microscope stage so that the piece was rotatable at all angles. Further imaging was done with a Leica DFC420 C camera

attached to a Leica M205 C microscope. Figure 3.3 is a stack of three images merged using Helicon Focus software (www.heliconsoft.com/heliconfocus.html).

3.3 Abbreviations

Leg formula (e.g. 1423) indicates the length of each leg relative to the other legs from longest to the shortest (in the example, leg 1 is longest, followed by leg 4). Abbreviations are as follows: ALS = anterior lateral spinnerets, AME = anterior median eyes, BL = book lung, cl = claw, co = colulus, cx = coxa, EF = epigastric furrow, fe = femur, LC = left chelicera, mt = metatarsus, mx = maxilla, op = opisthosoma, PLS = posterior lateral spinnerets, pp = pedipalp, ps = prosoma, pt = patella, RC = right chelicera, sr = spiracle, st =sternum, T = trichobothrium, ti = tibia, tr = trochanter, ts = tarsus, 2–4 = walking legs 2–4. All measurements are in mm.

3.4 Preservation and morphological interpretation

The specimen is preserved in a piece of cloudy, light orange amber; approximately 4.5 mm x 3.5 mm. Prior to receipt by the authors, the piece of amber containing the specimen had been cleaved in half to the left of the abdomen and subsequently glued back together. Small air bubbles and pieces of organic material are present. The opisthosoma of the spider is translucent and the spinneret attachment points can be viewed internally. Many features of the specimen are difficult to study due to the cloudiness of the amber (many, tiny air inclusions). No other syninclusions co-occur with the specimen.

Penney (2003b) considered the wrinkled opisthosoma in his Cretaceous Burmese amber specimen of *Afrarchaea grimaldii* (Araneae: Archaeidae) to be the

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consequence of typical preservational processes that occur in amber. Repeated mention, however, of a wrinkled abdomen in archaeids, and the presence of wrinkles in our specimen, leads us to suggest this may be a specific preservational trait of mecysmaucheniids and closely related families. Koch & Berendt (1854, figs 9 & 10) figured parallel abdominal folds in their drawings of Baltic amber archaeids, and Eskov (1992), Penney (2003b) and Wunderlich (2004) all mention wrinkles and folds in the abdomens of their archaeid amber specimens.

The organic material has shrunk in most of the specimen, as is the rule in amber preservation, leaving a ghostly but faithful outline of the original surface. The cuticle has shrunk from the distal end of the leg segments, leaving only the outline of the original surface (Fig. 3.1E). In the tarsi, however, the cuticle is absent from the proximal end of the podomere, and a slight constriction occurs, indicating the area was unsclerotized in the living organism (a character that is present in both archaeids and mecysmaucheniids).

3.5 Systematic Paleontology

Order ARANEAE Clerck, 1757

Suborder OPISTHOTHELAE Pocock, 1892

Superfamily PALPIMANOIDEA *sensu* Forster & Platnick, 1984

Family MECYSMAUCHENIIDAE Simon, 1895

Remarks: Mecysmaucheniidae are diagnosed as having two spinnerets and chelicerae originating from a foramen in the carapace. Although our specimen has four spinnerets and we cannot be certain the chelicerae originate from a foramen in the carapace, we place the specimen in Mecysmaucheniidae on account of the following

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characters: The unsclerotized, constricted area on the base of the tarsal segments in our specimen appears to be a synapomorphy uniting the archaeids and mecysmaucheniids (Forster & Platnick, 1984; H. Wood pers. comm.) and places our specimen firmly among these families. The lack of a constricted neck or greatly heightened cephalic area (characteristic of Archaeidae), and the presence of four spinnerets (cf. six in archaeids), suggests our specimen should be included within Mecysmaucheniidae. Our reasoning is that, while mecysmaucheniids have only two spinnerets, this is a reduction from the plesiomorphic six (i.e. an apomorphy). Loss of spinnerets (or their reduction to patches of spigots) has occurred several times within the Palpimanoidea (Forster & Platnick, 1984) and is a character of known polarity. It is likely that reduction is a trend within the Mecysmaucheniidae and the condition in *Archaemecys* n. gen. represents a stage in the reduction. Archaeids have two spiracle openings, unlike the single opening seen in the mecysmaucheniids and our specimen. Additionally, Forster & Platnick (1984) mentioned that the spiracle is often sclerotized in mecysmaucheniids, a character observed in our fossil. *Archaemecys*, like other mecysmaucheniids, does not have tubercles on the carapace, and the chelicerae in the fossil are shorter and stouter than those usually found in archaeids. Archaeids have spatulate hairs on the tibia and metatarsus of leg 1 (Forster & Platnick, 1984), but the Mecysmaucheniidae, including our specimen, do not. Additionally, our specimen does not have a femoral hump, as is present in archaeids (see Wunderlich, 2004). A Pararchaeidae affinity can be ruled out because, as mentioned above, the pararchaeids do not possess the unsclerotized, constricted area at the bases of the tarsi. This aside, our specimen has plumose leg setae, not the

serrate or smooth setae found in pararchaeids, and the legs are stout, unlike the slender legs characteristic of pararchaeids.

Genus *Archaemecys* n. gen.

Figures 3.1– 3.3

Type species: Archaemecys arcantiensis n. sp., by present and monotypic designation

Material examined: Holotype and only known specimen, subadult male, MNHN ARC11R deposited in the Muséum national d'Histoire naturelle, Paris.

Etymology: The genus name is derived from the Greek *archae*, meaning primitive or ancient, and the modern genus *Mecysmauchenius,* which the fossil somewhat resembles.

Stratigraphic horizon: Lower Cretaceous, Uppermost Albian, subunit A1s12 (Néraudeau *et al.,* 2002).

Diagnosis: Archaemecys can be distinguished from all other genera of Mecysmaucheniidae by the presence of four spinnerets, a strongly sclerotized ring around the spinnerets, and a sclerotized tracheal spiracle.

Remarks: The genus differs from other mecysmaucheniids by the presence of four spinnerets. All extant Mecysmaucheniidae have only two spinnerets, a derived condition. Additionally, *Archaemecys* has a particularly robust sclerotized ring around the spinnerets, and its legs are much shorter and stouter than in extant mecysmaucheniids.

Archaemecys arcantiensis n. sp.

Figures 3.1– 3.3

Arachnida Salticidae—Néraudeau *et al.* (2002, fig. 6.8)

Type locality: Archingeay-Les Nouillers, Charente-Maritime, south-west France.

Etymology: The specific epithet is based on *Arcantiatum*, former Latin name of the locality Archingeay from which the fossil originates.

Diagnosis: As for the genus.

Description: Body length 3.10. Carapace 1.31 long, 0.94 wide, $\geq$ 0.66 high; pars cephalica highly elevated so that carapace, when viewed from side, appears subrectangular in outline; without tubercles. Only AME visible on anterior face of carapace. Chelicerae with $\geq$ 11 peg teeth (Fig. 3.3); peg teeth ~0.17 long, chelicerae 0.71 long; fang $\geq$ 0.35 long; chelicerae appear to originate from a foramen, although this is not certain; sclerotized lip/projection above where chelicerae originate (Fig. 3.3). Sternum 0.34 wide, 0.57 long, lateral margins project slightly between coxae.

Maxillae converge slightly, almost circular in shape. Petiole encircled by sclerotized plate (Fig. 3.2A); rugose epigastric plate, flanked by book lung covers (Fig. 3.2B). Opisthosoma 1.42 long, approximately 1.10 wide, height uncertain; likely sub-globular in life; dorsal surface not preserved so presence of scutum not known. Opisthosomal cuticle wrinkled in subparallel lines, bearing short, plumose setae, each originating from a prominent follicle. Four spinnerets and anal tubercle surrounded by well-developed chitinous ring (Fig. 3.2B); ALS well defined in two segments (Fig.

3.1D), posterior spinnerets smaller; patch of cuticle with short setae in front of ALS, possibly a colulus. Spiracle situated well anterior to spinnerets; fortified with cuticle ring (Figs 3.1A, B, C).

Leg formula 1423; leg 1 cx 0.23, tr 0.16, fe 0.57, pt 0.25, ti 0.39, mt, 0.39, ts 0.39, total 2.38; leg 2 cx 0.18, tr 0.19, fe 0.52, pt 0.20, ti 0.38, mt 0.33, ts 0.33, total 2.13; leg 3 cx 0.17, tr 0.18, fe 0.45, pt 0.21, ti 0.39, mt 0.33, ts 0.28, total 2.01; leg 4 cx 0.25, tr 0.16, fe 0.54, pt 0.20, ti 0.44, mt 0.41, ts 0.33, total 2.33. Plumose setae on all leg segments; no spines; each metatarsus with single trichobothrium, most likely on dorsal surface (trichobothrium located seven-tenths of way along metatarsus from proximal end in legs 2–4); tibiae 2–4 with at least one (up to 3) trichobothria (Fig. 3.2). Legs relatively short and stout. Tarsi with unsclerotized constriction at the base of the tarsus (Fig. 3.1E). Three tarsal claws on unsclerotized onychium; paired claws with 4, possibly 5 teeth, unpaired claw simple. Pedipalp rounded and bulbous, 0.37 long, 0.16 wide.
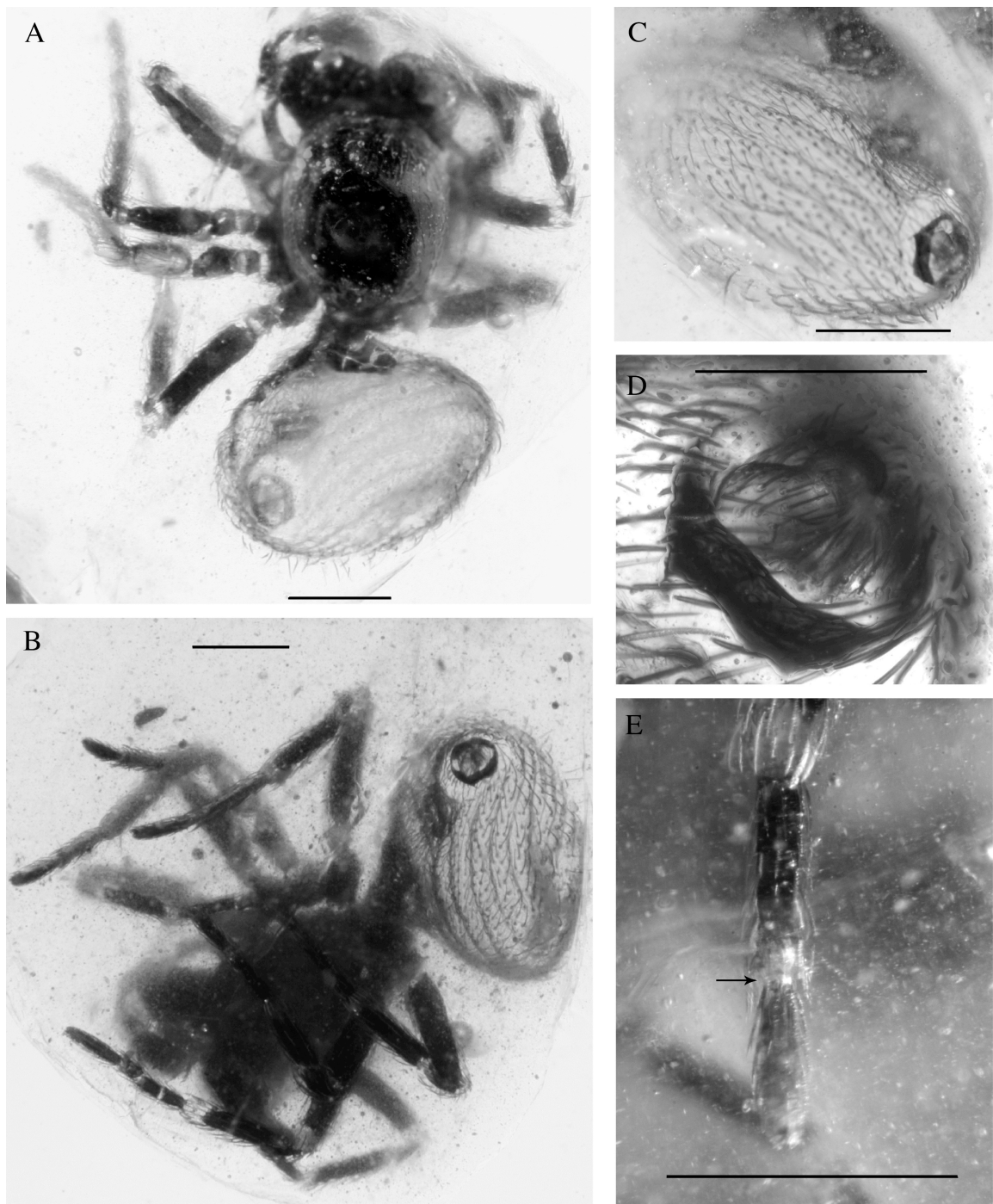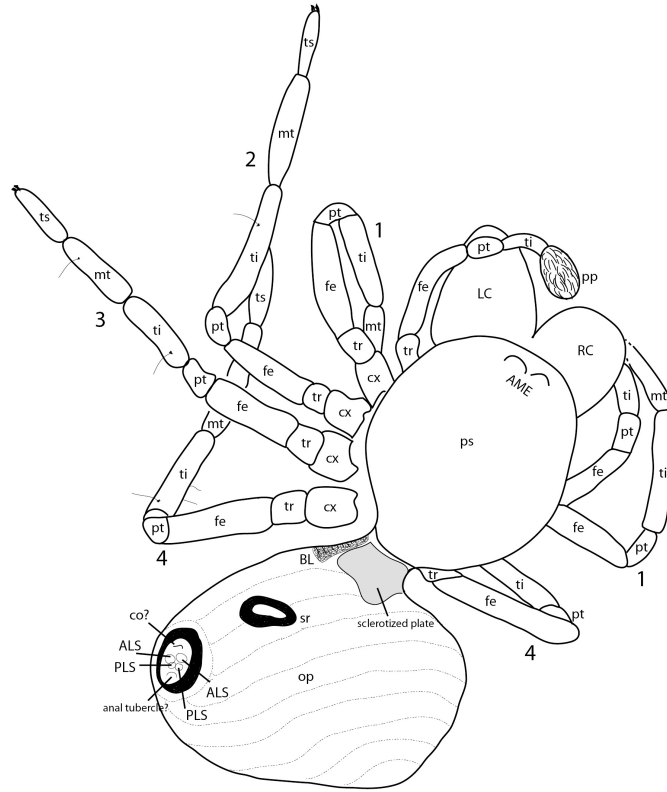
Fig. 3.1 A–E. *Archaemecys arcantiensis* n. gen., n. sp. **A**. dorsal view of the specimen; **B**. ventral view of the specimen; **C**. opisthosoma. Notice the pronounced wrinkling of the cuticle and the sclerotized rings around the tracheal spiracle and the spinnerets; **D**. lateral view of the spinnerets, anterior to the left. The anterior two spinnerets (left) are relatively large, with two segments, while the posterior two spinnerets (right) are smaller; **E**. close-up of metatarsus and tarsus third leg segment showing the unsclerotized portion at the base of the tarsus. Scale bars: 0.5 mm, except for C., which is 0.2 mm.
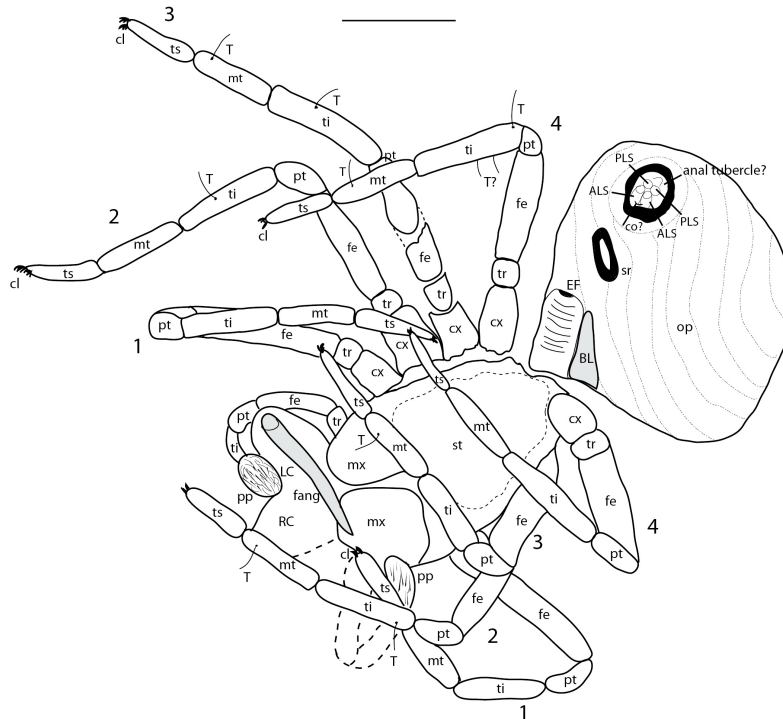
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Fig. 3.2 A–B. Interpretive drawings of *Archaemecys arcantiensis* **n. gen., n. sp. A**. dorsal view of specimen; **B**. ventral view of specimen. See text for explanation of abbreviations. Scale bar = 0.5 mm.
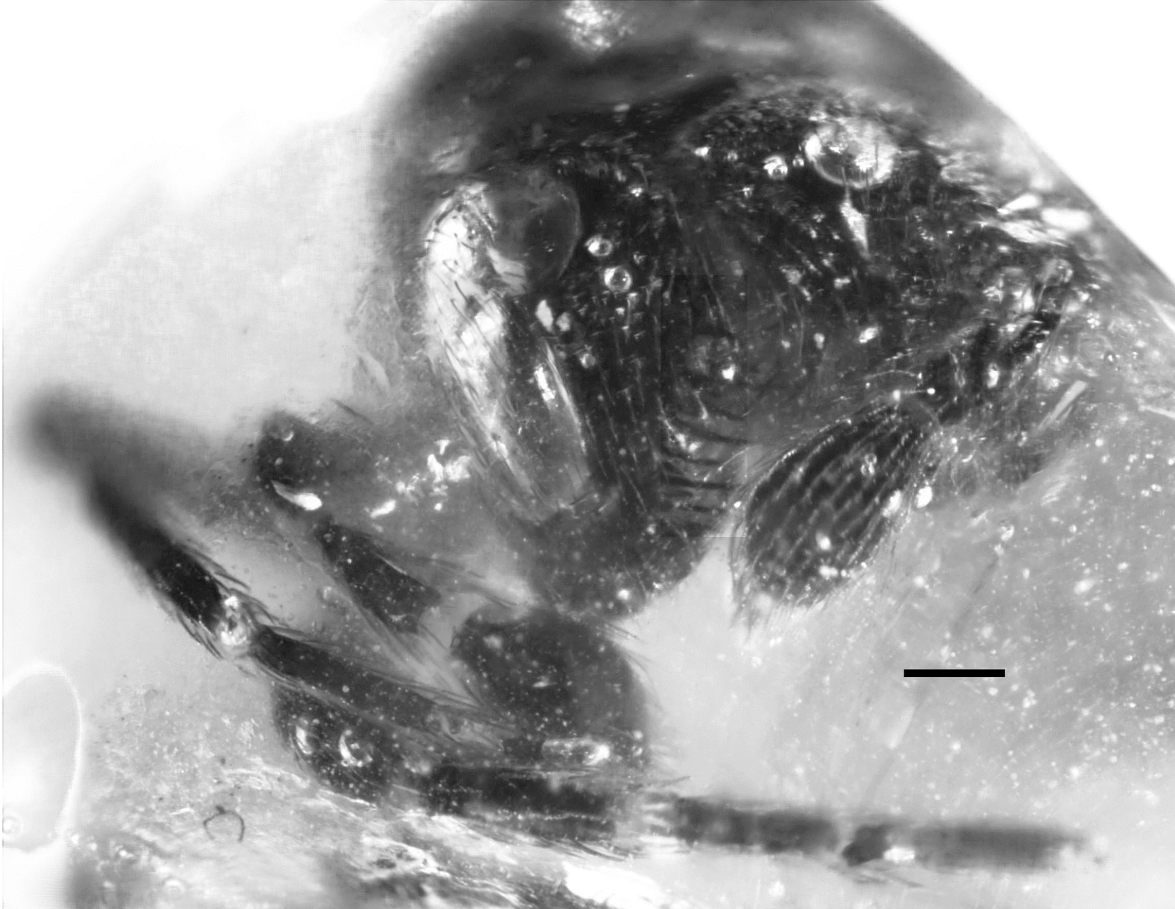
Fig. 3.3. *Archaemecys arcantiensis* n. gen. n. sp. Anterior view of the chelicerae and pedipalps. Notice the peg teeth on the chelicerae and the heightened profile of the carapace. Scale bar = 0.1 mm.

3.6 Remarks

While we are only able to view four spinnerets, we cannot completely rule out the possibility of 6, as there may be a very small median pair (this it is unlikely since we are able to view inside the opisthosoma to the point of spinneret attachment). Regardless, even if the specimen possesses six spinnerets, this would not change its placement within the Mecysmaucheniidae. Although the archaeids and pararchaeids

have 6 spinnerets, these families do not share the other characters found in our specimen (see remarks section above). Additionally, losing spinnerets is a fairly common phenomenon within the Araneae. Extant mecysmaucheniids have lost four spinnerets in the reduction to the two the family currently possesses; given this, it seems quite possible that a primitive mecysmaucheniid would have four, or even six, spinnerets.

3.7 Discussion

This is the first description of a fossil mecysmaucheniid and extends the range of the family back to the Cretaceous (Late Albian). Archaeids have been described from Late Cretaceous (Penney, 2003b) amber and are known from the Jurassic (Eskov, 1987; Selden *et al.,* 2008); it follows that mecysmaucheniids are also present in the Mesozoic, since they are sister to the archaeids.

Mecysmaucheniids are commonly found in the litter layer of forests (Forster & Platnick, 1984; Jocqué & Dippenaar-Schoeman, 2006). Since the Archingeay amber fauna is considered a unique representative of a litter fauna (Néraudeau *et al.,* 2002; Perrichot *et al.,* 2007), our spider specimen corroborates this observation and supports the hypothesis that resin flowed directly onto the forest floor, thereby engulfing our spider and the many other organisms found in this amber.

Recent mecysmaucheniids occur only in New Zealand and South America (specifically Argentina and Chile) (Jocqué & Dippenaar-Schoeman, 2006; Platnick, 2008), while archaeids are found only in Australia, South Africa and Madagascar. The presence of fossil archaeids and mecysmaucheniids in Eurasia poses interesting biogeographical questions. Although the present distribution of mecysmaucheniids

and archaeids may be an artifact of sampling bias, this seems unlikely, and it is especially curious that mecysmaucheniids occur in precisely those parts of Gondwana from which archaeids are absent. The particular distributions of these two families may represent a case of competitive exclusion or, more likely, since they are sister taxa, may result from a divergence in the distant geological past and/or extinction due to climatic or geological events.

3.8 Note on Wunderlich (2008)

A work published recently by Wunderlich (2008) referred to *Archaemecys arcantiensis* n. gen. n. sp. (this paper) as *Palaeomecysmauchenius* (this was a manuscript name—we provided Wunderlich with a preliminary draft of the present paper in 2007) and placed our specimen in his new subfamily Lacunaucheniinae. We refute this placement on the following grounds: *Archaemecys* possesses a ring around the spinnerets (*contra* members of Lacunaucheniinae) and does not, to our knowledge, have three pairs of spinnerets (a trait of Lacunaucheniinae). Furthermore, Wunderlich (2008) indicated we support the theory of ousted relics (the hypothesis that northern lineages were ousted to the southern hemisphere by more competitive taxa). This is false: we simply stated that Archaeidae and Mecysmaucheniidae may have had a more widespread distribution in the Mesozoic, so their extant range is perhaps a relict of a previous pancontinental distribution, although this remains to be tested within a rigorous scientific framework.

3.9 Acknowledgements

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