

Editorial

Phylogenomic, Biogeographic, and Evolutionary Research Trends in Arachnology

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1. Introduction

Textbook knowledge tells us that arachnids are a hyper diverse clade of chelicerates that have taken on terrestrial lifestyles. Original papers published in prestigious venues routinely reconstruct details of this purported single terrestrialization event that would have been followed by arachnid diversification on land. However, we are beginning to understand that arachnids are very likely paraphyletic; as such, Arachnida can only circumscribe an assemblage of chelicerates that live terrestrially. If so, arachnid terrestrialization may have taken several independent routes at different historic times. While the diversity and phylogeny of spiders, scorpions and harvestmen may be relatively well documented and understood, additional groups that we deem to be arachnids remain enigmatic and will likely continue to be more or less neglected after this Special Issue. We have here assembled examples of contemporary studies that include both original research as well as reviews focusing on “arachnids” and cover loosely defined biological subdisciplines of phylogenomics, biogeography, and evolution. The latter includes systematics, taxonomy, DNA barcoding, and trait evolution. In this editorial, I introduce the authors of these papers and their featured research, and through this narrative, I pose two questions. The first one is what is arachnology given that arachnids may not be monophyletic? The second question is where should our field be headed toward in the near future?

2. What Is Arachnology?

In a paper titled “What Is an “Arachnid”? Consensus, Consilience, and Confirmation Bias in the Phylogenetics of Chelicerata” [1], Prashant Sharma and colleagues review the systematics of the group we refer to as arachnids. They focus on the evidence for arachnid monophyly; it seems to be weak at best and seems to have been repeatedly confirmed through biased interpretations of hypotheses and the evidence in their support. By showing the fragility of phylogenies and the research bias of works that confirm rather than challenge classification hypotheses, as well as the paucity and deficiency of classical morphological characters, these authors question the standards and trends in the field.

Arachnologists such as myself have rarely doubted the validity of the classical arachnid orders, such as spiders, scorpions, harvestmen, and mites, and classical systematic literature would additionally suggest that these major groups share common ancestry with other terrestrial chelicerates that are known as arachnids. However, if the time has arrived to reassess our understanding on what an arachnid really is, as questioned by Sharma and colleagues, then by extension we need to ask ourselves this: What is arachnology and who is an arachnologist? To scientists who have considered themselves as arachnologists



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throughout their careers, this is a tough question indeed. A handy explanation, considering all evidence from the above review, is this. Having a basis in morphological and ecological definitions and perhaps defying a solid phylogenetic definition, arachnology refers to any biological investigation of the terrestrial (and secondarily aquatic) lineages of chelicerates, both extinct as well as extant. Arachnologists, by extension of this logic, study these organisms.

Even if arachnology unites students of a paraphyletic assemblage of evolutionary lineages, arachnologists will continue our quest in getting to know our organisms and their role in ecosystems. In this respect, arachnology resembles other thriving biological disciplines that study non-monophyletic groups, for example, ichthyology, herpetology, or microbiology. Even if these fields are defined as research of para- or polyphyletic groups of organisms, they nonetheless continue to unite practical societies and produce relevant science.

3. Phylogenomic and Evolutionary Research Trends in Arachnology

Taxonomy has been and remains the fundamental biological discipline that provides the token of biological communication as it defines and describes species and classifies them in the tree of life. Its importance notwithstanding, taxonomy has stagnated recently despite the availability of modern tools that the discipline should utilize. In the paper titled “Improving taxonomic practices and enhancing its extensibility—an example from araneology” [2], Jason Bond and colleagues review a decade of publications on spider taxonomy. They evaluate the types of data used to delineate species, whether data were made freely available, whether an explicit species hypothesis was stated, what types of media were used, the sample sizes, and the degree to which species constructs were integrative. The results they report are worrying, and they may be true for most invertebrate groups and not only spiders. Namely, the study concludes that taxonomy remains largely descriptive, not integrative, and provides no explicit conceptual framework. Bond et al. make four recommendations that would, if the taxonomic community implements them, enhance the rigor, repeatability, and scientific standards in taxonomy.

Systematics has seen tremendous leaps towards phylogenomic data capture as genomic sequencing in non-model organisms has become routine. However, given that whole genome or transcriptome capture is not always feasible and its costs are substantial, research groups have focused on developing protocols for reduced representation sequencing. Among these efforts, the most widely used approach is to focus on ultra-conserved elements (UCE). Indeed, arachnology has hopped on this train early on, and papers continue to demonstrate the effectiveness of modern phylogenomics using UCE. In a paper titled “In Silico Assessment of Probe-Capturing Strategies and Effectiveness in the Spider Sub-Lineage Araneoidea (Order: Araneae)” [3], Yi-Yen Li and colleagues report on development of a probe set specific for orb-weaving spiders, lineage Araneoidea. This research opens the doors for numerous studies that require araneoid UCE data at the species or higher levels.

Why are some clades hyper rich with species while other clades of similar ages are species poor? Many factors can be at play, including diversification and extinction tempos. In a paper titled “*Solenysa*, a Cretaceous Relict Spider Group in East Asia” [4], Jiahui Tian and colleagues explore the long evolutionary history of one of the major clades of linyphiids and the reasons for its relative poverty in species diversity compared with the other linyphiid lineages. The authors found that *Solenysa* diverged from other linyphiids in the Cretaceous and underwent diversification stasis well into Oligocene. They explained this stasis followed by modest diversification with the Cenozoic ecosystem transition triggered by global climate changes. Jiahui Tian and colleagues conclude that *Solenysa* is a Cretaceous relict that has survived mass extinction around the K-T boundary.

The next title refers to arachnid specimens, not to arachnologists, as one might incorrectly think. In a paper titled “Old Brains in Alcohol: The Usability of Legacy Collection Material to Study the Spider Neuroarchitecture” [5], Andres Rivera-Quiroz and Jeremy

Miller explore whether or not the central nervous system in spiders can be reconstructed with minimal invasion and from old museum specimens. It can. Using a minimally destructive method of specimen preparation for micro-CT investigation of ganglia on a range of specimens of varying ages, these authors found no significant differences in the brain shape nor brain relative volume. This is good news for students of soft internal anatomies who should go ahead and study important, rare, legacy specimens along with newly collected ones.

4. Biogeographic Research Trends in Arachnology

The chelicerate orders collectively referred to as arachnids show diverse, and oftentimes clade-predictable patterns in dispersal biology. As their consequence, some clades have become textbook examples of vicariant biogeography, e.g., trapdoor and liphistiid spiders, scorpions, and harvestmen. Other arachnids, such as spiders that balloon (that is, haphazardly travel aerially by silken sails), maintain lively patterns of gene flow over continents. In the best dispersing groups, such as long-jawed spiders (*Tetragnatha*) and the giant golden orb web spiders (*Nephila* and *Trichonephila*), uninterrupted gene flow can easily span intercontinentally and over thousands of kilometers. Biogeography of arachnids can help us better understand the history of the Earth's biotas and the evolution of complex biodiversity hotspots.

Indeed, biogeography and the history of hotspot formation feature prominently in this Special Issue. In a paper titled "Incorporating Topological and Age Uncertainty into Event-Based Biogeography of Sand Spiders Supports Paleo-Islands in Galapagos and Ancient Connections among Neotropical Dry Forests" [6], Ivan Magalhaes and colleagues present an elegant biogeographic study of sand spiders (Sicariidae: *Sicarius*) from Neotropical xeric biomes. This research found that *Sicarius* must have dispersed to the Galapagos Islands when the archipelago consisted of paleo-islands that are now submerged; thus, this colonization must have occurred before the emergence of modern Galapagos Islands. This paper is likely to advance the analytical methods applied in historical biogeography as it presents an approach for evaluating competing hypotheses given phylogenetic topological instability and vagueness in time split estimation.

In another biogeographical paper titled "A Natural Colonisation of Asia: Phylogenomic and Biogeographic History of Coin Spiders (Araneae: Nephilidae: *Herennia*)" [7], Eva Turk and colleagues report on a reconstructed evolutionary history of the nephilid spider genus *Herennia*. Known as coin spiders for their undulating abdominal shape, *Herennia* features numerous species that are narrow endemics in Southeast Asia and Australasia, as well as one widespread and common species, *H. multipuncta*. Based on a phylogenomic scaffold and an ultrametric phylogeny, these authors tested and discarded the hypothesis of a human mediated colonization of *H. multipuncta* in favor of its alternative, paraphrasing this as a natural "coinquest". This study further used an innovative biogeographic approach with dispersal probabilities depending on continental and island tectonic histories in appropriate time slices in Earth's past, as well as the natural history of the organisms. First proposed for nephilid spiders globally, Turk et al. [7] modified this novel approach here.

No fewer than three original papers dissected the biogeography of the Caribbean archipelago, one of the global biodiversity hotspots. In a paper titled "Single-Island Endemism despite Repeated Dispersal in Caribbean *Micrathena* (Araneae: Araneidae): An Updated Phylogeographic Analysis" [8], Lily Shapiro and colleagues reconstruct the biogeographic history of spiny orb weavers. *Micrathena*, according to these authors, colonized the archipelago on five occasions, but despite such efficiency at crossing the ocean barrier, which might be seen as facilitating continuous gene flow, the patterns of diversification on islands resulted in a pronounced single-island endemism in *Micrathena*. This study and the next one both failed to find corroborative evidence for the existence of a land bridge that may have connected the Greater Antilles with the American mainland—the GAARlandia scenario.

Also focusing on the Caribbean biogeographic history is the paper by Klemen Čandek and colleagues titled “Biogeography of Long-Jawed Spiders Reveals Multiple Colonization of the Caribbean” [9]. Čandek and colleagues provided a phylogenetic context for originally collected representatives of *Tetragnatha* spanning the Caribbean islands by adding numerous global terminals. The resulting chronogram and the reconstructed ancestral areas both revealed a pattern that contrasts the one from a spiny orb weaver; *Tetragnatha* instead showed low levels of island endemism despite its high species richness on the archipelago. These authors also attempted to test the predictions from the Intermediate dispersal model of biogeography, something that would require an a priori definition of three categories of dispersers. However, long-jawed spiders did not fit one of these three categories as the genus uniquely comprises both excellently and poorly dispersing species. Čandek et al. concluded that *Tetragnatha* represents a ‘dynamic disperser’, i.e., a taxon that readily undergoes evolutionary changes in dispersal propensity.

These papers do not yet exhaust the studies on Caribbean biogeography as reported in this Special Issue of *Diversity*. In a paper titled “Island-to-Island Vicariance, Founder-Events and within-Area Speciation: The Biogeographic History of the Antillattus Clade (Salticidae: Euophryini)” [10], Franklyn Cala-Riquelme and colleagues study the Antillattus clade of jumping spiders (genera *Antillattus*, *Truncattus*, and *Petemethis*) of the archipelago. This study particularly tested the GAARlandia land bridge scenario to explain spider diversity of the Greater Antilles. In contrast to the above studies, Franklyn Cala-Riquelme and colleagues found GAARlandia as a credible explanation of the biogeographic patterns, with an inferred historic dispersal from northern South America to Hispaniola. Subsequently to that inferred event, jumping spiders show imprints of vicariance, founder-events, within-island speciation, as well as multiple dispersal events in parts of the phylogeny.

The Baja peninsula in Mexico is among the biogeographically understudied yet diverse areas of the New World. In a paper titled “New Distributional Records of *Phidippus* (Araneae: Salticidae) for Baja California and Mexico: An Integrative Approach” [11], Luis Hernández Salgado and colleagues report on a survey of *Phidippus* jumping spiders of Baja using DNA barcoding combined with morphology. They augment the species list of Baja to now comprise 10 *Phidippus* species with evidence of an undescribed one.

Moving south to the Guayana region of South America, a paper titled “Beta Diversity along an Elevational Gradient at the Pico Da Neblina (Brazil): Is Spider (Arachnida-Araneae) Community Composition Congruent with the Guayana Region Elevational Zonation?” [12] authored by André Nogueira and colleagues reports on a thorough sampling of spiders from a Brazilian mountain along an elevation gradient. These authors detected high beta diversity among the sites, but they found several unexpected patterns related to species abundances and dominance. Samplings of arachnids as intensive as the one reported in this paper are rare indeed, but they are critical to begin to understand geographical variation in species diversity.

5. Arachnology's Direction

If arachnology is the study of terrestrial chelicerate lineages, where is our field headed? More and more arachnid genomes are being annotated on a yearly basis, and genomic data are beginning to be utilized in phylogenetic analyses at the species and higher taxonomic levels. In fact, systematics focusing on several arachnid lineages has been at the forefront of this discipline, with recent contributions uncovering the utility of transcriptomic and genomic data in deciphering the tree of life and in testing evolutionary and biogeographic hypotheses and scenarios. Into this wealth of phylogenomic data, arachnologists routinely weave phenotypic and ecological variables for truly integrative evolutionary studies.

Nature has selected the evolution of certain traits and animal products that arachnids are renowned for. Take spider silk, for example, which represents nature's toughest biomaterial. Only recently have we found that silk proteins are many times as diverse as we understood only a decade ago. Genomic and transcriptomic analyses are helping us discover new and new genes that code for various types of silk, and proteomics and functional

ecology of silk are emerging fields that may potentially revolutionize biotechnological efforts towards utilizing these amazing materials. Spider and scorpion venoms are another wealth of animal products worthy of precise biochemical and genomic scrutiny and call for medical applications. Finally, morphology is not going to retire any time soon. Spider orb weaver lineages, such as the giant wood spider (*Nephila*), widow spiders (*Latrodectus*), jewel spiders (*Gasteracantha*), and others, have reached, evolutionarily speaking, nature's greatest differences in male and female shape and size, and students of sexual size dimorphism regularly make these their model organisms.

In closing, let me call for even higher outputs and standards in arachnological research. Considering arachnid age and deep phylogenetic splits, their evolutionary landscape is uniquely diverse, and this calls for continuous original and synthetic research. Our Special Issue should serve as an invitation to arachnology for the new generation of biologists. Come equipped with specialized skills, join the existing labs, and create new ones; then, help us transform arachnology into modern science.

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