

Drivers of Spider Body Plans: Time, Geography or Climate?

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## Abstract

Spiders are a highly diverse order that are present across practically all terrestrial environments. Many aspects of their morphological characteristics have been studied, but what is not as well-known is the impact that climate has on their body-plan diversity and body plan overall. Spiders from differing climates or continents could have differing morphological variation. Spiders from five sites across climates, geographies and slices of geological time were measured and mapped on a two-dimensional representation of morphological space. One modern and one fossil site were specifically matched for climate, the two modern sites were matched for geography and two fossil sites were matched for geological epoch. From the analysis, it was shown that neither climate nor geography played any role in separating the sites in morphological space. The sites from the same epoch (Eocene for fossil, and modern) were identical to one another across the critical axis of the morphospace, which separated spiders by the ratio between their body length and leg length. Based on the family composition in sites and how well-constrained morphology was within a family, it seems most likely that phylogenetics or ecology dictate a spiders body plan. However close examination of a single family could yet yield other interesting results.

This thesis is written in the form of a journal article from The Journal of Arachnology

### **Declaration**

I declare that the thesis submitted here has never been submitted to another institution as part of a higher degree research degree. Work by Alexander Petrunkevitch and Jorg Wunderlich, as well as the work conducted for the Atlas of Living Australia were critical to the project and formed data sources, but such work was utilised in a way it had not been before. No ethics approval was needed for the work described herein. All other work was completely my own work.

### **Signature**

A handwritten signature in black ink, appearing to read 'Wunderlich', written in a cursive style.

Signed 05/10/2017

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## INTRODUCTION

The fossil record can be an invaluable tool for understanding current biodiversity and predicting biotic changes. It is the best source for examining trends over long periods of time, informing us when certain taxa evolved and under what circumstances they did so, as well as how the diversity of organisms has fluctuated over time. Palaeobiology can therefore inform many areas of modern biology.

One of the most important issues for current and near-term science is anthropogenic climate change. It is believed that climate change today is more rapid than it has been at any point during the past 100,000 years, the period for which we have highly reliable climate data (Petit et al. 1999). This fact is reinforced by studies of the fossil record that show that our average global temperature has gone up by an amount in the past couple of centuries that would have taken millions of years in the pre-industrial Earth (Oreskes 2004). It is important to stress that while the climate has shifted before, humans are causing very rapid change, and thus there is a need to undertake studies that will allow us to more accurately predict its effects.

There are many aspects of an organism's biology that could be affected by shifts in climate. Aspects such as sexual behaviour or growth already have been shown to respond to changes like higher temperatures (Møller 2004; Morison & Morecroft 2008). Species have also been shown to constrict or expand their ranges as areas become too hot to actually be amenable (Dukes et al. 2009). However, potential changes in body plans or body sizes of organisms have not been studied as extensively.

In order to best predict such effects, comparisons between different climates, locations, and times need to be undertaken. Therefore, at least one location relatively rich in fossils and a number of modern locations need to be chosen. To be valid, a comparison would likely have to be restricted to one taxonomic group such as an order to make sure the results are not confounded by variation in body plans. It is for this reason that the order Araneae (Spiders) was chosen, as they are more structurally uniform than many other orders. One might expect that spiders will have changed physically over time. The question is whether this is due to climatic effects, geographical isolation or merely evolutionary time.

To separate these three potential drivers, a number of different sites would need to be chosen. Such sites would need to be a mixture of both modern and fossil locations, as well as originating from different continents and climates. The fossil sites would need to be split again into an earlier time period and one between the earlier interval and the present day.

By using a combination of five sites and taxa pairings, the effects of climate, geography and time can be addressed. The sites would be three fossil and two modern locations. Two of the fossil sites (F and B) are from the same time period, while the third (D) is from a point in time midway between those sites and the modern (T and C). F and B would be geographically distinct from one another, while T and C would intentionally be close to one another but of a distinct climate. All fossil sites would aim to be climatically comparable to one of the modern sites, but F and T would intentionally have to be matched closely. If the two most similar sites are F and T, then climate is the major factor driving the spider body plan. If T and C are similar, but F and B are not then it is a geographic signal, by contrast if B and D are also similar it is an evolutionary trend. Such a pattern would be reinforced if D is different to every other site, as it is positioned between F and T and C timewise.

Any scenario in which more than one of these cases are true, or even all sites are different from one another, it would indicate some form of multivariate response in spider morphology. Conversely if none of these combinations occurs then some other untested factor would be most relevant. While unlikely, it is possible that all the sites could be similar to one another, which would indicate spider morphology being very uniform and ubiquitous.

A number of background areas need be examined first to answer this question. First, the fossil record of spiders will need to be looked at in order to determine which geological time intervals and physical locations should be used. Aspects of spider biogeography also will need to be looked at, as well as how morphometrics can be used to analyse populations. Palaeoclimate studies and their accuracy will be addressed to provide context to the fossil sites. Finally, the responses of arthropods to current climate change will be addressed.

**Fossil Record of Spiders.--** Understanding when spiders as a group have diversified and when members of particular families or clades began to resemble modern species is key to locating spatially and temporally appropriate fossil sites for study. While it is not expected that the same number of species will be present in the fossil sites as there are in modern locations, if the same genera occur at the different sites that should validate the comparison.

Spiders originated in the Middle Devonian interval around 380-390 Ma (Selden et al. 1991). A now-extinct group of arachnids appeared that possessed almost all of the key spider-like features of its modern representatives. While it is debatable whether they could really be classified as 'true' spiders, these fossils likely represent the stem group to modern Araneae. The fossils from this period are believed to be some of the earliest terrestrial arthropods, and they rapidly developed the ability to produce silk, but lacked true spinnerets (Selden et al. 2008; Penney and Selden 2011), a key feature of the spider body plan. While the exact time

that they or their ancestors colonised the land cannot be stated with any certainty, they could have been terrestrial for even a several to tens of millions of years before appearing in the fossil record. The first definitive spider appears much later in the Carboniferous around 300 Ma (Penney and Selden 2011), possessed all of the key characters, including spinnerets.

Unfortunately, the spider fossil record remains patchy for much of the Phanerozoic, with some continents and land masses possessing very few recorded specimens (Selden et al. 2009). The overwhelming majority of material is found in Cenozoic rocks (Dunlop et al. 2015; Penney and Langan 2006; Penney and Selden 2007), but there does appear to be a spike in fossil finds during the Cretaceous Period (Penney 2003) that coincides with the most recent radiation of insects, which in turn follows the rise of angiosperms. There also is an increase in the number of fossils preserved in amber starting from the Late Cretaceous (Penney and Langan 2006; Penney and Ortuño 2006; Grimaldi 2009), which accounts in part for the increased number of spider fossils. Amber is a mode of fossilisation that results in excellent three-dimensional preservation of soft-bodied organisms like insects and spiders (Martínez-Delclòs et al. 2004; Penney and Langan 2006; Perkovsky et al. 2007). Preservation of spiders in other modes of fossilisation, such as compression-impression fossils, is generally considered poor (Penney and Selden 2007) and specimens are rarely found complete. This condition presents an issue when it comes to examining the fossil record of spiders, as there are large portions of geological time that cannot be examined due to a global lack of specimens (Dunlop et al. 2008). This pattern significantly narrows those locations temporally appropriate for sampling.

In addition to having a patchy record, fossil spiders simply have not been paid enough attention by researchers. Most of the work has been done by only a few people, some having worked considerable amount of time ago (e.g., Petrunkevitch 1942) and others more recently (e.g., Penney 2003). Palaeoarachnology is a narrow field and it is not surprising that the research base is small, and consequently most publications are produced by a small group of researchers (Penney and Selden 2007). These factors limit the kinds of analytical research that can be undertaken using existing data and further limits the choice of study sites. It may also explain why some continents such as North America and Asia are represented by more specimens than others. However, these complications do not mean that there are not well-sampled locations to enable a reliable analysis.

Based on the information above, the Florissant fossil beds of Colorado (Site F) were chosen as a starting point for the analysis. Florissant is a well-sampled location from a time interval when spiders had already undergone much of their radiation and were likely similar

at the genus level to those found today (Bodner and Maddison 2012; Boyle et al. 2008; Roberts et al. 2008; Veatch and Meyer 2008). The assemblage is of late Eocene age (approx 34-37 Mya) and is known for its excellent preservation of plant, insect, and spider compression fossils. The other two fossil sites were chosen on this basis. The site representing B is the Baltic amber, a middle Eocene (44-40 Mya) site with a wealth of amber spider fossils and an inferred warm-temperate climate similar to the Florissant. The temporally intermediate fossil site is the Dominican amber (Site D), which is early to middle Miocene (15-20 Mya) (Iturralde-Vinent and MacPhee 1996) and has a more sub-tropical climate.

**Spider Biogeography.--** Changes in the geographic ranges of spiders, whether they are attributable to extensions, contractions, or latitudinal or longitudinal shifts, are another aspect that is important to understand. Other factors will play less prominence than geographic ones, but ensuring that the modern sites used in the study are relevant for purposes of comparison is a highly desirable goal.

Generally, it is claimed that spiders are limited in their ability to disperse compared to their insect prey, particularly as they do not possess wings that would allow them to bypass some geographic obstacles (Platnick, 1976; Raven, 1980; Yoo and Framenau, 2007). This lack of dispersability would impact their ability to cross barriers such as rivers and potentially mountain ranges. Although spiders are capable of aerial dispersal via ballooning (Duffey 1998), this method would likely only facilitate local dispersal as it requires specific weather conditions. Therefore, while spiders are present on nearly every continent, there should be significant differences in species composition on either side of major geographic barriers (Crews et al. 2006). There have been studies on their movements over geological time (Hendrixson and Bond 2007). While some of these studies are dated, they nevertheless indicate that the dispersal ability of spiders has been heavily affected by continental separation. Most spider cross-continental dispersal occurs in one of two modes. Processes such as rapid sea level change (Miller et al. 2005) would have allowed sporadic dispersal across the continents during periods of lower sea level. Land bridges also would have improved dispersal. The other major way that spiders could have dispersed would have been by rafting, that many smaller organisms accomplish (Gillespie 2011).

Additionally, the vast majority of basal spider divergences occurred in the Cenozoic or later in the Cretaceous. Specifically, many of the modern families originated during this time, including the most speciose one, the Salticidae (Bodner and Maddison 2012; Garrison et al. 2016). Most spider families occur on every continent bar Antarctica, therefore each of



those families subsequently has colonised the world and overcame any geographic barriers that limited their dispersal. The implications of the biogeographic patterns for how spider body plans vary between continents is unclear, but it could indicate that major body plans are ubiquitous across space. To test if this is the case, sites separated by large geographic distances would have to be breached.

The predominant conclusion in the literature is that individual populations of spiders are limited in their dispersal, which likely limits options for comparisons between modern sites and the Florissant. Therefore, if the intention was to eliminate the effect of biogeography then the modern sites would have occur in North America. However, the effect of environment also is important, so initially it may be useful to focus on similarities in topography rather than geographical matching. Furthermore, geography is a key factor that could be driving spider body plans; consequently establishing modern sites based on proximity to the fossil sites is unnecessary.

The preceding discussion implies that spider geographic distributions that are a result of anthropogenic climate change may likewise be limited. The role of climate refugia may be greater for spiders than for other taxa (Ashcroft 2010), though the outcomes would likely be affected by the ecosystems in which they live (Parmesan 2006). This pattern is most likely due to the speed with which human-generated climate change is occurring (IPCC 2011).

**Morphometric Analyses of Spiders.**—The creation of morphospaces populated with the populations at our sites, will require a form of morphometric analyses. The term morphospace could loosely be defined as a representation of a population's morphological variation in two-dimensional space. Morphometrics involves analysing details of the size and shape of an organism to assess structural and evolutionary relationships (Fig. 1 provides a simple example). It focuses on the relative distance in geometric space between species based on measurements of body parts (Adams et al. 2004; Mitteroecker and Gunz 2009). Morphometrics can be used to generate two-dimensional plots of a group of specimens, that summarise their body plans and structural differences. These analyses can quantify some of the evolutionary relationships between fossil specimens and living organisms (Nazzi 1992), as well as features of highest importance to taxonomy (Roberts et al. 2008). The accuracy of these analyses is, however, directly related to the completeness of the specimens, their orientation, the number of measurements taken, and the preserved dimensionality (i.e., 2D versus 3D). Fewer preserved dimensions will likely yield a less robust morphometric analysis, as this reduces the complexity of the data. Loss of accuracy will be true if there are

fewer measurements in the analysis. Therefore, it would be advantageous to maximise the number of measurements taken.

Though there is consensus in the literature about the efficacy of morphometrics, highlighting the approach's accuracy prior to its application is a valuable approach. Morphometrics as a field is rapidly evolving and developing (Adams et al. 2004) and there is a wide variety of forms and methods (Mitteroecker and Gunz 2009), all of which generate some geometric representation of the organisms used in the analysis. Though there are issues with some of the methods such as those that use landmark features (von Cramon-Taubadel et al., 2007), there is nonetheless evidence that morphometrics can produce reliable results and separate organisms both taxonomically and structurally (Francoy et al., 2008; Sasakawa, 2015). For example, Francoy et al. (2008) separated bees at a subspecies level based on wing structure. Consequently, morphometrics should have few problems with showing relationships between species.

Morphospaces have also been used effectively in many studies, not only involving spiders (Wood 2017) but also a variety of other taxa including mammals (Grossnickle and Polly 2013), fish, vertebrates overall (Ward and Mehta 2014), and birds (McGowan and Dyke 2007; Riegner 2008). Such morphospaces have been used to answer questions relating to competition (McGowan and Dyke 2007), differences in the vertebral column structure (Ward and Mehta 2014), and even trends in colour and plumage (Riegner 2008). Morphospaces can also show structural changes over long periods of time (Wood 2017), by using fossil and modern data effectively in combination (McGowan and Dyke 2007; Roberts et al. 2008). Indeed, the idea that morphospaces could be used to investigate whether climate has a significant impact on spider body plans is not inconceivable. Given that both strict morphological (Grossnickle and Polly 2013) and more behavioural/ecological studies (McGowan and Dyke 2007) have been done, there could be detection of whether climate has influenced a robust morphospace. However, a robust morphospace would require measuring a large number of body parts and a significant number of specimens at each site. It also necessitates that the characteristics used in the analysis generate a complex enough picture to differentiate potentially closely related species. The nature of the structures that are measured are key to the reliability of the analysis.

For spiders, one of the key characteristics for identification by morphometrics appears to be carapace or cephalothorax shape, followed by opisthosoma or abdomen shape. Studies have found that landmark features are not reliable for identification of fossil spiders (Bond

and Beamer, 2006). Based on the conclusions of von Cramon-Taubadel et al. (2007) the outline or overall shape of both carapace and opisthosoma is more accurate for determining taxonomy and relationships (Bond and Beamer, 2006). For fossils, it is entirely possible that this fact is attributable to the rarity with which landmark features are identifiable, even within amber (Roberts et al., 2008). Therefore, fossil outlines may be more reliable simply because they preserve more easily in both two dimensional and three-dimensional fossils. However, such outline approaches are not without their issues either (Penney and Langan, 2010) and while carapace and opisthosoma outlines may be reliable when determining specimens to the family level (Roberts et al., 2008), they may be less useful when determining taxa to a lower taxonomic level. Given that the focus of our study is the morphospace each population of spiders occupies, it is their population structure, and consequently evolutionary relationships between them should not present a problem.

In terms of the morphometrics of the fossil spiders, the spiders from the Florissant fossil beds are compression fossils with only two dimensions preserved rather than the ideal three (Martínez-Delclòs et al., 2004). The two amber sites should have amber inclusions preserved three dimensionally. Thus, should a morphometric analysis be undertaken that includes the Florissant specimens, it would only be able to use two-dimensional data on either the dorsal or ventral plane. The use of the same number of dimensions across all sites would allow for an accurate comparison. Morphometric analyses of the Florissant spiders have been done before using the outline approach (Roberts et al. 2008), but such a study was concerned with checking identification of specimens, and did not involve comparisons of morphospace between sites. There have not been morphometric studies on either of these amber fossil sites, nor have their been morphometric studies on the modern sites.

**Palaeoclimatic Studies.--** Palaeoclimatology is the science of estimating the climate of a past environment based on a deposit's flora (more often) or fauna (less often), as well as chemical signals (Mosbrugger and Utescher 1997; Poole et al. 2005). For example, palaeoclimatology has provided data to infer that the Mesozoic was warmer and wetter than now (Fletcher et al. 2008; Keller 2008; Wilkinson et al. 2012). As with the morphometric analysis, it is important that we ensure that use of such methods will be accurate and reliable. In order to arrive at an accurate analogue for the Florissant biota a suitable method must be found. A proper analogue should have a similar temperature, level of rainfall, rainfall pattern and elevation. These environmental variables might produce a flora and fauna which is similar in terms of morphological structure, if climate is the primary factor in determining body plan/structure.

The most common method of determining palaeoclimate in Late Cretaceous and Cenozoic terrestrial fossil assemblages is to document the morphology of fossil leaves within a given assemblage. Specifically an evaluation of their overall area and margin shape (Wolfe 1979; Uhl et al., 2003). This form of analysis assumes that average leaf-margin shape and leaf area will be fairly uniform across a temperature or rainfall zone. This assumption has been shown to be accurate based on the results of several studies (Bailey and Sinnott 1915; Wolfe 1979; 1995, Greenwood et al. 2004). Leaf morphology analysis is generally considered to be an accurate method of analysing palaeoclimate (Mosbrugger and Utescher, 1997; Wilf 1997). The nearest fossil relative approach is another method of using plant fossils. It involves comparing fossil to modern taxa, and examines the overlap of temperature ranges of the living taxa that are present in the fossil assemblage (Uhl et al. 2003; Xing et al. 2012). This method of palaeoclimatic estimation has been refined more recently. There are other methods that incorporate and expand on these previous methods, such as CLAMP (Wolfe 1995; Xing et al. 2012), theoretically enabling a more accurate result.

Exact climate data is not readily available for either Baltic or Dominican amber, although the former is generally considered to be warm-temperate and the latter sub-tropical. However there have already been many reconstructions of climatic conditions of the Florissant beds (Boyle et al. 2008; Smith 2008; Veatch and Meyer 2008; Zaborac-Reed and Leopold 2016), which offer a range of values with respect to temperature, rainfall, and elevation. Zaborac-Reed and Leopold (2016) would seem to be the most comprehensive study. Their analysis pools the results of a number of other studies together. Using multiple methods from other studies corroborate their new approach, such as the nearest living relative approach and CLAMP, thus lending validity to their findings. The authors determined that the Florissant environment likely had a mean annual temperature (MAT) between 14.3 and 18.2 °C and that conditions of frost were rare. This is a fairly large MAT range, but there is always error in palaeoclimate estimation, and based on other analyses of the Florissant presented in Zaborac-Reed and Leopold (2016), it is more likely that MAT sat towards the lower half of that range. Likewise, mean annual precipitation (MAP) estimates have a range of  $720 \pm 310$ mm, placing the Florissant beds in a warm-temperate yet dry climate. The rainfall pattern is believed by Zaborac-Reed and Leopold (2016) to be predominantly summer wet ( $570 \pm 160$ mm over the summer) and winter dry. The remaining variable of elevation has been a point of contention in the literature. However, a value of around 1500 m (Zaborac-Reed and Leopold 2016) would seem to be reasonable, as there is evidence of continuous uplift since the late Eocene and Florissant currently lies at around 2500m above sea level.

Based on this and other studies, the necessary criteria for finding an extant climate analogue of the Florissant fossil beds have all been well-constrained.

**Responses of Modern Arthropods to Different Climates.--** Human-generated climate change has already had impacts on contemporary organisms, with the arthropods being no exception. Climate change responses that account for distribution and morphology of life will enhance our understanding of the responses spiders have historically made and will make in the future. If certain spider body types are specific to or favoured by certain climates, and those climates become restricted in distribution because of climate change, then those spider body types could therefore become restricted as well. This could even be defined as functional types of spiders if a certain climate suits a certain habitat, which in turn suits a certain type of spiders such as burrowers. If indeed burrowers have a distinct body type.

With a warming climate, the environment will eventually approach similar conditions to that of the Eocene (Fletcher et al. 2008; Poole et al. 2005). Therefore, it could be expected that many taxa including insects will reoccupy locations they inhabited before the climate began to cool during the Cenozoic (Parmesan, 2006). It already has been noted that some species of insect pests have expanded their ranges and as a result have increased in abundance in recent years (Cannon 1998; Dukes et al. 2009). Climate change may not be the only cause for this phenomenon, as human activity and expansion have also resulted in range expansions of invasive species (Mooney and Cleland 2001). Nevertheless it seems plausible that pest species or insect species with higher limits to their typical thermal tolerances will spread quickly as a result of climate change. Pest species have a wider tolerance than non-pest species (Dukes et al. 2009), so they may extend their geographical range to a greater extent than non-pest species.

It is also important to consider the different potential impacts of climate change on different life stages of insects. Juveniles are more vulnerable to variation in temperature than adults (Kingsolver et al. 2011), meaning that areas where insect species can breed may be a subset of those in which the adults can populate. However, the rate at which climate change currently is occurring may inhibit range expansions particularly if the process happens too fast for populations to move. This could be the case for species that do not have wings, such as spiders, or for insects that are less able fliers.

A decline in overall body size has been suggested to be as a result of global warming (Clyde and Gingerich 1998; Sheridan and Bickford 2011) in fossil organisms, a phenomenon that could also be possible in modern populations. While overall body size is not indicative of anything in particular regarding body plans, it nonetheless is a crucial aspect of biology.

Whether this is a universal response has been disputed (Gardner et al. 2011). It is important from these findings that the implication of organisms occurring in warmer environments are smaller than the same organisms in cooler environments. However, when looking at spiders specifically, reductions in body size with a commensurate warming climate does not appear to happen. A study by Entling et al. (2010) showed spiders from warm and dry environments are larger than those in cool and moist environments. Entling et al. (2010) do state that some part of the observed pattern could be explained by a turnover in family composition. However, they do believe their results to be consistent with changes in physiological processes as a result of the climate gradient.

Therefore, examples of altered arthropod morphology in response to or as a result of climate in are relevant. One study examined beetles (Babin-Fenske et al. 2008) that showed an increase in both size and in the fineness ratio (ratio between body length to width) that indicates a more streamlined body. While Babin-Fenske et al. (2008) show clear results, their applicability to this study is somewhat in question. Their results show a population-wide response and do not necessarily indicate whether beetles in a warmer location always have higher fineness ratios than those from colder localities. Nonetheless, this association could indicate that spiders would have a similar response to warmer climates, as Entling et al. (2010) already indicate by suggesting larger spider bodies in warmer climates. However, none of these studies make mention of distinct differences in functional composition across climates.

The responses of spiders to climate change are therefore likely to mirror largely that of insects. Comparing the Florissant fossil bed spiders to the modern sites will presumably show a clear distinction between the body plans of spiders in warmer compared to cooler environments. This distinction should follow either the predictions of Sheridan and Bickford (2011) that body size would decrease or those of Entling et al. (2010) and Babin Fenske et al. (2008), that body size and the ratio between length and width should increase. The outcome will indicate whether structural responses to climate change in animals are largely universal or specific to lower taxonomic levels such as orders, the latter possibility is the most consistent with the available data. If spiders have no differential structural response to various climates, then the morphological diversity of spiders will not be adversely affected by anthropogenic climate change. This notion is one of the key hypotheses this study aims to test. The other two being the impact of geographical separation and trends in body plans over time.

**Overall Predictions.--** Climate conditions should have an impact on how spider body plans are constructed. Given what has been presented in the previous sections, the comparison among sites will yield one of four possible scenarios. All of the sites being similar to one another is possible, but highly unlikely given the variety of environments that are present. The same is true for a scenario in which all sites are significantly different from one another. The two scenarios that are more likely are one in which sites are separated by climate, and another in which sites are separated by geography. These scenarios are likely because it has been shown that spider body size distributions change as a result of climate change (Entling et al. 2010) and because species composition that turn over through space should also cause differences in body-shape distributions (Crews and Hedin 2006).

## METHODS

**Site selection.--** To generate as many combinations as possible and practicable, a total of five sites were chosen. As mentioned in the previous chapter, these sites are the fossil locality of the Florissant beds, the two Australian sites chosen to represent modern spider populations, and the two amber-bearing fossil sites of Baltic amber and Dominican amber. The Florissant site is in Colorado, USA, near the city of Colorado Springs, and has been extensively studied since the late 1800s (Scudder 1890). Its temporal position and climate estimates were presented in the previous chapter, the selection of the modern sites had to take that information into account. Therefore, the nature of the climate data for the Florissant and its late Eocene age were critical in the selection of all the other sites.

The modern sites had to be distinct from each other as well as from Florissant. It was decided that one modern site would be a climate analogue of the Florissant and the other would be a control for the Florissant site of today. (Figure 1 shows the Florissant during the Eocene and 2 shows the locality of the fossil beds). Using the palaeoclimate data and the analysis by Zaborac-Reed and Leopold (2016), it was determined that the most similar site in the Americas was a district in the state of Puebla in Mexico. However, this region was too poorly sampled to be included, and a substitute was the Mescalero Apache tribe reservation (38 species) in New Mexico. Unfortunately, there are few publications that take a comprehensive view of modern spider populations within a site, so museum collections were used. The process of obtaining specimen data from those locations proved to be unsuccessful, as it was logistically difficult to obtain a sufficient number of photos necessary for comprehensiveness.



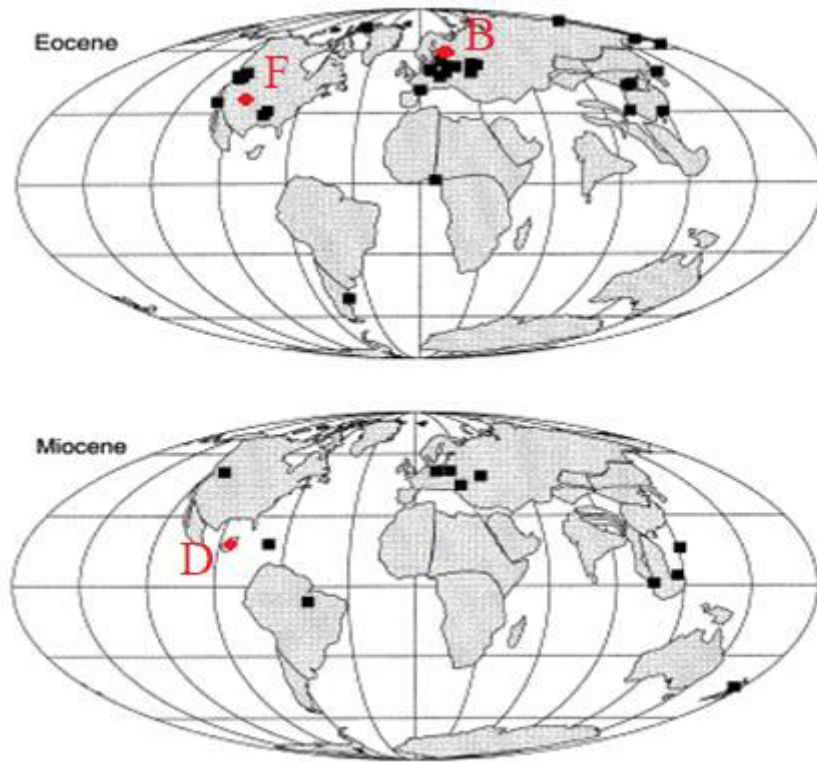


Figure 1. Approximate geographic positions of the fossil sites in our analysis, marked in red. Eocene has Florissant (F) and Baltic (B) Miocene point is the Dominican Amber (D), modified from Martinez-Delclòs et. al. (2004). The black squares are not related to this study.

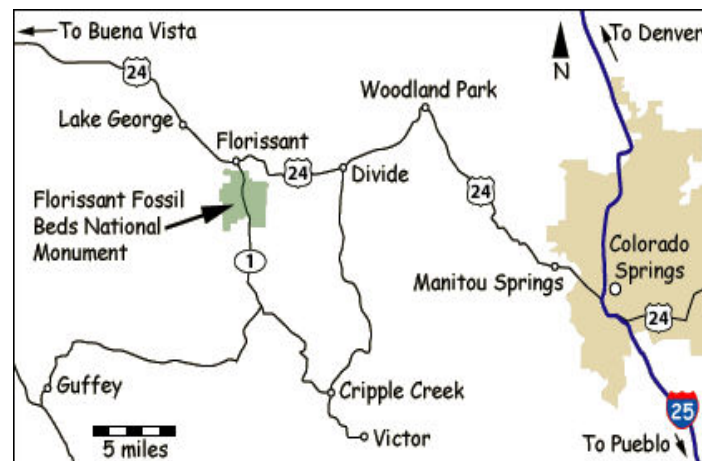


Figure 2. Florissant Fossil beds (Site F) locality and surrounds.

As a result, sites from Australia were used instead, which seemed appropriate as sampling of different environments is fairly complete and the material was easy to access. To find these sites the Atlas of Living Australia (ALA) was used along with Australian Bureau of Meteorology climate data. The selected climate analogue site was Barrington Tops National Park and State Forest (Figure 3) (designated as site T for Tops). It has a MAT of

15.2°C, which places it at the lower end of the 14.3-18.2 °C range that Zaborac-Reed and Leopold (2016) gave for the Florissant beds, which as stated is plausible. The MAP for Barrington Tops is 920 mm and it shares its rainfall pattern with the Florissant beds in that most of the rain falls during summer. Barrington Tops' last attribute, elevation, is also similar to that of the Florissant, as the maximum elevation is approximately 1540 m. These features made Barrington Tops an excellent candidate for a climate analogue.

The other modern site needed to be climatically distinct from the first, but still geographically close in order to minimise the chances of geographic differences between the sites impacting the pattern of similarity between their morphospaces. Therefore, the most logical choice would be of a site adjacent to the coast with very low elevation. Using both elevation and proximity to Barrington Tops as criteria, I delineated a coastal arc from Port Stephens to Forster (thus site C) that encapsulated parts of the inland region as well (Figure 3). The MAT for this entire area is between 18-19 °C and the MAP is close to 1100mm. This geographical position made the site significantly warmer on average and slightly wetter, with the rainfall pattern distributed more throughout the year than the one found in Barrington

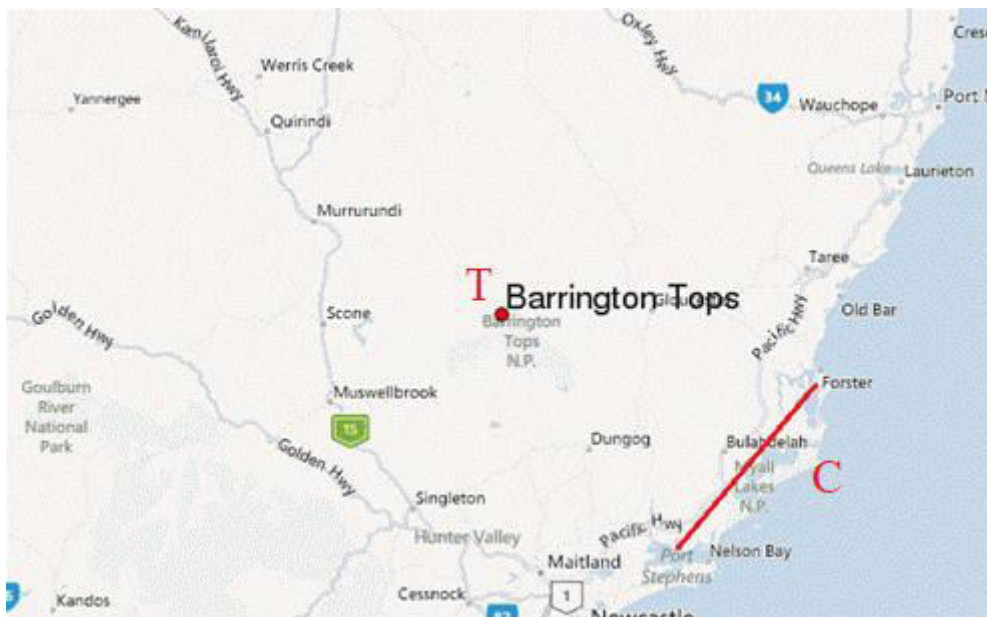


Figure 3. Map of a portion of New South Wales (NSW) showing both Barrington Tops National park and the rough extent of the coastal arc. Modified from [www.mountain-forecast.com](http://www.mountain-forecast.com) (accessed 05/07/17).

Tops.

Additional fossil sites also have been well sampled and extensively studied. The site chosen to represent B (same time as F yet geographically isolated) was Baltic amber. The

Baltic amber is middle Eocene (44-40 Ma), whereas the Florissant is late Eocene (37 Ma), but its position in Europe makes it geographically distant from the Florissant, which was the case even at their times of deposition (Figure 1 and 4). Baltic amber has been well-studied and presents a large number of spider inclusions (Perkovsky et al. 2007; Wunderlich 2004), which allows creation of a robust dataset. It has been suggested that the climate of the Baltic region was warm temperate during the Late Eocene, making it not radically dissimilar from any of our other sites, but likely to be most similar to our modern coastal arc.

The remaining fossil site (D), placed between the Florissant and the modern sites on the geological timescale, is the Dominican amber. Like the Baltic amber, this site has many spider species in its inclusions (Penney 2008; Wunderlich 2004; Wunderlich 2008). It is mid-Miocene in age (15-20 Ma). It is also geographically isolated from Florissant, but the ability of spiders to migrate across ocean barriers (Bodner and Maddison 2012, Gillespie et al. 2012) could decrease the impact of that biogeographical distance (Figure 1a shows the geography during the Miocene). In terms of climate, the Dominican amber is considered to be sub-tropical in environment (Grund 2006), and therefore is significantly different from the other sites. Nevertheless, it is still a useful site because it represents a midpoint in time between the



Figure 4. Locations of Baltic amber deposits (Site B) that have been sampled, highlighted in yellow. Taken from Weitschat et al. (2010)

late Eocene and the Recent.

**Data Sources.--** The specimen data for the Florissant site were obtained through the works of Scudder (1890) and Petrunkevitch (1922). While these studies are dated, they each provide numerous scaled drawings of specimens that can be used to collect the necessary measurements from each spider. From these papers, only those specimens which were associated with drawings were considered. Plate XI in Scudder (1890) and every spider

drawing within Petrunkevitch (1922) were used. Taxonomy of specimens was cross-checked using Roberts et al. (2008), Dunlop et al. (2015), and the Palaeobiology Database (fossilworks.org) and the currently accepted names were used. This was done due to the systematics of older works such as Petrunkevitch (1922) likely having errors. Combined, these works gave a total of 50 species for the Florissant site.

For modern spiders, the arachnology collection at the Australian Museum was used. This collection houses hundreds of thousands of spiders from throughout Australia, which are stored in 70-75% ethanol (Figures 5 and 6). The extent of occurrences within each site was determined using polygons created in ALA (Figures 7a and b). The number of specimens that met the selection criteria at each of the modern sites was far greater than the numbers found at fossil sites, so only one specimen per species was used. The specimen chosen to represent each species was chosen at random. A few species had only one representative and some of the more common ones had somewhat over 15. This was done based on the concept that intraspecific variation at a location would be small compared to interspecific variation in terms of overall morphology. As a result, the total number of species thought to be available for Barrington Tops was 44 and for the Coastal arc was 52. However, not every specimen could be located within the collection, and the actual numbers used were 42 and 49 respectively.



Figure 5. Photo of a specimen jar from the Australian museum arachnology collection.



Figure 6. Photo of *Longepi boyd* from the Australian museum arachnology collection

For both Baltic and Dominican Amber, the works of Wunderlich (1988; 2004) were used. Photos were made of these specimens preserved in amber, though only some of the photos present from each volume were used. Photos were chosen based on clarity and maximising the number of measurements obtainable; thus photos with dorsal or ventral aspects were primarily used. Appendices 3 and 4 detail which photos were used and on what

pages they appear. As before, only those images identified to species level were used, and to ensure as many body measurements as possible could be taken, the preference was for dorsal

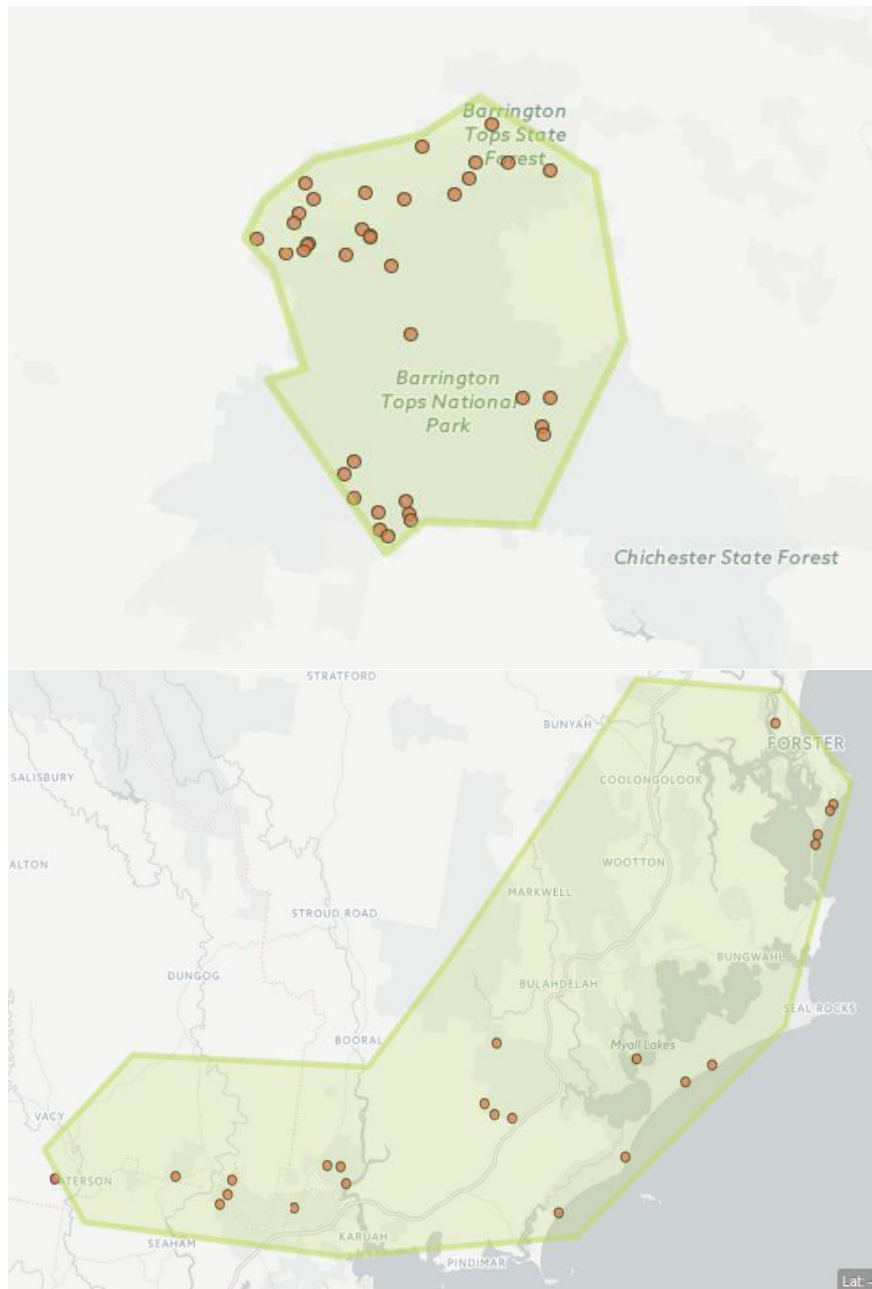


Figure 7. Polygons generated on ALA for site T Barrington Tops (top) and site C the coastal arc (bottom). The red dots indicate collection events/sites that resulted in species level occurrences that are housed in the Australian Museum Arachnology collection.

or ventral images. However, some other aspects of these specimens did need to be used. A total of 45 species were extracted from the Baltic Amber and 38 from Dominican amber. This brought the total number of specimens/individuals used in the analysis to 224.

**Measurements.**-- The fossil images were initially measured and processed, prior to measurement of modern specimens. This procedure enabled measurements that did not appear reliably in the fossils (i.e., less than 33% of the time) to be removed from the analysis. The total number of measurements taken from each spider was 24. The measurements used were the length and width of the prosoma and opisthosoma and the lengths of the five major segments for one member of each leg pair (Figure 8 shows the external anatomy of a spider). A total body length measurement was also either taken from the relevant literature (Scudder

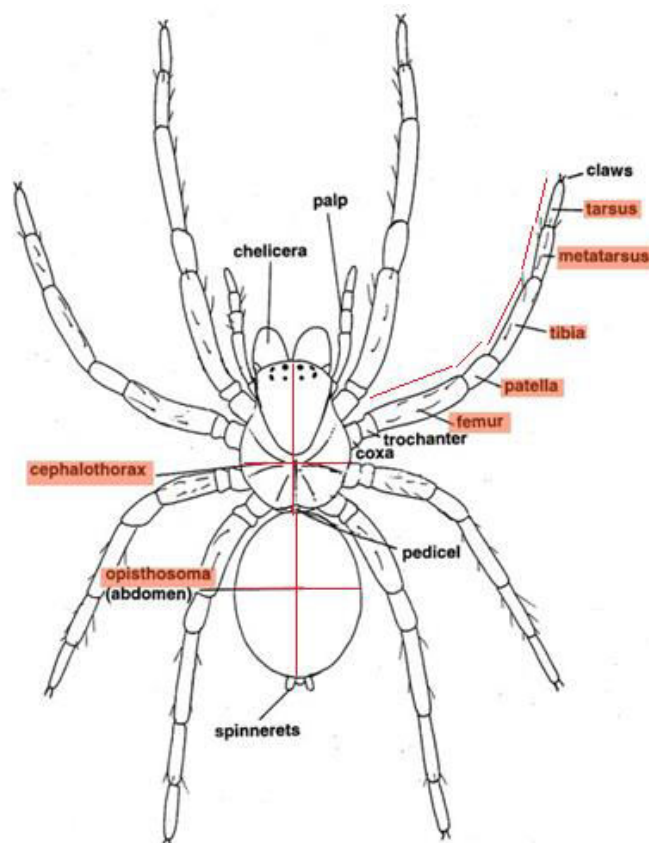


Figure 8. External anatomy of a spider, with measurement points indicated by red lines and labels in orange.

in orange and

1890; Petrunkevitch 1922) or alternatively calculated using the body segment lengths in which measurements were taken using a 15cm ruler with 0.5 mm gradations up to 5 cm. Measurements taken from the literature were used initially for each specimen to calculate the scaling of the other measurements. The sizes of the spinnerets and chelicera were not taken as these could not be obtained from the fossils reliably. In addition, the supposed sex of the specimen was noted alongside family and species names.

The modern specimens were measured on site at the Arachnology section of the Australian Museum. As the measured material were physical specimens, as opposed to drawings or pictures of fossils, they could be rotated and manipulated to maximise the number of measurements taken. Some specimens were missing anatomical elements, due to

certain legs being removed for taxonomic studies or to other disturbances prior to this study. The specimens were measured under a stereo microscope with an eyepiece graticule and a 1 mm micrometer scale. At each magnification level the graticule could be calibrated using the micrometer, generating a number of gradations on the graticule per mm (Table 1). Once calibrated, the specimens were removed carefully from the specimen jars and placed into an observation well with white sand and additional 70% ethanol to maintain moisture. The white sand was used as an aid in appropriate positioning of the spiders, portions of which could be buried under the sand when measuring certain body parts. Care was taken at all times to manipulate specimens as little as possible, as some were very small and often exceptionally delicate.

The specimens from the Baltic and Dominican Amber were measured in a similar fashion to the fossil specimens from the Florissant material. The initial body length measurement was used to calculate the scale for each photo used in the Baltic amber, and then measurements were calculated using the ruler and scale as mentioned before. However, for Dominican Amber the photos in Wunderlich (1988) were often not in an ideal position, and the quality was such that the measurements given in the book itself were added to supplement measurements taken from the photos.

**Table 1.** Micrometer calibrations for each optical zoom on the stereo microscope.

Magnification Level	Gradations per 1mm
1x	20
2x	40
3.2x	65
4x	80
5x	100

**Statistical Analyses.--** The statistical program R (version 3.3.1) was used for all analyses in this study. Initially, each dataset was read into R and log transformed. The transformed data were then scaled and centred around zero before being transformed into a distance matrix by subtracting the mean and dividing by the standard deviation. Each distance matrix was then run through a principal coordinates analysis (PCoA) to generate a unique morphospace for each site. The function `cmdscale` in the R stats package was used. PCoA was used because the data contained a large number of missing data points or measurements, hereafter referred to as not applicable/available (NAs). This ruled out use of both factor

analysis and principal components analysis (PCA). A transposed version of each of these matrices was also used to generate morphospaces that had body parts as data points rather than species as data points. Both the transposed and the complete data sets were analysed using both Euclidean and Gower's distance measures (Gower 1971). Gower's distances are more appropriate for an incomplete dataset, and so they were used as an additional means of checking the robustness of the results.

The individual morphospaces could not be compared to one another directly because ordination produces scores with different distributions, depending on the relative intensity of sampling across gradients. Thus, in order to compare sites, the datasets were combined into one matrix and a new morphospace was generated that depicted all of them simultaneously. Sites could as a result be compared statistically on a pairwise basis, as well as visually. The pairwise comparisons allowed testing the three hypotheses concerning potential drivers of spider body plan variation (climate, geography, and time/evolution). The Wilcoxon test implemented by `wilcox()` in R was used to make comparisons of both axis 1 and axis 2 PCoA scores. Each site was compared to every other site, resulting in a total of ten pairings per axis.

To test the robustness the results generated, the data were cleaned (missing or unreliable data removed) in a number of different ways and the analyses were re-run. The cleaning was necessary due to the large number of NAs in the data matrices, with data for certain individual spiders being highly incomplete. The first method of cleaning was on a taxon-by-taxon basis. Any individual spider with nine or more NAs (over a third of the measurements) was removed from the dataset before the all-sites matrix was remade and transformation and scaling was undertaken. The figure of nine measurements was selected after considering several options and it was determined that nine NAs as a cut-off presented a balance between retaining as much of the sample size as possible and improving reliability of the data. This method of cleaning resulted in the following reductions in sample size for the sites: 24 for Florissant, 41 for Barrington Tops, 49 for coastal arc, 37 for Baltic amber and 17 for Dominican amber.

The second method of cleaning also involved removing data based on an a maximum NA threshold, but in this case measurements were removed rather than taxa. The threshold this time was applied to the matrix of all sites, not each individual site matrix. This criterion applied to the all-sites matrix, as each individual site would have different measurements that would not meet the threshold and thus could not be compared if cleaned individually. The



threshold chosen for this method was 35 NAs, meaning that roughly one quarter of spiders in the analysis were missing the relevant measurement. This cut-off of one quarter was chosen for the same reasons as for the threshold of the taxon-cleaned dataset, as well as because more stringent thresholds (fewer NAs) did not significantly alter the number of measurements retained after cleaning. This method of cleaning reduced the total number of measurements in the analysis to eleven: body length total, cephalothorax length and width, abdomen length and width, leg I femur length, leg II femur length, leg III femur length, leg IV femur length, leg I patella length and leg I tibia length.

The third and final method of cleaning used to check for robustness in the results involved replacing NAs with the row and column means. The protocol for this method was to replace any cell in the all-sites matrix that had an NA with the average of the corresponding row and column means, effectively 'filling in' the missing data points. Because this procedure left no NAs in the matrix, PCA and factor analysis (FA) could then be implemented. The PCA and FA loadings were then used to see which variables most likely contributed the most to the structuring of the PCoA ordinations, which was not always obvious based on examining the morphospaces generated by the PCoAs. Wilcoxon tests were run on all of the cleaned datasets as well.

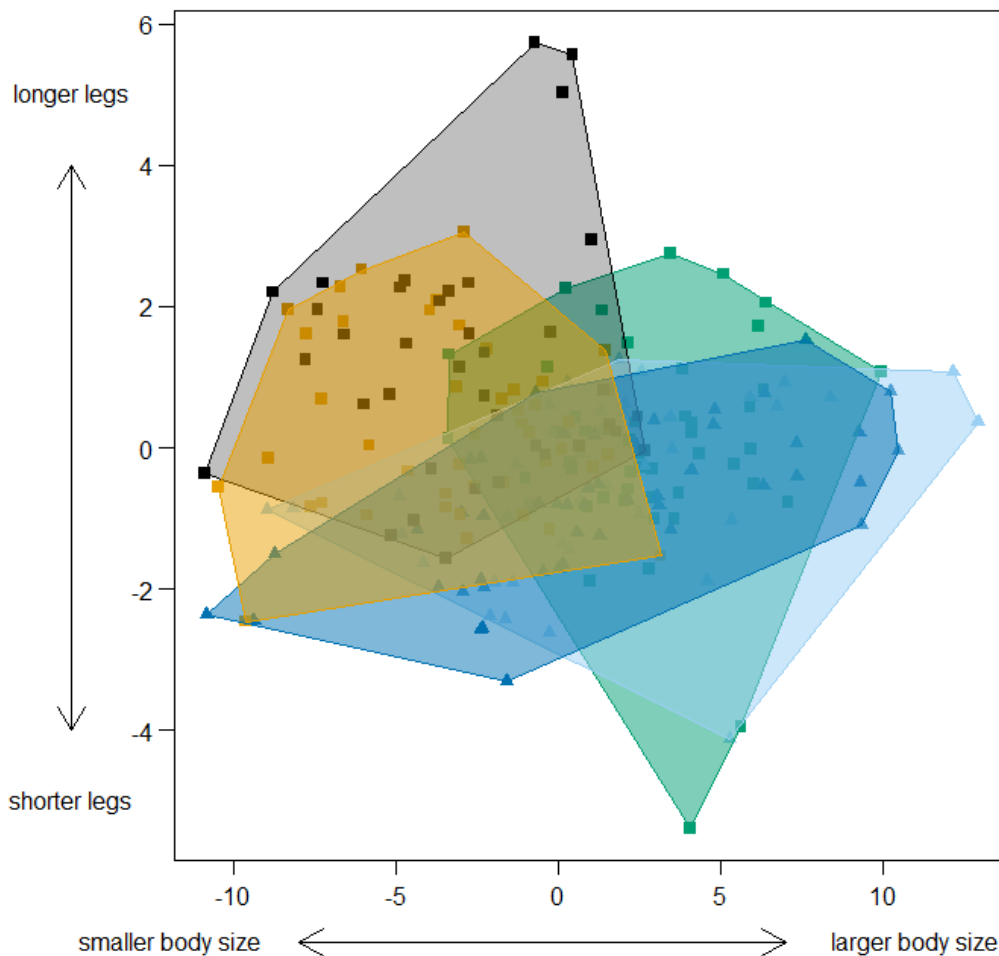
Note that another method of data-checking not used in this analysis was the process of randomly knocking out taxa or measurements regardless of missing data points. It was felt that the level of checking these various methods allowed was sufficient and thus a randomised check was not critical to testing the robustness of the obtained results.

After the cleaning and conducting all Wilcoxon tests, a final set of morphospaces was constructed for each site to quantify the role of family level composition. Specifically, each taxonomic family in each site which was represented by five or more specimens was included to see if individual families occupied narrow regions of the morphospaces. An exception was made for the Baltic Amber dataset because no family included more than five specimens, so the cut-off for that site was four. The premise of this analysis is that if families are strongly clustered, then gaps between sites can be explained by phylogenetic effects. A similar morphospace representing all five sites at once was constructed that included the five most numerous families overall. This was done to see if family level morphological space was more or less constrained across sites than within each site, such as if there were large numbers of a particular family in multiple sites.



## RESULTS

The morphospaces generated for all sites combined using the complete data set are presented in figure 9, with the version that employed Gower's distances in figure 10. The two modern Australian sites overlap almost completely, and each of the fossil sites overlap with them. However, each site occupies its own unique area of morphospace. The same patterns are seen in the morphospaces generated from the cleaned and filled in datasets, and are shown



in figures 11, 12 and 13.

The two modern sites spread across axis 1 in the complete dataset (fig 9) and are separated on axis 2 from the fossil sites. The Florissant site overlaps with the two amber sites only partially, but almost entirely with the modern sites. The morphospace generated using Gower's distances (fig 10) distinguishes the sites in the same way, though axis 2 had to be

flipped to match the orientation to figure 9. The taxonomically cleaned dataset (fig 11) is differently oriented relative to the complete dataset, but presents a similar pattern of separation between the five sites. The amount of space dedicated to the modern sites has increased compared to the complete data, and that occupied by the fossil sites has decreased.

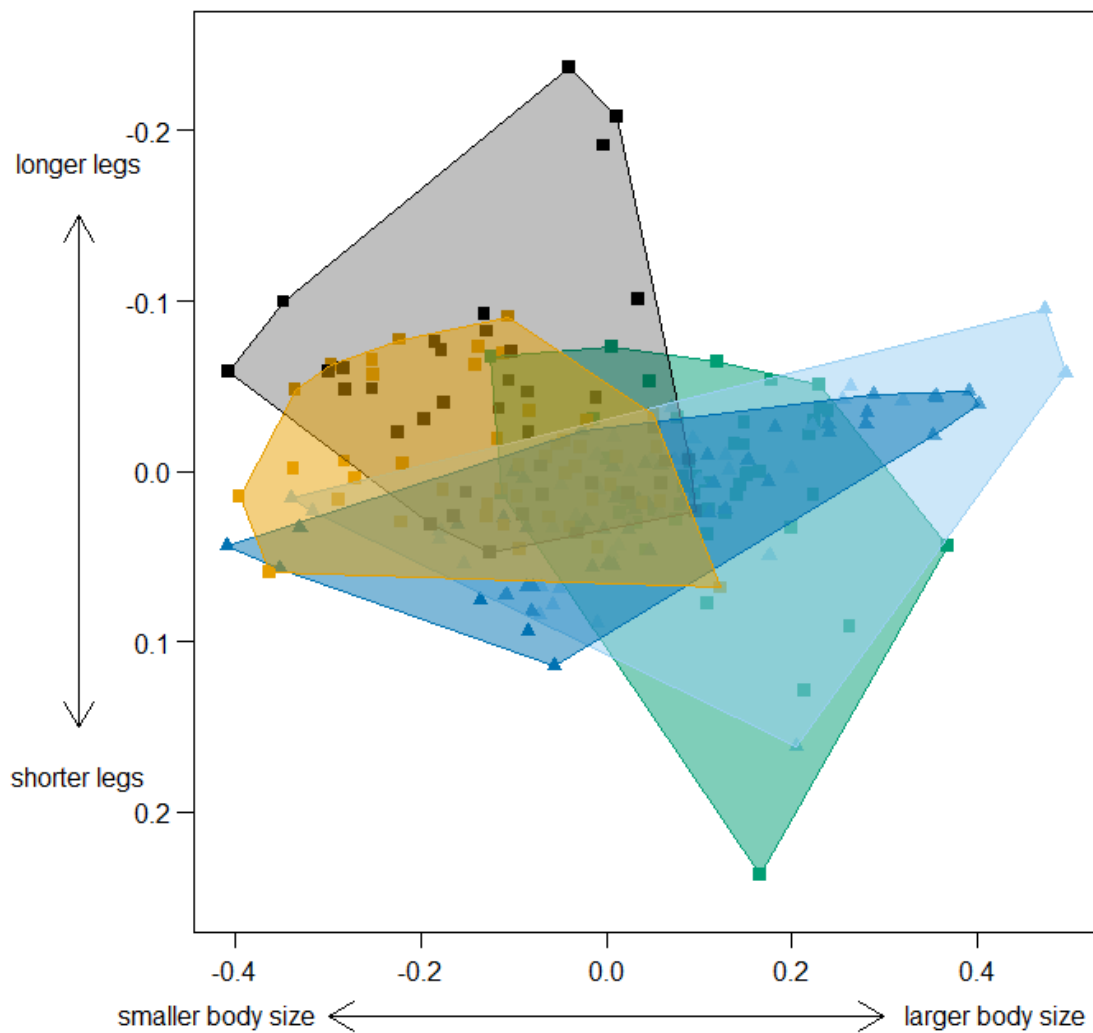


Figure 10. Morphospace of all sites generated using Gower's rather than Euclidean distance. Colours of sites are identical to figure 9. Note the Y axis limits are flipped to correct the orientation.

The 'mean filled' dataset (fig 12) presents yet another shift in the orientation of the sites, but also provides a similar pattern of separation. The overall morphological space occupied by all the sites is reduced, as evidenced by the shorter axes, and once again the modern sites appear to have a larger share. The extent of the overlap between the two amber

sites is reduced, with more data points appearing outside the shared space. The measurement-cleaned dataset (fig 13) more closely resembles the complete dataset (fig 9), with a more restricted spread of the modern sites on axis 2. The spread of the sites on axis 1 does not appear to change at all regardless of the cleaning method, suggesting that axis 2 is more sensitive for and important for separating the sites and that the results are robust to transformation and cleaning. The factor analysis morphospace is not shown here because it is virtually identical to the mean-filled dataset.

Across all four datasets, axis 1 represents an overall size axis. Those species that are very small or very large in body size consistently lie at the extremes. Therefore, sites that separate along axis 1 could be considered to sample fundamentally different size distributions. Axis 2 predominantly reflects an inverse relationship between body size and leg length. Those spiders with significantly longer legs than bodies lie at one end, such as those from family Pholcidae, while spiders with leg lengths similar to overall body length lie at the other end. This pattern seems present irrespective of overall species body size. The loadings from the factor analysis suggest that the result is being driven by body segment length (loadings range from 0.7-0.9 for all body measurements).

The Wilcoxon test results for axis 1 and axis 2 for all four methods are presented in table 2 and 3. They show whether a particular pair of sites differs significantly in morphospace occupation. Any  $p$ -value  $< 0.001$  was considered significant, meaning that those two sites differed significantly on that axis. On axis 1, all comparisons were significantly different from one another in at least one dataset except for Barrington Tops vs coastal arc and the Baltic amber vs Dominican amber. This means that the two modern sites and the two amber sites are essentially the same on axis 1.

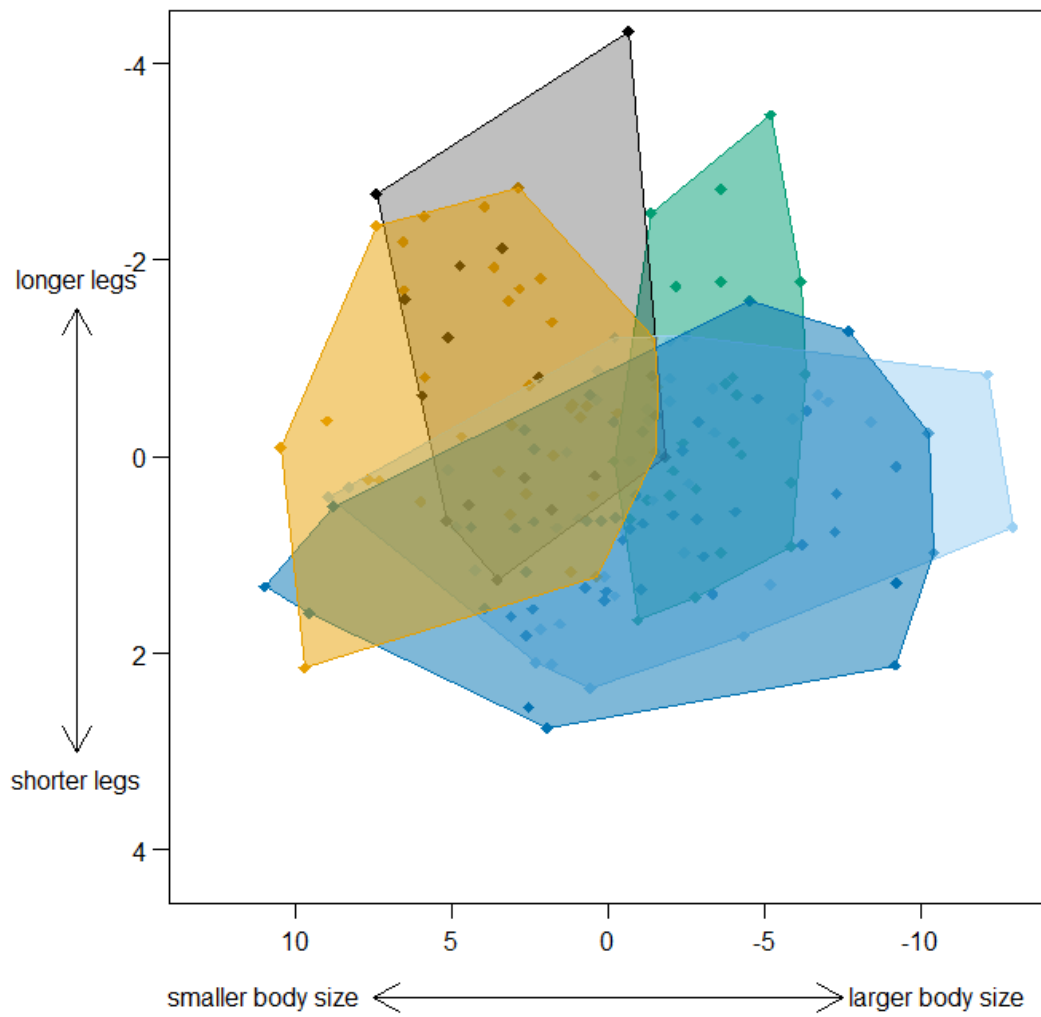


Figure 11. The overall morphospace for the taxonomically cleaned dataset, with colour codes identical to figure 9. X and Y axis orientation is again flipped to make morphospaces easy to visually compare



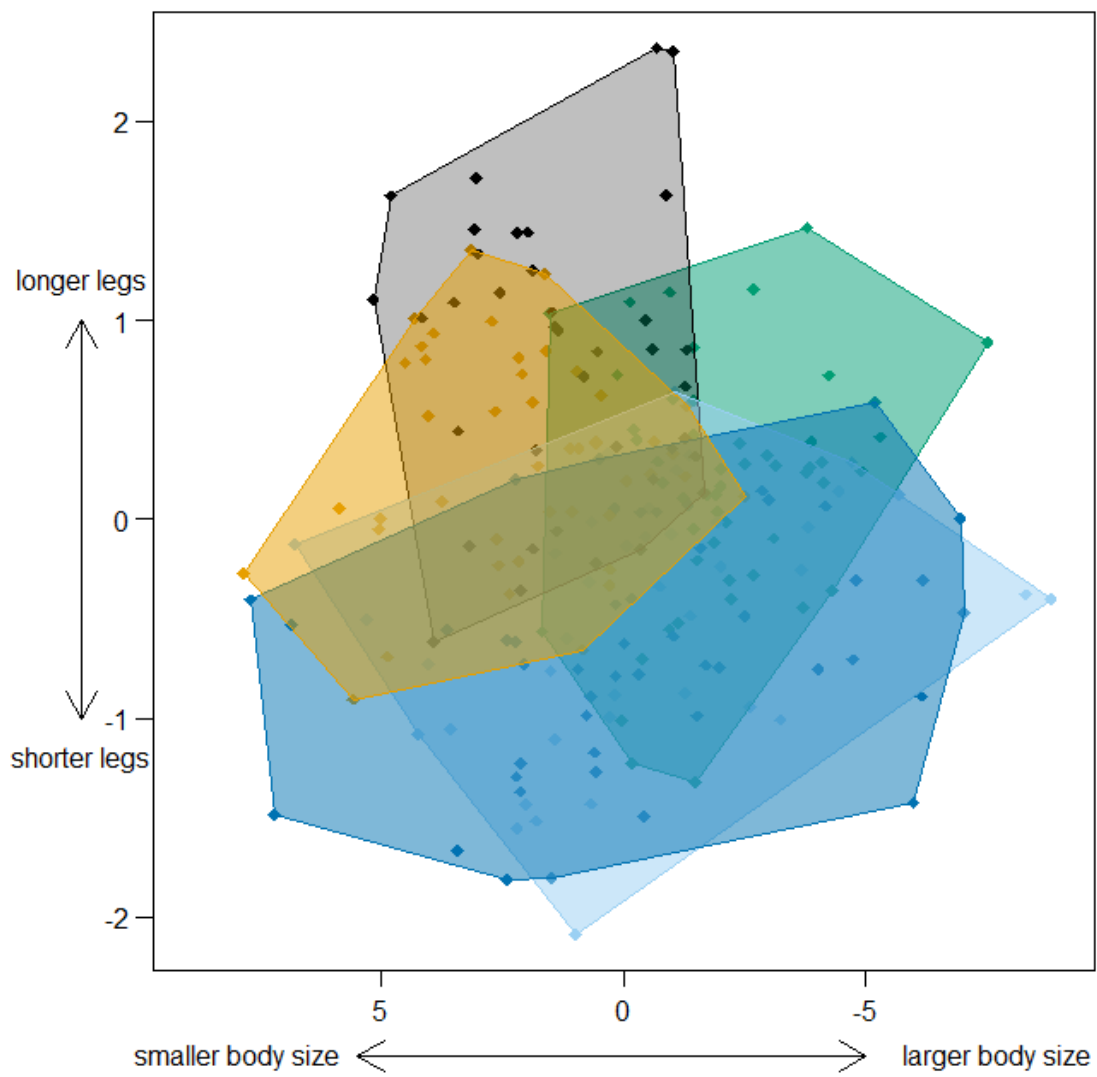


Figure 12. Morphospace of the mean filled dataset, with colours identical to figure 9. X axis limits are flipped to correct orientation.





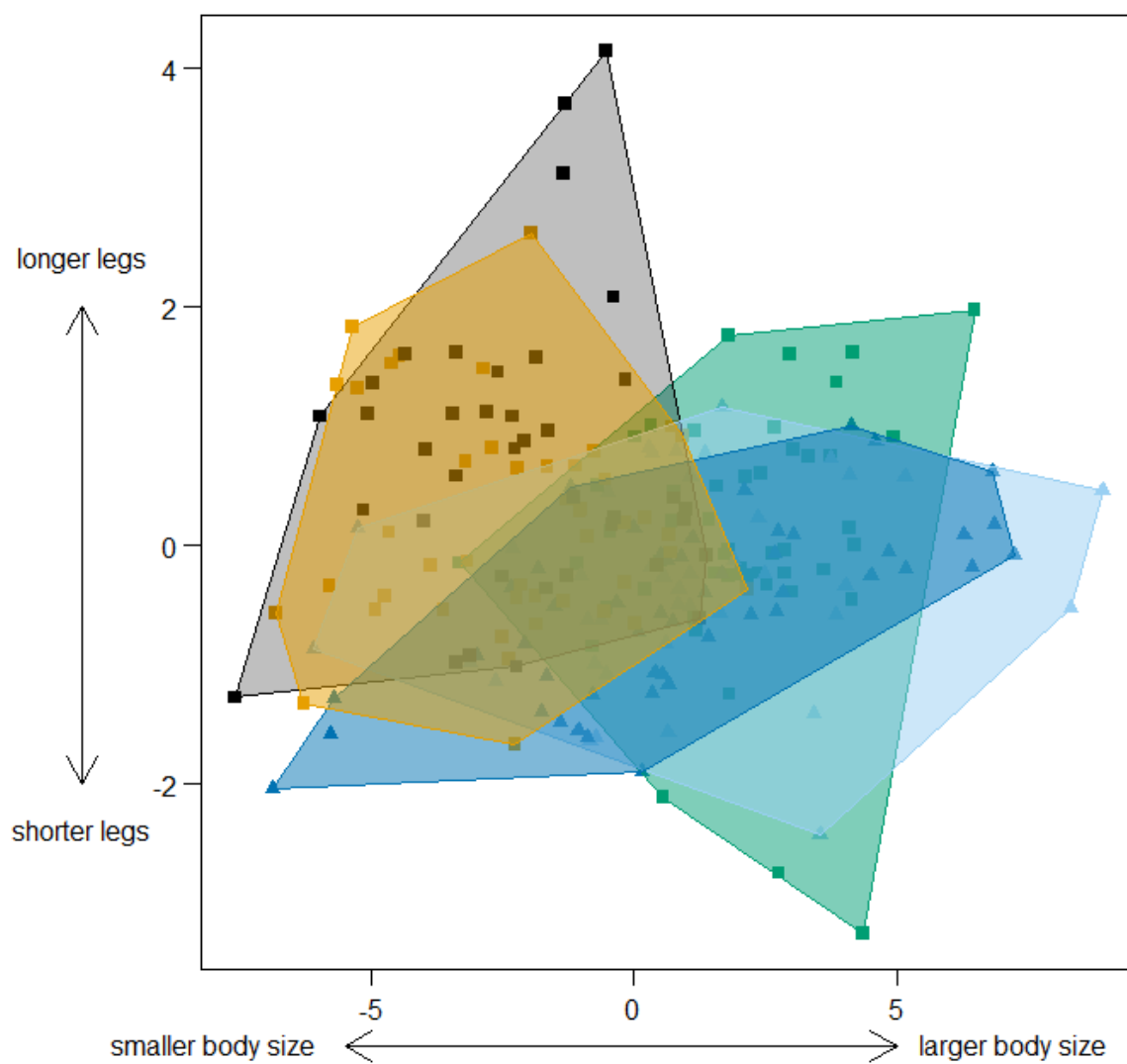


Figure 13. Morphospace of all sites with data cleaned based on missing measurements, colours of sites are identical to figure 9.

**Table 2.** Pairwise Wilcoxon test results for each of the four datasets. Critical value is  $p < 0.001$ . The four datasets are from left to right: the complete dataset with all missing measurements (NAs) included, data with taxa removed based on the number of NAs, data with NAs replaced by the average of the row and column means, and data with measurements removed based on the number of NAs. Significant values are in bold.

Pair	Complete data set	Taxon Cleaned	Mean Filled	Measurement Cleaned
Florissant vs Barrington Tops	0.006	<b>0.001</b>	<b>&lt;0.001</b>	0.007
Florissant vs coastal arc	0.02	0.011	<b>0.001</b>	0.028
Florissant vs Baltic amber	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Florissant vs Dominican amber	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Barrington Tops vs coastal arc	0.9809	0.9165	0.9271	0.9211
Barrington Tops vs Baltic amber	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Barrington Tops vs Dominican amber	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Coastal arc vs Baltic amber	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Coastal arc vs Dominican amber	<b>&lt;0.001</b>	<b>0.001</b>	0.01871	<b>&lt;0.001</b>
Baltic amber vs Dominican amber	0.6526	0.6849	0.08832	0.7886

One of the pairings found to be indistinguishable from one another on axis 1 follows on in axis 2. Barrington Tops and Coastal arc are again highly comparable across all datasets, but Baltic amber and Dominican amber differ in the mean-filled dataset. Instead, Florissant and Baltic amber are indistinguishable on axis 2. Also of note is that the Coastal arc is significantly different from all three fossil sites on axis 2 for all four datasets.

**Table 3.** Pairwise comparisons of the sites for axis 2 based on Wilcoxon test results. The critical value here is  $p < 0.001$ . Columns are identical to table 2 and significant values are in bold.

Pair	Complete Data set	Taxon Cleaned	Mean Filled	Measurement Cleaned
Florissant vs Barrington Tops	0.063	0.067	<b>&lt;0.001</b>	0.011
Florissant vs coastal arc	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Florissant vs Baltic amber	0.4952	0.4325	0.309	0.9732
Florissant vs Dominican amber	<b>0.001</b>	0.4874	<b>&lt;0.001</b>	0.01
Barrington Tops vs coastal arc	0.1755	0.05455	0.2217	0.3272
Barrington Tops vs Baltic amber	0.01	<b>0.001</b>	<b>&lt;0.001</b>	0.016
Barrington Tops vs Dominican amber	<b>&lt;0.001</b>	0.008	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Coastal arc vs Baltic amber	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Coastal arc vs Dominican amber	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Baltic amber vs Dominican amber	0.013	0.9119	<b>0.001</b>	0.022

Transposing the data for each site made it possible to create body plan morphospaces. The transposed PCoAs for the sites are presented in Figs. 14 and 15, with Fig. 14 representing the transposed PCoA for all sites combined with Euclidean distances and figure 15 using Gower's distances. The transposed PCoAs for individual sites are shown in appendix 6. These plots show each measurement as a separate data point and utilise the complete dataset so that all measurements and taxa are included, thus maximising the number of measurements behind each data point. In, addition the Wilcoxon test indicates that the results obtained are relatively robust to data manipulation.

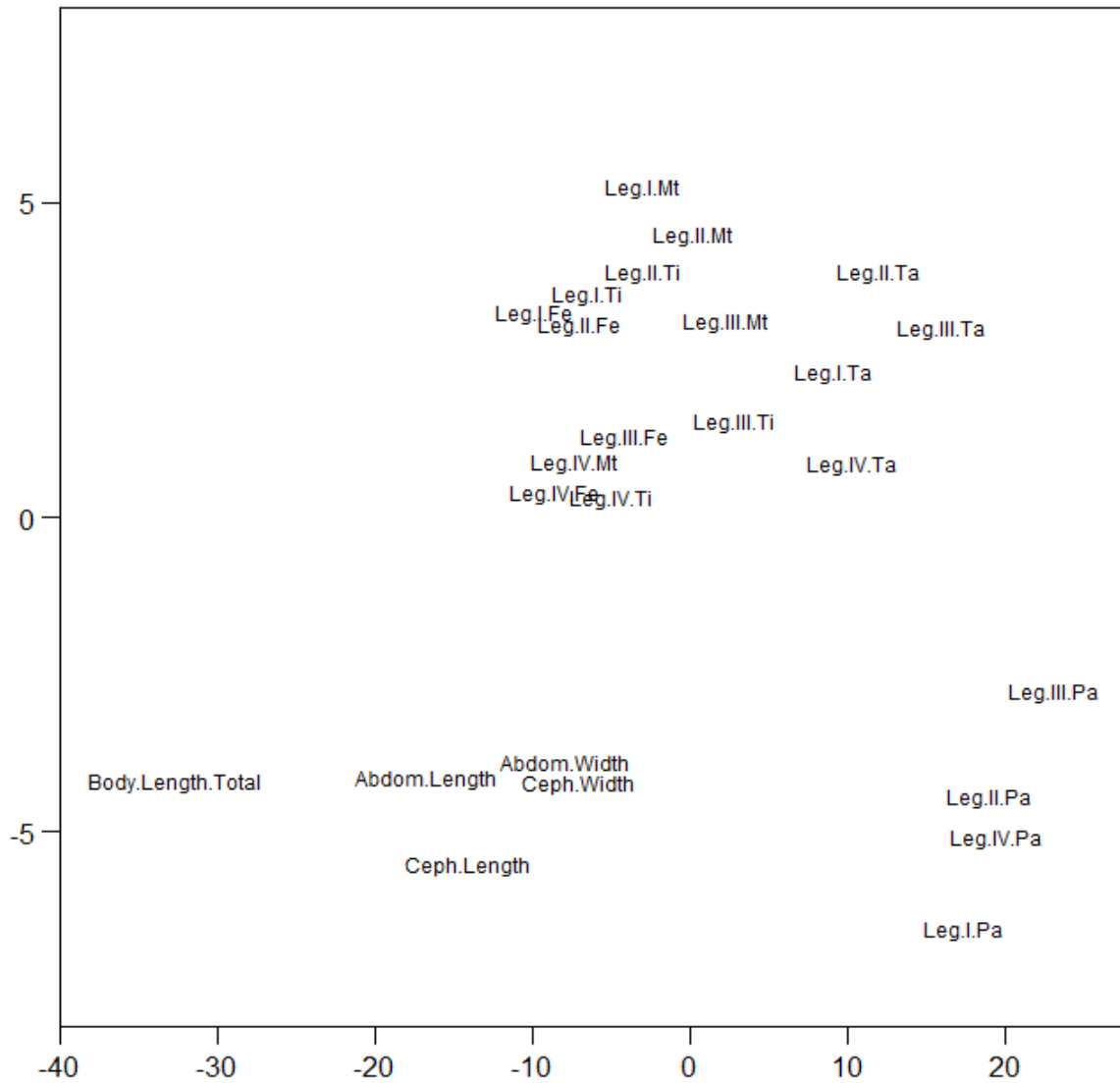


Figure 14. Body plan PCoA for the all-sites matrix. Measurements are labelled using the first four letters of the segment in the case of body segments and the first two (except for the metatarsus) alongside leg number in the case of leg measurements.

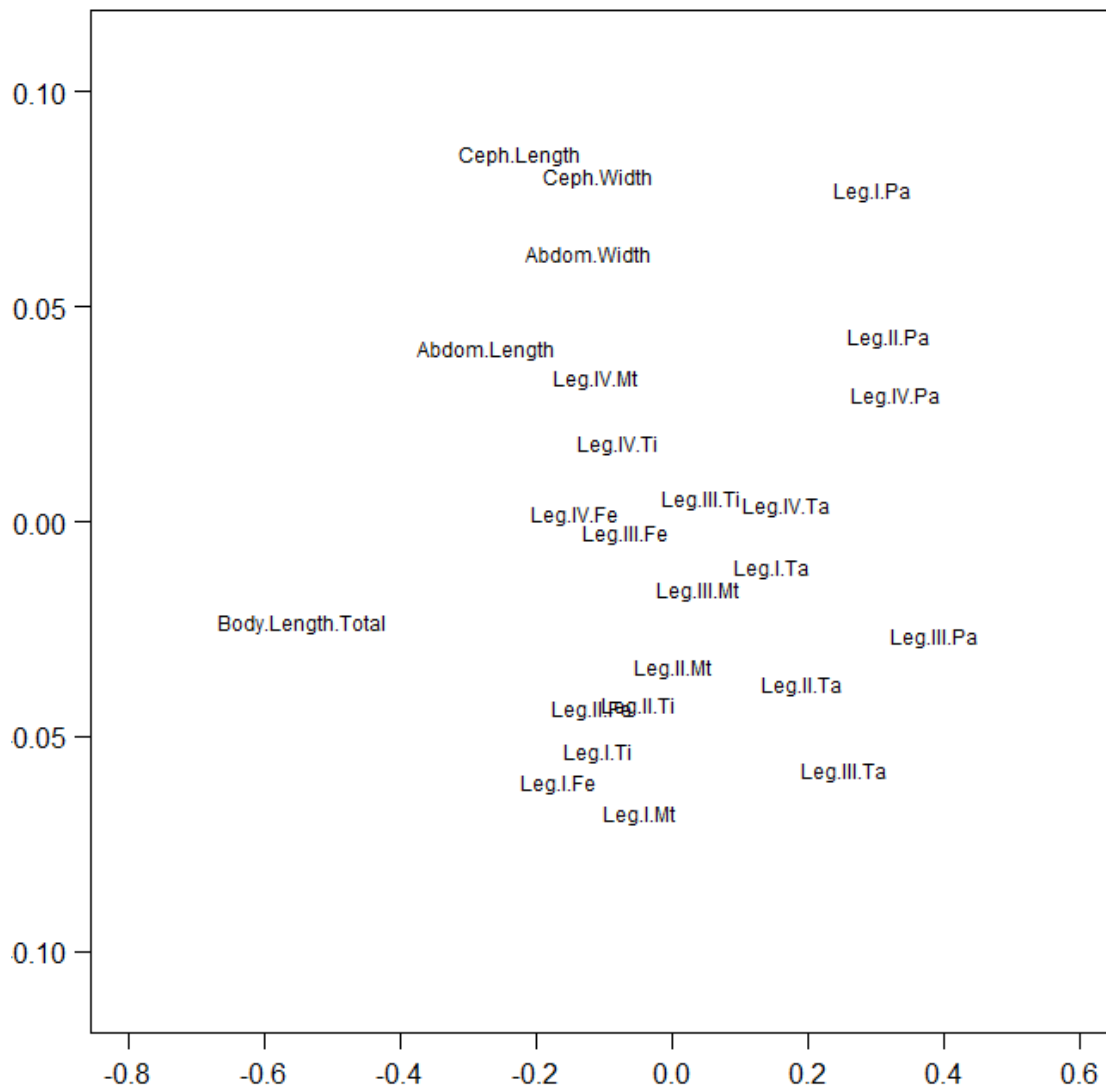


Figure 15. Body plan morphospace of all sites using Gower's distance rather than Euclidean distance. Contractions of measurements identical to figure 14.

In all of the body-plan morphospaces, there is a clear indication that the x-axis (axis 1) represents measurement size or length. The 'Body length total' and the body segment measurements lies at one extreme and the patellae and tarsal measurements sit at the other extreme. All of the body-part measurements cluster together in all five sites, and individual leg segments cluster together as well. However, there does not appear to be any consistent order within a site with respect to the separation of segments on axis 2. Almost none of the measurements are in actual leg order, and no leg measurements consistently ordered in all the sites.

The meaning of axis 2 is less clear. It separates the body measurements from most of the leg measurements, as they overlap on axis 1. Leg segments are independent of body size

based on this separation (figure 14), which varies between sites and between segments. There does appear to be a level of similarity in shape across all sites except Florissant (Appendix 6A). The leg segment measurements are also less clustered in the Florissant compared to other sites (Appendix 6A), with the Leg III patella measurement farther away from the other patella points than the other leg III measurements are to each other.

The body plan morphospaces for all sites (Fig. 14 and 15) separates the measurements more clearly than the ones for each site do individually. There is a clear gap between body measurements and leg measurements. Patella measurements occur isolated from the other leg segments as well. Axis 1 is still a size axis, but again there is no clear ordering of the legs between segments on axis 2. There appears to be less clustering and less dispersion when Gower's distances are used, as opposed to Euclidean distances.

The family-level morphospaces for individual sites are detailed in Figures 16-20, while the five most numerous families across all sites are shown in figure 21. Based on these plots, there is a high degree of clustering at the family level. The family Gnaphosidae clusters closely in the Florissant morphospace (Fig. 16), while the Lamponidae and Zodariidae both cluster with the Australian morphospaces (Fig. 17 & 18). Dictynidae clusters in the Baltic amber (Fig. 19), and both Pholcidae and Theridiidae seem to cluster in the Dominican amber (Fig. 20). Regardless of whether they cluster or not, each family seems to occupy a unique part of the morphospace, although there is always some overlap with other families. The exception to both of these is the pattern for the family Araneidae (orb weavers) at Florissant (Fig 16). Araneids do not cluster, but instead occupy the extremes of the morphospace as well as some of the centre. Consequently, Araneidae almost totally overlaps the other two families present in Figure 16. This result suggests that Araneidae are more variable in their body plans than are other spider families.

The same patterns are seen in the morphospace of the most speciose families across all sites (figure 21.). Araneidae covers the largest area of the morphospace and entirely overlaps with Clubionidae, with some overlap on the other three families as well. Lycosidae, Lamponidae and Zodariidae are all as clustered, as they were in some of the individual sites, if not more so. Zodariidae especially occupies a small part of the morphospace, despite being the most speciose family with 23 species. The fact that there is no spread of the morphospaces as a result of combining sites suggests that the body plan within a family is constrained.

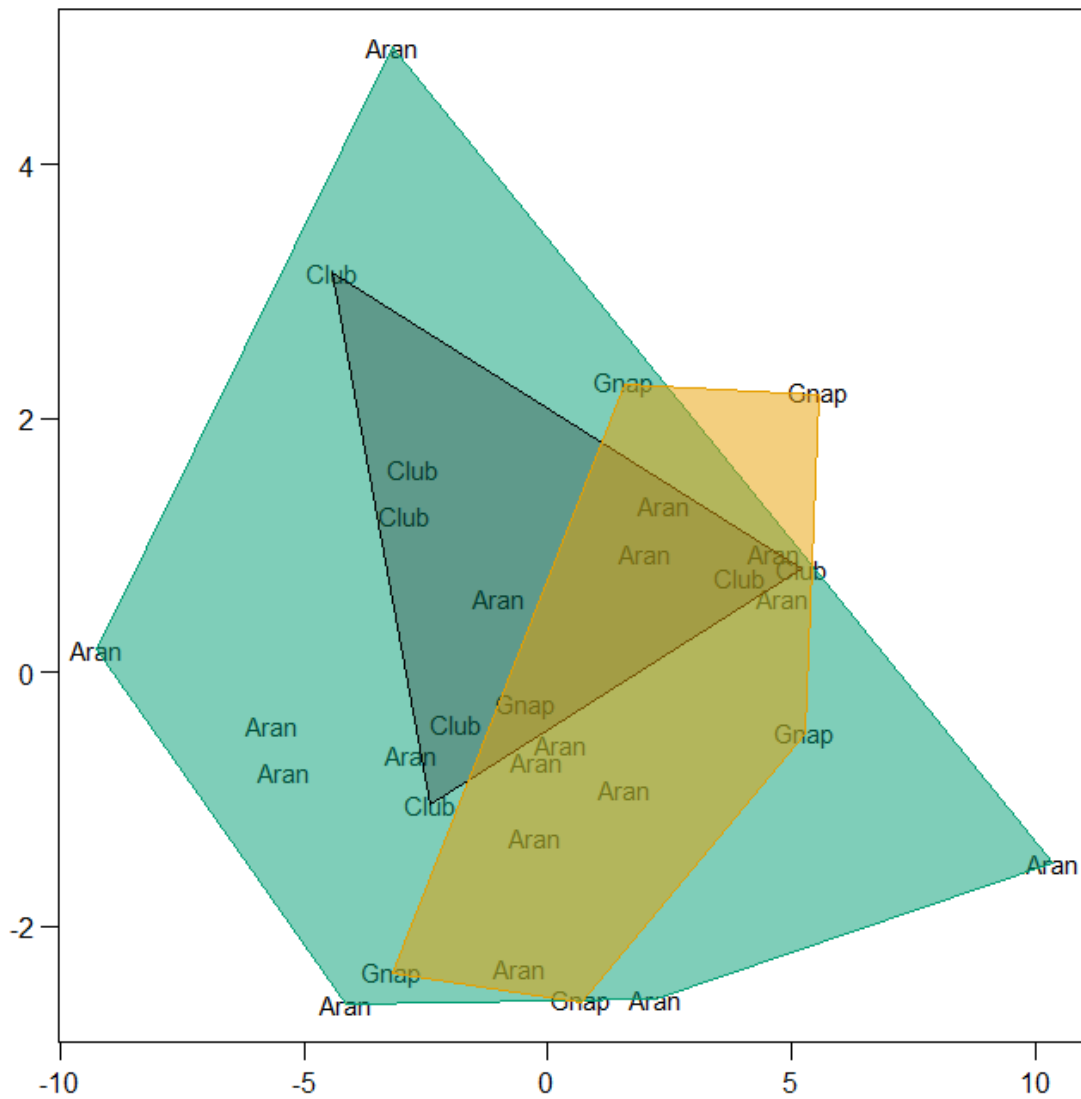


Figure 16. Family level morphospace of the Florissant with families with over 5 species. Families are Aran=Araneidae, (green) Gnap=Gnaphosidae (yellow) and Club=Clubionidae (grey).



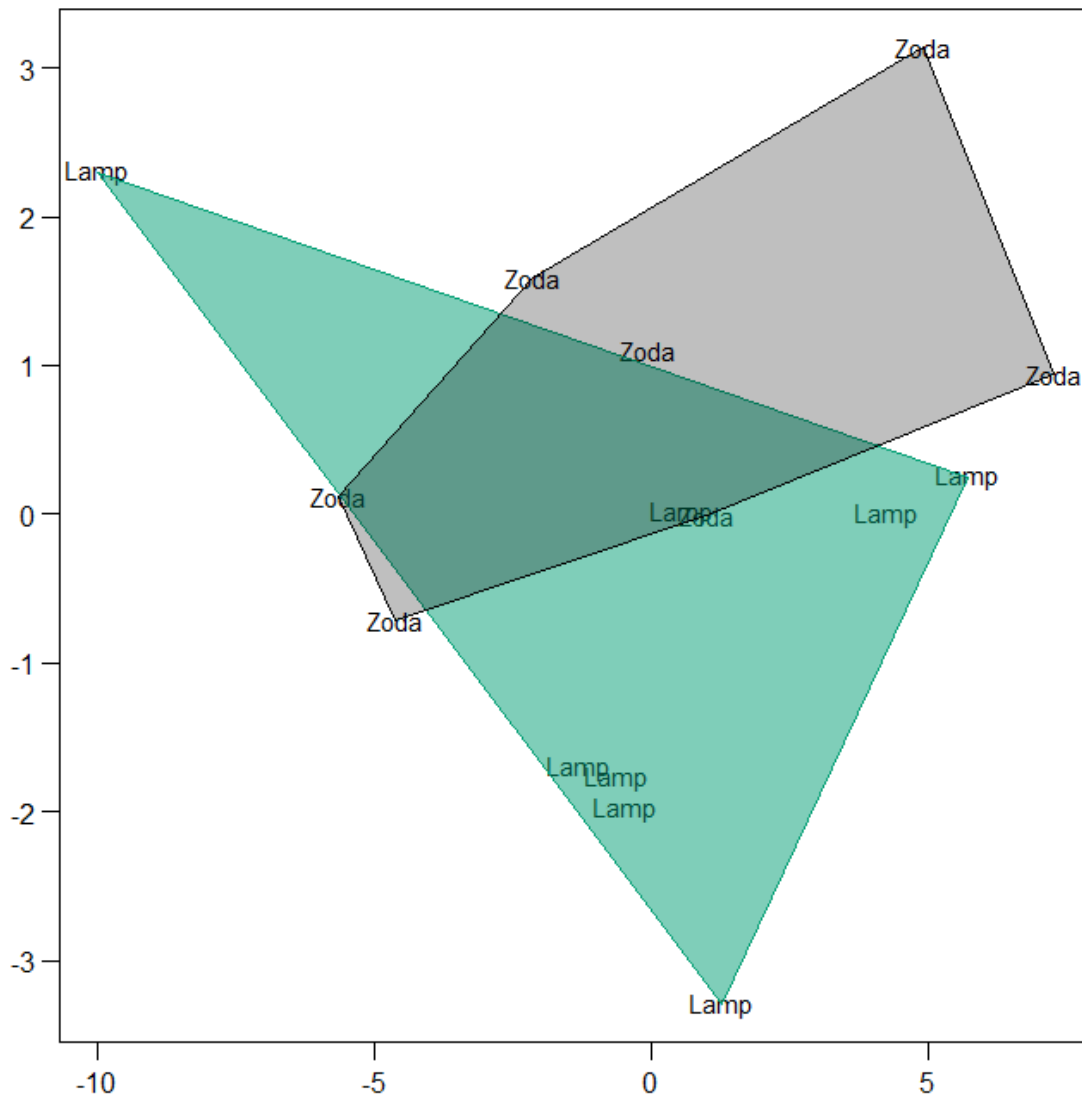


Figure 17. Family level morphospace of the Barrington Tops spiders with the families being Lamp=Lamponidae (green) and Zoda=Zodariidae (grey)

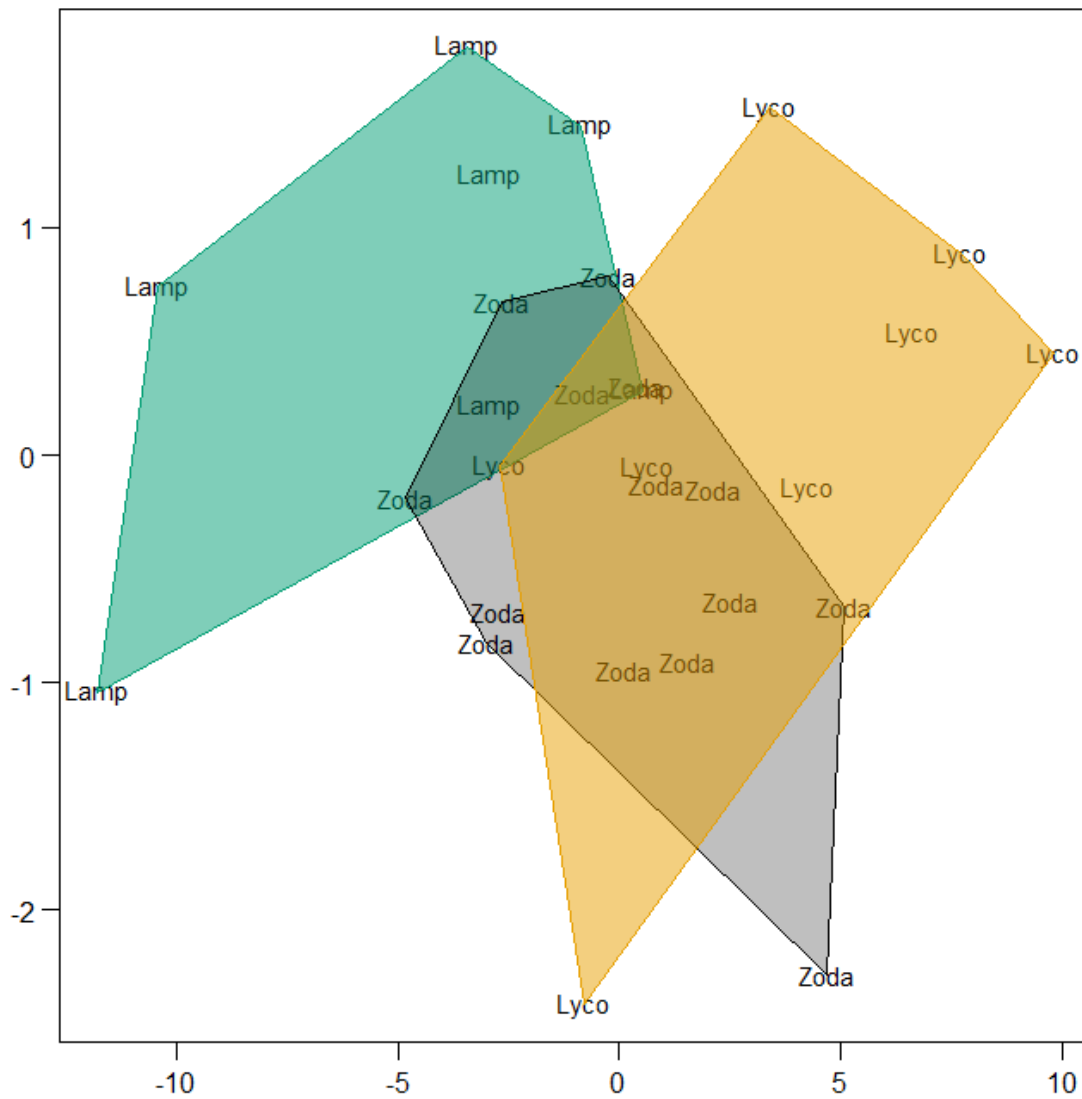


Figure 18. Family level morphospace for the coastal arc site, with the most speciose families being Lamponidae (green), Zodariidae (grey) and Lyco=Lycosidae (yellow).

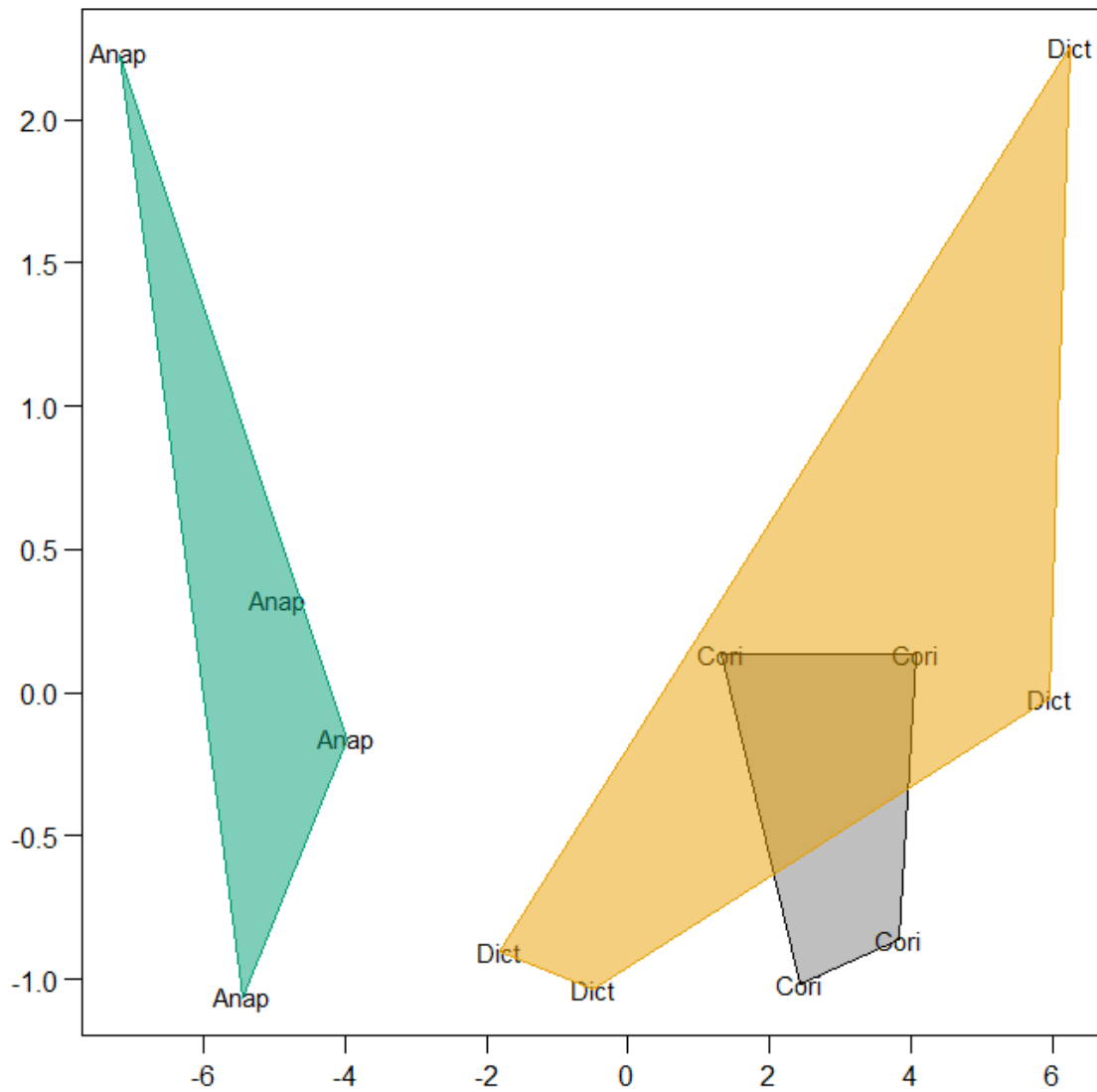


Figure 19. Family level morphospace for the Baltic amber using families with four species present. Families are Anap=Anapidae (green), Dict=Dictynidae (yellow) and Cori=Corinnidae (grey).

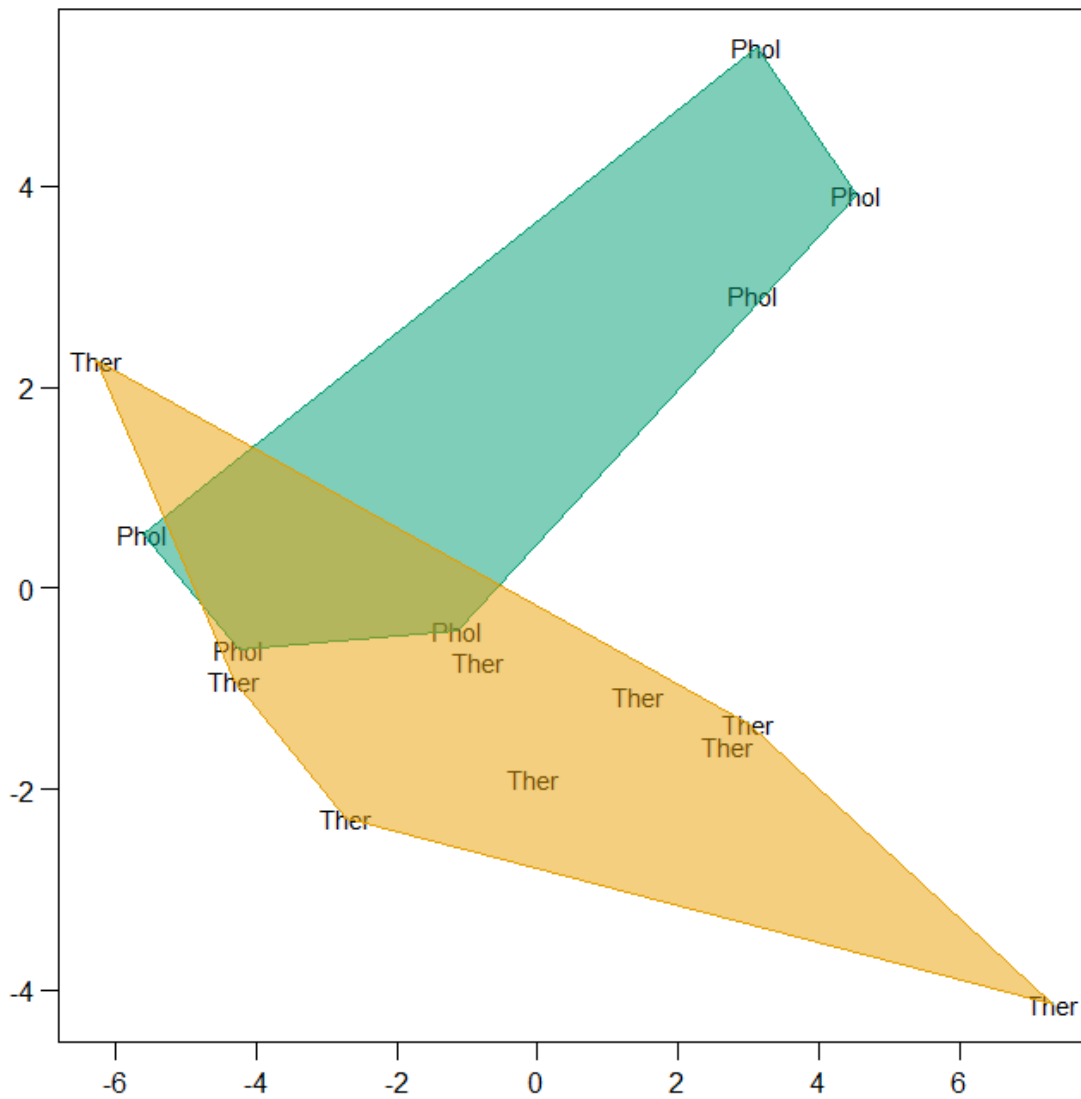


Figure 20. Family level morphospace for the Dominican amber site with the most speciose families being Phol=Pholcidae (green) and Ther=Theridiidae (grey).

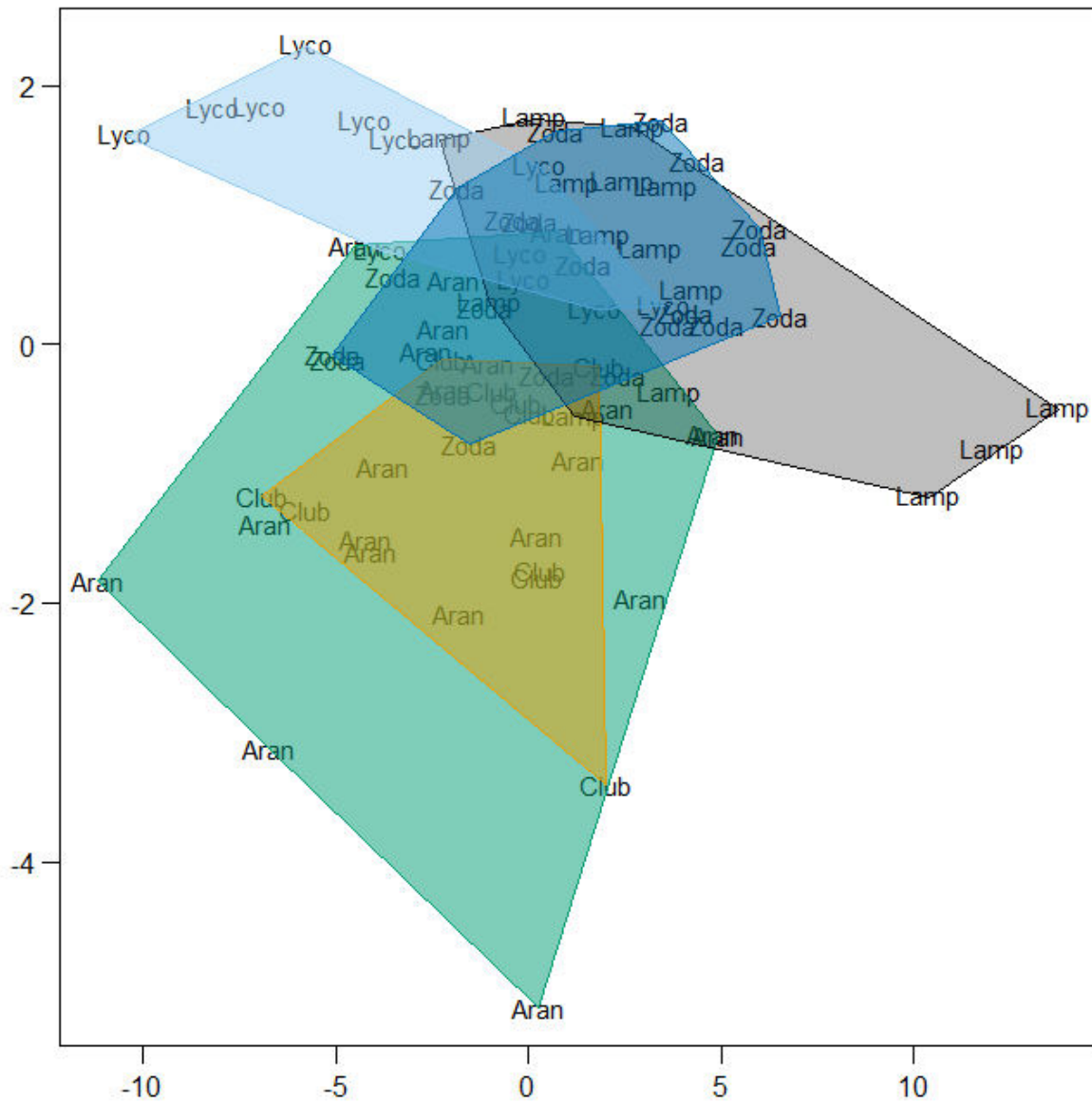


Figure 21. Morphospace of the five most speciose families across all sites. Families are Araneidae (green), Clubionidae (yellow), Lamponidae (grey), Lycosidae (pale blue) and Zodiariidae (dark blue).

## DISCUSSION

**All-site Morphospaces.--** The primary result of the analyses is that there is no apparent relationship between climate and spider body plans. The original prediction made prior to this study is not fulfilled by these results, and one of the alternative hypotheses should be accepted. The Barrington Tops and Coastal arc sites differ in their MAT by around 3°C, yet are shown to be similar on both axes (Figures 9-13). Barrington Tops is also different from its climatic analogue, Florissant. The difference in MAT between Barrington Tops and the Coastal arc is environmentally significant. Because no difference exists climate is unlikely to be important. Of the other two explanations for differences between sites, time is the one with the strongest support. The two modern sites are similar on both axis 1 and 2 (Tables 2 and 3) and the two Eocene sites are similar on axis 2 (Table 3). Thus, those sites from the same period show similarity, despite considerable geographic distance in the case of the Florissant and Baltic amber.

However, merely stating the apparent differences is not enough: determining what each axis represents and how the separations of sites could be interpreted is crucial. Axis/factor 1 is an overall size axis. The majority of spiders from the Florissant site occupy the middle of this axis, suggesting they are effectively of 'medium' or average size. Both amber sites occupy the smaller half of axis 1. Therefore, these samples apparently draw from a smaller body-size class than Florissant. The modern sites, however, range across the entirety of axis 1. Indeed, some of the smallest and largest spiders come from Barrington Tops and Coastal arc. Any changes over time in overall spider size therefore are unclear. While the largest spiders are modern and both Australian sites are considered different to all

other sites on axis 1, there are some large spiders in Florissant, and there is significant overlap with other sites.

A possible explanation for the differences seen on axis 1 is evidenced by the similarity of the Baltic and Dominican amber on axis 1. The two amber sites can be considered insignificantly different and the two non-fossil sites are considered comparable on this axis indicating that any differences are a result of preservation mode. It may be that larger spiders are not as easily preserved as amber inclusions (Labandeira 2014), leading to only smaller spiders being present in the analysis. Amber could also be favouring climbing spiders or those that predominately live in trees, but the breadth of families in the Dominican amber (Penney 2008) does not support this. The compression fossils of the Florissant could, as a result of taphonomic processes, knock both the largest and smallest spiders out of the population, due to the fragility of the latter and the burial likelihood of the former. If this explanation is correct, then the three fossil sites would have looked more like the modern ones on axis 1 if the entire population had been preserved.

If, however, the differences are not due to taphonomy, then the results have some interesting implications for spider evolution. The differences on axis 1 could indicate that during or after the Miocene the size range of spiders increased, with larger spiders becoming more common. An exact reason for this trend would not be clear. Entling et al. (2010) suggest that spiders grow larger in warmer and drier conditions, while the planet as whole has gotten slightly cooler as well as more arid since the Miocene. The authors do not suggest any mechanism that might explain an increase in size range. So, either Entling et al. (2010) are incorrect in their findings or the true size range of spiders has not changed appreciably over time. That spider size range has remained unchanged seems more likely, given the likelihood that taphonomy has curtailed the size ranges sampled in our sites.

With axis 1 of the morphospaces separating the spiders by size, axis 2 must therefore separate them by some aspect of their body plan. As stated in the previous chapter, there is evidence that axis 2 is determined by the ratio between body length and leg length. Barrington Tops and Coastal arc are once again similar on this axis, as are the Baltic amber and Florissant. This could indicate that since the Eocene, spiders have become more balanced in the ratio between body size and leg size, as the two modern sites lie closer to a 1:1 ratio than either of the Eocene sites. However, the Dominican amber lies even further from the 1:1 ratio than the Eocene sites, which calls into question the idea that spider body plans have

changed over time. The currently studied associations between body length and leg length in spiders are within a single species and do not appear to be related to any of the drivers tested here (Foellmer and Fairbairn 2005). However, the suggestion that the apparent ratio between body and leg size has changed more than once over the past 40 million years is not implausible.

A possible explanation for the spread of sites across axis 2 is family composition. The Dominican amber is the only site to possess a significant number of species from the family Pholcidae (6) ( Figure 20), with the only other site having having this family is the Baltic amber (1). This could mean that the differential sampling of families in each site could result in there being fundamentally different morphospaces. There are also many families that are sampled across sites, such as Salticidae and Tetragnathidae. However, these families are usually lower in species richness than those families which dominate particular sites, such as Zodariidae in the modern sites and Araneidae at Florissant. As a result, it is unclear if family composition has an effect. In order to ascertain if it is, each site would need to be reanalysed using at least 10-15 specimens per site all from the same family. This is not possible given the availability of published data used in this analysis, but museum collections could provide clarity. In any case, such an analysis would test to for the separation of sites in the same way particularly within a single family and therefore whether the axes result from the same factors.

Given the breadth of families occurring in these sites, and Baltic amber in particular, it is also possible that any phylogenetic signal is being overridden. Thus the differences between the sites are actually result from trends over time. If this is the case and if spiders have grown to be more balanced in their body/leg ratio since the Eocene, what are the possible explanations for this pattern? Considering that the loadings generated by the factor analysis (Appendix 7) indicate that this trend would be driven by changes in body length rather than leg length, then evolutionary pressure on spiders must have selected for longer and wider body segments. Perhaps some change in prey habits favoured body shape, or certain families that evolved after the fossils were sampled had life habits that favoured such a shape. The first explanation seems possible given that spiders have coevolved with their predominant prey, insects, in the past (Penney and Selden 2007), but the only trend that has occurred in insect body size during that time is towards a smaller wingspan and body size (Clapham and Karr 2012). It is unclear how such a trend could shift spiders to have a more balanced ratio between body and leg length, but it is possible that spiders could have been



placed under the same pressures as insects resulting from, for example, predation from birds that reinforced such a body plan. As for the second explanation, families that are more dominant in the fossil samples, such as Araneidae and Pholcidae, are theoretically older than families dominant in the modern sites, such as Lamponidae and Zodariidae. However, none of the fossil sites are from a time interval before these families evolved. Given how spiders seem to be able to colonise habitats regardless of barriers (Bodner and Maddison 2012, Platnick 1976, Raven 1980), all of the sites in the analysis could in theory contain all the families in both the fossil and modern sites. Nevertheless, it is unclear what drove the change in spider body proportions if indeed the differences and similarities between sites are due to an overall shift.

Based solely on the five morphospaces created for all five sites, it is difficult to say what is driving the differences between them. While climate is patently not affecting spider body plans in any way, there is ambiguity in regards to some of the other possible drivers. Taphonomy clearly affects the samples obtained, which should come as no surprise, and explains any differences on axis 1. The majority of the confusion is with respect to whether sites are also being separated by evolutionary time, phylogeny or simple life habits. The all-sites morphospaces alone are unable to answer this question. Hence other types of analyses were undertaken.

**The Family-level Morphospaces.--** In an attempt to determine whether evolutionary or phylogenetic factors are responsible for shifts over time, morphospaces of key families were generated for both individual sites (Figures 16-20) and all sites combined in one morphospace (Figure 21). There is no overlap between fossil and modern sites with respect to which families are dominant. Both modern sites are dominated by the same two families (Lamponidae and Zodariidae), but these families do not appear in the fossil sites. The Eocene sites do not share dominant families; however, there are many families that are held common between the Florissant and the Baltic amber. This fact makes comparing sites in terms of evolution difficult, but some insights can still be made.

Spiders from the same family usually cluster together tightly in any given morphospace, both within a site and across sites. Therefore, not only do spider families have specific body plans that do not vary significantly, but this pattern is consistent across geographic space. As stated previously, the exception to this rule appears to be the family Araneidae, which could have highly varied body plans simply because they are orb-web

builders. The araneid life habit potentially makes fewer demands on body proportions than do other predation modes such as ground hunting and ambush predation. In any event, the clustering of spider species within families is probably responsible for much of the overlap between sites, and does lend support to the notion that the differences between sites are due to taxonomic composition.

On the other hand, the fact that the Florissant and the Baltic amber samples do not share a most dominant family, yet are similarly distributed on axis 2, does not support the theory that the differences are due to taxonomic composition. While it is true that some of the families are common to both sites, many are not, and those that are shared include only 1-3 species per family. Thus, there is actually very little taxonomic overlap between the Baltic amber and Florissant sites from the species in our analysis. Based on the list of taxa for these sites (Dunlop et al. 2015), this is not actually the case, as there are large numbers of araneid spiders identified to the species level in the Baltic amber. However, these Baltic amber species either do not appear in Wunderlich (2004), or they did not meet the criteria of being represented by both measurements and photos. This means that the taxonomic composition of the amber sites may not be indicative of their resident population. If there was limited taxonomic overlap, and insofar as the sites are still considered to be similar, then sampling artifacts may not affect the analyses. Consequently, the differences between sites may indeed be due to evolutionary change. However, the similarity could also be due to the two sites sampling effectively similar sets of life habits or spider ecologies.

The family-level morphospaces have therefore provided some clarification of the results presented here, but there is also still some doubt. As mentioned previously, without an analysis that includes many species from the same family and from all the sites there can be no certainty as to the reasons for the differences between sites. Despite this fact, the most logical explanation for what has been found so far is that some combination of phylogenetic signals and life habits are the principal drivers of spider body plan distributions. The high level of constraint within each family and the lack of family overlap between the fossil and modern sites most likely combines to generate the results seen in this study. The family-level morphospaces have done little to explain the exceptionally high level of similarity between the Baltic amber and Florissant on axis 2 (Table 3), so there remains potential for an evolutionary trend to still be the cause of the differences.

**The Issue of Missing Measurements.**-- Unfortunately, there is another issue with the data that could have caused the differences between the sites, namely, that of completeness of fossil specimens. Very few of the fossil specimens present no missing measurements (NAs) leading to certain comparisons in the PCoA being omitted due to the lack of data. This means that the morphospaces representing fossil sites have been constructed with less data than those representing the modern sites. In turn, this raises the possibility that taphonomy could be responsible for the differences observed on both of the axes of the morphospaces. However, if this were the case then the Baltic and Dominican ambers would probably show similarity on both axes, not just the overall size axis. They do not. This is not to say that the presence of the NAs does not have an effect, but the patterns shown here are stronger than one would expect if taphonomy was the underlying factor generating the results.

Another, more simple, explanation for the high level of NAs is that the data sources used for the modern and fossil sites differ fundamentally. All modern specimens were measured using actual specimens, while the fossil specimens were represented by photographs and drawings. While this may not be a great issue for the Florissant and its compression fossils, the fact that the spiders from Baltic and Dominican amber could not be rotated as needed for adequate observation and may have resulted in there being more NAs. Obviously, the results obtained here would be more accurate if the actual specimens could be acquired and manipulated, but they could still be accurate enough without them.

It is for this reason that the various methods of data 'cleaning' were used to remove or replace NAs. If pairs of similar sites stayed the same on each axis regardless of how the data were cleaned, meaning that the *p*-values stayed within a reasonable range, then NAs are not a major issue with respect to those particular pairs. Unfortunately, the first method of data cleaning -that of removing species which have a certain number of measurements missing- fails in this regard. It results in certain pairs becoming similar when they are classed as different in the complete dataset. Though nothing changes on axis 1 or on axis 2, Baltic and Dominican amber switch from being different to similar, while the other two cleaning methods again indicate them to be different. The differences in *p*-values are dramatic (rising from 0.01 to 0.9), so there must be an aspect of these two datasets that is causing this change. The altered sample sizes for these sites make them the least well sampled, which could mean that there are too few species within them to make the analysis reliable. Conversely, the taxonomic cleaning method is the only method that keeps Florissant and Barrington Tops similar to one another on axis 2, and fewer taxa were removed from these sites than the

previous pair. Therefore, it is likely that the taxa removed from the Florissant and Barrington Tops are similar with respect to measurement patterns to those that remain. If so, then taxonomic cleaning should not have altered the morphospace radically. Regardless, there is some doubt as to the effectiveness of this data-cleaning method.

The second method of data cleaning involved removing measurements that included too many NAs. This measurement-based method of culling seems to have been more effective than taxonomic cleaning, as only one comparison involving axis 2 differs with respect to what is seen in the full dataset. In addition, removing measurements rather than taxa makes more sense from an analytical viewpoint. If a measurement does not appear consistently in the dataset, then it is more likely that those species that remain after taxonomic cleaning will have it as an NA anyway, ultimately making the impact of this measurement on the analysis minimal. It is for this reason that the threshold of 35 spiders missing a given measurement was proportionately more conservative than the threshold for taxonomic cleaning of nine measurements missing from a given spider.

There is a similar level of confidence in the third method of cleaning, specifically the replacement of NAs with the averages of the row and column means (the mean-filled dataset). Although this method did alter the actual dataset, it allowed a PCA and factor analysis to be run rather than a PCoA, which enabled identification of the variables that drive each axis. Furthermore, the results are once again consistent with those based on the original dataset. This level of consistency suggests that the choice of methods is not crucial and that the results obtained are robust.

**Body Plan Morphospaces.--** The last set of morphospaces analyses to be discussed are the transposed PCoAs or body-plan plots. These graphs are essential for identifying the most important measurements both within and across sites. They represent the morphological 'footprint' of each site, and should in theory include axes that are similar to the ones found in the species-by-species morphospaces.

Some trends do emerge. Total body length is always at the extreme end of the morphospace, and the other body measurements are clustered near it. Axis 1 is a size axis as in the species-based morphospaces and ultimately provides little information about differences between sites. The lengths and widths of the respective body segments are tightly clustered, suggesting that there is generally little difference in scaling among the segments within sites. The fact that the body segments cluster in general suggests that spiders generally

have a round shape and that cylindrical or elliptical abdomens/cephalothoraxes are rare, at least in these sites.

The three morphological modules that are present are Body, Legs and Patellae, and indicate that these measurements are strongly independent of one another. Conversely those measures within a module are strongly dependent on one another. If, for example, an individual spider is large in one body measurement it is likely to be large in all of them and so on. The same is true for the leg module, and the seemingly random clustering mentioned previously could suggest that the legs are generally of consistent length among each other and that spiders with exceptionally long pair of legs compared to its other pairs are rare. Why the Patellae are independent from the rest of the leg segments is not immediately apparent. It appears that the length of the patellae is operating under a different pressure from the rest of the leg segments, and why that would be is not explained by the analyses.

In regard to selection pressure, the independence of the leg segments and the body segments suggest that they are operating under differing constraints as well. Clapham and Karr (2012) suggest that the pressure on body size could be related significantly to predation, as well as fluctuations in the partial pressure of atmospheric oxygen. Leg length is likely to be under similar pressure from the latter, but ease of locomotion and prey capture are likely to be the principal aspects driving shifts in leg length.

**Implications for Spider Morphology.--** These findings have a number of implications regarding the construction of spider body plans and the potential effect of changing climate. Given that there appears to be no significant morphospace difference among sites that have different climates, it can be suggested that a reduction in cold-climate areas will likely not reduce the morphological diversity of spiders. While the findings of Entling et al. (2010) would suggest that smaller spiders would be disadvantaged, it is more likely that colder climates are less suitable for colonisation by larger spiders than warmer climates are disadvantageous for smaller spiders. As such, the size range of spiders should not change dramatically with anthropogenic climate change. As for shape, if trends were to follow those predicted by Babin-Fenske et al. (2008), then surviving spiders would have less round and more cylindrical bodies, as a warmer climate would drive spiders to increase their 'fineness' ratio. Based on both the body plan plots for Barrington Tops (Appendix 6B) and the Coastal arc (Appendix 6C) and the all sites morphospace (Figure 9), this is not the case

because they have very different climates and plot similarly. From a purely morphological point of view, spiders will most likely be unaffected by anthropogenic climate change.

The majority of morphological diversity in spiders therefore relates to phylogeny, or more accurately the ecological roles that phylogenetic groupings represent. This is not a surprising conclusion. Indeed, this conclusion could be interpreted as the null hypothesis for this study, as the differing families of spiders conduct differing activities in terms of habitat and prey capture. Families that primarily use orb- or sheet-webs for prey capture (Araneidae and Theridiidae) appear to be more variable in their morphology than those that are predominately ground- or plant-dwelling chase hunters or ambush predators (Lycosidae and Zodariidae), at least based on the set of spiders studied here. The degree of variation within a family seems to be consistent across environmental variables, and has likely been consistent for some time as well. The principal driver of spider body plan variation and thus spider morphology is therefore the method of predation.

For the araneid spider (orb-weavers), the reason for having a larger size range and more morphological variation is unclear. It could be that the internal structure of the web has some impact on morphology, or the location of the spider within the web. Web-building spiders also seem to have a less balanced ratio between body length and leg length compared to chase-hunting spiders, as they occupy parts of the morphospace closer to the extreme, such as pholcids, than pure chase-hunting species like lycosids. It may well be that in order to effectively use a web, a spider needs longer legs to better sense vibrations of captured prey or perhaps to provide greater security of movement along the web. However, given that the separation along axis 2 seems to be being driven by differences in body length rather than leg length, it is more likely that spiders that rely on webs for prey capture do not need large bodies compared to their legs. The absence of large bodies is attributable to a lack of a need to physically subdue their prey. However, there would likewise be no direct disadvantage to having body segments and legs of more similar length. There would also likely be limited pressure for a particular overall size, explaining why spiders that build more structured webs have greater morphological variation.

This relationship is not the case with the ground-dwelling spiders such as Lycosidae. Lycosids have to rely on the subduing of prey, and might therefore need to have larger bodies. Similarly, lycosids need to move rapidly, and the small body/long legs body plan may not be advantageous. A body plan with the ratio between leg length to body length of closer

to 1:1 would likely be advantageous. Families such as Lycosidae are also at the larger end of the size spectrum, so combined with the potential need for a more balanced ratio between body and leg length, an explanation is in the offing for their reduced morphological variation.

A relationship between body plan and web-building in spiders is a simple albeit understudied notion. Logically, certain body plans would work best for particular hunting methods. However, there has been little study of the effect of web structure on spider body plans. The minimal work devoted to this issue focuses on one or two species at a time (McReynolds and Polis 1987; Vincent and Lailvaux 2006) or alternatively looks not at body structure but at web structure and behavioural differences (Sensenig et al. 2010). There is therefore little additional evidence to support the claim that web structure drives or highly affects morphological variation, although the results here suggest that this is the case. Any study that would clarify this problem needs to focus on a broader population with a more balanced proportion of families, as well as separate the body plan morphospaces by family rather than site.

One of the only studies to have related spider structure to predation was that of Craig (1987). This study compared spider size to web architecture in orb weavers. It determined that smaller spiders generally build webs that are not of orb-design and that many larger spiders in the superfamily Araneioidea do not build webs, but rather use alternate means of prey capture. While this study is interesting, it did look at size only, not body plan, and thus is only partially related to the findings presented here. However, the fact that orb-webs are built by spiders of all sizes (Craig 1987) and that other web designs are constrained does imply that orb-webs are more versatile in their morphology.

**Future Avenues.--** The next steps in terms of research have been implied by the previous sections. There is a lack of evidence for an effect of climate, but the apparent absence of a relationship cannot be rejected totally. A study of a family that occupies many climates would be able to settle that unanswered question. More importantly, an extensive study of spiders from multiple families and multiple locations would be able to assess constraints on spider morphological diversity and demonstrate how constrained different spider families are. The majority of families would resemble the orb-weavers, exhibiting wide morphological diversity regardless of their method of prey capture. Alternatively, each family could have a highly conserved body plan that differs based on prey capture method or habitat. Some aspects of spider body plans could even be particular to subsets within families.

For example, it is possible that the family Pisauridae (nursery web spiders) includes a genus with a unique body plan: the fishing spider genus *Dolomedes*.

In the near future, additional studies would allow understanding of how spiders evolved morphologically during their radiation during the Cretaceous and the Cenozoic (Penney and Selden 2011). Spiders could have evolved more cylindrical bodies that re-evolved to rounder ones. Is the leg formula of a lineage or clade consistent, or does it vary, and at what point in time did certain changes in body plans occur? These are all potentially answerable questions if extensive work on spiders from a wide geographic range and a variety of environments can be carried out. This goal could be achieved by studying arachnology collections in Australia as they are comprehensive and well preserved, as well as being easily accessible. Accordingly, follow-up studies to this one could focus on the modern Australian fauna in an effort to avoid the added complications presented by fossil datasets like the ones presented in this analysis. However, if the collections that the fossil sites used in these analyses were based on could be used, then those complications could be mitigated. Alternatively, if a strong base of modern Australian data could be established, any fossil results that are unclear could be compared with that to improve clarity. An Australian baseline would be reliable as the analyses presented here do not appear to show a geographic trend in spider morphology.

An effort to fully understand the morphology of spiders from a purely phylogenetic context would also help considerably. As such, constructing a supertree for the purpose of analysis via comparative methods such as phylogenetic generalised least squares (PGLS) would enable close examination of particular morphological aspects of spiders and determine the extent to which they phylogenetically cluster. Such phylogenies could provide inferences regarding convergent evolution in spider body plans. This could also be done for a number of other traits in spiders, such as the size ranges, shape and more ecological traits. However a study focusing on the linkage between spider phylogenetics and the ratio between leg length and body length would be of interest.

The findings presented here open an avenue of research that should result in a clearer understanding of the nature of spider morphology, as well as the resilience of spiders to environmental disturbances and differences. This research also could have implications for understanding insects, which are tightly linked to spiders in both an ecological and phylogenetic sense. Therefore, what affects one group may affect the other in the same way.



If spiders and insects are resilient in terms of their morphology, regardless of environmental disturbances or differences in climate, and if morphology is ecologically constrained, then it bodes well for the ability of both groups to adapt in response to any major environmentally disruptive event.

## CONCLUSIONS

This study set out to ascertain the vulnerability of spiders to climate change in terms of their morphology, and it has achieved that goal. Unexpectedly, it has presented some evidence that spider body plans are not likely to be driven by climatic factors, nor are they likely to be driven by geography. Instead, the principal driver of differences in spider morphology across different biotas is life habit. Web structure, predation method and habitat all likely determine the degree of morphological variation within a family and the location of that family within the overall morphospace. Spiders are animals whose morphology and ecology are closely linked, and it is important to achieve a greater understanding of those links in the near future.

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## APPENDICES

### *Appendix 1- Baltic amber photos*

Following table depicts the Baltic amber spiders used from Wunderlich (2004), listing species, photo number and page number of the photo.

Species	Photo	Page Number
<i>Ummidia malinowskii</i>	4	335
<i>Clostes priscus</i>	7	337
<i>Segestria flexio</i>	15/16	342
<i>Segestria tomentose</i>	18	343
<i>Vetsegestria quinquespinosa</i>	21	344
<i>Eoarchaea hyperoptica</i>	72	364
<i>Eoarchaea vidua</i>	74	365
<i>Myrmecarchaea petiolus</i>	76	366
<i>Eometa perfecta</i>	116	382
<i>Nephila dommeli</i>	127	387
<i>Palaeonephila curvata</i>	129	387
<i>Balticoroma gracilipes</i>	145	394
<i>Balticoroma serafinorum</i>	149	395
<i>Fossilanapis unispinum</i>	163/164	400/401
<i>Ruganapis scutata</i>	167	402
<i>Praetheridion fleissneri</i>	188	409
<i>Spinilipus curvatus</i>	193	411
<i>Acrometa eichmanni</i>	214	419
<i>Eopopinus rarus solitarius</i>	238	427
<i>Heteronesticus magnoparacymbialis</i>	235	426
<i>Succiphantes velteni</i>	263	438
<i>Eocryphoecara abicera</i>	272	442
<i>Eocryphoeca gracilipes</i>	296	450
<i>Cymbiohahnia parens</i>	299	451
<i>Protohahnia antiqua</i>	320	459
<i>Succiniropsis samlandica</i>	346	469
<i>Adorator hispidus</i>	352	471
<i>Spinozodarion ananulum</i>	357a	473
<i>Eodoter magnificus</i>	364	476
<i>Palaeospinisoma femoralis</i>	368	478
<i>Ablator depressus</i>	370	478
<i>Ablator splendens</i>	373	479
<i>Cryptoplanus complicatus</i>	380	482
<i>Protoorthobula bifida</i>	392	487
<i>Trochanteridromulus glabripes</i>	393	487
<i>Trochanteridromulus scutatus</i>	416	496
<i>Distanilinus paranutus</i>	422	498
<i>Gorgospina amabilis</i>	423	498

<i>Ummidia damzeni</i>	1	334
<i>Harpactea communis</i>	24	345
<i>Scytodes weitschati</i>	38	357
<i>Oligoleptoneta altoculus</i>	48	354
<i>Eoleptoneta similis</i>	47	354
<i>Balticoblemma unicorniculum</i>	51	356
<i>Paraspermophora perplexa</i>	52	357

*Appendix 2- Dominican amber photos.*

Following table is similar to appendix 1, all spiders taken from Wunderlich (1988) have their species listed alongside the photo used and the page number of both the photo and the measurements in text. The first spider in the table however comes from Wunderlich (2004).

Species	Photo	Page Number Photo	Page Number Measurements
<i>Parvomygale distincta</i>	11/12	339	NA
<i>Masteria sexoculata</i>	704/705	341	46
<i>Stenoonops incertus</i>	710	343	60
<i>Mosdisimus calcar</i>	715	343	78
<i>Mosdisimus calcaroides</i>	716	345	79
<i>Mosdisimus tuberosus</i>	717	345	81
<i>Pholcophora brevipes</i>	718	345	82
<i>Pholcophora longicornis</i>	719	345	83
<i>Serratochorus pygmaeus</i>	720	345	85
<i>Prototama minor</i>	721	345	89
<i>Oecibus piliformis</i>	722	347	86
<i>Cyrtognatha weitschati</i>	725	347	97
<i>Azilia hispaniolensis</i>	727	347	102
<i>Araneometa herrlingi</i>	729	349	109
<i>Custodela lamellata</i>	731	349	121
<i>Faiditus crassipatellaris</i>	732	349	129
<i>Spintharus longisoma</i>	734	349	136
<i>Chryso dubia</i>	735	351	163
<i>Stemmops prominens</i>	736	351	145
<i>Stemmops incertus</i>	737	351	146
<i>Styopsis pholcoides</i>	738	351	146
<i>Theridion wunderlichi</i>	744	353	169
<i>Cornutioidion elongatum</i>	745	353	174
<i>Chrosiothes curvispinosus</i>	746	353	141
<i>Mimetus bituberculatus</i>	747	353	176
<i>Succinyna pulcher</i>	750	353	190
<i>Hispaniolyna magna</i>	751	355	193
<i>Nanoctenus longipes</i>	753	355	199
<i>Corinna flagelliformis</i>	756	355	203
<i>Veterator angustus</i>	757	355	211
<i>Veterator ascutum</i>	760	357	208



<i>Chemmisomma dubia</i>	761	357	216
<i>Wulfila spinipes</i>	762-763	357	218
<i>Lupettiana ligula</i>	765	359	221
<i>Elaver nutua</i>	766	359	222
<i>Strotarchus heidti</i>	767	359	224
<i>Lyssomanes pulcher</i>	773	361	238
<i>Corythalia ocululiter</i>	779	363	241

*Appendix 3- Barrington Tops record table.*

Following table contains the Family, species and record number of all the spiders used in the Barrington Tops site.

Family	Species	Record Number
Amaurobidae	<i>Storenosoma altum</i>	KS.104654
Amaurobidae	<i>Storenosoma terraneum</i>	KS.41367
Anapidae	<i>Maxanapis dorrigo</i>	KS.103904
Archaeidae	<i>Austarchaea milledgei</i>	KS.103340
Corinnidae	<i>Nyssus albopunctata</i>	KS.40429
Corinnidae	<i>Nyssus coloripes</i>	KS.120760
Corinnidae	<i>Poecilopta lugubris</i>	KS.102029
Gradungulidae	<i>Tarlina smithersi</i>	KS.122667
Hexathelidae	<i>Hadronyche formidabilis</i>	KS.41227
Hexathelidae	<i>Paraembolides tubrabucca</i>	KS.41359
Idiopidae	<i>Misgolas billsheari</i>	KS.38602
Lamponidae	<i>Centroina macedon</i>	KS.37393
Lamponidae	<i>Graycassis barrington</i>	KS.95584
Lamponidae	<i>Graycassis chichester</i>	KS.37354
Lamponidae	<i>Lampona allyn</i>	KS.103339
Lamponidae	<i>Lamponicta cobon</i>	KS.104181
Lamponidae	<i>Lamponoides coottha</i>	KS.103297
Lamponidae	<i>Longepi boyd</i>	KS.104751
Lamponidae	<i>Paralampona kiola</i>	KS.37395
Lycosidae	<i>Artoria versicolor</i>	KS.39783
Lycosidae	<i>Artoria lineata</i>	KS.39725
Lycosidae	<i>Venatrix pictiventris</i>	KS.122939
Mimetidae	<i>Australomimetes pseudomaculosus</i>	KS.103231
Mimetidae	<i>Australomimetes tasmaniensis</i>	KS.103932
Miturgidae	<i>Miturga gilva</i>	KS.42935
Nicodamidae	<i>Ambicodamus darlingtoni</i>	KS.103960
Nicodamidae	<i>Ambicodamus sororius</i>	KS.101654
Nicodamidae	<i>Oncodamus decipiens</i>	KS.101991
Salticidae	<i>Lycidas nigriceps</i>	KS.42979
Salticidae	<i>Prostheclina amplior</i>	KS.103279
Sparassidae	<i>Isopeda villosa</i>	KS.16669
Stiphidiidae	<i>Couranga kioloa</i>	KS.122567
Stiphidiidae	<i>Pillara griswoldi</i>	KS.101690

Stiphidiidae	<i>Pillara karuah</i>	KS.103921
Theridiidae	<i>Theridion pyramidale</i>	KS.103285
Zodariidae	<i>Asteron grayi</i>	KS.39485
Zodariidae	<i>Asteron zabkai</i>	KS.39143
Zodariidae	<i>Habronestes grahami</i>	KS.39459
Zodariidae	<i>Habronestes piccolo</i>	KS.39144
Zodariidae	<i>Nostera nadgee</i>	KS.39140
Zodariidae	<i>Pentasteron osticans</i>	KS.77592
Zodariidae	<i>Storosa obscura</i>	KS.39464

*Appendix 4- Coastal arc record table*

As per appendix 3, except for the spider species present in the coastal arc site.

Family	Species	Record Number
Corinnidae	<i>Nyssus albopunctata</i>	KS.60416
Corinnidae	<i>Nyssus coloripes</i>	KS.63934
Gallieniellidae	<i>Oreo renmark</i>	KS.122896
Gradungulidae	<i>Tarlina smithersi</i>	KS.122636
Hexathelidae	<i>Paraembolides tubrabucca</i>	KS.40820
Hexathelidae	<i>Asadipus kunderang</i>	KS.57592
Lamponidae	<i>Asadipus longforest</i>	KS.57609
Lamponidae	<i>Graycassis bruxner</i>	KS.39597
Lamponidae	<i>Lamponella beaury</i>	KS.39607
Lamponidae	<i>Paralampona domain</i>	KS.57621
Lamponidae	<i>Paralampona Sherlock</i>	KS.57620
Lamponidae	<i>Prionosternum nitidiceps</i>	KS.57594
Lamponidae	<i>Erigone prominens</i>	KS.62268
Linyphiidae	<i>Artoria versicolor</i>	KS.39780
Lycosidae	<i>Artoria triangularis</i>	KS.61970
Lycosidae	<i>Kangarosa tristicula</i>	KS.122824
Lycosidae	<i>Venator spenceri</i>	KS.63922
Lycosidae	<i>Venatrix australiensis</i>	KS.39714
Lycosidae	<i>Venatrix furciliata</i>	KS.67465
Lycosidae	<i>Venatrix picitiventris</i>	KS.62025
Lycosidae	<i>Venatrix micarioides</i>	KS.122889
Salticidae	<i>Clynotis albobarbatus</i>	KS.42272
Salticidae	<i>Helpis minitabunda</i>	KS.97256
Salticidae	<i>Myrmarachne simoni</i>	KS.101696
Salticidae	<i>Saitis virgatus</i>	KS.124093
Sparassidae	<i>Heteropoda procera</i>	KS.15768
Sparassidae	<i>Isopedella pessleri</i>	KS.67824
Stiphidiidae	<i>Barahna myall</i>	KS.107595
Stiphidiidae	<i>Couranga kioloa</i>	KS.62463
Stiphidiidae	<i>Corasoides australis</i>	KS.92740
Thomisidae	<i>Saccodomus formivus</i>	KS.73157
Thomisidae	<i>Sidymella rubrosignata</i>	KS.118365
Thomisidae	<i>Sidymella trapezia</i>	KS.66189
Trochanteriidae	<i>Morebilus plagusius</i>	KS.35518

Trochanteriidae	<i>Rebilus griswoldi</i>	KS.123620
Zodariidae	<i>Asteron hunti</i>	KS.55995
Zodariidae	<i>Habronestes bradleyi</i>	KS.39431
Zodariidae	<i>Habronestes grahami</i>	KS.56010
Zodariidae	<i>Habronestes hunti</i>	KS.39183
Zodariidae	<i>Habronestes minor</i>	KS.55991
Zodariidae	<i>Habronestes piccolo</i>	KS.59647
Zodariidae	<i>Habronestes pictus</i>	KS.71605
Zodariidae	<i>Hetaerica scenica</i>	KS.39414
Zodariidae	<i>Neostorena minor</i>	KS.56057
Zodariidae	<i>Nostera nadgee</i>	KS.39445
Zodariidae	<i>Pentasteron isobelae</i>	KS.56082
Zodariidae	<i>Pentasteron simplex</i>	KS.55650
Zodariidae	<i>Storosa obscura</i>	KS.59571
Zodariidae	<i>Zillimata scintillans</i>	KS.59578

#### Appendix 5- Taxonomic checks

A number of species, particularly fossils ones, have had their species names changed since the publications used in this study. These tables look at only those species in each site that have had their name changed. Original name and most recent name used in this analysis are listed.

#### 5A- Florissant Taxonomic checks.

Original name	Current Name
<i>Epeira meekii</i>	<i>Araneus meekii</i>
<i>Theridium opertaneum</i>	<i>Palaeometa opertanea</i>
<i>Anyphaena interita</i>	<i>Palaeodrassus interitus</i>
<i>Epeira delita</i>	<i>Araneus delitus</i>
<i>Epeira abscondita</i>	<i>Araneus absconditus</i>
<i>Epeira emertoni</i>	<i>Araneus emertoni</i>
<i>Epeira cinefacta</i>	<i>Araneus cinefactus</i>
<i>Clubiona latebrosa</i>	<i>Eobumbatrix latebrosa</i>
<i>Theridium seclusum</i>	<i>Linyphia seclusa</i>
<i>Clubiona ostentata</i>	<i>Eostentatrix ostentata</i>
<i>Epeira vulcanalis</i>	<i>Araneus vulcanalis</i>
<i>Epeira longimana</i>	<i>Araneus longimanus</i>
<i>Epeira indistincta</i>	<i>Araneus kinchloae</i>

#### 5B- Barrington Tops taxonomic checks

Original name	Current Name
<i>Artoria berenice</i>	<i>Artoria versicolor</i>

#### 5C- Coastal Arc taxonomic checks

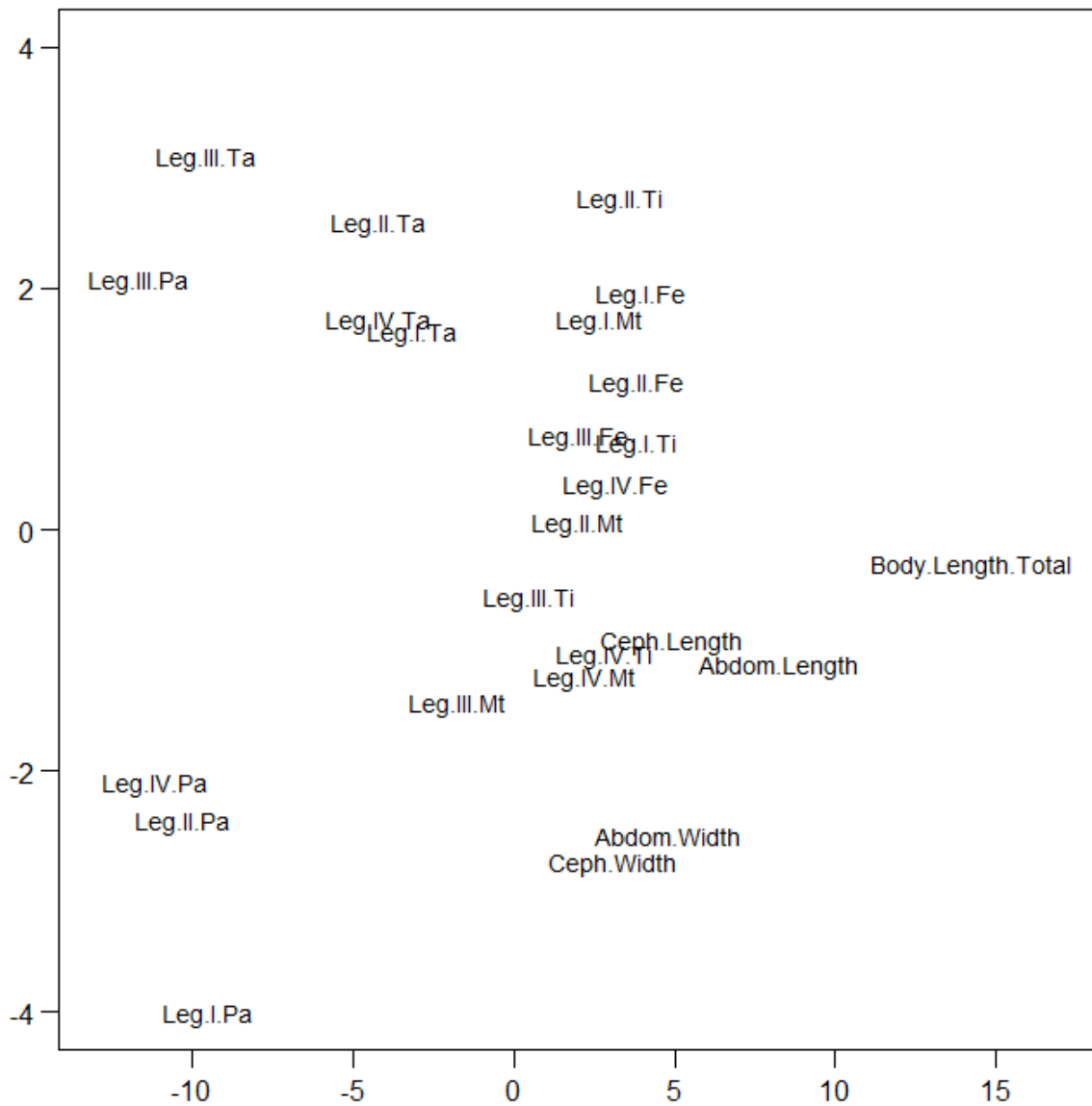
Original name	Current Name
<i>Artoria berenice</i>	<i>Artoria versicolor</i>

5D- Dominican amber taxonomic checks

Original name	Current Name
<i>Microsteria sexoculata</i>	<i>Masteria sexoculata</i>
<i>Gamasomorpha incerta</i>	<i>Stenoonops incertus</i>
<i>Tama minor</i>	<i>Prototama minor</i>
<i>Lepthyphantes lamellatus</i>	<i>Custodela lamellata</i>
<i>Argyrodes crassipatellaris</i>	<i>Faiditus crassipatellaris</i>
<i>Theridion ovale</i>	<i>Theridion wunderlichi</i>
<i>Teudis ligula</i>	<i>Lupettiana ligula</i>
<i>Clubionoides nutua</i>	<i>Elaver nutua</i>

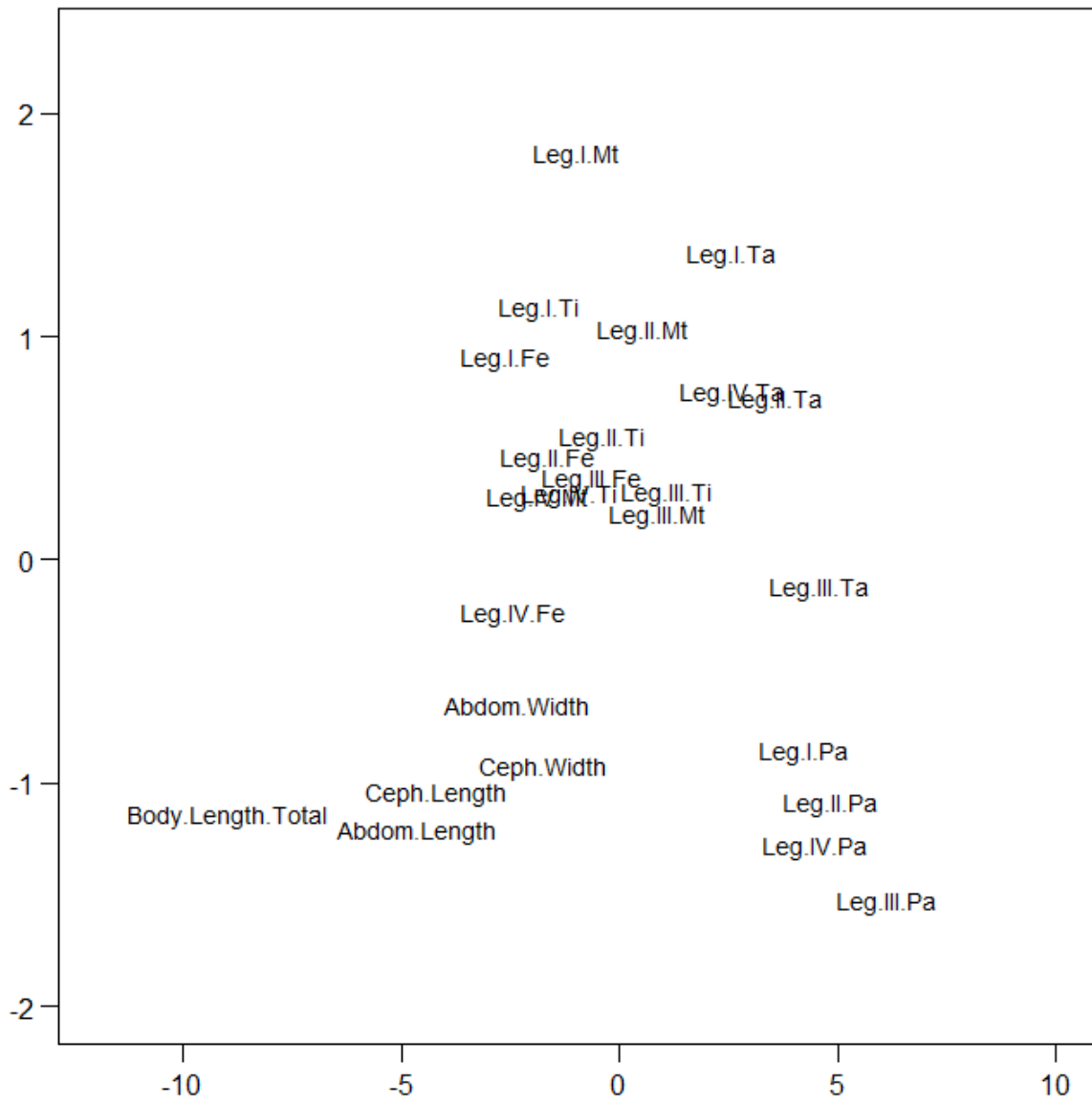
Appendix 6- Body Plan Morphospaces

The morphospaces for the transposed data in each individual site are shown here. These morphospaces were generated using the complete dataset.

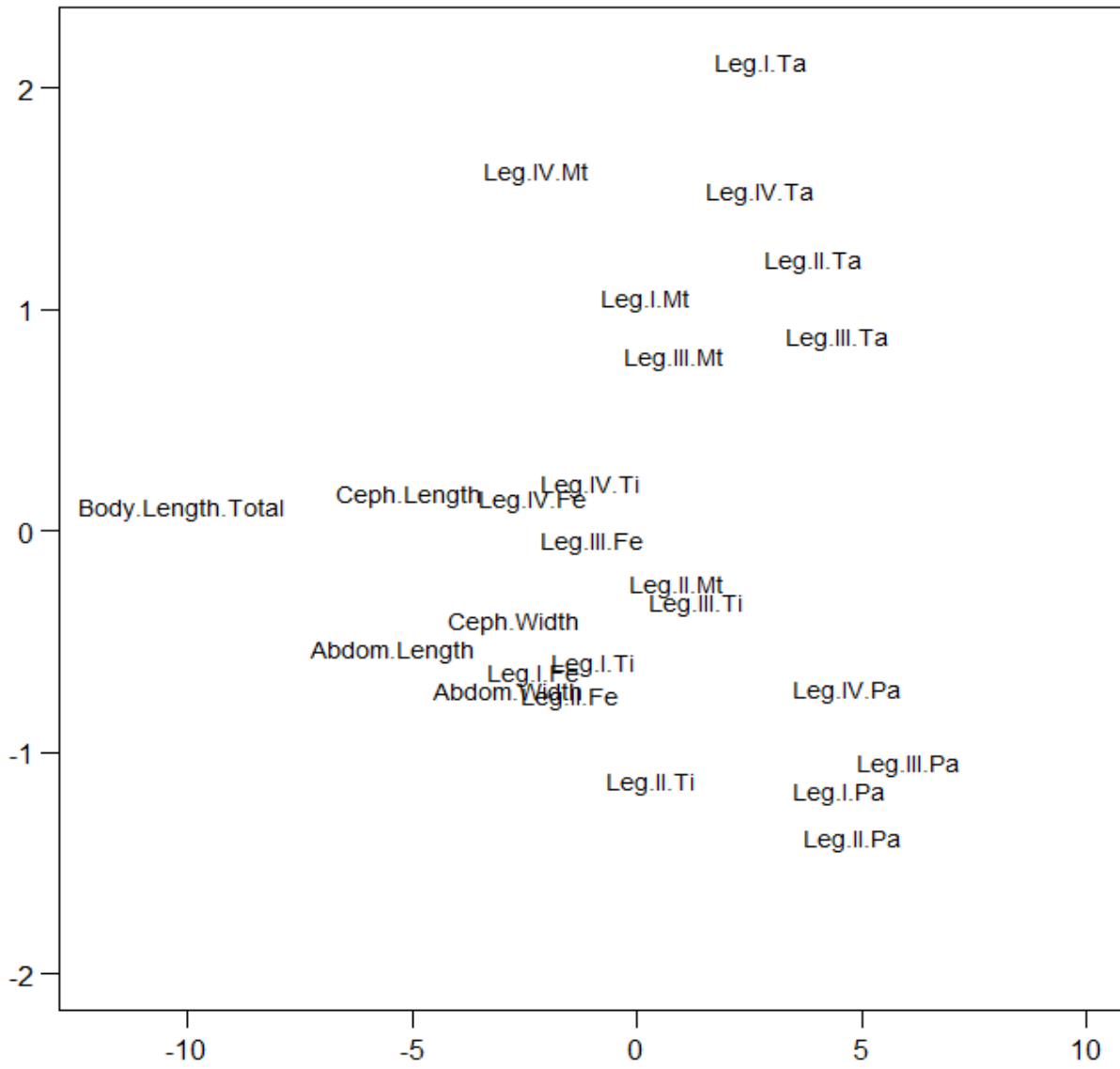


6A Florissant body plan morphospace

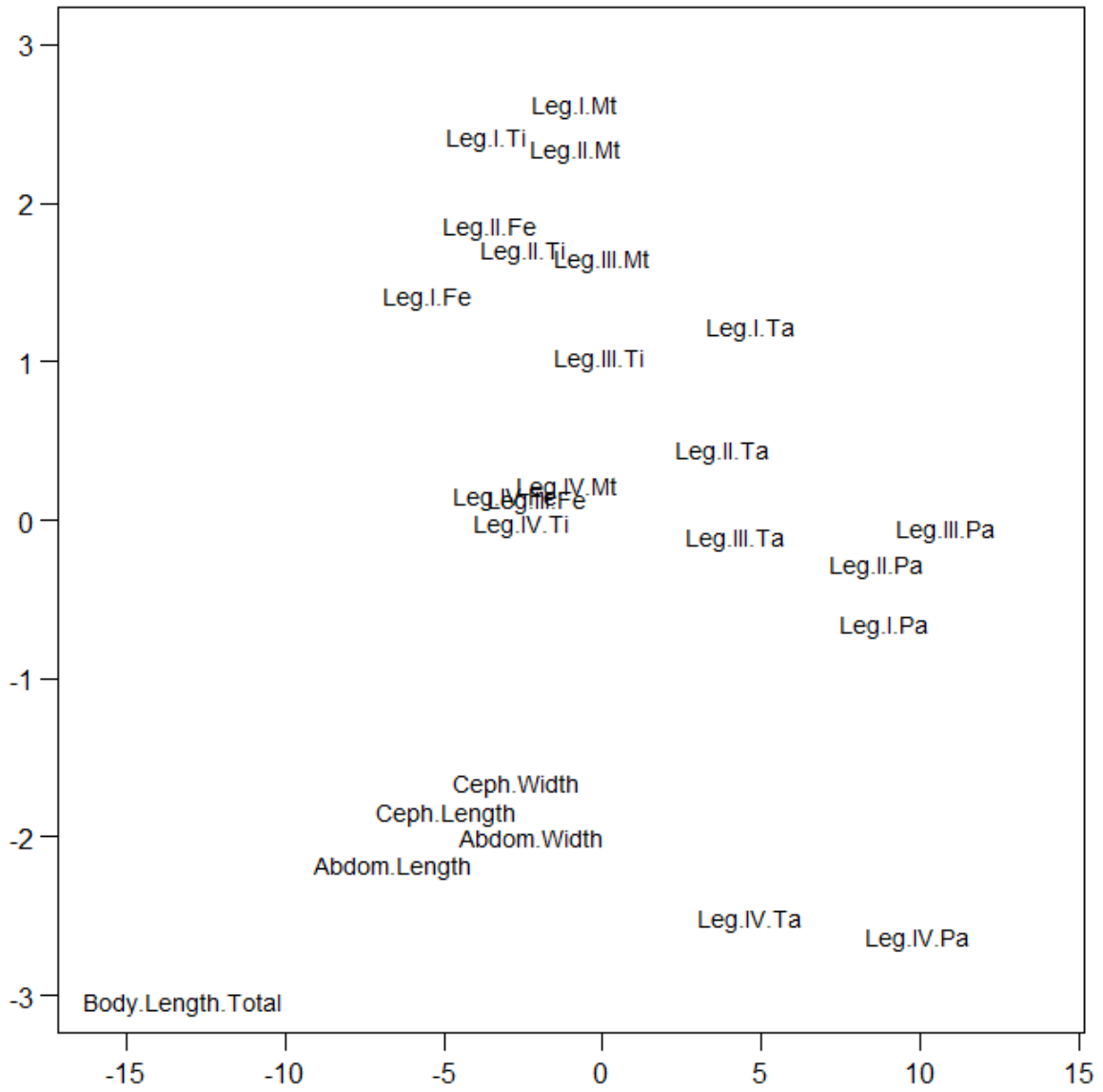
6B- Barrington Tops body plan morphospace



6C- Coastal arc body plan morphospace



6D- Baltic amber body plan morphospace







Appendix 7- Factor Analysis Loadings

Loadings:

	Factor1	Factor2	Factor3
Body.Length.Total	0.315	0.902	0.286
Ceph.Length	0.328	0.849	0.290
Ceph.Width	0.396	0.730	0.390
Abdom.Length	0.329	0.864	0.313
Abdom.Width	0.364	0.709	0.415
Leg.I.Fe	0.436	0.444	0.719
Leg.I.Pa	0.410	0.610	0.395
Leg.I.Ti	0.401	0.456	0.749
Leg.I.Mt	0.473	0.371	0.714
Leg.I.Ta	0.534	0.389	0.530
Leg.II.Fe	0.528	0.442	0.633
Leg.II.Pa	0.492	0.487	0.392
Leg.II.Ti	0.613	0.384	0.582
Leg.II.Mt	0.645	0.335	0.574
Leg.II.Ta	0.725	0.274	0.436
Leg.III.Fe	0.589	0.492	0.506
Leg.III.Pa	0.623	0.486	0.281
Leg.III.Ti	0.626	0.445	0.496
Leg.III.Mt	0.714	0.349	0.439
Leg.III.Ta	0.751	0.276	0.328
Leg.IV.Fe	0.545	0.510	0.502
Leg.IV.Pa	0.602	0.495	0.219
Leg.IV.Ti	0.558	0.529	0.454
Leg.IV.Mt	0.654	0.439	0.355
Leg.IV.Ta	0.698	0.336	0.294

	Factor1	Factor2	Factor3
SS loadings	7.559	7.114	5.625
Proportion Var	0.302	0.285	0.225
Cumulative Var	0.302	0.587	0.812

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