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What does the history of Theraphosidae systematics tell us about the future of tarantula taxonomy?

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Systematics provides the foundational knowledge about the units of biodiversity, i.e., species, and how we classify them. The results of this discipline extend across Biology and can have important impacts on conservation. Here we review the systematic and taxonomic practices within Theraphosidae over the last 260 years. We examine the rate of newly described species and investigate the contemporary practices being used in the description of new genera and species. There have been two large waves of theraphosid taxonomy, with an explosive growth of newly described species and author combinations in the last 60 years. We look back and find that during 2010–2024 contemporary practices in theraphosid systematics and taxonomy have remained largely static, being dominated by morphology-based approaches. Over this period, only 10% of newly described species incorporated DNA data or explicitly stated the species concept used. Similarly for genera, only five of the 37 newly described genera over that time were supported as distinct and monophyletic by DNA. We highlight the taxonomic movement of species among Theraphosidae, Barychelidae, and Paratropididae; however, given the limited molecular sampling for the two latter families, the boundaries of these families remain a significant area of needed research. To promote inclusivity, we provide a copy of this paper in Spanish as supplementary material.

KEYWORDS
Barychelidae, Paratropididae, spider, review, Mygalomorphae, species concept

1 Introduction

The fields of taxonomy and systematics form the foundation for all research in Biology. Because of this, the implications of accurately understanding classification and defining species boundaries extends beyond these two disciplines (Dayrat, 2005). These interwoven fields share objectives and methodologies, with taxonomy focused on the identification, delimitation, and description of new species and understanding how organisms are hierarchically ranked (i.e., alpha and beta taxonomy), while systematics endeavors to refine our comprehension of relationships between species, as well as higher taxonomic levels. Researchers from other scientific disciplines and policy makers rely on an accurate understanding of species because incorrect identifications can impact the interpretation of research (e.g., evolutionary, ecological, biochemical) (Bortolus, 2008; Bennett and Balick, 2014). Furthermore, the over-splitting or lumping of species can greatly impact conservation if species are overlooked, or conservation approaches are inappropriately applied to species or populations where it is not needed (Ely et al., 2017).

Being able to organize Earth's biodiversity into unambiguous taxonomic ranks (e.g., species, genera, tribes, families, subfamilies) challenges biologists, even with modern data and techniques. Within the Araneae Clerck, 1757, there are over 52,000 described and valid spider species (World Spider Catalog WSC, Accessed 16 April 2024). The infraorder Mygalomorphae Pocock, 1892 comprises approximately 3000 valid species in 31 families (World Spider Catalog, 2024). These spiders (the tarantulas, trapdoor spiders, and funnel web spiders) pose several challenges to taxonomists because morphological homoplasy and morphological stasis are common (Wilson et al., 2023). These conserved morphologies have often stifled accurate classification and species delimitation, as well as obscuring evolutionary relationships (Opatova et al., 2020) – likely due to distantly related lineages having similar ecologies and niche preferences (Wilson et al., 2023). For example, the former Ctenizidae Thorell, 1887, Dipluridae Simon, 1889, and Nemesiidae Simon, 1889 families were found to be non-monophyletic and constituted multiple independent lineages that were raised to family status once genomic data was investigated (Opatova et al., 2020). Because of these morphological issues, Theraphosidae has been referred to as a "…nomenclature and taxonomic nightmare" (Raven, 1990a).

Of all the spiders, tarantulas (Theraphosidae Thorell, 1869) may be the most well-known to the general public (or at least most recognized) because of their large size, hairy appearance, and charismatic presence in popular culture (Figures 1A–K). This one family comprises over one-third of described mygalomorph diversity with over 1,100 valid species (as of 16 April 2024; World Spider Catalog, 2024). However, this does not include the many specific epithets that are now considered junior synonyms or have been classified as *nomina dubia*. Interestingly, because of their size and charisma there are likely significant numbers of undescribed species sitting in natural history collections waiting to be "discovered" (Paknia et al., 2015; Hilton et al., 2021). Compared to most mygalomorph families, theraphosid diversity is widespread with a near global, largely pan-tropical distribution. As such, tarantula systematics and taxonomy is a global endeavor with research being undertaken on species from all continents (except Antarctica): North America (Hendrixson et al., 2015; Ortiz and Francke, 2015, 2016, Hamilton et al., 2016; Turner et al., 2018; Graham et al., 2020; Mendoza and Francke, 2020); South America (Pérez-Miles and Locht, 2003; Bertani and Fukushima, 2009; Guadanucci, 2011, 2014; Perafán et al., 2015; Cifuentes et al., 2016; Ferretti et al., 2018; Hüsser, 2018; Nicoletta et al., 2020; Candia-Ramírez and Francke, 2021; Cifuentes and Bertani, 2022; Gabriel et al., 2023; Galleti-Lima et al., 2023; Kaderka et al., 2023; Sherwood et al., 2023; Ferretti et al., 2024; Peñaherrera-R et al., 2024); Europe (Korba et al., 2022); Africa (Gallon, 2003, 2005, Midgley and Engelbrecht, 2019); Asia (Schmidt and von Wirth, 1996; West et al., 2012; Prasanth and Jose, 2014; Sanap & Mizra 2014; Nunn et al., 2016; Montemor et al., 2020; Sivayyapram et al., 2020; Yu et al., 2021; Songsangchote et al., 2022; Chomphuphuang et al., 2023); and Australia (Raven, 2005; Briggs et al., 2023).

Our current understanding of the Theraphosidae Tree of Life is largely developed from a handful of molecular phylogenies (Hüsser, 2018; Lüddecke et al., 2018; Turner et al., 2018; Foley et al., 2019, 2021; Korba et al., 2022; Ortiz, 2023). These phylogenies challenged the results of the past (i.e., those that only used morphology), and began to provide a better understanding and stability of relationships through inter-subfamily sampling (Table 1; Figure 2). The subfamily rank has long been used to accommodate theraphosid diversity (Simon, 1892; Pocock 1895a), and over time many subfamilies have been modified to either expand their definition or new subfamilies have been erected to accommodate newly described or 'hard-to-place' species (Smith, 1990, 1995; Schmidt, 1993; Samm and Schmidt, 2008, 2010; Guadanucci, 2014) (Table 1). As of 2024, 13 extant subfamilies are largely accepted. These include the Aviculariinae Simon, 1892, Eumenophorinae Pocock, 1897, Harpactirinae Pocock, 1897, Ischnocolinae Simon, 1892, Ornithoctoninae Pocock, 1895a, Poecilotheriinae Simon, 1892, Psalmopoeinae Samm and Schmidt, 2010, Schismatothelinae Guadanucci, 2014, Selenocosmiinae Simon, 1889, Selenogyrinae Smith, 1990, Stromatopelminae Schmidt, 1993, Theraphosinae Thorell, 1870, and Thrigmopoeinae Pocock, 1900. Additionally, there is one extinct subfamily, Prototheraphosinae Wunderlich and Müller, 2020, known only from a single, mid Cretaceous fossil in Myanmar (Wunderlich and Müller, 2020) and is thought to be closely related to the Selenocosmiinae. Sanger sequencing phylogenies that used a handful of loci provided broad taxon sampling and were among the first to reject several morphological hypotheses; however, the limited phylogenetic signal in that data left many relationships unresolved (Hüsser, 2018; Lüddecke et al., 2018; Korba et al., 2022). The use of transcriptome-based phylogenies with hundreds of loci, albeit with less samples, lead to highly supported relationships within and between subfamilies for the first time, while also confirming the monophyly of most of the subfamilies found in Lüddecke et al. (2018). Several studies have since built on the Foley et al. (2019) phylogeny by adding the barychelid *Rhianodes atratus* (Thorell, 1890; Foley et al., 2021) and *Bonnetina* Vol, 2000 (Ortiz, 2023). These phylogenies all recover largely the same relationships, with all acknowledging the same basal node was unstable and sensitive to the data used. Importantly though, these phylogenies all suffer from the same issue, limited taxon sampling. With less than 5% of the known tarantula diversity sampled, there is significant room to explore and test hypotheses in Theraphosidae systematics.

In this review, we highlight the surge in Theraphosidae systematic research over the past six decades, offer insights into the current diversity and classification landscape, and summarize the contemporary trends and methodologies employed up to this point. Extending beyond Theraphosidae, we explore the taxonomic boundaries between Theraphosidae and Barychelidae Simon, 1889 (Figure 1L), as well as the more recent inclusion of some Paratropididae Simon, 1889 species into Theraphosidae. Finally, we

FIGURE 1
Theraphosidae diversity. **(A)** Theraphosinae, *Aphonopelma* sp. **(B)** Aviculariinae, *Typhochlaena seladonia*. **(C)** Psalmopoeinae, *Psalmopoeus irminia*. **(D)** Eumenophorinae, *Hysterocrates* sp. **(E)** Harpactirinae, *Augacephalus* sp. **(F)** Stromatopelminae, *Stromatopelma* sp. **(G)** Selenocosmiinae, *Selenocosmia crassipes*. **(H)** Poecilotheriinae, *Poecilotheria* sp. **(I)** Ischnocolinae, *Ischnocolus* sp. **(J)** Ornithoctoninae, *Cyriopagopus lividus*. **(K)** Thrigmopoeinae, *Thrigmopoeus* sp. **(L)** Barychelidae, *Rhianodes atratus*. Photos used from iNaturalist were cropped to size. Photo credit in the same order: Chris Hamilton, Joao Mendes & Dimenor Santos (joaomendes/iNaturalist), Allan Hopkins (hoppy_1951/iNaturalist), Eric (Toganim/iNaturalist), Joubert Heymans (jouberth/iNaturalist), Nael Ajm (naelajm/iNaturalist), Michelle Woolley, Sanjaya Kanishka (Sanjaya_kanishka/iNaturalist), Vojtěch Vita (vojtechvita/iNaturalist), Wich'yanan L (plains-wanderer/iNaturalist), P. S. Sivaprasad (sivabirds/iNaturalist), Tan Kok Hui (kokhuitan/iNaturalist).

will show how this significant burst in recent theraphosid taxonomic work has provided the foundation for global researchers to collaborate and advance our understanding of the Theraphosidae Tree of Life.

2 Methods

2.1 Data acquisition & analysis

Theraphosidae systematics has been built cumulatively on the backs of many researchers, scholars, naturalists, and enthusiasts alike. While not every piece of work can be acknowledged here, this effort should not be considered overlooked or unrecognized. To investigate the general trends and statistics of Theraphosidae diversity through time, we downloaded species data from the World Spider Catalog (World Spider Catalog, 2024, Accessed 16 April 2024). The WSC is regarded as one of the best public, online taxonomic databases, with up-to-date decisions and access to all Araneae taxonomic papers. Only genera and species that are considered valid have data readily available for export, therefore readily downloadable statistics do not include data for nominal species considered as junior synonyms, *nomina dubia*, or *nomina nuda*. To accommodate the common use of subfamilies in Theraphosidae (Thorell, 1870; Raven, 1985; Lüddecke et al., 2018; Foley et al., 2021; Biswas et al., 2023), we added this data to our matrix (Supplementary Datasheet 1) by following Tarantupedia (Kambas, 2024) and the literature. Because there are some differences, we make several deviations from the classification

TABLE 1 Changes in the number of recognized Theraphosidae subfamilies from 1985–2019. *, Newly described subfamily; +, subfamily raised from synonymy; ~, subfamily moved to Theraphosidae from another family.

Raven, 1985	Smith, 1990	Schmidt, 1993	Raven, 1994	Smith, 1995
8	9	11	12	13
Aviculariinae	Aviculariinae	Aviculariinae	Aviculariinae	Acanthopelminae*
Eumenophorinae	Eumenophorinae	Eumenophorinae	Eumenophorinae	Aviculariinae
Harpactirinae	Harpactirinae	Harpactirinae	Harpactirinae	Eumenophorinae
Ischnocolinae	Ischnocolinae	Ischnocolinae	Ischnocolinae	Harpactirinae
Ornithoctoninae	Ornithoctoninae	Ornithoctoninae	Ornithoctoninae	Ischnocolinae
Selenocosmiinae	Selenocosmiinae	Poecilotheriinae+	Poecilotheriinae	Ornithoctoninae
Theraphosinae	Selenogyrinae*	Selenocosmiinae	Selenocosmiinae	Poecilotheriinae
Thrigmopoeinae	Theraphosinae	Selenogyrinae	Selenogyrinae	Selenocosmiinae
	Thrigmopoeinae	Stromatopelminae*	Stromatopelminae	Selenogyrinae
		Theraphosinae	Theraphosinae	Spelopelminae*
		Thrigmopoeinae	Thrigmopoeinae	Theraphosinae
			Trichopelmatinae~	Thrigmopoeinae
				Trichopelmatinae

Rudloff, 2001	Pérez-Miles and Locht, 2003	Gallon, 2003	West et al., 2008	Guadanucci, 2012
11	10	11	10	10
Aviculariinae	Aviculariinae	Aviculariinae	Aviculariinae	Aviculariinae
Eumenophorinae	Eumenophorinae	Eumenophorinae	Eumenophorinae	Eumenophorinae
Harpactirinae	Harpactirinae	Harpactirinae	Harpactirinae	Harpactirinae
Ischnocolinae	Ischnocolinae	Ischnocolinae	Ischnocolinae	Ischnocolinae
Ornithoctoninae	Ornithoctoninae	Ornithoctoninae	Ornithoctoninae	Ornithoctoninae
Poecilotheriinae	Poecilotheriinae	Poecilotheriinae	Poecilotheriinae	Selenocosmiinae
Selenocosmiinae	Selenocosmiinae	Selenocosmiinae	Selenocosmiinae	Selenogyrinae
Selenogyrinae	Selenogyrinae	Selenogyrinae	Selenogyrinae	Stromatopelminae
Spelopelminae	Theraphosinae	Stromatopelminae+	Theraphosinae	Theraphosinae
Theraphosinae	Thrigmopoeinae	Theraphosinae	Thrigmopoeinae	Thrigmopoeinae
Thrigmopoeinae		Thrigmopoeinae		

West et al., 2012	Guadanucci, 2012	Fukushima and Bertani, 2017	Lüddecke et al., 2018	Foley et al., 2019
10	11	10	13	13
Aviculariinae	Aviculariinae	Aviculariinae	Aviculariinae	Aviculariinae
Eumenophorinae	Eumenophorinae	Eumenophorinae	Eumenophorinae	Eumenophorinae
Harpactirinae	Harpactirinae	Harpactirinae	Harpactirinae	Harpactirinae
Ischnocolinae	Ischnocolinae	Ischnocolinae	Ischnocolinae	Ischnocolinae
Ornithoctoninae	Ornithoctoninae	Ornithoctoninae	Ornithoctoninae	Ornithoctoninae
Selenocosmiinae	Schismatothelinae*	Schismatothelinae	Poecilotheriinae+	Poecilotheriinae
Selenogyrinae	Selenocosmiinae	Selenocosmiinae	Psalmopoeinae+	Psalmopoeinae
Stromatopelminae	Selenogyrinae	Selenogyrinae	Schismatothelinae	Schismatothelinae

(Continued)

TABLE 1 Continued

West et al., 2012	Guadanucci, 2012	Fukushima and Bertani, 2017	Lüddecke et al., 2018	**Foley et al., 2019**
10	11	10	13	13
Theraphosinae	Stromatopelminae	Theraphosinae	Selenocosmiinae	Selenocosmiinae
Thrigmopoeinae	Theraphosinae	Thrigmopoeinae	Selenogyrinae	Selenogyrinae
	Thrigmopoeinae		Stromatopelminae+	Stromatopelminae
			Theraphosinae	Theraphosinae
			Thrigmopoeinae	Thrigmopoeinae

provided by Kambas (2024). We place six genera as *incertae sedis* due to their uncertain placement (e.g., many have been placed in Barychelidae at some point in their taxonomic past); these include *Acanthopelma* F.O. Pickard-Cambridge, 1897, *Cyrtogrammomma* Pocock, 1895b, *Melloina* Brignoli, 1985, *Psalistops* Simon, 1889, *Reichlingia* Rudloff, 2001, and *Thalerommata* Ausserer, 1875. Most of these currently reside in Ischnocolinae, a subfamily that has been used as a historical 'trash bin' or 'dumping ground' to place species that do not fit into the other subfamilies (Guadanucci, 2014). Furthermore, we find that *Neoheterophrictus* Siliwal et al., 2012 and *Heterophrictus* Pocock, 1900 should be listed under Eumenophorinae rather than Ischnocolinae, as per Guadanucci (2011); Siliwal et al. (2012), and Mirza et al. (2014). Lastly, we find that *Yanomamius* Bertani and Almeida, 2021 should be listed under Schismatothelinae rather than Psalmopoeinae, as per the authorities of the genus (Bertani and Almeida, 2021).

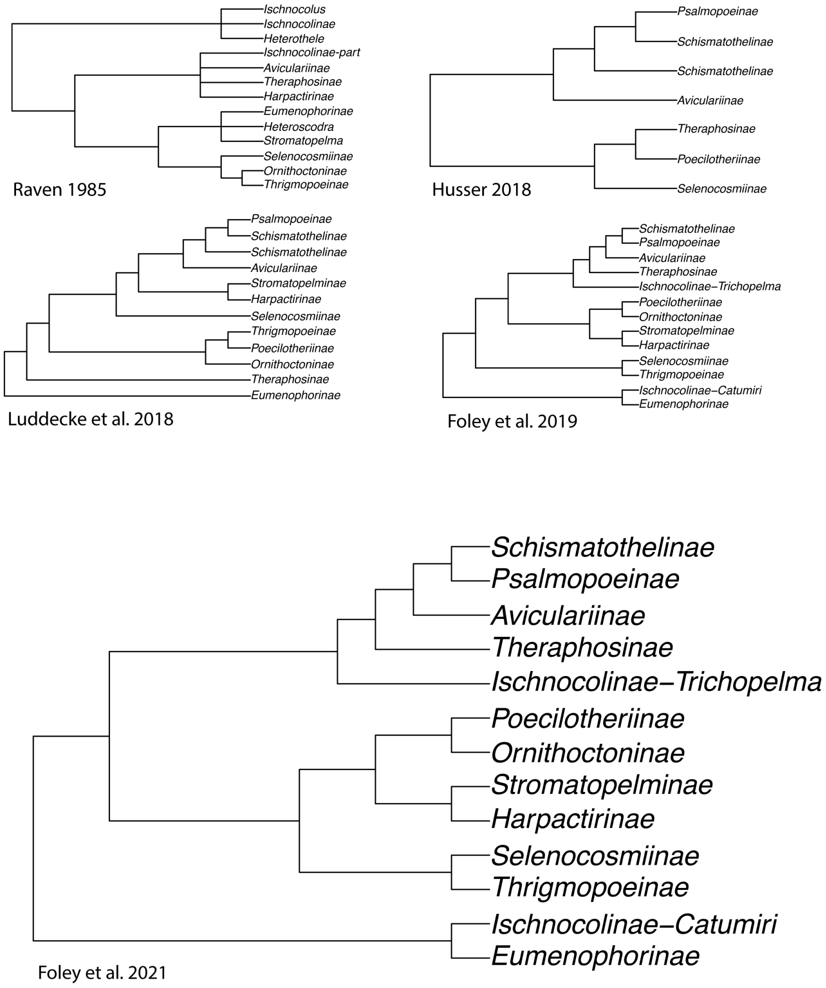

FIGURE 2
Simplified cladograms from key studies that have widespread taxon sampling in Theraphosidae systematics.

To investigate contemporary trends in theraphosid taxonomy and systematics, we recorded the approach and data type used for newly described and currently valid genera and species, from 1 Jan 2010 to 16 April 2024. Newly described genera were categorized as one of the following: 1) Morphology – Descriptive; 2) Morphology – Cladistics; or 3) DNA+Morphology. Genera were categorized as Morphology – Descriptive if the study did not explicitly describe their testing framework to erect new genera. Genera were categorized as Morphology – Cladistics if a morphological cladistic analysis was included, supporting the monophyly of the new genera. Genera were categorized as DNA+Morphology if DNA and morphology were both used to confirm monophyly of the new genus. For species data, we followed Bond et al. (2022) and also recorded if a species concept was explicitly stated when testing species boundaries, and if so, which species concept. The approach used to delimit species were again categorized three ways: 1) Morphological – Descriptive; 2) Morphological – Cladistics; and 3) DNA+Morphology. Species were recorded as Morphological – Descriptive if no testing framework was stated. Species were recorded as Morphological – Cladistics if a morphological phylogeny was used to delimit species. Finally, species were recorded DNA+Morphology if DNA was used in any capacity that led to a new species being described, this included studies that produced a DNA barcode without phylogenetic context and studies using hundreds of loci. For DNA+Morphology, we also noted how morphology was used (e.g., cladistics, morphometrics, or descriptive), as well as if ecological information was used. Given the importance of preserving all aspects of holotypes, we also recorded if the holotype was sequenced and whether the sequence data was publicly available. To examine the proportion of valid names and synonyms for genera and species, we manually counted the number of generic and species synonyms for each valid genus, as well as the number of *nomina dubia* from WSC. Additionally, we examined which sex or sexes were described at the time of the species description (Supplementary Datasheets 2–4). Data was analyzed and plotted using Rstudio (R Core Team, 2024) and the following R packages: tidyverse (Wickham et al., 2019), RColorBrewer (Neuwirth, 2014), Patchwork (Pedersen, 2019), and ape (Paradis et al., 2004).

3 Results & discussion

3.1 The explosive waves of Theraphosidae taxonomy

Theraphosidae taxonomy is over 260 years old, with the majority of theraphosid species described during two large “waves” (Figure 3). Beginning in 1758, theraphosid taxonomic work slowly rose until the 1870s when the first, large burst of descriptions occurred, peaking in 1897 with 38 species. Following this peak, the number of species described each year decreased until the 1950s–1960s. In the 1980s a second, more explosive burst of activity began and continues to this day (Figure 3). During the first wave, a period of just over 200 years (1758–1960), 57 author combinations described 508 species which are still valid today; this makes up almost half of today’s formally recognized diversity with 46.1% (508/1110). This wave of theraphosid taxonomy was most prolific in Europe and North America, with 20 of the top 21 theraphosid taxonomists (measured in described and currently recognized species) coming from those two regions – all of which described at least six currently recognized species. However, it should be acknowledged that Brazilian arachnologist Cândido Firmino de Mello-Leitão described 36 tarantula species during this time. Only two prevalent theraphosid taxonomists described

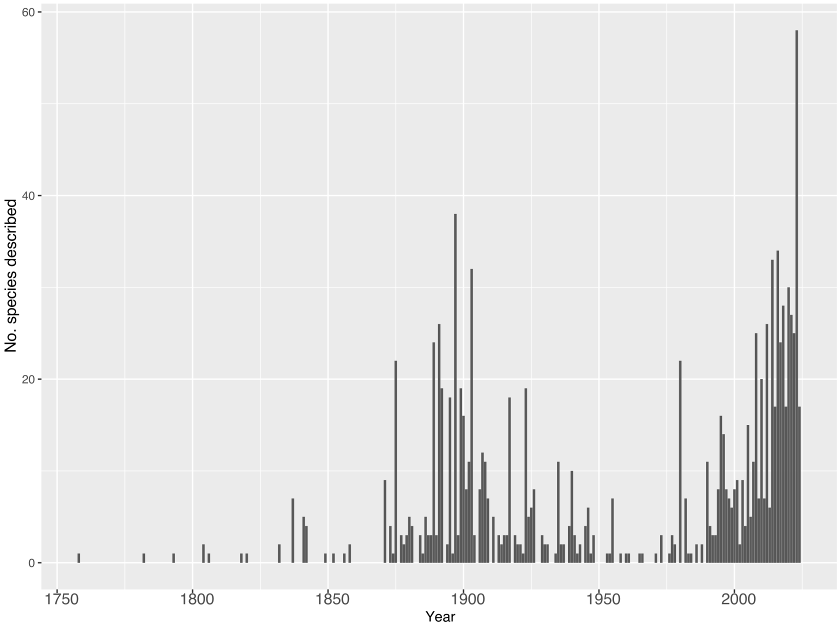

FIGURE 3
The number of valid species described per year. Data collected from the World Spider Catalog on 16 April 2024.

more, Reginald Pocock and Eugène Simon with 96 and 90 currently valid species, respectively.

Currently, we are in the midst of a great resurgence or "second wave" in theraphosid taxonomy (Figure 3). From 1961 to 16 April 2024 (a 62-year span), arachnologists have described 592 currently valid species, more than 50% of the described tarantula diversity. In 2023 alone, 58 new theraphosid species were described. Interestingly, this second wave is occurring not only in species diversity, but also in the diversity of taxonomists describing these species – approximately half of the described species over the last 60 years were carried out by 204 author combinations, an almost 400% increase when compared to the 57 in the 200 years prior. This is important because these authors are living and working on the continents where the tarantulas they are describing live. Even though taxonomy is a field in crisis, where less and less taxonomists are employed due to underfunding (Bacher, 2012; Sluys, 2013; Bond et al., 2022), the number of theraphosid taxonomic papers and authors has been trending upwards.

The diversity of tarantulas, while nearly globally distributed, is far from uniform. On a continental scale, we see large disparities in the number of species. Regions such as Australia and Europe are relatively poor, with Australia having only six described species, while species from Europe/Eurasia are only found along the fringes of the Mediterranean. Africa and Asia have comparatively far more diversity, with ~150 and ~200 species respectively, yet all these regions are dwarfed by the Americas, where ~650 described species reside. When we compare diversity using geopolitical boundaries, we find several countries contain a relatively large proportion of diversity. The three countries with the most currently recognized species are Brazil, Mexico, and Peru, possessing ~210, ~100, and ~80 described species respectively (and a vast amount of undescribed diversity), making up ~35.4% (390/1100) of all described Theraphosidae diversity. There are likely a combination of factors contributing to the disparity in theraphosid diversity between subfamilies and regions, for example taxonomic bias, geology, and evolutionary innovation. One potential taxonomic bias is that the Americas have contributed much more taxonomic research in the last 60 years than other regions. Is this because more undescribed diversity has been examined here compared to other parts of the world? Are there more theraphosid taxonomists working on these continents? Or do the Americas truly harbor more diversity? These cannot be answered at this time, but we do know that Brazil, Mexico, and Peru are well known biodiversity hotspots, where factors such as long-term stability (Marin et al., 2018) and topographical complexity (Moeslund et al., 2013) can facilitate the accumulation and generation of new species. Additionally, evolutionary innovation often leads to differences in diversity, and the development of urticating hairs – an effective anti-predator mechanism found in two American subfamilies, has likely contributed to an increase in diversity, either through increased diversification or reduced extinction within the Theraphosinae subfamily (Biswas and Karanth, 2024).

We also investigate the breakdown of Theraphosidae classification across taxonomic levels, namely genus and subfamily. Here we acknowledge that measures of diversity above the species level may not be meaningful, as division between (and among) ranks above species (particularly genera and subfamily) can be arbitrary (Avise and Mitchell, 2007; Stork et al., 2015), but interesting nonetheless. As one taxonomist might determine a large clade to be one genus, another might recognize multiple smaller genera (see proposed changes to anole lizards: Nicholson et al., 2012, 2014, Poe, 2013; Poe et al., 2017). Currently, Theraphosidae includes 167 recognized genera. Of these, an astounding 25.1% (42/167) are monotypic! Most of these monotypic genera reside within the Theraphosinae subfamily – the dominant lineage throughout North, Central, and South America. Conversely, there are 11 genera with at least 20 species, comprising 28.9% (318/1100) of described tarantula diversity. When we look at subfamily classification, a notable pattern emerges (Figure 4). Within most subfamilies, one or two genera contain more diversity than the other genera in the same subfamily (Figure 4). This result begs the question: Is this a real, biological result or a taxonomic bias? In some cases, the more diverse genera could perhaps be a 'dumping ground' (like the Ischnocolinae), where new species with uncertain placement are put into these genera. Another answer is that there are more taxonomists working on these genera. Yet another potential

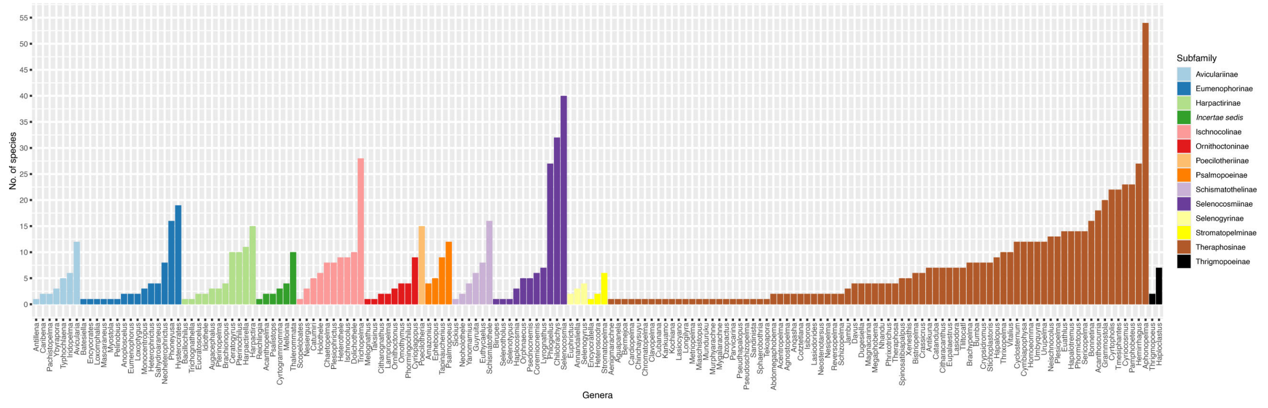

FIGURE 4
The number of valid species per genus. Genera are colored by subfamily classification. Data collected from the World Spider Catalog on 16 April 2024.

answer lies in our desires to answer one of evolutionary biology's most interesting questions – what mechanisms allowed some lineages on the Tree of Life to become more diverse than others? While the dumping of species into some genera helps reduce the inflation of monotypic genera, they may not always reflect natural monophyletic lineages. For example, the two most diverse genera *Aphonopelma* Pocock, 1901 (54 species) and *Selenocosmia* Ausserer, 1871 (40) (Figure 4), are likely not monophyletic (Schmidt, 1995; Raven, 2000; Hamilton et al., 2016; Turner et al., 2018), and will probably split into multiple genera after future revisions. Questions like these will only be answered by future collaborative research.

3.2 Contemporary practices in Theraphosidae systematics

It is well understood that the boundaries of different taxonomic ranks is hotly debated (Mahner, 1993; Mallet, 1995; Wheeler and Meier, 2000; De Queiroz, 2005, 2007; Kallal et al., 2020; Turk et al., 2020; Hormiga et al., 2023; Kuntner et al., 2023; Maddison and Whitton, 2023). Because of this, many researchers agree that taxonomy and systematics should be rigorous and employ "best practices" and current theory, as in any other scientific discipline (Dayrat, 2005; Cook et al., 2010; Kaiser et al., 2013; Wheeler, 2018, 2020; Bond et al., 2022; Valdecasas et al., 2022). In our field, "best practices" is synonymous with integrative taxonomy – i.e., using multiple data types (morphology, DNA, ecology, etc.) to test hypothesized taxonomic boundaries. Across Theraphosidae systematics, we have seen a variety of practices and methods, ranging from descriptive with no mention of a species hypothesis testing framework, to the "best practices" that utilizes morphology, DNA, and ecology.

Morphological data dominates theraphosid classification, particularly at the generic and species level. Since 2010, several years after the development of molecular tools that could be used for taxonomy (Hebert et al., 2003, 2004), there have been 38 theraphosid genera described (excluding *Bumba* Pérez-Miles et al., 2014 which is a replacement name for *Maraca* Pérez-Miles, 2006, which was also a replacement for *Iracema* Pérez-Miles, 2000). Surprisingly, only five genera (*Lasiocyano, Parvicarina, Tekoapora* Galleti-Lima et al., 2023, *Tliltocatl* Mendoza and Francke, 2020, and *Urupelma* Kaderka et al., 2023) used genetic data to support them as distinct monophyletic lineages – four of these were published in 2023 (Galleti-Lima et al., 2023; Kaderka et al., 2023). The other 33 genera can be considered untested hypotheses. Though nine of these 33 genera were supported as monophyletic by a morphological phylogeny, our understanding of these genera could change heavily following molecular investigations.

Molecular data can provide significant insight into theraphosid systematics by reconstructing evolutionary history and inferring extent of geneflow – a measure that cannot be tested using morphology. For example, molecular data revealed significant over-splitting in the North American *Aphonopelma* and aided in 33 synonymies, highlighting where morphology failed to accurately delimit species as distinct, independently evolving lineages. A recent review of taxonomic practices in Araneae between 2008–2018

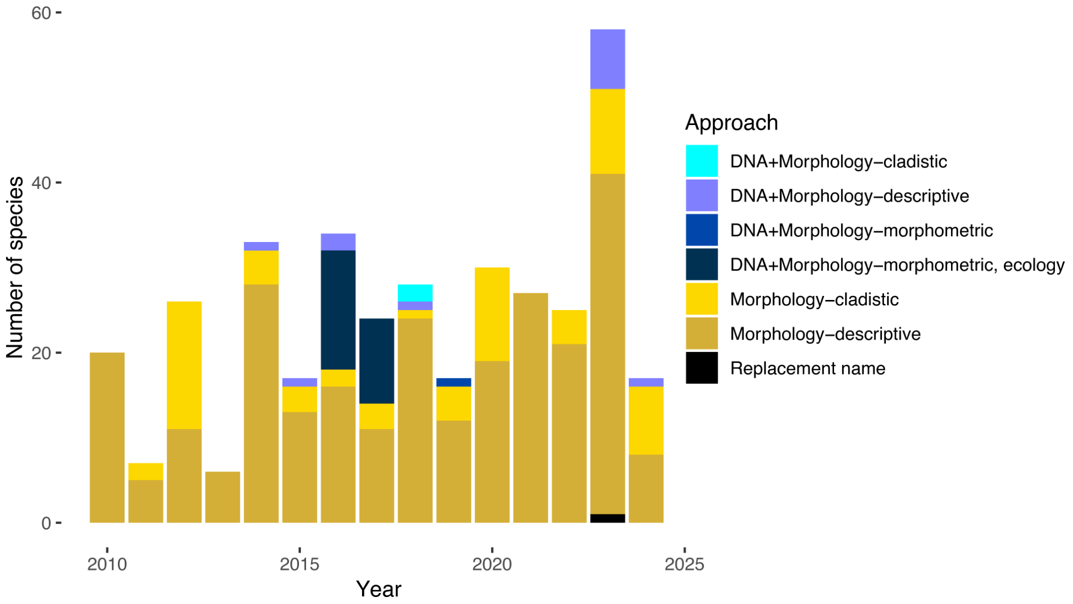

FIGURE 5
Approaches and data types used for newly described species from 2010–2014. Approaches were classified in the following ways: DNA+Morphology – cladistic if DNA and morphological cladistics were used for describing new species, DNA+Morphology – morphometrics if DNA and morphometrics were used, DNA+Morphology – morphometrics, ecology if DNA, morphometrics, and ecology was used, DNA+Morphology – descriptive if DNA and descriptive morphology was used, Morphology – cladistics if morphological cladistics was used, Morphology – descriptive if a descriptive taxonomic approach was used. Replacement name for cases where a species had to be renamed to avoid taxonomic confusion due to the species being a homonym.

revealed the use of molecular data was startlingly low at ~6% (see Bond et al., 2022). When we look at Theraphosidae, only 10.8% (40/369) of the newly described species during 2010–2024 were delimited with DNA (Figure 5) – interestingly this is biased by 2016 and 2017 where almost half of all newly described species included DNA. This trend of incorporating DNA quickly diminishes, with no new species described using DNA from 2020 to 2022. There are only a handful of studies that have incorporated molecular data into their species delimitation studies and generic revisions including: *Aphonopelma* (Hendrixson et al., 2013; Hamilton et al., 2011, 2014, 2016), the Australian species (Briggs et al., 2023), *Bonnetina* (Ortiz and Franke 2015; 2016, 2017), *Brachypelma* Simon, 1891 (Mendoza and Francke, 2017), *Davus* O.Pickard-Cambridge, 1892 (Candia-Ramírez and Francke, 2021), *Grammostola* Simon, 1892 (Montes de Oca et al., 2016), *Ischnocolus* Ausserer, 1871 (Korba et al., 2022), *Pamphobeteus* Pocock, 1901 (Cifuentes et al., 2016), *Plesiopelma* Pocock, 1901 (Ferretti et al., 2024), *Tliltocatl* Mendoza and Francke, 2020 (Mendoza and Francke, 2020), *Lasiocyano, Parvicarina, Tekoapora* (Galleti-Lima et al., 2023), and *Urupelma* (Kaderka et al., 2023).

Of the 40 species that have used DNA to aid in species delimitation, only 29 of them sequenced the holotype. However, in several studies it was unclear if the holotype was sequenced – i.e., the published phylogenies did not provide specimen identifiers or accession numbers, instead only supplying the species name, therefore it could not be confidently inferred if the holotype was used in the molecular phylogeny. In other studies, it was found that individual specimens had multiple codes, for example a holotype specimen was given one code in the species description (presumably a museum accession number) but another code in the molecular phylogeny and tables (presumably collection/collector identifiers). Additionally, some specimen codes were only able to be linked based on data in the Supplementary Material. For most holotypes, the sequence data was publicly available at the time of this publication; there were only two cases where a holotype's data was not publicly available (Hüsser, 2018; Galleti-Lima et al., 2023).

Another important component of modern taxonomy and the "best practices" would be to explicitly state the species concept that was used. Species concepts provide a framework to test species hypotheses, however their use in theraphosid taxonomy has been very low, with only 10% (37/369) of new species (2010–2024) being described under a defined species concept. Of these 37 species, three species concepts have been utilized: the Phylogenetic Species Concept (inferred as Cracraft, 1983), the Unified Species Concept (sensu De Queiroz, 2007), or the Morphological Species Concept (MSC – generally using a typological viewpoint). Historically, theraphosid taxonomy has been based on the MSC, though not explicitly stated.

As of 1st April 2024, there have been 98 generic and 291 species synonyms within Theraphosidae taxonomic history, and a further two genera and 141 species considered *nomina dubia* (Figure 6). To put this into perspective, 36.9% of all available generic names (98/265) and 20.9% (291/1391) of all available species names are junior synonyms, comparable to previous examinations of similar statistics at the species level (see Platnick and Raven, 2013). We know that the "cryptic species problem" (i.e., morphologically indistinguishable using traditional approaches) is common throughout mygalomorphs. When using morphology alone for delimitation and classification, researchers must try to accurately find the boundary between intra- and inter-specific variation. Given the number of junior synonyms, both at the species and genus level in theraphosids, this is clearly difficult to do accurately. This should make taxonomists wary of inferring boundaries when only investigating morphology.

When we look for potential biases in the sex of described species, we find that for most theraphosid species described since 2010, both sexes were described (Both: 226, Female only: 61, Male only: 82). In subsequent years, since their description, an additional six females were described for species that were only known from the male (Both: 232, Female: 55 and Male: 82). This is important to point out because Theraphosid taxonomists have described only one sex in 38.7% (143/369) of the examined species (from 2010–2024), comparable to the 35.6% of all spider species examined in Bond et al. (2022) from 2008–2018. While being able to describe males and females is of course best practice, we acknowledge the difficulty of being able to collect mature specimens of both sexes,

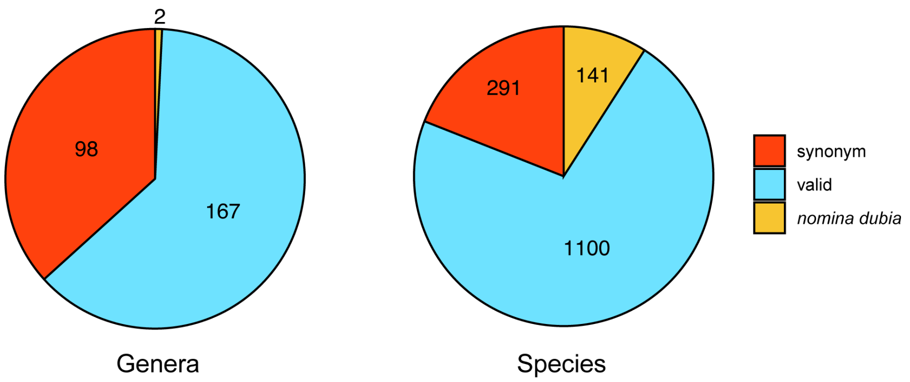

FIGURE 6
The proportion of species synonyms and *nomina dubia* for Theraphosidae genera and species, as of 16 April 2024.

based on our own experiences. In many cases, females can remain elusive with cryptic burrows and collecting mature males in the breeding season may not be possible based on location and climatic challenges. Furthermore, traits or character states can sometimes be hard to quantify objectively, particularly in the continuum of morphological variation. As such, different scoring of characters can lead to different inferred phylogenies (see Mori and Bertani, 2020; Goloboff-Szumik and Ríos-Tamayo, 2022), as well different opinions on what characters should define different genera and species (see Nunn et al., 2016; Sivayyapram et al., 2020). For example, theraphosids (and mygalomorphs, in general) have "simple" copulatory organs that do not provide many effective characters for comparison with other species. Because of this, small intraspecific variation in these simple structures might be perceived as interspecific ones by many taxonomists.

One of the best examples of convergent morphological evolution misleading theraphosid taxonomists is the arboreal African genera *Stromatopelma* Thorell, 1869 and *Heteroscodra* Pocock, 1900. They were placed into their own subfamily (Stromatopelminae) by Schmidt in 1993, though previously they had been placed in Eumenophorinae by Raven (1985) after being transferred from Aviculariinae. In 2003, Gallon included both genera in Stromatopelminae while also including *Encyocratella olivacea* Strand, 1907, one of only two tarantula species known to lack spermathecae (Bertani and da Silva Junior, 2002; Gallon, 2003), and proposing another African subfamily, the Harpactirinae, as the sister lineage. In later years, subsequent morphology-based phylogenies inferred the Stromatopelminae resided within the Aviculariinae once again (West et al., 2008; Fukushima and Bertani, 2017). Eventually, molecular data would refute the placement in either Aviculariinae or Eumenophorinae, affirming the positions of Schmidt (1993) and Gallon (2003, 2005) that the Stromatopelminae was an independent lineage, sister to Harpactirinae (Lüddecke et al., 2018; Foley et al., 2019). This is not a criticism of the use of morphology. The desire to use molecular data is prevalent but the funding is not. These research funding inequities are important because the vast majority of new diversity being described is coming from regions with the highest biodiversity, yet these researchers are not being supported.

There will be times when DNA is inaccessible and morphological data may be the only option. Many putatively undescribed species reside in biological collections around the globe, but because of their age or storage may not be suitable for DNA sequencing because of their preservation technique or a hesitancy to destructively sample small or very rare specimens. In these cases, researchers are left with few choices. They can either wait to resample fresh material, which of course requires additional time and resources, or proceed using a morphological-only approach. This is problematic due to significant anthropomorphic change where species are going extinct before being described (Bond, 2012). Ultimately, the more information researchers can use, the more robust our species and classification hypotheses will be. While species can be delimited and described solely from DNA sequence data following a hypothesis testing framework (Cook et al., 2010; Jörger and Schrödl, 2013; Renner, 2016; Briggs et al., 2023), systematics and taxonomy carried out only using DNA does not provide context about the organisms or their evolution, potentially leaving many interesting evolutionary stories behind (Wheeler, 2018). As said by Wheeler (2020): "But no single source of evidence can eclipse the others without sacrificing valuable knowledge". Only an integrative approach using morphology, ecology, and molecular data will give a robust and informative classification.

3.3 Theraphosidae, Barychelidae, Paratropididae: Where to draw the line?

Phylogenomics has provided the much-needed stabilizing insight to the Mygalomorphae Tree of Life (Bond et al., 2014; Garrison et al., 2016; Starrett et al., 2017; Hedin et al., 2019; Kulkarni et al., 2020; Opatova et al., 2020; Kulkarni et al., 2023), however achieving widespread taxon sampling for phylogenomics is difficult given the sheer diversity of the group and the costs involved. Many taxonomically important genera and species have not yet been sampled in this context, leaving many untested hypotheses in mygalomorph systematics. In the case of the families Theraphosidae, Barychelidae, and Paratropididae, the frequent transfer of genera and species back and forth has blurred the taxonomic limits of these groups.

The Barychelidae (sometimes called brush-footed trapdoor spiders) are a widespread group of mygalomorphs, currently comprising 39 genera and 285 valid species. Barychelids are the sister lineage to Theraphosidae, with both families sharing many characteristics such as claw tufts, dense tarsal scopula, and hirsute appearance (Opatova et al., 2020), however recent phylogenetics suggest the family may not be monophyletic (Kulkarni et al., 2023). Barychelids have a broad distribution and can be found in Central and South America, Africa, Asia, and Australia. Interestingly, they are also found throughout Oceania in many of the pacific islands such as Hawaii, New Caledonia, and Fiji – areas where tarantulas have not been recorded. When compared to Theraphosidae, Barychelidae has received very limited taxonomic attention, with most studies focusing on Oceania and Asia (Raven, 1986, 1988, 1990b, 1994, 2008; Churchill and Raven 1992; Yu et al., 2023), as well as a handful of studies from South America (Guadanucci, 2012; Mori and Bertani, 2016, Rios-Tamayo, 2023), Africa (Benoit, 1965, 1966, Gonzalez-Filho et al., 2023), and India (Jose and Sebastian, 2008; Siliwal and Molur, 2009; Siliwal et al., 2009). For example, where 38 new theraphosid genera have been erected since 2010, no new Barychelidae genera have been erected since 1995.

The boundary between the Theraphosidae and Barychelidae has been vague for a very long time. This can be attributed to their similar morphology and lack of genetic taxon sampling. Barychelidae is thought to be distinct from Theraphosidae based on the number of cuspules and shape of the maxillary anterior lobe (Raven, 1985). However, this distinction does not represent a clear boundary as several barychelid genera (*Brachionopus* Pocock, 1897, *Cyrtogrammomma*, *Dolichothele* Mello-Leitão, 1923, *Euthycaelus* Simon, 1889, *Harpactirella* Purcell, 1902, *Idiothele* Hewitt, 1919, *Psalistops*, *Reichlingia*, *Thalerommata*, and *Trichopelma* Simon, 1888) have been transferred to Theraphosidae during the 1970s to 2023 (Bücherl et al., 1971; Raven, 1985; Mori and Bertani, 2020; Bertani and Raven, 2023) – and sometimes moving back and forth between the two families. Most of these decisions were based on morphology, though sometimes cladistics. Of these genera, only a small number of *Brachionopus*, *Euthycaelus*, *Harpactirella*, and *Trichopelma* species have been confirmed as theraphosids by molecular data (Bond et al., 2012; Wheeler et al., 2017; Opatova et al., 2020; Foley et al., 2021; Kulkarni et al., 2023; Yu et al., 2023). As such, barychelids are poorly represented in online repositories such as GenBank, SRA, or Dryad, and as argued in Mori and Bertani (2020) a wider sampling of Barychelidae should be a priority. A better understanding of the limits of Barychelidae would in turn dramatically impact our understanding of Theraphosidae classification, as well as providing further insight into their evolution and biogeography.

The Paratropididae are an enigmatic group of mygalomorph spiders due to them being rare, reclusive, and hard to find (Perafán et al., 2019), characteristics that have caused them to be difficult to place in the mygalomorph Tree of Life. Though Raven (1985) suggested they were sister to Theraphosidae, early molecular data had difficulty placing paratropidids in phylogenies, often with weak support (Hedin and Bond, 2006; Bond et al., 2012). Once phylogenomics were used, the family has been recovered either as an early branching and species poor lineage of Bipectina or sister to the Domiothelina (Opatova et al., 2020; Kulkarni et al., 2023) – though they have only ever been represented by *Paratropis* Simon, 1889. Recent work has questioned the placement of certain lineages, with *Melloina* being moved to Theraphosidae (Mori and Bertani, 2020; Goloboff-Szumik and Ríos-Tamayo, 2022) and morphological cladistic analyses placing the *Melloina* and *Paratropis* inside Theraphosidae (Mori and Bertani, 2020; Goloboff-Szumik and Ríos-Tamayo, 2022). Additionally, the Glabropelmatinae Raven, 1985 (and in particular *Melloina*) was placed in Theraphosidae (Echeverri et al., 2023). The cladistic analyses that placed *Melloina* in Theraphosidae (Mori and Bertani, 2020; Goloboff-Szumik and Ríos-Tamayo, 2022) conflicts with recent molecular phylogenies with regards to theraphosid subfamily relationships (Foley et al., 2019, 2021; Ortiz, 2023). The morphological phylogenies that proposed Eumenophorinae as sister to Selenocosmiinae, Theraphosinae sister to Ornithoctinae + Poecilotheriinae, and Psalmopoeinae sister to Stromatopelminae – all have been rejected in phylogenomic studies (Foley et al., 2019, 2021; Ortiz, 2023). Similar to the Barychelidae, increasing sampling for molecular work from paratropidid genera, such as *Melloina*, will be key to testing the correct placement and composition of this family.

3.4 The future of Theraphosidae systematics and taxonomy

From this review it is clear that the taxonomic practices throughout the history of Theraphosidae have remained largely static. Theraphosid systematists have been slow to adopt modern techniques and apply best practices, some of which we attribute to resource inequities – something global collaboration can help mitigate. If the fields of Theraphosidae taxonomy and systematics want to be more rigorous, then we must move toward a more integrative approach and explicit testing of species boundaries (i.e., hypothesis testing). Having a clear, reproducible framework for testing species or generic boundaries, even without DNA, will only help to increase the rigor and robustness of taxonomy. However, in cases where DNA can be used, sequencing of holotypes (either newly described species or historical specimens – more feasible now than ever before due to high-throughput sequencing methodologies) will be critical for future theraphosid and barychelid taxonomy by adding stability and clarity, and by providing the ability to confidently identify species regardless of stage of life or sex.

The systematics and taxonomy of Theraphosidae and their close relatives remains a fruitful area for discovery. While the number of newly described species continues to increase exponentially, there are likely still many more to be named. As mentioned earlier, widespread taxon sampling for molecular phylogenetics continues to be an issue, leaving many parts of the Theraphosidae (and Barychelidae) Tree of Life unknown and untested. With these spiders occurring across multiple continents, this is an opportunity for international collaboration in the face of disparity in resources. Global collaboration will help balance certain resource and acknowledgement inequities, collectively elevating the standard of Theraphosidae systematics and evolution. Theraphosid researchers, keep up the great work, collaborate, and continue this second wave of taxonomic research we are currently experiencing.

Author contributions

EB: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. CH: Conceptualization, Funding acquisition, Investigation, Methodology, Resources, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/frchs.2024.1445731/full#supplementary-material

SUPPLEMENTARY DATA SHEET 1

THERAPHOSIDAE_species_export_20240416.csv, data downloaded from World Spider Catalog, 16 April 2014 with subfamily column added.

SUPPLEMENTARY DATA SHEET 2

Theraphosidae_2010_2024_FINAL.csv, reduced dataset for valid species described 2010-2024 with records of species concept, data type, approach, holotype sequences and availability.

SUPPLEMENTARY DATA SHEET 3

synonyms_nomina_dubia.xlsx, simple tally of the number of synonyms and for genera and species for each valid genus as well as records of *nomina dubia*.

SUPPLEMENTARY DATA SHEET 4

genera_described_post_2010.csv, dataset to record approach used for valid genera described from 2010-2024.

SUPPLEMENTARY DATA SHEET 5

español_MS_Briggs&Hamilton.pdf.

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