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EVOLUTION OF STENOPHAGY IN SPIDERS (ARANEAE): EVIDENCE BASED ON THE COMPARATIVE ANALYSIS OF SPIDER DIETS

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Stenophagy (narrow diet breadth) represents an extreme of trophic specialization in carnivores, but little is known about the forces driving its evolution. We used spiders, the most diversified group of terrestrial predators, to investigate whether stenophagy (1) promoted diversification; (2) was phylogenetically conserved and evolutionarily derived state; and (3) was determined either by geographical distribution and foraging guild. We used published data on the prey of almost 600 species. Six categories of stenophagy were found: myrmecophagy, araneophagy, lepidopterophagy, termitophagy, dipterophagy, and crustaceophagy. We found that the species diversity of euryphagous genera and families was similar to stenophagous genera and families. At the family level, stenophagy evolved repeatedly and independently. Within families, the basal condition was oligophagy or euryphagy. Most types of stenophagy were clearly derived: myrmecophagy in Zodariidae; lepidopterophagy in Araneidae; dipterophagy in Theridiidae. In contrast, araneophagy was confined to basal and intermediate lineages, suggesting its ancestral condition. The diet breadth of species from the tropics and subtropics was less diverse than species from the temperate zone. Diet breadth was lower in cursorial spiders compared to web-building species. Thus, the evolution of stenophagy in spiders appears to be complex and governed by phylogeny as well as by ecological determinants.

KEY WORDS: **Polyphagy, predator, prey, prey specificity, trophic niche.**

Since defining the specialist–generalist dichotomy (Levins and MacArthur 1969), ecologists have investigated the forces driving the evolution of these ecological strategies. In terms of diet, specialists and generalists represent two extremes of trophic breadth, often termed stenophagy and euryphagy, respectively. Stenophagy is the use of a narrow trophic niche and occurs in many animal taxa, particularly herbivores (e.g., Jermy et al. 1990) and parasites (e.g., Poulin 1992), but occasionally also in carnivores (e.g., Hodek and Honěk 1996). Stenophagous predators often possess specialized morphological, behavioral, and physiological traits that increase utilization efficiency of their exclusive prey. Thus, diet breadth often correlates with morphological, behavioral, and physiological traits (Huey and Pianka 1981; Sasal and Morand 1998; Šimková et al. 2001) that have an evolutionary basis (Caldwell 1996).

A number of hypotheses explain the evolution of stenophagy, particularly in herbivores: increased physiological efficiency, use of enemy-free space, optimal foraging, neural constraints, interspecific competition avoidance, coevolutionary interactions, and trade-offs (Jermy et al. 1990; Singer 2008). However, can the distribution of stenophagy among taxa also be explained by phylogeny? At least some studies suggest that stenophagy is phylogenetically constrained (Gilbert et al. 1994; Stireman 2005). The role of diet breadth in macroevolutionary processes has been studied in several invertebrate and vertebrate taxa (e.g., Darst et al. 2005; Sasal et al. 1998). Adaptation to new trophic zones, such as terrestrial habits in frogs (Darst et al. 2005), is an important driving force in the diversification of predators (Futuyma 1986; Brooks and McLennan 1993). But, opinions contrast on whether species diversification is promoted more in stenophagous or euryphagous predators. In some taxa, stenophagous lineages are less likely to diversify than euryphagous lineages (Toft 1995) whereas in other taxa, specialization appears to promote diversification by reducing gene flow (Futuyma and Moreno 1988). Thus, there is substantial need to explore phylogenetic and ecological correlates with stenophagy across large clades.

Ecological specialization, including stenophagy, is typically considered a derived state (Nosil and Mooers 2005) because it results in trade-offs that can have dramatic effects on how predators interact with nonpreferred prey (Joshi and Thompson 1995; Fry 1996). Over evolutionary time scales, such trade-offs should constrain the direction of evolution and the rate of speciation. This predicts that specialization and stenophagy are evolutionary dead ends due to increased susceptibility to extinction (e.g., Moran 1988). Transitions from euryphagy to stenophagy should therefore be more frequent than the reverse. But, the accumulated evidence is largely ambiguous. Although shifts from generalist to specialist strategies are common in frogs and insects (Nosil 2002; Darst et al. 2005; Gilbert et al. 1994), parasitoids instead commonly revert from specialists to generalists (Stireman 2005).

Spiders (Araneae) are the seventh most diverse order of animals, and are noteworthy because they are exclusively terrestrial carnivores (Coddington and Levi 1991). Not surprisingly, all trophic strategies, including stenophagy, oligophagy, and euryphagy exist within spiders, except for monophagy. Most spiders seem to be euryphagous, that is, capturing and consuming a wide variety of largely invertebrate prey (Nentwig 1987). Quite a few species appear to be oligophagous, that is, targeting particular prey groups but supplementing their diets sporadically with various other prey types. For example, the salticid *Portia* spp. feeds primarily on other spiders, but occasionally takes insects as prey (Li et al. 1997). Far fewer species are stenophagous, that is, foraging on only a single prey group. For example, the zodariids *Zodarion* spp. capture and consume only ants (Pekár 2004).

Yet, the mechanisms underlying the evolution and maintenance of stenophagy in spiders, and the implication of stenophagy for speciation, are unknown. However, such investigation is now feasible given the many rigorous studies on the diets of diverse spider species over the last 100 years and the considerable progress made in the phylogeny of spiders at various taxonomic levels. The evolutionary diversification of spiders is not coupled with major trophic shifts, as occurs in other megadiverse groups of arthropods. Instead, spider diversification is linked to key innovations in how silk is used to capture prey (Bond and Opell 1998). Spiders use several distinct silks to produce many different types of webs that vary in architecture and microhabitat (Blackledge et al. 2009). Some of these webs are likely specialized for the capture of specific prey types (Stowe 1986; Bond and Opell 1998; Blackledge et al. 2009). For instance, spiders hunting with extremely reduced webs, such as the single-thread bolas used by *Mastophora*, *Ordgarius,* and *Cladomelea* (all Araneidae) are often very specific in capture of moths, whereas the orb spinning relatives of these spiders catch diverse prey (e.g., Yeargan 1994). Therefore, web-building spiders are in general thought to be less selective in their diet. In contrast, few attempts have been made to disentangle the evolution of prey specialization among cursorial spiders that do not use silk for the capture of prey, even though multiple foraging strategies have clearly evolved (Foelix 1996).

Our goals here are to describe the phylogenetic pattern of stenophagy among spiders and to determine which types of stenophagy predominate. Using this information, we then test several hypotheses about how diet breadth interacts with ecology and evolutionary diversification in spiders. The "diversification" hypothesis is that diet breadth differs between stenophagous and euryphagous genera and families. We predict that the evolution of stenophagy reduces species diversification. The "phylogenetic constraint" hypothesis is that either stenophagy or euryphagy is primarily a derived condition. We predict that stenophagy is primarily a derived condition that is restricted to few clades. Finally, there are two "ecological constraint" hypotheses. The first one states that diet breadth differs among geographical regions. We predict that stenophagy is more frequent in the tropical zone, the latter states that diet breadth differ between foraging guilds. We predict that stenophagy is most common in cursorial species because most types of webs function as nonselective traps.

Material and Methods

Data on the prey of spiders were taken from more than 400 articles published between 1903 and 2009 (Appendix). All together, we found data on 587 species of spiders belonging to 311 genera and 65 families. We used all available information, but excluded data for 25 species represented by a single unsupported observation each. The quality of the data varied from anecdotal notes to rigorous analyses. Qualitative observations, such as reports of seeing a species feeding on a certain prey, were turned into quantitative data using binary scores. The number of prey records per species varied between 1 and 24,319 specimens, with the median = 26 (SD = 1268). For 186 species included in the analysis, the number of prey was lower than 10. Most data on prey came from field observations (73.3%, $N = 562$), fewer from laboratory experiments (20%), and 7.6% were from combined field and laboratory observations. The laboratory data were mainly results of acceptance experiments. In 4% of species, data from preference experiments were included. Because preference experiments remove many of the constraints on prey selection by spiders in the field, they tend to overestimate selectivity. However, these studies are still informative and make up only a small proportion of our data. Of all data, 4.1% were for cosmopolitan species, 52.6% for temperate, 25.4% for subtropical, and 17.9 % for tropical spider species.

Prey species were categorized to order (from Gastropoda to Vertebrata), with one exception. Hymenoptera was split to three groups (Formicidae, Apidae, and other Hymenoptera), because many species captured ants but not other hymenopteran taxa. For each spider species, diet breadth was computed using the Shannon–Wiener index (Weaver and Shannon 1949). This index (H) was chosen because other indices, such as the Simpson formula (Simpson 1949), are more sensitive to the enormous variation in sample sizes. The diversity index varied between 0 and 3. Because "specialization" and "stenophagy" are "in the eye of the beholder" (Futuyma and Moreno 1988), we defined heuristic thresholds for stenophagy ($H = 0$–0.3), oligophagy ($H = 0.31$–1.1), and euryphagy ($H = 1.11$–3). Using these thresholds, we found 156 stenophagous, 144 oligophagous, and 262 euryphagous species in the dataset.

To test the diversification hypothesis, we selected stenophagous and euryphagous genera and families and compared their diet breadth. We used families and genera for which the index of prey diversity fell within the thresholds for stenophagy (mean of H for species in a genus/family < 0.3) and the number of prey was at least 10. There were six such families and 45 such genera. However, we excluded 14 of these genera because their phylogenetic positions were unknown. For each stenophagous family/genus, we next selected the most closely related sister family/genus for which evidence of euryphagy (mean of H for species of a genus/family > 1.1) was available. The following sister–family comparisons were therefore made (stenophagous/euryphagous): Caponiidae/Segestriidae, Oonopidae/Dysderidae, Archaeidae/Eresidae, Palpimanidae/Eresidae, Mimetidae/Eresidae, Zodariidae/Amaurobiidae, Ammoxenidae/Gnaphosidae. The list of sister–genera comparisons is shown in Table 1. The number of species for each genus and family was found in Platnick (2010). Number of described species for a stenophagous family/genus versus nearest euryphagous family/genus was compared using paired Wilcoxon tests (Mitter et al. 1988).

To test the phylogenetic hypotheses, we first constructed the phylogenetic trees and then used comparative methods (Stireman 2005). Phylogenetic trees were constructed by combining phylogenetic and taxonomic information from published data, assuming identical branch distances because these were typically unreported. For phylogeny at the family level, we used the most recent hypothesis for Araneae (Coddington 2005). However, this phylogeny lacked a few newly designated families, namely Cybaeidae, Hahniidae, Homalonychidae, and Nephilidae. Their positions were resolved using additional sources (Jocqué and Dippenaar-Schoeman 2006; TOL 2009). Generic level phylogenies were constructed for each family that (1) included at least four genera with data on prey; (2) included more than one stenophagous species; and (3) for which a phylogenetic analysis was available. These conditions were met for eight families whose phylogenies were collected from the following sources: Araneidae (Scharff and Coddington 1997; Agnarsson and Blackledge 2009), Corinnidae (Bosselaers and Jocqué 2002; J. Bosselaers, pers. com.), Dysderidae (Arnedo et al. 2007b), Salticidae (Maddison and Hedin 2003; Maddison et al. 2008; W. Maddison, pers. com.),

Table 1. **List of sister-genera and their family affiliation used in the comparison of diversification.**

Stenophagous	Euryphagous
Araneidae	
Kaira	*Metepeira*
Mastophora	*Metepeira*
Pasilobus	*Metepeira*
Cladomelea	*Metepeira*
Celaenia	*Metepeira*
Corinnidae	
Falconina	*Phruronellus*
Dysderidae	
Tedia	*Harpactea*
Linyphiidae	
Tenuiphantes	*Linyphia*
Walckenaeria	*Erigone*
Ummeliata	*Erigone*
Salticidae	
Tutelina	*Menemerus*
Anasaitis	*Euophrys*
Siler	*Menemerus*
Microheros	*Aelurillus*
Stenaelurillus	*Aelurillus*
Theridiidae	
Dipoena	*Latrodectus*
Euryopis	*Latrodectus*
Chrosiothes	*Latrodectus*
Neospintharus	*Latrodectus*
Asagena	*Steatoda*
Phycosoma	*Latrodectus*
Yaginumena	*Latrodectus*
Thomisidae	
Amyciaea	*Xysticus*
Aphantochilus	*Misumenops*
Tmarus	*Diaea*
Zodariidae	
Zodarion	*Pax*
Habronestes	*Pax*

Theridiidae (Arnedo et al. 2004; 2007a; I. Agnarsson, pers. com.), Thomisidae (Benjamin et al. 2008; P. Lehtinen, pers. com.), Tetragnathidae (Álvarez-Padilla et al. 2009), and Zodariidae (Jocqué 1991).

Generalized least squares (GLS) were used to test the effect of branch distance on the continuous response variable (H) at the family level. The response variable was logarithmically transformed to approach normal distribution, homoscedasticity of residuals, and to stay within positive bounds for predicted values (Pinheiro and Bates 2000). The correlation structure among observations was created from the family trees using a Brownian motion model of character evolution (Hansen and Martins 1996). The linear model also included a linear variance function to weight the effect of prey sample size (N per species). To test the hypotheses within selected families at the species level, we primarily used generalized estimating equations with the binomial error structure (GEE) from the ape package (Paradis 2006) that includes methods for phylogenetic and evolutionary analyses. We modeled the relationship between proportions of a certain prey category in the diet (response variable) and branch distance. As the low diversity index, an indication of stenophagy, is a result of high proportion of certain prey, we expected that the relationship between the proportion of certain prey and branch distance would decrease linearly on a logit scale if stenophagy was a basal condition, increase linearly, if stenophagy was a derived condition, or be quadratic, if stenophagy was at an intermediate position within the tree. The analysis within eight families was performed only for prey categories that were captured by at least three genera within the family. We fitted quadratic logit models to the relationship between proportions of certain prey, but if the quadratic coefficient was not significantly different from zero then it was removed from the model.

The branch distances were estimated by the number of nodes separating each species from the root of the tree (Stireman 2005). Initially, we ran analyses with both full (including all taxa) and reduced (including only taxa with prey data) phylogenies. As the results were similar, we used the latter ones. The variance of the binomial model includes in its definition weighing according to N, thus no extra weights to account for different prey numbers needed to be specified. Corrected number of degrees of freedom for the Wald test of parameters was used. GEE requires estimation of a correlation structure that was based upon the constructed phylogenetic trees. If the GEE did not converge, Generalized linear models (GLM) with a quasi-binomial setting were used to correct for large SE of parameter estimates (and associated P-values). Bonferroni correction was applied to the significance level for the multiple tests of each prey group within a single spider family. The relationship between the diversity index and species number at the family level was tested using Moran's I autocorrelation (Gittleman and Kot 1990). In addition, ancestral states for continuous characters (prey diversity or prey proportion) for each node were estimated within the eight families (both at the genus and species levels) using maximum likelihood assuming Brownian motion (Schluter et al. 1997) within the ace function from the ape package. Ninety-five percent confidence intervals (CI_{95}) for these estimations were computed from logarithmically transformed diversity values or angularly transformed proportions to stay within positive range.

The two methods used to test hypotheses on the position of stenophagy along the phylogeny, logit regression using GEE (mentioned above) and ancestral state estimation using ace, are similar but not identical. The logit regression works with observed data, allows for weighting, and produces simple linear trends (on logit scale) but not a detailed prediction for each node. Ancestral state estimation works with estimates (each having inherent uncertainty), does not allow for weighting, but produces detailed estimates for each node. The results of these methods are thus complementary. As the estimations by ancestral state estimation are approximate, the pie charts are figured in gray color in all figures to contrast with empirical estimates of prey diversities for each species displayed in black.

To test the two ecological constraints hypotheses, we used GLS to compare prey diversities among geographical zones and among foraging guilds. Furthermore, we used GEE with a binomial error structure to compare proportions of a certain prey category in the diet among geographical zones or between foraging guilds. Geographic areas of distribution for each species, classified as tropical, subtropical, temperate, and cosmopolitan, were taken from Platnick (2010). The classification of predatory strategies (cursorial or web building) was species-specific and was taken from the various literature sources (Appendix). The web-building guild, species using web for prey capture, contained 255 species, and the cursorial guild, species capturing prey without the use of web, contained 308 species.

All analyses were performed in R (R Development Core Team 2009). Data deposited in the Dryad repository: doi:10.5061/dryad.1d8761h1.

Results

The prey data came both from field and laboratory studies. The laboratory acceptance experiments provide estimates of fundamental trophic niche, whereas that of natural prey are estimates of realized niche. The former was expected to be wider, but comparison of prey diversities between laboratory and field studies did not support this expectation (Analysis of variance [ANOVA], $F_{1,471} = 0.7$, $P = 0.41$). The prey data also differed dramatically in sample size (N) among species. As precision of the estimated prey diversity increases with N, weighting according to N was used in every regression analysis. Weighting adjusted the effect of each species giving large power to species with high N.

Taken together all gathered data on the prey of spiders, the most frequent prey of extant spider species was Diptera (42.9% of prey records, $N = 134{,}956$), followed by Homoptera (17%), Coleoptera (8%), and Formicidae (8%). Stenophagous spiders specialized on Formicidae (50% of species, $N = 156$), followed by Araneae (18%), Lepidoptera (14%), Isoptera (10%), Diptera (7%), and Crustacea (2.6%).

DIVERSIFICATION

The number of species of stenophagous genera was lower than that of euryphagous genera, but not significantly (Wilcoxon rank paired test, $V = 115$, $P = 0.08$). The number of species in the stenophagous families was also lower than in euryphagous families, but also not significantly (Wilcoxon rank paired test, $V = 13$, $P = 0.94$).

PHYLOGENETIC CONSTRAINT

Prey diversity was not significantly related to the branch distance at the family tree (GLS, $F_{1561} = 3.8$, $P = 0.053$, Fig. 1) suggesting that stenophagy is rather derived than basal. Moran's I revealed significant but weak (negative) spatial autocorrelation ($I = -0.016$, $P < 0.0001$) suggesting rather independence of stenophagy from phylogeny at the family level. Mapping of stenophagy on the tree showed that stenophagy is completely absent in Mygalomorphae, very rare in Haplogynae, and most frequent in RTA (i.e., species with a retrolateral tibial apophysis on the male palp) clade and Orbiculariae. We recognized two clusters of stenophagous species in the family-level topology. One is in the Palpimanoidea (Mimetidae, Archaeidae, Palpimanidae) and the other in the Gnaphosoidea (Ammoxenidae, Gallieniellidae). Low prey diversity for Gradungulidae, Telemidae, Lamponidae, and Gallieniellidae is, however, supported by anecdotal records only. In case of Oonopidae and Caponiidae, it is based only on a single species. Therefore, only Ammoxenidae, Archaeidae, Palpimanidae, Mimetidae, and Zodariidae are considered stenophagous at the family level.

Using the ancestral estimation method, oligophagy was the estimated very ancestral condition in the eight families for which phylogenies were available: Araneidae (mean = 0.5, CI_{95} = 0.01–3.8), Corinnidae (0.65, 0.01–4.01), Salticidae (1.03, 0.02–4.8), Tetragnathidae (0.49, 0.02–1.07), Theridiidae (0.39, 0.03–0.75), Thomisidae (0.65, 0.01–4.2), and Zodariidae (0.61, 0.19–1.94), except for Dysderidae, in which it was euryphagy (1.33, 0.26–2.39) (Figs. 2 and 3). Stenophagy (supported by prey records with $N > 4$) was found once within Corinnidae (Fig. 2B) in a clade including *Falconina* and *Attacobius*; within Dysderidae (Fig. 2C) in *Tedia* only; within Tetragnathidae (Fig. 3A) in *Arkys* and *Neoarchemorus* clade. Within Theridiidae (Fig. 3B), it has six independent occurrences and within Zodariidae (Fig. 3D), there are three independent occurrences. Three independent occurrences of stenophagy were found within both Araneidae (Fig. 2A) and Thomisidae (Fig. 3C), and five in Salticidae (Fig. 2D).

Stenophagous fly-eaters included *Mastophora* (Araneidae), *Tetragnatha* (Tetragnathidae), *Cryptachea,* and *Phoroncidia* (Theridiidae). The proportion of dipterans in the diet increased in a quadratic fashion with branch distance on the family level (GEE, $t_{72.1} = 7.3$, $P < 0.0001$, Fig. 4A), suggesting that dipterophagy is an intermediate condition. It was not related to the branch distance within Araneidae (GEE, $t_{12.5} = 1.6$, $P = 0.14$), Dysderidae (GEE, $t_{4.7} = 1$, $P = 0.39$), Corinnidae (GEE, $t_{5.8} = 1.2$, $P = 0.29$), Salticidae (GEE, $t_{18} = 0.5$, $P = 0.63$), or within Tetragnathidae (GEE, $t_{8.1} = 0.8$, $P = 0.48$). Within Thomisidae, the proportion of Diptera in the diet decreased significantly with the branch distance (GEE, $t_{7.9} = 3.9$, $P = 0.008$, Fig. 5A, B), suggesting that dipterophagy was a basal condition. Within Theridiidae, dipterophagy occurs independently in three clades and the proportion of Diptera in the diet increased with the branch distance (GLM, $t_{61} = 49.7$, $P < 0.0001$, Fig. 5C, D). The estimated ancestral condition in this family included a large proportion of Diptera (0.69, 0.5–0.88).

Stenophagous termite-eaters were found in *Ammoxenus* (Ammoxenidae), *Stenaelurillus*, *Microheros* (both Salticidae), and *Chrosiothes* (Theridiidae). The proportion of termites in the diet increased slightly with the branch distance at the family level, but the effect was not significant after Bonferroni adjustment (GEE, $t_{72.1} = 2.2$, $P = 0.03$, $\alpha = 0.008$). The proportion of termites was not related to the branch distance within Salticidae (GEE, $t_{18} = 0.4$, $P = 0.69$) and Zodariidae (GLM, $t_{38} = 0.3$, $P = 0.35$).

Stenophagous crustacea-eaters included *Amaurobioides* (Anyphaenidae) and *Tedia* (Dysderidae). The proportion of isopods or amphipods in the diet increased with the branch distance at the family level (GEE, $t_{72.1} = 2.9$, $P = 0.005$, Fig. 4B), suggesting that crustaceophagy was a derived condition. The estimated line is shallow due to few cases of crustaceophagy.

Stenophagous ant-eaters were found in *Falconina* (Corinnidae), *Galianoella* (Gallieniellidae), *Callilepis* (Gnaphosidae), *Oecobius* (Oecobiidae), *Anasaitis*, *Siler*, *Tutelina* (all Salticidae), *Asagena*, *Dipoena*, *Euryopis*, *Phycosoma*, *Steatoda*, *Yaginumena* (all Theridiidae), *Amyciaea*, *Aphantochilus*, *Tmarus* (all Thomisidae), and *Habronestes*, *Trygetus*, *Zodarion, Zodariellum* (all Zodariidae). The proportion of ants in the diet decreased with the branch distance on the family level but the effect was not significant after Bonferroni adjustment (GEE, $t_{72.1} = 2.2$, $P = 0.03$, $\alpha = 0.008$). Within Araneidae, the proportion of ants increased with the branch distance at quadratic fashion (GEE, $t_{12.5} = 6.1$, $P = 0.0001$, Fig. 6A, B), suggesting that myrmecophagy was an intermediate condition. The proportion of ants

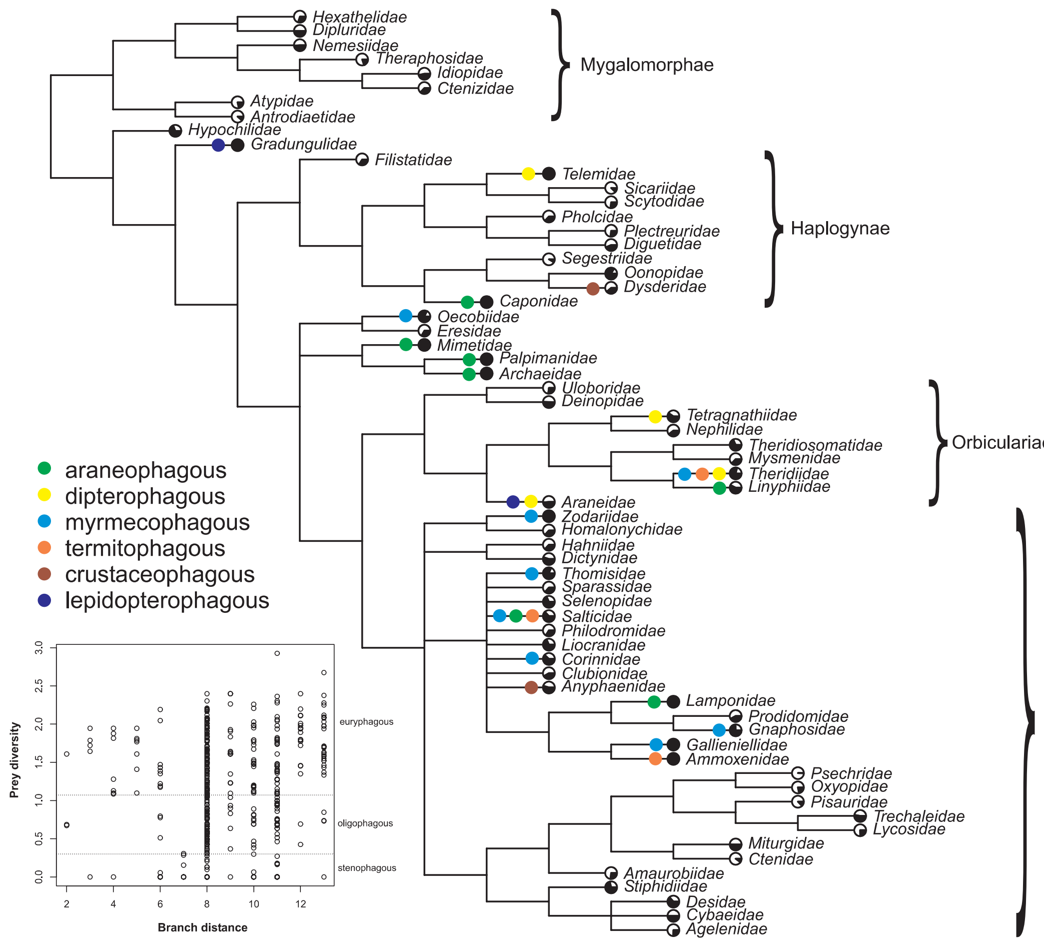

Figure 1. Topology of families within Araneae and their diet breadth. The colored dots indicate the types of stenophagy occurring within each family. The black and white pie chart indicates mean prey diversity, calculated using the Shannon–Weaver index and scaled from $H = 0$ to 3. The proportion of the pie colored white indicates H, with a fully white pie equaling the maximum, $H = 3$ (euryphagy), and a fully black pie indicating $H = 0$ (stenophagy). Only families for which prey data were available are shown. Insert: Relationship between the prey diversity and branch distance of the family tree for 562 species of spiders. Horizontal dotted lines identify borders for each trophic category.

in the diet increased with the branch distance within Salticidae (GEE, $t_{18} = 3.6$, $P = 0.002$, Fig. 6C, D) and Zodariidae (GEE, $t_{7.4} = 5.6$, $P = 0.003$, Fig. 6E, F), suggesting that myrmecohagy was a derived condition. The very ancestral condition in Araneidae was sufficiently euryphagous to include portion of ants in the diet (0.03, 0.001–0.05). Ant eating occurs in this family in several clades. In Salticidae, ant eating occurs at least in three independent lineages. But in Zodariidae, all ancestral estimations included ants in the diet. The proportion of ants in the diet was not related to the branch distance within Corinnidae (GEE, $t_{5.8} = 0.1$, $P = 0.93$), within Thomisidae (GEE, $t_{22} = 2.4$, $P = 0.024$), or within Theridiidae (GLM, $t_{61} = 5.5$, $P = 0.02$, $\alpha = 0.013$) after Bonferroni adjustment.

Stenophagous lepidoptera-eaters included *Celaenia*, *Cladomelea*, *Kaira*, *Mastophora*, and *Pasilobus* (all Araneidae). The proportion of Lepidoptera in the diet did not change with branch distance at the family level (GEE, $t_{72.1} = 1.7$, $P = 0.10$). Within Araneidae, the proportion increased with the branch distance and the effect was just marginally significant after Bonferroni adjustment (GLM, $t_{70} = 2.5$, $P = 0.013$, $\alpha = 0.013$, Fig. 7A, B), suggesting that lepidopterophagy was a derived condition. The ancestral condition in Araneidae included portion of lepidopterans in the diet (0.03, 0.01–0.07). Lepidoptera eating occurs in two clades in Araneidae. Within Thomisidae, the proportion of Lepidoptera in the diet decreased with the branch distance but not significantly after Bonferroni correction (GEE, $t_{7.9} = 2.9$, $P = 0.03$). The proportion of Lepidoptera in the diet was not related to the branch distance within Theridiidae (GEE, $t_{14.9} = 1.5$, $P = 0.16$) or within Tetragnathidae (GLM, $t_{21} = 1.5$, $P = 0.24$).

Stenophagous spider-eaters were found in *Orthonops* (Caponiidae), *Walckenaeria* (Linyphiidae), *Australomimetus*, *Mimetus* (both Mimetidae), *Palpimanus* (Palpimanidae), and *Portia* (Salticidae). The proportion of spiders in the diet decreased

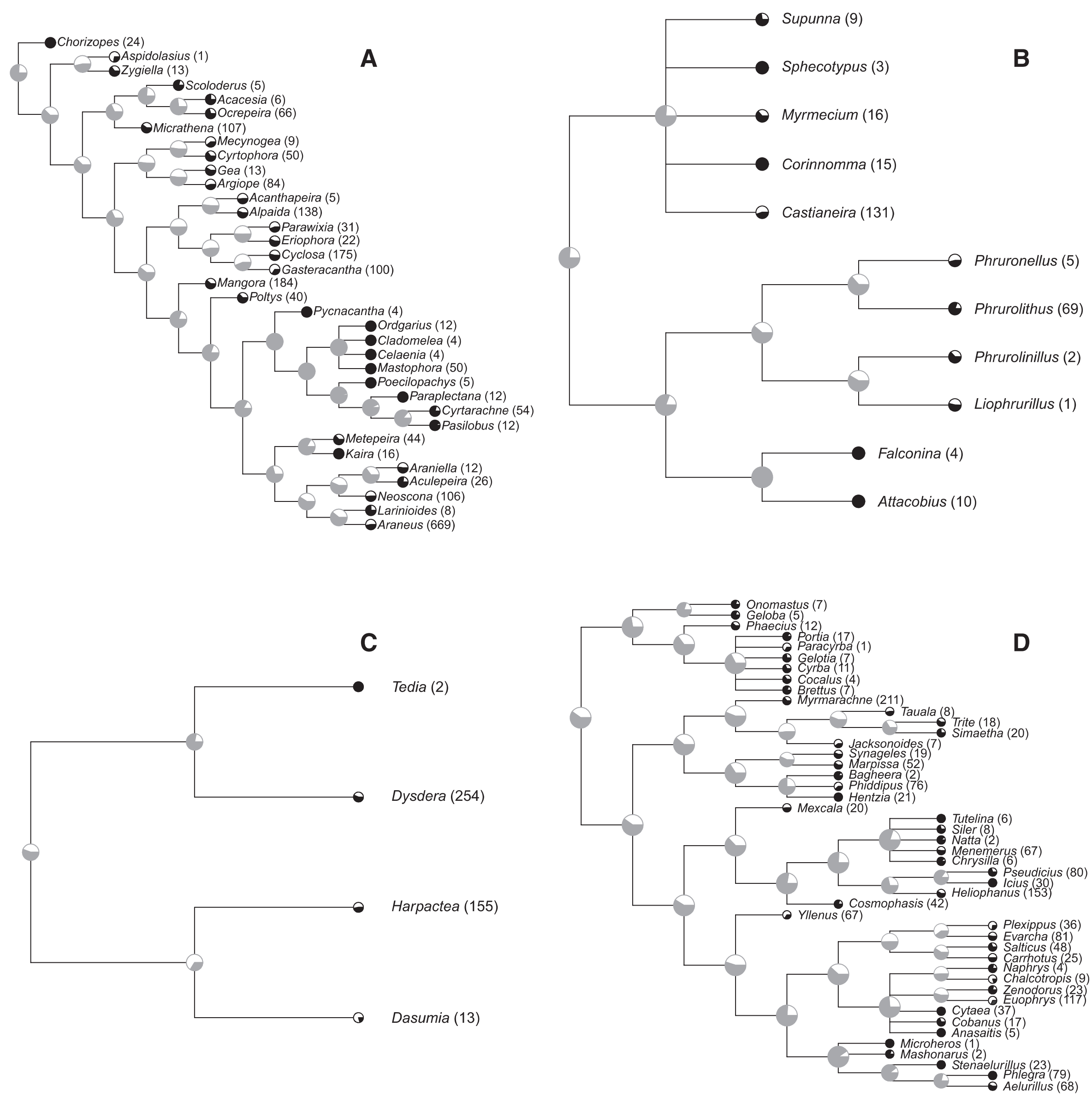

Figure 2. Topology of araneid (A), corinnid (B), dysderid (C), and salticid (D) genera with mean prey diversity. The pie charts at the terminals show the diversity of captured prey for each genus, calculated from the mean of *H* for all species within that genus. The proportion of the pie filled white indicates *H*, with a fully white pie equaling the maximum, *H* = 3 (euryphagy), and a fully black or gray pie indicating *H* = 0 (stenophagy). Ancestral conditions were estimated using maximum likelihood and are indicated in gray. Numbers of species in each genus, according to Platnick (2010), are given in parentheses.

with the branch distance at the family level in a quadratic fashion (GEE, $t_{72.1} = 6.1$, $P < 0.0001$, Fig. 4C), suggesting that araneophagy was an intermediate condition. The proportion of spiders in the diet also decreased with the branch distance within Salticidae (GEE, $t_{18} = 3.5$, $P = 0.003$, Fig. 8A, B) and Zodariidae (GEE, $t_{6.7} = 11.4$, $P = 0.0001$, Fig. 8C, D), suggesting that araneophagy was a basal condition. In Salticidae, spider eating was found in one large clade, whereas in Zodariidae, a high proportion of spiders in the diet was ancestral (0.18, $CI_{95} = 0.14, 0.22$). The proportion of spiders in the diet was not related to the branch distance within Araneidae (GLM, $t_{70} = 1.4$, $P = 0.16$), Corinnidae (GLM, $t_9 = 1.9$, $P = 0.1$), Dysderidae (GLM, $t_7 = 2.9$, $P = 0.13$), Tetragnathidae (GLM, $t_{21} = 0.4$, $P = 0.69$), Theridiidae (GLM, $t_{61} = 0.8$, $P = 0.36$), and Thomisidae (GEE, $t_{7.9} = 2.4$, $P = 0.05$).

ECOLOGICAL CONSTRAINTS

Prey diversity differed significantly among the geographical zones (GLS, $F_{3559} = 7.9$, $P < 0.0001$, Fig. 9A): cosmopolitan and temperate spider species had significantly higher prey diversity than subtropical and tropical species (GLS, contrasts, $F_{1559} = 9.9$,

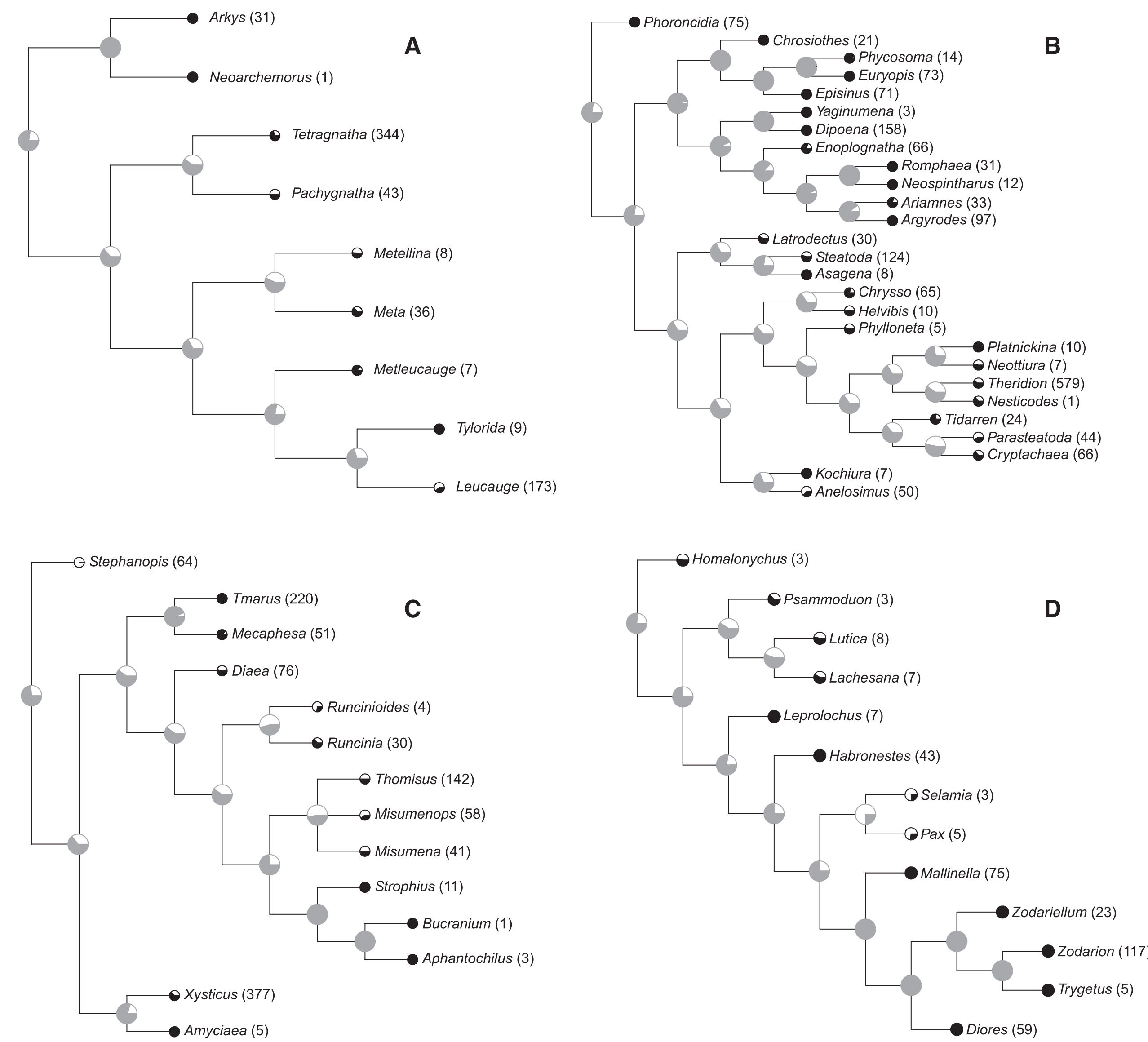

Figure 3. **Topology of tetragnathid (A), theridiid (B), thomisid (C), and zodariid (D) genera with mean prey diversity. The pie charts at the terminals show the diversity of captured prey for each genus, calculated from the mean of *H* for all species within that genus. The proportion of the pie filled white indicates *H*, with a fully white pie equaling the maximum, $H = 3$ (euryphagy), and a fully black or gray pie indicating $H = 0$ (stenophagy). Ancestral conditions were estimated using maximum likelihood and are indicated in gray. Numbers of species in each genus, according to Platnick (2010), are given in parentheses.**

$P < 0.002$). As concerns the proportion of a certain prey in the diet, there was not significant difference among the geographical zones in the proportion of termites (GEE, contrasts, $t_{72.1} < 0.6$, $P > 0.58$), isopods or amphipods (GEE, contrasts, $t_{72.1} < 0.9$, $P > 0.39$), and spiders (GEE, contrasts, $t_{72.1} < 1.3$, $P > 0.19$). The proportion of dipterans in the diet was significantly higher in cosmopolitan and temperate species than in subtropical and tropical ones (GEE, contrasts, $t_{72.1} > 5.3$, $P < 0.0001$, Fig. 10A). The proportion of ants in the diet was significantly higher in cosmopolitan than in subtropical and tropical species (GEE, contrast, $t_{72.1} > 2.5$, $P < 0.01$) and the lowest in temperate species (GEE, contrast, $t_{72.1} = 7.6$, $P < 0.0001$, Fig. 10A). The proportion of Lepidoptera in the diet was significantly lower in cosmopolitan and temperate than in subtropical and tropical spiders (GEE, contrasts, $t_{72.1} > 4.4$, $P < 0.0001$, Fig. 10A).

The prey diversity was significantly lower in cursorial than in web-building species (GLS, $F_{1,561} = 7.6$, $P < 0.0001$, Fig. 9B). As concerns the proportion of a certain prey in the diet, there was not significant difference between cursorial and web-building species in the proportion of termites (GEE, $t_{72.1} = 1.9$, $P = 0.06$), isopods or amphipods (GEE, $t_{72.1} = 0.3$, $P = 0.76$), and Lepidoptera (GEE, $t_{72.1} = 1$, $P = 0.32$). Fly eating was significantly more

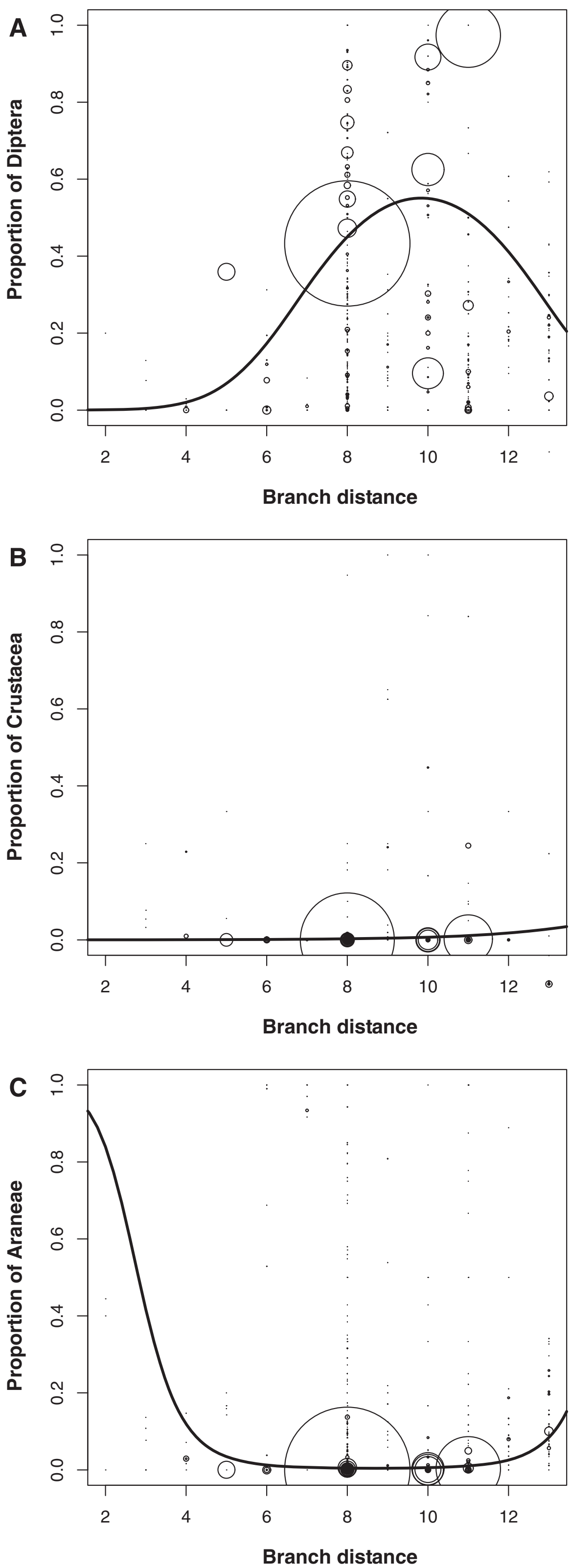

Figure 4. Relationship between proportion of Diptera (A), Crustacea (B), and Araneae (C) in the diets of 562 spider species and the branch distances of the family tree, using quadratic logit models. The sizes of points was scaled to *N* (prey sample size) and corresponds to their weight during analysis.

common in web building than in cursorial species (GEE, $t_{72.1} = 9.2$, $P < 0.0001$, Fig. 10B). Cursorial spiders had significantly higher proportion of ants (GEE, $t_{72.1} = 7.2$, $P < 0.0001$, Fig. 10B) and spiders (GLM, $F_{1561} = 150.6$, $P < 0.0001$, Fig. 10B) than web-building species.

Discussion

We find only weak support for the "diversification hypothesis," which predicts that stenophagy reduces species diversification in spiders. Although many stenophagous genera and families are species-poor compared to most euryphagous genera (Figs. 2 and 3), these differences were not statistically significant given the available data. Reduced diversification in specialist taxa was confirmed for some parasites (Desdevises et al. 2001), but a meta-analysis by Thompson (1994) revealed that prey specificity did not in general reduce diversification. Therefore, the effect of stenophagy on diversification rates in spiders is difficult to determine and our result will have to be re-evaluated once better data are available.

The "phylogenetic constraint" hypothesis received mixed support. Our prediction that stenophagy in general is a derived condition is not strongly supported at the family level among spiders. However, estimation of diet breadth on the tree at the generic level showed that oligophagy was the ancestral strategy for most nodes. Stenophagy then subsequently evolved for such prey that the oligophagous species included in their diet. We suspect that trophic adaptation results first from evolution of behavioral and morphological traits that initially enabled the ancestral species to catch these prey followed by subsequent evolution of more specialized traits, such as aggressive chemical mimicry in lepidopterphages and myrmecophages. Such adaptations are known also from other predatory groups (Sloggett and Majerus 2000). It should be emphasized that with the current datasets, it was not possible to estimate accurately the ancestral trophic states at all levels because of partially unresolved phylogenies (Paradis 2006) and absence of prey data for several genera/species.

Within families, some types of stenophagy are clearly characteristic for derived clades, whereas other types occur in basal and intermediate lineages. Myrmecophagy was clearly derived in Salticidae and Zodariidae. All other types of stenophagy in spiders were most frequent in the intermediate levels of the tree topologies, suggesting that either transitions from euryphagy or oligophagy to stenophagy were as likely as the reverse at the family level, or that species divergence was reduced in the stenophagous clades. All in all, derived spiders are not more stenophagous than basal taxa. Similar results were found in fish parasites (Desdevises et al. 2002). The derived origin of myrmecophagy agreed with the pattern of trophic evolution in other

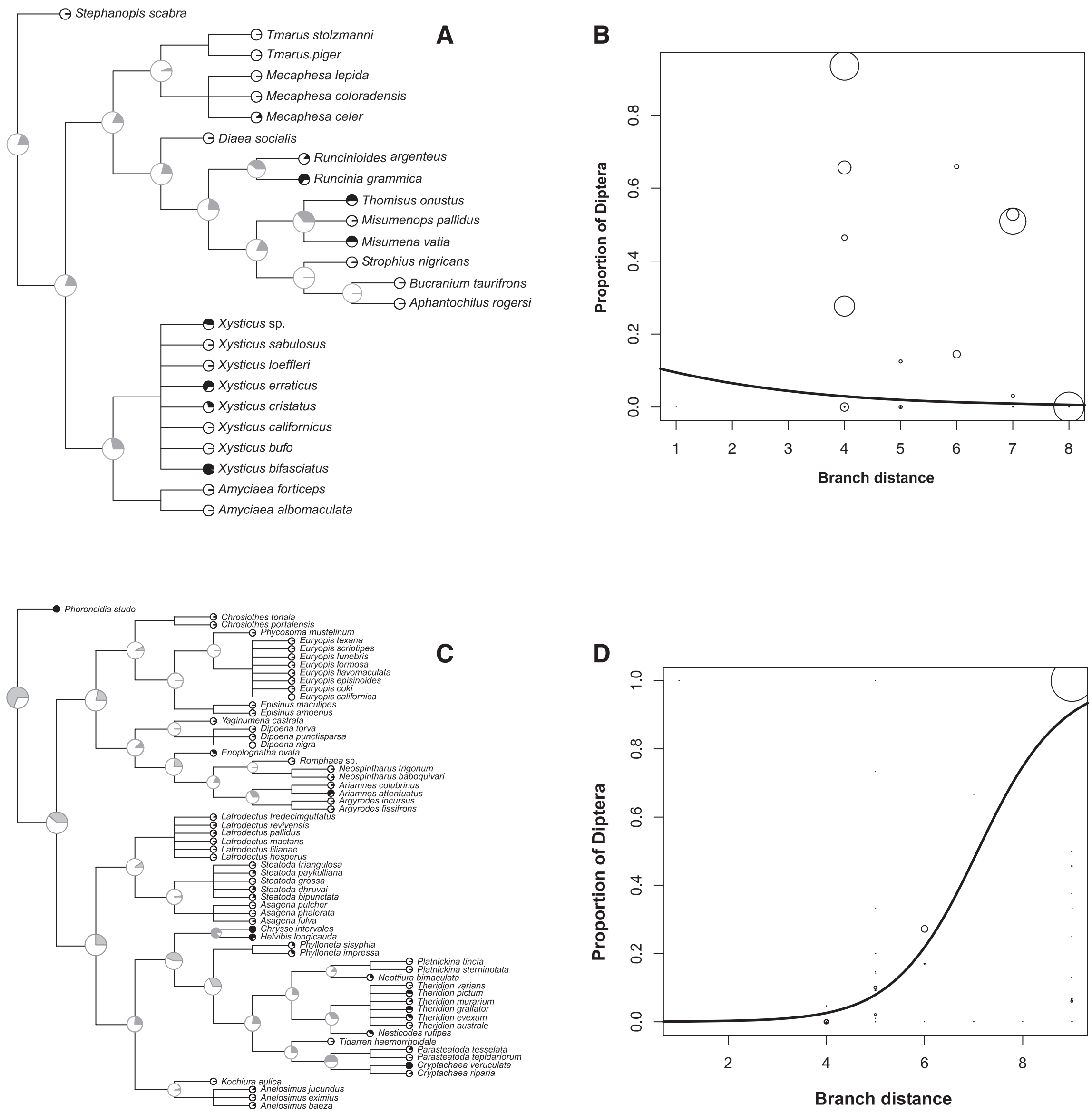

Figure 5. Topology of thomisid (A) and theridiid (C) species with the proportion of Diptera in the diet indicated by the amount of black in each pie chart. Ancestral conditions were estimated using maximum likelihood and are indicated in gray. Relationship between proportion of Diptera in the diet and the branch distance for 25 thomisid (B) and 67 theridiid (D) species using the logit models. The size of points was scaled to *N* (prey sample size) and corresponds to their weight during analysis.

taxa. Basal (primitive) species of Dendrobatid frogs were euryphagous and derived species stenophagous upon ants (Caldwell 1996). Similarly, in Coccinellidae, myrmecophagy was derived from coccidophagy (Giorgi et al. 2009).

Spider eating and araneophagy were found predominantly in species near the bases of trees, suggesting its ancestral state. Spiders were among the first predators to invade the land (Pisani et al. 2004). In the Devonian, before insects diversified, spiders likely preyed on spiders and other arachnids (Vollrath and Selden 2007). However, spider eating is still frequent even among extant cursorial spiders (e.g., Rypstra and Samu 2005). Spider eating has several forms: sexual cannibalism (e.g., Elgar 1992), cannibalism (e.g., Polis 1981), intraguild predation (e.g., Wise and Chen 1999), and oophagy (e.g., Valerio 1974). Interestingly, araneophagy is either homogeneously distributed (Theridiidae, Tetragnathidae, Corinnidae, Thomisidae) or more frequent in basal taxa (Salticidae, Zodariidae, Araneidae). As predicted, crustaceophagy occurs only in one primitive family Dysderidae that originated around the same time as their isopod prey during the Permian (Grimaldi and Engel 2005; Vollrath and Selden 2007).

All other types of stenophagy include flying insects that first appeared in the Triassic or Jurassic. Dipterophagy was most frequent in two-dimensional web-building species (Orbiculariae) that likely originated in the Jurassic (Ayoub et al. 2007).

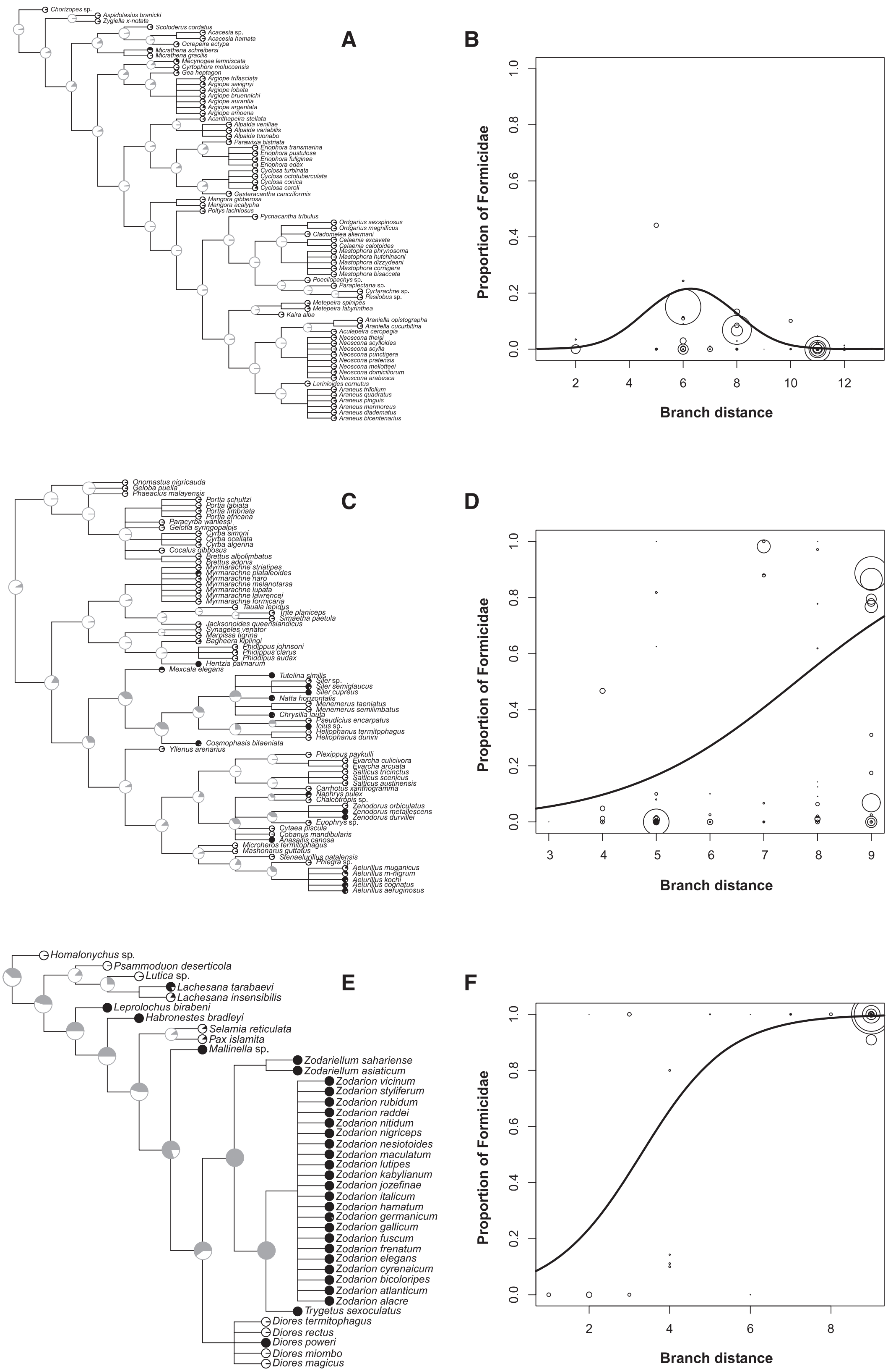

Figure 6. Topology of araneid (A), salticid (C), and zodariid (E) species with the proportion of ants in the diet indicated by the amount of black in each pie chart. Ancestral conditions were estimated using maximum likelihood and are indicated in gray. Relationship between proportion of ants in the diet and the branch distance for 72 araneid (B), 74 salticid (D) and 40 zodariid, and one homalonychid (F) species with the logit models. The size of points was scaled to *N* (prey sample size) and corresponds to their weight during analysis.

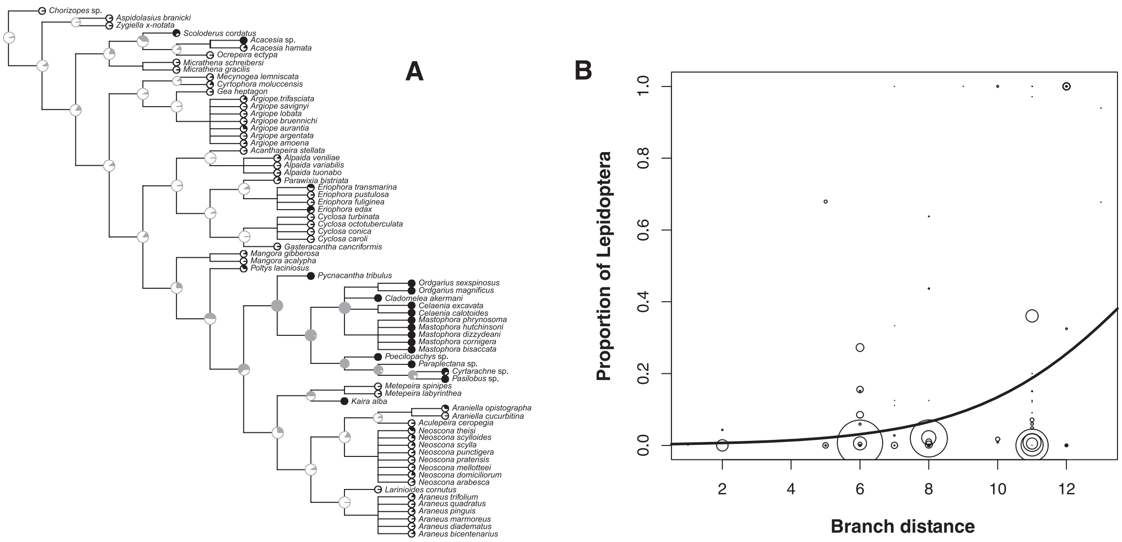

Figure 7. **Topology of araneid (A) species with the proportion of lepidopterans in the diet indicated by the amount of black in each pie chart. Ancestral conditions were estimated using maximum likelihood and are indicated in gray. Relationship between proportion of lepidopterans in the diet and the branch distance for 72 araneid (B) species with the logit model. The size of points was scaled to *N* (prey sample size) and corresponds to their weight during analysis.**

Lepidopterophagy was derived in Araneidae. Again both lepidopteran prey (Grimaldi and Engel 2005) and araneid predators (Ayoub et al. 2007) first appeared in the Jurassic. Termitophagy also appears derived at the family level. However, the relationship failed to be significant, probably due to scarce evidence for termitophagous species. Termites originated in the Cretaceous as did their theridiid specialists (Grimaldi and Engel 2005; Vollrath and Selden 2007). Myrmecophagy is most common in more derived families and species. This is not surprising for theridiid spiders because ants appeared in the Cretaceous (Grimaldi and Engel 2005) and are thus younger than the origin of Theridiidae. But, a few nonweb building families (RTA clade) with myrmecophagy (Zodariidae, Salticidae, Corinnidae, Thomisidae) are younger than the origin of ants (Vollrath and Selden 2007). However, even for these families, myrmecophagy is characteristic for derived species. More precise interpretations of coevolution will be possible only with more accurate estimates of origins and better resolved family and generic trees. In particular, the large polytomy in the non-web-building (RTA) clade, where most stenophagy occurs, and missing data for many other species, makes it impossible to draw any firmer conclusions.

The comparative analysis revealed that stenophagy occurs in several spider families at various positions in the tree topology. Such multiple origins are reported for other predatory groups too. For example, in Coccinellidae, myrmecophagy and acarophagy were found at the distal branches, coccidophagy and psyllophagy were found at the intermediate tree positions, whereas aphidophagy has occurred both at intermediate and distal tree topologies (Giorgi et al. 2009).

The "ecological constraint" hypothesis was supported by the significant effect of geographic zone on spider diet breadth. Spiders from the tropics and subtropics displayed lower diet breadth compared to taxa from the temperate zone. This pattern did not result from a greater proportion of stenophagous species in the subtropical and tropical zones (36%, $N = 246$) compared to temperate species (23%, $N = 294$). Instead, diet breadth of tropical and subtropical spiders is in general narrower. The geographic effects varied for different prey types. Frequency of spiders, crustaceans, and termites in the diet was similar across all zones. But, lepidopterans were most frequent in spider diets in subtropical and tropical zones, whereas dipterans were more frequent in the temperate zone. Also, ants were more common prey in cosmopolitan species compared to other zones, and were rarest in the temperate zone.

Guild type also correlated with diet breadth. Interestingly, diet breadth was lower in cursorial spiders compared to web-building species, in contrast to previous findings by Nyffeler (1999). Reduced diet breadth in cursorial spiders was not caused by a greater abundance of stenophagous species in the cursorial guild. It instead reflects the more opportunistic nature of web-building species. This pattern may also reflect an artificial bias resulting from an inability of researchers to recognize invertebrates trapped in webs that are consumed versus not-consumed prey (see also Blackledge 2011). In this respect, the analysis of diet of cursorial spiders is more precise as only prey held in chelicera are recorded.

With respect to guild types, two major radiations occurred in Araneae, cursorial spiders diversified within the RTA

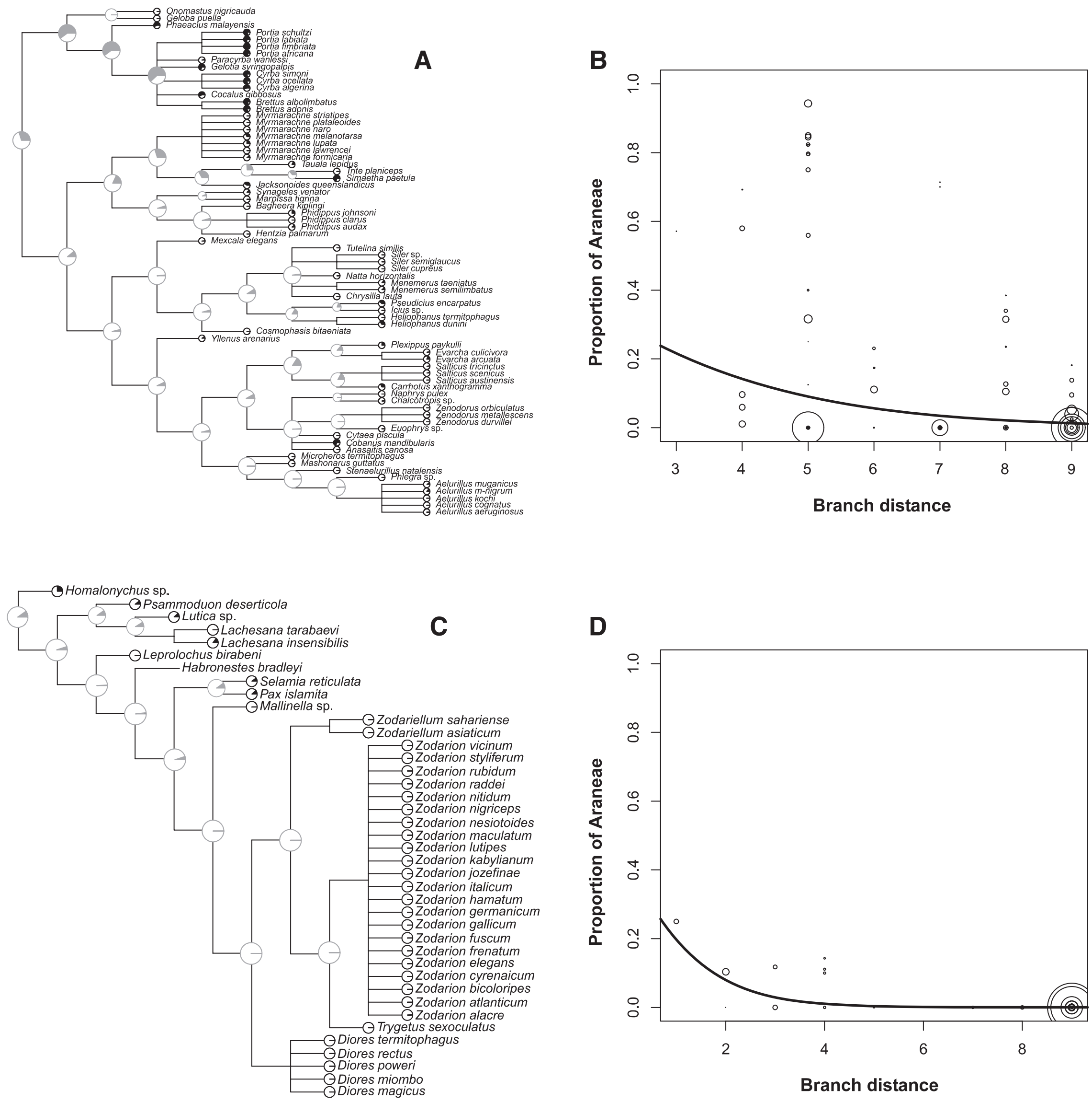

Figure 8. **Topology of salticid (A) and zodariid (C) species with the proportion of spiders in the diet indicated by the amount of black in each pie chart. Ancestral conditions were estimated using maximum likelihood and are indicated in gray. Relationship between proportion of spiders in the diet and the branch distance for 24 salticid (B) and 40 zodariid and one homalonychid (D) species with the logit models. The size of points was scaled to *N* (prey sample size) and corresponds to their weight during analysis.**

clade whereas aerial web-building species diversified within the Orbiculariae (Bond and Opell 1998; Blackledge et al. 2009). Among both groups, stenophagy evolved for the types of prey that their ancestral predatory strategies made each taxon most likely to encounter. Not surprisingly, dipterans were the most frequent prey of web-building species, whereas ants and spiders were more frequent prey of cursorial species. Termites, crustaceans, and lepidopterans were captured by both guilds at similar frequencies.

How many stenophagous spider species are there? Our analysis is based upon data of almost 600 species of spiders. Although that number might appear high, in fact, it represents only 1.4% of the 41,000 known spider species (Platnick 2010). Overall, 156 of 562 species (28%), for which reasonable data on prey were obtained met our criterion for stenophagy. This frequency is likely overestimated due to more intensive research on species suspected to be stenophagous and due to the low number of prey records for some species, reducing their diversity indices. We expect that future research will reveal new types of stenophagy among spiders. Specifically, there is preliminary evidence for stenophagy on Collembola, Blattodea, Homoptera, and Coleoptera (Pratt and Hatch 1938; Austin and Blest 1979; Nyffeler et al. 1988; Alderweireldt 1994; Downes 1994; Yamanoi and Miyashita 2005; Rybak 2007).

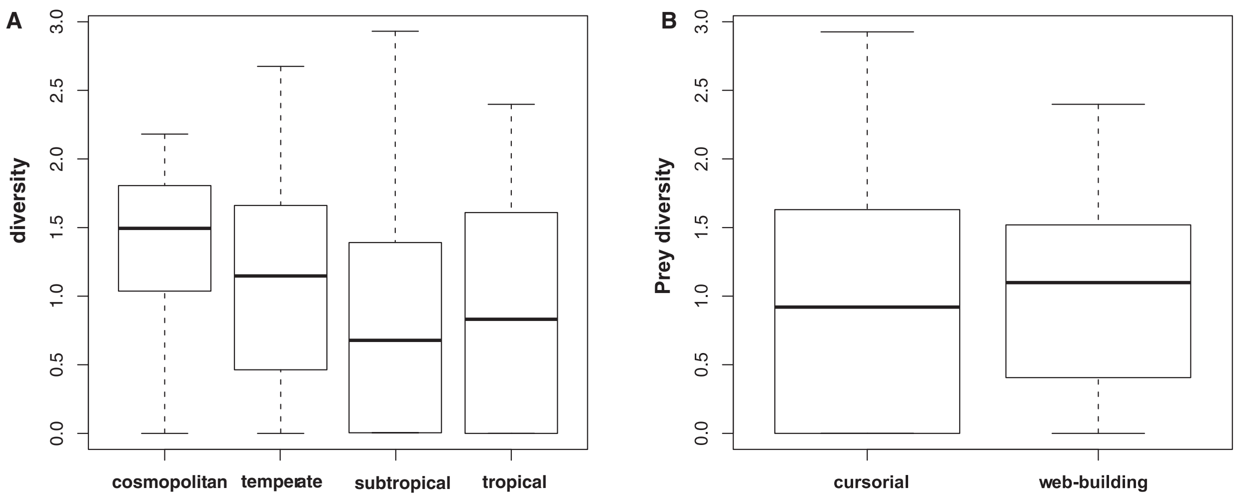

Figure 9. Comparison of prey diversity for four geographical regions (A) and two guilds (B). Lines are medians, boxes are quartiles, and whiskers are 1.5× interquartile range.

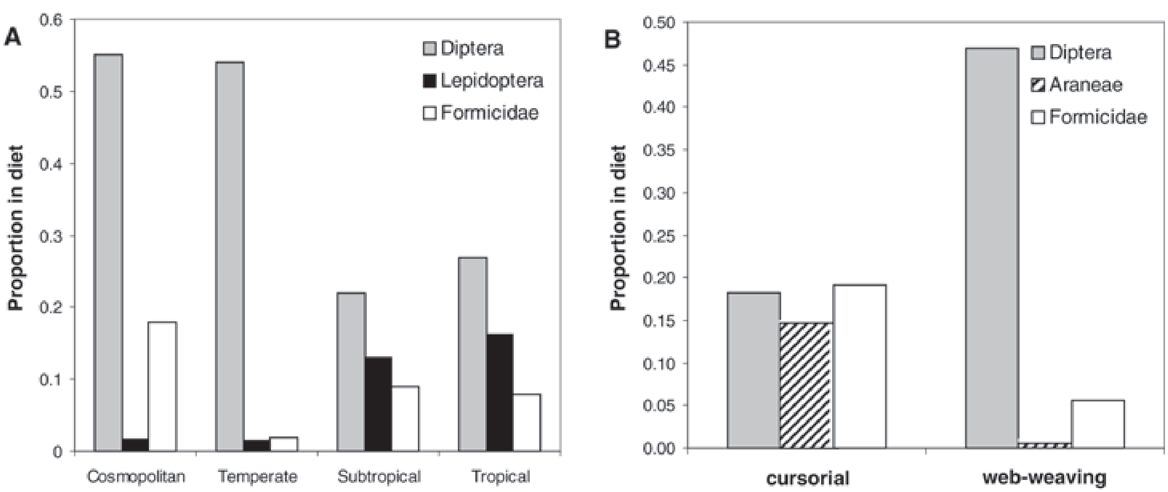

Figure 10. (A) Comparison of the proportion of Diptera, Lepidoptera, and Formicidae in the diets of cosmopolitan, temperate, subtropical, and tropical spiders. (B) Comparison of proportion of Diptera, Araneae, and Formicidae in the diets of cursorial and web-building species.

We conclude that the evolution of stenophagy in spiders appears to be governed by multiple determinants, including phylogeny and ecology. Stenophagy cannot unambiguously be considered as either limiting or promoting diversification. However, stenophagous genera were in general species-poor suggesting that improved analyses will support a limiting influence of stenophagy on diversification of spiders once more trophic data are available. Regardless, specialization of prey included in the diets of euryphagous ancestors appears to be the primary pathway for the evolution of stenophagy among spiders and stenophagy correlates significantly with both tropical/subtropical distribution and cursorial hunting strategies. Future analysis should aim to identify the adaptations that limit capture and processing of prey by stenophagous spiders and seek to incorporate both ecological and phylogenetic information to obtain more informative results about the evolution of stenophagy.

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Appendix

List of species used in the analyses and the sources of references. Estimated diet breadth index (*H*) is given for each species in square brackets.

Agelenidae: *Agelena labyrinthica* (CLERCK) (Nyffeler 1982) [1.47], *Agelenopsis aperta* (GERTSCH) (Riechert & Tracy 1975) [1.49], *A. naevia* (WALCKENAER) (Bilsing 1920) [2.26], *Allagelena gracilens* (C. L. KOCH) (Nyffeler 1982) [1.13], *Malthonica ferruginea* (PANZER) (Nentwig 1983) [2.21], *Tegenaria atrica* C. L. KOCH (Bristowe 1939) [1.79]. Amaurobiidae: *Amaurobius ferox* (WALCKENAER) (Nentwig 1987) [0.94], *A. similis* (BLACKWALL) (Bristowe 1939) [2.40], *Coelotes terrestris* (WIDER) (Petto 1990) [1.23], *Coelotes* sp. (Sechterová 1992) [2.26], *Coras medicinalis* (HENTZ) (Bilsing 1920) [1.61]. Ammoxenidae: *Ammoxenus amphalodes* DIPPENAAR & MEYER (Van den Berg & Dippenaar-Schoeman 1991, Dippenaar-Schoeman et al. 1996a,b, Haddad & Dippenaar-Schoeman 2006) [0], *A. coccineus* SIMON (Dean 1988, Van Den Berg & Dippenaar-Schoeman 1991) [0], *A. daedalus* DIPPENAAR & MEYER (Van Den Berg & Dippenaar-Schoeman 1991) [0], *A. pentheri* SIMON (Dippenaar-Schoeman et al. 1996a,b) [0], *Rastellus sabulosus* PLATNICK & GRIFFIN (Henschel 1997) [0]. Antrodiaetidae: *Aliatypus* sp. (Coyle & Icenogle 1994) [1.95]. Anyphaenidae: *Amaurobioides africana* HEWITT (Lamoral 1968) [0.21], *Anyphaena accentuata* (WALCKENAER) (Korenko & Pekár, unpublished) [1.79]. Araneidae: *Acacesia hamata* (HENTZ) (Bilsing 1920) [1.49], *Acacesia* sp. (Stowe 1986) [0], *Acanthapeira stellata* (WALCKENAER) (Nyffeler et al. 1989) [1.54], *Aculepeira ceropegia*

(Walckenaer) (Nyffeler & Benz 1979) [0.68], *Alpaida tuonabo* (Chamberlin & Ivie) (Shelly 1983) [1.50], *A. variabilis* (Keyserling) (Florez et al. 2004) [1.08], *A. veniliae* (Keyserling) (Saavedra et al. 2007) [1.43], *Araneus bicentenarius* (McCook) (Bilsing 1920) [2.05], *A. diadematus* Clerck (Nyffeler & Benz 1989) [1.42], *A. marmoreus* Clerck (Pasquet 1984) [1.17], *A. pinguis* (Karsch) (Endo 1989) [1.87], *A. quadratus* Clerck (Nyffeler 1982) [1.13], *A. trifolium* (Hentz) (Bilsing 1920) [1.88], *Araniella cucurbitina* (Clerck) (Nyffeler & Benz 1979) [1.36], *A. opistographa* (Kulczyński) (Klein 1988) [1.50], *Argiope amoena* L. Koch (Murakami 1983) [1.52], *A. argentata* (Fabricius) (Nentwig 1985a) [1.66], *A. aurantia* Lucas (Bilsing 1920, Uetz et al. 1978) [2.21], *A. bruennichi* (Scopoli) (Nyffeler & Benz 1978, Ludy 2007) [0.85], *A. lobata* (Pallas) (Richter 1960) [1.79], *A. savignyi* Levi (Nentwig 1985a) [1.47], *A. trifasciata* (Forsskal) (Bilsing 1920, Uetz et al. 1978) [2.02], *Aspidolasius branicki* (Taczanowski) (Calixto & Levi 2006) [2.17], *Celaenia calotoides* Rainbow (McKeown 1952) [0], *C. excavata* (L. Koch) (Stowe 1986) [0.13], *Chorizopes* sp. (Eberhard 1983) [0], *Cladomelea akermani* Hewitt (Leroy et al. 1998) [0], *Cyclosa caroli* (Hentz) (Ibarra-Núñez et al. 2001) [2.06], *C. conica* (Pallas) (Nentwig 1983) [1.29], *C. octotuberculata* Karsch (Baba 2003) [0.78], *C. turbinata* (Walckenaer) (Nyffeler & Sterling 1994) [1.42], *Cyrtarachne* sp. (Miyashita et al. 2001) [0.63], *Cyrtophora moluccensis* (Doleschall) (Lubin 1974) [1.05], *Eriophora edax* (Blackwall) (Ceballos et al. 2005) [1.08], *E. fuliginea* (C. L. Koch) (Nentwig 1985a) [1.22], *E. pustulosa* (Walckenaer) (Laing 1988) [1.70], *E. transmarina* (Keyserling) (Herberstein & Elgar 1994) [1.26], *Gasteracantha cancriformis* (Linnaeus) (Gregory 1989, Yoshida 1989a, Ibarra-Núñez et al. 2001) [1.97], *Gea heptagon* (Hentz) (Nyffeler et al. 1989, Nyffeler & Sterling 1994) [1.25], *Kaira alba* (Hentz) (Stowe 1986) [0], *Larinioides cornutus* (Clerck) (Nyffeler & Benz 1979, Ysnel 1993) [0.75], *Mangora acalypha* (Walckenaer) (Nyffeler & Benz 1979) [1.12], *M. gibberosa* (Hentz) (Bardwell & Averill 1997) [1.19], *Mastophora bisaccata* (Emerton) (Stowe 1986, Yeargan & Quate 1996) [0], *M. cornigera* (Hentz) (Stowe 1986) [0], *M. dizzydeani* Eberhard (Eberhard 1980) [0], *M. hutchinsoni* Gertsch (Yeargan 1988, Yeargan & Quate 1996) [0], *M. phrynosoma* Gertsch (Stowe 1986, Yeargan & Quate 1996) [0], *Mecynogea lemniscata* (Walckenaer) (Wise & Barata 1983) [1.82], *Metepeira labyrinthea* (Hentz) (Bilsing 1920, Wise & Barata 1983) [1.77], *M. spinipes* F. O. P.-Cambridge (Uetz 1989) [0.44], *Micrathena gracilis* (Walckenaer) (Uetz & Biere 1980) [0.91], *M. schreibersi* (Perty) (Shelly 1984) [1.49], *Neoscona arabesca* (Walckenaer) (Bilsing 1920, Culin & Yeargan 1982) [1.90], *N. domiciliorum* (Hentz) (Bilsing 1920) [1.91], *N. mellotteei* (Simon) (Yamanoi & Miyashita 2005) [1.44], *N. pratensis* (Hentz) (Bardwell & Averill 1997) [0.95], *N. punctigera* (Doleschall) (Yamanoi & Miyashita 2005) [1.35], *N. scylla* (Karsch) (Yamanoi & Miyashita 2005) [1.22], *N. scylloides* (Bösenberg & Strand) (Yamanoi & Miyashita 2005) [1.58], *N. theisi* (Walckenaer) (Tahir et al. 2009) [1.84], *Ocrepeira ectypa* (Walckenaer) (Stowe 1978) [0.89], *Ordgarius magnificus* (Rainbow) (Stowe 1986) [0], *O. sexspinosus* (Thorell) (Shinkai & Shinkai 2002) [0], *Paraplectana* sp. (Stowe 1986) [0], *Paraplectanoides crassipes* Keyserling (Stowe 1986) [1.10], *Parawixia bistriata* (Rengger) (Fowler & Diehl 1978, Fowler & Gobbi 1988) [1.68], *Pasilobus* sp. (Robinson & Robinson 1975) [0.23], *Poecilopachys* sp. (Stowe 1986) [0], *Poltys laciniosus* Keyserling (Smith 2008) [1.10], *Pycnacantha tribulus* (Fabricius) (Dippenaar-Schoeman & Leroy 1996) [0], *Scoloderus cordatus* (Taczanowski) (Stowe 1978) [0.63], *Taczanowskia* sp. (Eberhard 1981a, Stowe 1986) [0], *Zygiella x-notata* (Clerck) (Nentwig 1983) [1.05]. Archaeidae: *Eriauchenius jeanneli* (Millot) (Legendre 1961) [0], *E. workmani* O. P.-Cambridge (Legendre 1961) [0], Atypidae: *Atypus affinis* Eichwald (Bristowe 1971, Hiebsch & Krause 1976, Stein et al. 1992) [1.72], *Sphodros abboti* Walckenaer (Coyle & Shear 1981) [1.79], *S. rufipes* (Latreille) (Coyle & Shear 1981) [1.64]. Caponiidae: *Caponia* sp. (Dippenaar-Schoeman 2002) [0], *Orthonops* sp. (Platnick 1995, Ubick et al. 2005) [0.29]. Clubionidae: *Clubiona corticalis* (Walckenaer) (Bristowe 1939) [1.24], *C. cycladata* Simon (Austin 1984) [1.53], *C. phragmitis* C. L. Koch (Nentwig 1982a) [1.10], *C. robusta* L. Koch (Austin 1984) [1.32]. Corinnidae: *Attacobius attarum* (Roewer) (Erthal & Tonhasca 2001) [0], *Castianeira descripta* (Hentz) (Bilsing 1920) [1.66], *Corinnomma suaverubens* Simon (Hawkeswood 2003) [0], *Falconina gracilis* (Keyserling) (Fowler 1984) [0], *Liophrurillus flavitarsis* (Lucas) (Pekár & Jarab 2011) [1.39], *Myrmecium gounellei* Simon (Oliveira 1988) [1.10], *Phrurolinillus lisboensis* Wunderlich (Pekár & Jarab, unpublished) [1.10], *Phrurolithus festivus* (C. L. Koch) (Pekár & Jarab 2011) [0.57], *Phruronellus formica* (Banks) (Gertsch 1979) [1.61], *Sphecotypus niger* (Perty) (Oliveira 1988) [0], *Supunna picta* (L. Koch) (Jackson & Poulsen 1990) [0.83]. Ctenidae: *Ancylometes concolor* (Perty) (Menin et al. 2005, L. F. García, pers. com.) [1.04], *Cupiennius salei* (Keyserling) (Nentwig 1986a, 1990) [2.93]. Ctenizidae: *Ummidia* sp. (Bond & Coyle 1995) [1.39]. Cybaeidae: *Argyroneta aquatica* (Clerck) (Nielsen 1932) [1.10]. Deinopidae: *Avella unifasciata* L. Koch (Austin & Blest 1979) [0.36], *Deinopis subrufa* L. Koch (Austin & Blest 1979) [1.83]. Desidae: *Badumna insignis* (L. Koch) (Henderson & Elgar 1999, Downes 1993) [1.99], *B. longinqua* (L. Koch) (Laing 1988) [1.95], *Desis formidabilis* (O. P.-Cambridge) (Lamoral 1968) [0.81], *D. marina* (Hector) (Forster & Forster 1973) [0], *Phryganoporus candidus* (L. Koch) (Downes 1994) [0.07]. Dictynidae: *Dictyna arundinacea* (Linnaeus) (Heidger & Nentwig 1985) [1.48], *D. calcarata* Banks (Jackson 1979) [0.54], *D. civica* (Lucas) (Billaudelle 1957) [1.55], *D. coloradensis* Banks (Miliczky & Calkins 2001) [1.60], *D. foliacea* (Hentz) (Bilsing 1920, Heidger

& Nentwig 1985, Judd 1969) [1.14], *D. uncinata* THORELL (Nyffeler & Benz 1981) [0.87], *Dictyna* sp. (Jackson 1979, Pérez de la Cruz et al. 2007) [0.98], *Emblyna annulipes* (BLACKWALL) (Hagley & Allen 1989) [1.15], *E. jonesae* (ROEWER) (Nentwig 1982b) [0.70], *Mallos gregalis* (SIMON) (Tietjen et al. 1987) [0.43], *M. niveus* O. P.-CAMBRIDGE (Jackson 1979) [0.50], *Mexitlia trivittata* (BANKS) (Jackson 1979) [0.48], *Phantyna segregata* (GERTSCH & MULAIK) (Nyffeler et al. 1988b) [1.04]. Diguetidae: *Diguetia mojavea* GERTSCH (Nuessly & Goeden 1984) [1.23]. Dipluridae: *Euagrus mexicanus* AUSSERER (Coyle 1988) [1.95], *Ischnothele* sp. (Coyle & Ketner 1990) [1.09], *Thelechoris striatipes* (SIMON) (Baert & Murphy 1987) [1.10]. Dysderidae: *Dasumia carpatica* (KULCZYŃSKI) (M. Řezáč, pers. com.) [2.40], *Dysdera crocata* C. L. KOCH (Pollard et al. 1995) [1.91], *D. dentichelis* SIMON (Řezáč et al. 2008) [1.63], *D. dubrovninnii* DEELEMAN-REINHOLD (Řezáč et al. 2008) [1.04], *D. erythrina* (WALCKENAER) (Cooke 1965, Řezáč et al. 2008) [1.09], *D. spinicrus* SIMON (Řezáč et al. 2008) [0.9], *Harpactea hombergi* (SCOPOLI) (M. Řezáč, pers. com.) [1.83], *Harpactea rubicunda* (C. L. KOCH) (M. Řezáč, pers. com.) [1.35], *Tedia abdominalis* DEELEMAN-REINHOLD (Řezáč et al. 2008) [0]. Eresidae: *Eresus kollari* ROSSI (Norgaard 1941, Walter 1999) [1.22], *Eresus* sp. (Ergashev 1979) [2.05], *Seothyra henscheli* DIPPENAAR-SCHOEMAN (Henschel & Lubin 1992) [0.51], *Stegodyphus manicatus* SIMON (Nentwig 1982b) [2.19], *S. sarasinorum* KARSCH (Chandra 1987, Sekar & Shunmugavelu 1992) [1.47]. Filistatidae: *Filistata* sp. (Murphy 1991) [1.10], *Pritha nana* (SIMON) (Nentwig 1982) [1.81]. Gallieniellidae: *Galianoella leucostigma* (MELLO-LEITÃO) (Goloboff 2000) [0]. Gnaphosidae: *Aphantaulax stationis* TUCKER (Van den Berg & Dippenaar-Schoeman 1991) [0], *Asemesthes lineatus* PURCELL (Henschel 1997) [0.69], *Berlandina* sp. (Guseinov 2004) [0], *Callilepis nocturna* (LINNAEUS) (Heller 1974) [0], *Cesonia* sp. (Platnick & Shadab 1980) [0], *Drassodes lapidossus* (WALCKENAER) (Bristowe 1939, 1971, Van den Berg & Dippenaar-Schoeman 1991) [0.97], *D. neglectus* (KEYSERLING) (Jackson 1976) [0], *Drassodes* sp. (Vlassov & Systchevskya 1937) [0.27], *Eilica* sp. (Goloboff 2000) [0], *Gnaphosa lucifuga* (WALCKENAER) (Trautner 1994) [0.99], *Gnaphosa* sp. (Bristowe 1939, Heuts & Brunt 2001) [0.69], *Herpyllus hesperolus* CHAMBERLIN (Jackson 1976) [0], *Leptodrassus* sp. (Haddad & Dippenaar-Schoeman 2006) [0.67], *Micaria dives* (LUCAS) (Pekár, unpublished) [0.56], *M. sociabilis* KULCZYŃSKI (Pekár & Jarab 2011) [1.79], *Nomisia celerrima* (SIMON) (Soyer 1943) [0], *N. exornata* (C. L. KOCH) (Soyer 1943, Pekár & Henriques, unpublished) [2.06], *Pterotricha* sp. (Guseinov 2004) [0], *Scotophaeus blackwalli* (THORELL) (Bristowe 1939, Jager 2002) [1.79], *Taieria erebus* (L. KOCH) (Jarman & Jackson 1986) [0.76], *Zelotes fuligineus* (PURCELL) (Bristowe 1939, Haddad & Dippenaar-Schoeman 2006) [1.15]. Gradungulidae: *Progradungula carraiensis* FORSTER & GRAY (Gray 1983) [0]. Hahniidae: *Tuberta maerens* (O. P.-CAMBRIDGE) (Hambler 1995) [1.39]. Hexathelidae: *Macrothele calpeiana* (WALCKENAER) (Snazell & Allison 1989) [1.28], *Porrhothele antipodiana* (WALCKENAER) (Laing 1973) [1.82]. Homalonychidae: *Homalonychus* sp. (Ubick et al. 2005) [1.39]. Hypochilidae: *Hypochilus coylei* PLATNICK (Huff & Coyle 1992) [0.67], *H. gertschi* HOFFMAN (Shear 1969) [1.61], *H. sheari* PLATNICK (Huff & Coyle 1992) [0.69]. Idiopidae: *Misgolas rapax* KARSCH (Bradley 1996) [1.17]. Lamponidae: *Lampona cylindrata* (L. KOCH) (Platnick 2000) [0]. Linyphiidae: *Bathyphantes gracilis* (BLACKWALL) (Sunderland et al. 1986, Alderweireldt 1994) [0.86], *B. simillimus* (L. KOCH) (Rybak 2007) [0.52], *Collinsia inerrans* (O. P.-CAMBRIDGE) (Alderweireldt 1994, Sunderland et al. 1986) [0.96], *Diplostyla concolor* (WIDER) (Alderweireldt 1994) [1.39], *Erigone atra* BLACKWALL (Sunderland et al. 1986, Alderweireldt 1994) [1.12], *E. dentipalpis* (WIDER) (Sunderland et al. 1986, Alderweireldt 1994, Nyffeler & Benz 1988a) [1.38], *Frontinella communis* (HENTZ) (Nyffeler et al. 1988b, Suter et al. 1989, Bardwell & Averill 1997) [1.00], *F. frutetorum* (C. L. KOCH) (Herberstein 1997) [1.45], *Kratochviliella bicapitata* MILLER (Czajka & Bednarz 1971) [0.69], *Linyphia triangularis* (CLERCK) (Herberstein 1997) [1.74], *Linyphia* sp. (Nentwig 1983) [1.82], *Meioneta rurestris* (C. L. KOCH) (Sunderland et al. 1986, Alderweireldt 1994) [1.48], *Neriene clathrata* (SUNDEVALL) (Bristowe 1939, Alderweireldt 1994) [0.89], *N. radiata* (WALCKENAER) (Herberstein 1998) [0.94], *Oedothorax apicatus* (BLACKWALL) (Alderweireldt 1994) [0.94], *O. fuscus* (BLACKWALL) (Sunderland et al. 1986, Alderweireldt 1994) [0.69], *Prinerigone vagans* (AUDOUIN) (Alderweireldt 1994) [0.69], *Tenuiphantes tenuis* (BLACKWALL) (Sunderland et al. 1986, Alderweireldt 1994) [0.17], *Thyreosthenius biovatus* (O. P.-CAMBRIDGE) (Bristowe 1971) [1.09], *Ummeliata insecticeps* (BÖSENBERG & STRAND) (Zhang et al. 1999) [0], *Walckenaeria* sp. (Heuts & Brunt 2005) [0]. Liocranidae: *Agroeca* sp. (Ubick et al. 2005) [0.69]. Lycosidae: *Allocosa brasiliensis* (PETRUNKEVITCH) (Aisenberg et al. 2009) [1.63], *Alopecosa accentuata* (LATREILLE) (Bristowe 1939) [0.73], *Arctosa cinerea* (FABRICIUS) (Framenau et al. 1996) [1.61], *Arctosa littoralis* (HENTZ) (Punzo 2006) [2.28], *Geolycosa fatifera* (HENTZ) (Bilsing 1920, Hayes & Lockley 1990) [2.09], *Hogna antelucana* (MONTGOMERY) (Hayes & Lockley 1990) [1.97], *H. carolinensis* (WALCKENAER) (Bilsing 1920, Punzo 2003) [1.94], *H. lenta* (HENTZ) (Punzo 1991) [1.70], *Lycosa singoriensis* (LAXMANN) (Marikovskij 1956) [1.33], *L. tarentula* (LINNAEUS) (Moya-Larano et al. 2002) [1.37], *L. terrestris* BUTT, ANWAR & TAHIR (Tahir & Butt 2009) [1.59], *Pardosa agrestis* (WESTRING) (Schaefer 1974, Nyffeler & Benz 1988b, Samu et al. 1999) [1.71], *P. amentata* (CLERCK) (Edgar 1970, Nyffeler & Benz 1988b) [1.52], *P. birmanica* SIMON (Tahir & Butt 2009) [1.69], *P. floridana* (BANKS) (Breene et al. 1988, Bardwell & Averill 1997) [1.55], *P. hokkaido* TANAKA & SUWA (Suwa 1986) [1.98], *P. lugubris* (WALCKENAER) (Edgar 1969, 1970, Hallander 1970, Nyffeler & Benz 1981) [2.03], *Pardosa pauxilla*

Montgomery (Dean et al 1987) [1.70], *P. palustris* (Linnaeus) (Nyffeler & Benz 1988b, Hayes & Lockley 1990) [1.43], *P. pseudoannulata* (Bösenberg & Strand) (Kiritani et al. 1972, Kumar & Velusamy 1996, Ishijima et al. 2006) [0.74], *P. pullata* (Clerck) (Hallander 1970) [1.63], *P. ramulosa* (McCook) (Yeargan 1975) [2.09], *P. saxatilis* (Hentz) (Bardwell & Averill 1997) [1.58], *P. sierra* Banks (Punzo 2006, Punzo & Farmer 2006) [2.38], *Pirata piraticus* (Clerck) (Schaefer 1974, Gettmann 1978, Breene et al. 1988) [1.46], *P. piscatorius* (Clerck) (Gettmann 1978) [2.25], *P. subpiraticus* (Bösenberg & Strand) (Ishijima et al. 2006) [1.52], *Schizocosa avida* (Walckenaer) (Bilsing 1920, Wagner & Wise 1997) [2.12], *Sosippus floridanus* Simon (Punzo & Haines 2006) [2.67], *Trochosa ruricola* (De Geer) (Hackman 1957, Kielty et al. 1999) [0.85]. Mimetidae: *Australomimetus maculosus* (Rainbow) (Jackson & Whitehouse 1986) [0.06], *Ero aphana* (Walckenaer) (McCarthy 2002) [0], *E. furcata* (Villers) (Czajka 1963, Potzsch 1974) [0], *E. tuberculata* (De Geer) (Tutelaers 2009) [0], *Mimetus notius* Chamberlin (Kloock 2001) [1.35], *M. puritanus* Chamberlin (Cutler 1972) [0.78], *Mimetus* sp. (Jackson & Whitehouse 1986) [0]. Miturgidae: *Cheiracanthium mildei* L. Koch (Mansour et al. 1980) [1.47], *Cheiracanthium* sp. (Ubick et al. 2005) [0.69]. Mysmenidae: *Mysmenopsis furtiva* Coyle & Meigs (Coyle et al. 1991) [1.39]. Nemesiidae: *Acanthogonatus francki* Karsch (Pinto & Sáiz 1997) [1.88], *Nemesia caementaria* (Latreille) (Buchli 1969) [1.13], *N. congener* O. P.-Cambridge (Soyer 1943) [0]. Nephilidae: *Herennia multipuncta* (Doleschall) (Robinson 1980) [0.69], *Nephila clavipes* (Linnaeus) (Nentwig 1985a, Uhl & Vollrath 1998) [1.53], *N. pilipes* (Fabricius) (Robinson & Robinson 1973) [1.67], *N. plumipes* (Latreille) (Herberstein & Elgar 1994) [1.12]. Oecobiidae: *O. cellariorum* (Duges) (Glatz 1967) [0], *O. navus* Blackwall (Voss et al. 2007, Shear 1970, L. F. García, pers. com.) [1.19], *O. templi* O. P.-Cambridge (Debski 1923) [0], *Oecobius* sp. (Hingston 1925) [0.80], *Paroecobius* sp. (Dippenaar-Schoeman 2002) [0], *Uroctea durandi* (Latreille) (Nentwig 1987) [1.43]. Oonopidae: *Triaeris stenaspis* Simon (S. Korenko, pers. com.) [0.37]. Oxyopidae: *Oxyopes globifer* Simon (Huseynov 2006a) [1.46], *O. javanus* Thorell (Tahir & Butt 2009) [1.8], *O. lineatus* Latreille (Huseynov 2007a) [1.98], *O. salticus* Hentz (Nyffeler et al. 1992, Nyffeler & Sterling 1994) [2.11], *O. scalaris* Hentz (Wing 1983) [0.69], *Peucetia flava* Keyserling (Oliveira Gonzaga et al. 1998) [0.43], *P. viridans* (Hentz) (Nyffeler et al. 1992) [1.72]. Palpimanidae: *Palpimanus gibbulus* Dufour (Pekár et al. 2011b) [0.31], *P. orientalis* Kulczyński (Murphy 1991) [0], *P. stridulator* Lawrence (Henschel 1990, 1997) [0], *Palpimanus* sp. (Cerveira & Jackson 2005) [0.16]. Philodromidae: *Philodromus aureolus* (Clerck) (Hobby 1930, Bristowe 1939) [1.09], *P. cespitum* (Walckenaer) (Klein 1988) [1.27], *P. praelustris* Keyserling (Putman 1967) [1.91], *Thanatus fabricii* (Audouin) (Guseinov 2004) [1.35], *T. imbecillus* L. Koch (Guseinov 2004) [1.55], *T. vulgaris* Simon (Guseinov 2004) [1.66], *Tibellus macellus* Simon (Huseynov 2008) [1.23], *Tibellus oblongus* (Walckenaer) (Nentwig 1986a) [2.04]. Pholcidae: *Crossopriza lyoni* (Blackwall) (Shunmugavelu & Palanichamy 1995, Strickmann et al. 1997) [0.9], *Pholcus muraricola* Maughan & Fitch (Maughan 1978) [2.08], *P. phalangioides* (Fuesslin) (Nentwig 1983, Jackson & Brassington 1987, Uhlenhaut 2001) [1.01], *Physocyclus globosus* (Taczanowski) (Eberhard 1992) [1.61], *Smeringopus sambesicus* Kraus (Haddad & Dippenaar-Schoeman 2006) [1.39]. Pisauridae: *Architis tenuis* Simon (Nentwig 1985a) [2.40], *Dendrolycosa* sp. (Cerveira & Jackson 2002) [1.94], *Dolomedes aquaticus* Goyen (Williams 1979) [1.35], *D. fimbriatus* (Clerck) (Arnqvist 1992, Poppe & Holl 1995) [2.12], *D. tenebrosus* Hentz (Bilsing 1920) [1.45], *D. triton* (Walckenaer) (Zimmerman & Spence 1989) [2.01], *Hygropoda dolomedes* (Doleschall) (Cerveira & Jackson 2002) [1.78], *Pisaura mirabilis* (Clerck) (Nitzsche 1981) [1.89], *Pisaurina mira* (Walckenaer) (Young 1989) [1.95], *Thalassius spinosissimus* (Karsch) (Sierwald 1988) [1.79]. Plectreuridae: *Plectreurys tristis* Simon (Minch 1977) [1.61]. Prodidomidae: *Theuma fusca* Purcell (Haddad & Dippenaar-Schoeman 2006) [1.27]. Psechridae: *Fecenia* sp. (Robinson & Lubin 1979) [2.20]. Salticidae: *Aelurillus aeruginosus* (Simon) (Li et al. 1999a) [0.78], *A. cognatus* (O. P.-Cambridge) (Li et al. 1999a) [0.82], *A. kochi* Roewer (Li et al. 1999a) [0.66], *A. m-nigrum* Kulczyński (Huseynov et al. 2008) [2.07], *A. muganicus* Dunin (Huseynov et al. 2005) [2.08], *Anasaitis canosa* (Walckenaer) (Edwards et al. 1974, Jackson & Van Olphen 1991) [0.10], *Bagheera kiplingi* Peckham & Peckham (Meehan et al. 2009) [0.42], *Brettus adonis* Simon (Jackson 2000) [0.59], *B. albolimbatus* Simon (Jackson 2000) [0.49], *Carrhotus xanthogramma* (Latreille) (S. Korenko, pers. com.) [1.50], *Chalcotropis* sp. (Jackson et al. 1998) [2.40], *Chrysilla lauta* Thorell (Jackson & Van Olphen 1992) [0.36], *Cobanus mandibularis* (Peckham & Peckham) (Jackson 1989) [0.94], *Cocalus gibbosus* Wanless (Jackson 1990a, 2000) [1.04], *Cosmophasis bitaeniata* (Keyserling) (Curtis 1988, Allan & Elgar 2001) [0.60], *Cyrba algerina* (Lucas) (Guseinov et al. 2004) [1.63], *C. ocellata* (Kroneberg) (Jackson 2000) [0.64], *C. simoni* Wijesinghe (Jackson 2000) [0.59], *Cytaea piscula* (L. Koch) (Morrison 1981) [0], *Euophrys* sp. (Jackson et al. 1998) [2.08], *Evarcha arcuata* (Clerck) (Nentwig 1986a, Zolotarjov 2002) [2.04], *E. culicivora* Wesolowska & Jackson (Jackson et al. 2005) [0.76], *Gelotia syringopalpis* Wanless (Jackson 1990b) [0.83], *Goleba puella* (Simon) (Jackson 1990c) [0.65], *Heliophanus dunini* Rakov & Logunov (Huseynov 2006b) [1.71], *H. termitophagus* Wesolowska & Haddad (Wesolowska & Haddad 2002, Haddad & Dippenaar-Schoeman 2006) [0.78], *Hentzia palmarum* (Hentz) (Cutler 1980) [0], *Icius* sp. (Cutler 1980) [0], *Jacksonoides queenslandicus* Wanless (Jackson 1988a) [1.78], *Marpissa tigrina* Tikader (Sadana & Kaur 1980) [1.26], *Mashonarus guttatus* Wesolowska & Cumming (Wesolowska &

Cumming 2002) [0.57], *Menemerus semilimbatus* (Hahn) (Guseinov 2003) [1.14], *M. taeniatus* (L. Koch) (Huseynov 2005) [1.68], *Mexcala elegans* Peckham & Peckham (Pekár & Haddad 2011) [1.56], *Microheros termitophagus* Wesolowska & Cumming (Wesolowska & Cumming 1999) [0], *Myrmarachne formicaria* (De Geer) (Pekár, unpublished) [1.24], *M. lawrencei* Roewer (Jackson 1986) [1.10], *M. lupata* (L. Koch) (Jackson 1986a) [1.39], *M. melanotarsa* Wesolowska & Salm (Jackson et al. 2008) [1.16], *M. plataleoides* (O. P.-Cambridge) (Mathew 1934, Jackson 1986) [0.9], *M. striatipes* (L. Koch) (Jackson 1986) [0.69], *Naphrys pulex* (Hentz) (Cutler 1980) [0.67], *Natta horizontalis* Karsch (Jackson & Van Olphen 1992) [0.37], *Onomastus nigricaudus* Simon (Jackson 1990c) [0.57], *Paracyrba wanlessi* Zabka & Kovac (Zabka & Kovac 1996) [2.01], *Pelegrina galathea* (Walckenaer) (Dean et al. 1987) [0.46], *Phaeacius malayensis* Wanless (Jackson 1990d, Li 2000) [1.15], *Phiddipus audax* (Hentz) (Bilsing 1920, Dean et al. 1987, Johnson 1996, Okuyama 2007) [2.01], *P. clarus* Keyserling (Bilsing 1920) [1.56], *P. johnsoni* (Peckham & Peckham) (Jackson 1977) [1.96], *Phlegra* sp. (Van den Berg & Dippenaar-Schoeman 1991) [0], *Phyaces comosus* Simon (Jackson 1986b) [1.06], *Plexippus paykulli* (Audouin) (Jackson & MacNab 1989, Nyffeler et al. 1990) [2.18], *Portia africana* (Simon) (Li et al. 1997) [0.43], *P. fimbriata* (Doleschall) (Jackson & Blest 1982, Li & Jackson 1996, Clark & Jackson 2000) [0.28], *P. labiata* (Thorell) (Li et al. 1997) [0.56], *P. schultzi* Karsch (Li et al. 1997) [0.47], *Pseudicius encarpatus* (Walckenaer) (Dobroruka 1995, Kubcová & Buchar 2005) [0.90], *Salticus austinensis* Gertsch (Horner et al. 1988) [0.57], *Salticus scenicus* (Clerck) (Okuyama 2007) [0.82], *S. tricinctus* (C. L. Koch) (Guseinov 2005) [1.43], *Siler cupreus* Simon (Miyashita 1991, Touyama et al. 2008) [0.13], *S. semiglaucus* (Simon) (Jackson & Van Olphen 1992) [0.53], *Siler* sp. (Jackson et al. 1998) [1.95], *Simaetha paetula* (Keyserlin) (Jackson 1985) [0.80], *Stenaelurillus natalensis* Haddad & Wesolowska (Haddad & Wesolowska 2006) [0], *Synageles venator* (Lucas) (Pekár, unpublished) [1.32], *Tauala lepidus* Wanless (Jackson 1988b) [1.60], *Trite planiceps* Simon (Jackson & Van Olphen 1991) [1.24], *Tutelina similis* (Banks) (Denne 1982, Wing 1983) [0], *Yllenus arenarius* Menge (Bartos 2002, 2004) [1.98], *Zenodorus durvillei* (Walckenaer) (Jackson & Li 2001) [0.66], *Z. metallescens* (L. Koch) (Jackson & Li 2001) [0.56], *Z. orbiculatus* (Keyserling) (Jackson & Van Olphen 1991, Jackson & Li 2001) [0.76]. Scytodidae: *Scytodes longipes* Lucas (Nentwig 1985b) [1.64], *S. pallida* Doleschall (Li et al. 1999b) [0.83], *Scytodes* sp. (Gilbert & Rayor 1985) [1.61]. Segestriidae: *Segestria florentina* (Rossi) (Bristowe 1939) [2.08], *S. senoculata* (Linnaeus) (Bristowe 1939) [1.95]. Selenopidae: *Selenops* sp. (Ubick et al. 2005) [0.69]. Sicariidae: *Loxosceles intermedia* Mello-Leitão (Fischer et al. 2006) [1.93]. Sparassidae: *Carparachne aureoflava* Lawrence (Henschel 1994) [1.20], *Holconia immanis* (L. Koch) (Henle 1993) [1.85], *Leucorchestris arenicola* Lawrence (Henschel 1994) [1.16], *L. steyni* Lawrence (Henschel 1994) [1.39], *Olios* sp. (Jackson 1987) [1.61]. Stiphidiidae: *Tartarus mullamullangensis* Gray (Gray 1992) [0.64]. Telemidae: *Telema* sp. (Ubick et al. 2005) [0]. Tetragnathidae: *Arkys nitidiceps* Simon (Main 1982) [0], *Doryonychus raptor* Simon (Gillespie 1991) [1.2], *Leucage magnifica* Yaginuma (Yoshida 2000) [2.03], *L. mariana* (Taczanowski) (Ibarra-Núñez et al. 2001) [1.98], *L. venusta* (Walckenaer) (Bilsing 1920, Henaut et al. 2006) [1.45], *Menosira ornata* Chikuni (Shinkai 1998) [0.69], *Meta menardi* (Latreille) (Pötzsch 1966, Smithers 2005, K. Řeháková, pers. com.) [1.77], *M. reticuloides* Yaginuma (Yoshida 1990) [0.42], *Metellina merianae* (Scopoli) (Bristowe 1939) [1.79], *M. segmentata* (Clerck) (Nyffeler & Benz 1989) [1.17], *Metleucauge kompirensis* (Bösenberg & Strand) (Yoshida 1989b) [0.38], *M. yunohamensis* (Bösenberg & Strand) (Yoshida 1989b) [0.47], *Neoarchemorus speechleyi* Mascord (Stowe 1986) [0], *Pachygnatha degeeri* Sundevall (Bristowe 1939, Nyffeler & Benz 1981, Heuts & Brunt 2001) [1.48], *Tetragnatha eurychasma* Gillespie (Blackledge et al. 2003) [0.82], *T. extensa* (Linnaeus) (Nyffeler 1982) [0.76], *T. filiciphilia* Gillespie (Blackledge et al. 2003) [1.20], *T. javana* (Thorell) (Tahir et al. 2009) [1.73], *T. laboriosa* Hentz (LeSar & Unzicker 1978, Bardwell & Averill 1997, Nyffeler & Sterling 1994) [1.51], *T. montana* Simon (Dabrowska-Prot & Luczak 1968) [0.89], *T. praedonia* L. Koch (Yoshida 1987) [0.30], *T. reimoseri* (Rosca) (Wiehle 1963) [0], *T. squamata* Karsch (Hengmei & Joo-Pil 1994) [1.19], *T. stelarobusta* Gillespie (Blackledge et al. 2003) [0.74], *Tylorida* sp. (Robinson 1982) [0]. Theraphosidae: *Acanthoscurria atrox* Vellard (Lourenco 1978) [1.77], *Aphonopelma hentzi* (Girard) (Punzo & Henderson 1999) [1.41], *A. iodius* (Chamberlin & Ivie) (Prentice 1997) [1.61], *A. joshua* Prentice (Prentice 1997) [1.95], *A. mojave* Prentice (Prentice 1997) [1.79]. Theridiidae: *Anelosimus baeza* Agnarsson (Guevara & Avilés 2009) [1.61], *Anelosimus eximius* (Keyserling) (Christenson 1984, Nentwig 1985a, Pasquet & Krafft 1992) [2.28], *A. jucundus* (O. P.-Cambridge) (Nentwig & Christensin 1986) [1.81], *Argyrodes fissifrons* O. P.-Cambridge (Tanaka 1984, Tso & Severinghaus 2000) [0.36], *A. incursus* Gray & Anderson (Gray & Anderson 1989) [0], *Ariamnes attentuatus* O. P.-Cambridge (Eberhard 1979) [1.28], *A. colubrinus* Keyserling (Mascord 1980) [0], *Asagena fulva* (Keyserling) (Hölldobler 1970) [0], *A. phalerata* (Panzer) (Donisthorpe 1927, Soyer 1943) [0], *A. pulcher* (Keyserling) (MacKay 1982) [0], *Chrosiothes portalensis* Levi (Pérez de la Cruz et al. 2007) [0], *Chrosiothes tonala* (Levi) (Eberhard 1991) [0], *Chrysso intervales* Gonzaga, Leiner & Santos (Gonzaga et al. 2006) [0.64], *Cryptachaea riparia* (Blackwall) (Norgaard 1956) [1.94], *C. veruculata* (Urquhart) (Laing 1988) [0.18], *Dipoena nigra* (Emerton) (Archer 1946) [0], *D. punctisparsa* Yaginuma (Umeda et al. 1996) [0], *D. torva* (Thorell) (Simon 1997) [0], *Enoplognatha ovata* (CLERCK) (Hobby 1930, Heuts & Brunt 2001) [0.64], *Episinus amoenus* BANKS (Archer 1946) [0], *E. maculipes* CAVANNA (Pekár, unpublished) [0], *Euryopis californica* BANKS (MacKay 1982) [0], *E. coki* LEVI (Porter & Eastmond 1982) [0], *E. episinoides* (WALCKENAER) (Soyer 1943) [0], *E. flavomaculata* (C. L. KOCH) (Hirschberg 1968) [0], *E. formosa* BANKS (Clark & Blom 1992) [0], *E. funebris* (HENTZ) (Carico 1978) [0], *E. scriptipes* BANKS (Levi 1954) [0], *E. texana* BANKS (Gertsch 1979) [0], *Helvibis longicauda* KEYSERLING (Gonzaga et al. 2006) [1.41], *Kochiura aulica* (C. L. KOCH) (Soyer 1943) [0], *L. hesperus* CHAMBERLIN & IVIE (MacKay 1982, Schwammer & Baurecht 1988, Van den Berg & Dippenaar-Schoeman 1991) [0.94], *L. lilianae* MELIC (Hódar & Sánchez-Pinero 2002) [1.08], *L. mactans* (FABRICIUS) (Pratt & Hatch 1938, Nyffeler et al. 1988a) [0.74], *L. pallidus* O. P.-CAMBRIDGE (Shulov 1940) [1.39], *L. revivensis* SHULOV (Shulov & Wisemann 1959) [1.36], *L. tredecimguttatus* (ROSSI) (Schwammer 1988, Shulov 1940, Ponomarev 2006) [2.04], *Neospintharus baboquivari* (EXLINE & LEVI) (Smith Trail 1980) [0], *N. trigonum* (HENTZ) (Suter et al. 1989, Houser et al. 2005) [0], *Neottiura bimaculata* (LINNAEUS) (Bristowe 1939, Pekár, unpublished) [1.39], *Nesticodes rufipes* (LUCAS) (Rossi & Godoy 2006) [1.10], *Parasteatoda tepidariorum* (C. L. KOCH) (Guarisco 1988) [1.09], *Parasteatoda tesselata* (KEYSERLING) (Ibarra-Núñez et al. 2001) [2.36], *Phoroncidia studo* LEVI (Eberhard 1981b) [0], *Phycosoma mustelinum* (SIMON) (Umeda et al. 1996) [0.16], *Phylloneta impressa* (L. KOCH) (Scheidler 1989, Nyffeler & Benz 1979, Pekár 2000) [1.45], *P. sisyphia* (CLERCK) (Scheidler 1989) [1.28], *Platnickina sterninotata* (BÖSENBERG & STRAND) (Matsumoto et al. 1976) [0], *P. tincta* (WALCKENAER) (Bristowe 1939, Heuts & Brunt 2001) [0.46], *Romphaea* sp. (Whitehouse 1987) [0], *Steatoda bipunctata* (LINNAEUS) (Bristowe 1939, Nyffeler et al. 1986) [1.98], *S. dhruvai* PATEL, PILLAI & SEBASTIAN (Patel et al. 1987) [2.30], *S. grossa* (C. L. KOCH) (Barmeyer 1975) [0.74], *S. paykulliana* (WALCKENAER) (Kuznecov 1985) [1.75], *S. triangulosa* (WALCKENAER) (MacKay 1989) [0], *Theridion australe* BANKS (Nyffeler et al. 1988b) [0.69], *T. evexum* KEYSERLING (Barrantes & Weng 2007) [2.10], *T. grallator* SIMON (Gillespie & Tabashnik 1994) [1.22], *T. murarium* EMERTON (Putman 1967) [1.39], *T. pictum* (WALCKENAER) (Luczak & Dabrowska-Prot 1970) [1.77], *T. varians* HAHN (Bristowe 1939) [0.69], *Tidarren haemorrhoidale* (BERTKAU) (Nyffeler et al. 1988b) [0.75], *Yaginumena castrata* (BÖSENBERG & STRAND) (Umeda et al. 1996) [0]. Theridiosomatidae: *Theridiosoma* sp. (Ubick et al. 2005) [0.69]. Thomisidae: *Amyciaea albomaculata* (O. P.-CAMBRIDGE) (Main 1984, Williamson 1984) [0], *A. forticeps* (O. P.-CAMBRIDGE) (Mathew 1944) [0], *Aphantochilus rogersi* O. P.-CAMBRIDGE (Castanho & Oliveira 1997) [0], *Bucranium taurifrons* O. P.-CAMBRIDGE (Bristowe 1939) [0], *Diaea socialis* MAIN (Main 1988) [1.39], *Hedana valida* L. KOCH (Mascord 1970) [0], *Mecaphesa celer* (HENTZ) (Dean et al. 1987) [1.14], *M. coloradensis* (GERTSCH) (Hölldobler 1979) [0], *M. lepida* (THORELL) (Wing 1983) [0], *Misumena vatia* (CLERCK) (Lovell 1915, Bilsing 1920, Hobby 1930, 1940, Morse 1979, 1981, Erickson & Morse 1997, Ryazanova & Dzhangildin 2005) [1.59], *Misumenops pallidus* (KEYSERLING) (Cheli et al. 2006) [1.79], *Phrynarachne decipiens* (FORBES) (Pocock & Rothschild 1903) [0], *Runcinia grammica* (C. L. KOCH) (Huseynov 2007b) [1.07], *Runcinioides argenteus* MELLO-LEITÃO (Romero & Vaconcellos-Neto 2003) [2.19], *Saccodomus formivorus* RAINBOW (McKeown 1952) [0], *Stephanopis scabra* L. KOCH (Mascord 1970) [0], *Strophius nigricans* KEYSERLING (Oliveira & Sazima 1985) [0], *Thomisus onustus* WALCKENAER (Hobby 1930, Huseynov 2007c) [1.50], *Tmarus piger* (WALCKENAER) (Wunderlich 1994, Kubcová & Buchar 2005) [0], *T. stolzmanni* KEYSERLING (Lubin 1983) [0], *Xysticus bifasciatus* C. L. KOCH (Bristowe 1939, Ricek 1982) [0.32], *X. bufo* (DUFOUR) (Soyer 1943) [0.69], *X. californicus* KEYSERLING (Snelling 1983) [0.50], *X. cristatus* (CLERCK) (Hobby 1930, Bristowe 1939, Nentwig 1986a, Heuts & Brunt 2001) [2.12], *X. erraticus* (BLACKWALL) (Hobby 1930, Bristowe 1939, Nyffeler 1982) [1.42], *X. loeffleri* ROEWER (Guseinov 2006) [1.65], *X. sabulosus* (HAHN) (Soyer 1943) [0.69], *Xysticus* sp. (Nyffeler & Breene 1990) [1.87]. Trechaleidae: *Trechalea extensa* (O. P.-CAMBRIDGE) (Van Berkum 1982) [0], *Trechaleoides biocellata* (MELLO-LEITÃO) (van Berkum 1982, Cruz da Silva et al. 2005, Menin et al. 2005) [2.08]. Uloboridae: *Miagrammopes intempus* CHICKERING (Lubin et al. 1978) [1.66], *Miagrammopes* sp. (Lubin & Dorugl 1982) [1.79], *Octonoba sinensis* (SIMON) (Peaslee & Peck 1983) [1.39], *Philoponella republicana* (SIMON) (Binford & Rypstra 1992) [1.61], *Philoponella* sp. (Breitwisch 1989) [1.43], *Uloborus glomosus* (WALCKENAER) (Nyffeler & Sterling 1994) [0.39], *Uloborus* sp. (Pérez de la Cruz et al. 2007) [1.71]. Zodariidae: *Diores magicus* JOCQUÉ & DIPPENAAR-SCHOEMAN (Jocqué & Dippenaar-Schoeman 1992) [0], *D. miombo* JOCQUÉ (Jocqué & Dippenaar-Schoeman 1992) [0], *D. poweri* TUCKER (Haddad & Dippenaar-Schoeman 2006) [0], *D. rectus* JOCQUÉ (Jocqué & Dippenaar-Schoeman 1992) [0], *D. termitophagus* JOCQUÉ & DIPPENAAR-SCHOEMAN (Jocqué & Dippenaar-Schoeman 1992) [0], *Habronestes bradleyi* (O. P.-CAMBRIDGE) (Allan et al. 1996) [0], *Lachesana insensibilis* JOCQUÉ (Pekár & Lubin 2009) [1.95], *L. tarabaevi* ZONSTEIN & OVTCHINNIKOV (Zonstein & Ovtchinnikov 1999) [0.5], *Leprolochus birabeni* MELLO-LEITÃO (Jocqué 1988) [0], *Lutica* sp. (Ramirez 1995) [1.40], *Mallinella* sp. (T. M. Leong, pers. com.) [0], *Pax islamita* (SIMON) (Pekár & Lubin 2009) [2.20], *Psammoduon deserticola* (SIMON) (Rossl & Henschel 1999) [1.12], *Selamia reticulata* (SIMON) (Pekár, unpublished) [2.30], *Trygetus sexoculatus* (O. P.-CAMBRIDGE) (Pekár et al. 2005a) [0], *Zodariellum asiaticum* (TYSCHENKO) (Marikovskij & Tyschenko 1970, Pekár 2009) [0], *Z. surprisiense*

PEKÁR & CARDOSO (Pekár, unpublished) [0], *Z. bicoloripes* (DENIS) (Pierre 1959) [0], *Z. cyrenaicum* DENIS (Pekár et al. 2005a) [0], *Z. elegans* (SIMON) (Wiehle 1928) [0], *Z. frenatum* SIMON (Harkness 1976, Harkness & Harkness 1992) [0], *Z. fuscum* (SIMON) (Askins 1999) [0], *Z. gallicum* (SIMON) (Denis 1937) [0], *Z. germanicum* (C. L. KOCH) (Pekár 2004) [0.31], *Z. hamatum* WIEHLE (Pekár et al. 2005b) [0], *Z. italicum* (CANESTRINI) (Pekár et al. 2005b) [0], *Z. jozefienae* BOSMANS (Pekár et al. 2011a) [0], *Z. kabylianum* DENIS (Denis 1937) [0], *Z. lutipes* (O. P.-CAMBRIDGE) (Pekár et al. 2005a) [0], *Z. maculatum* (SIMON) (Pekár, unpublished) [0], *Z. nesiotoides* WUNDERLICH (Wunderlich 1991) [0], *Z. nigriceps* (SIMON) (Wiehle 1928) [0], *Z. nitidum* (AUDOUIN) (Pekár et al. 2005a) [0], *Z. raddei* SIMON (Vlassov & Systchevskya 1937) [0], *Z. rubidum* SIMON (Couvreur 1989, Pekár 2004, 2005) [0], *Z. styliferum* (SIMON) (Pekár, unpublished) [0], *Z. vicinum* DENIS (Snazell & Bosmans 1998) [0].

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