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SPIDERS OF IRAN

Systematics, diversity and distribution

Alireza Zamani



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The originality of this publication has been checked in accordance with the University of Turku quality assurance system using the Turnitin OriginalityCheck service.

Cover Images:

Background image: southern view of Mount Damavand from Lar National Park in Mazandaran Province, northern Iran (by Barbod Safaei-Mahroo).

Images of spiders, from left to right: *Loureedia phoenixi* Zamani & Marusik, 2020 (by Alireza Zamani), *Araniella villanii* Zamani, Marusik & Šestáková, 2020 (by Anatoly Ozerney) and *Lycosa aragogi* Nadolny & Zamani, 2017 (by Alireza Zamani).

ISBN 978-951-29-9252-2 (PRINT)
ISBN 978-951-29-9253-9 (PDF)
ISSN 0082-6979 (Print)
ISSN 2343-3183 (Online)
Painosalama, Turku, Finland 2023

تقدیم به عنکبوت‌ها، قهرمانان بی ادعای قلمرو حیوانات، که با تورهای پیچیده و مهارت‌های استثنائی‌شان در شکارگری تخیلات ما را تسخیر و شناخت ما را از جهان طبیعی غنی‌تر کرده‌اند.

به حیات وحش شکوهمند ایران، که گستره گوناگون گونه‌هایش ما را از شگفتی و تحسین سرشار می‌کند.

باشد که همچنان از شما بیاموزیم و برای حفاظت از شما تلاش کنیم تا نسل‌های آینده شاهد وجود شگفت‌انگیزتان باشند. این رساله به شما و آن دسته از افراد پرشور و خستگی‌ناپذیری که زندگی خود را وقف مطالعه و حفظ

تنوع ارزشمند حیات کرده‌اند تقدیم می‌شود.

To spiders, the unsung heroes of the animal kingdom, whose intricate webs and extraordinary hunting skills have captured our imaginations and enriched our understanding of the natural world.

To the magnificent wildlife of Iran, whose diverse array of species fills us with wonder and admiration.

May we continue to learn from you and strive to protect you, so that future generations can witness your awe-inspiring existence. This dissertation is dedicated to you, and to those passionate and tireless individuals who have devoted their lives to studying and preserving the invaluable diversity of life.

UNIVERSITY OF TURKU

Faculty of Science

Biodiversity Unit

ALIREZA ZAMANI: Spiders of Iran – Systematics, diversity and distribution

Doctoral Dissertation, 385 pp.

Doctoral Programme in Biology, Geography and Geology

April 2023

ABSTRACT

Spiders (Araneae) are the largest order of Arachnida and the sixth most speciose order of Animalia, comprising more than 50,000 extant species as well as over 1,400 species known from fossils. Despite this immense diversity that has been estimated to comprise 120,000–200,000 species, our knowledge of their systematics and distribution remains rather incipient. While attempts to evaluate the diversity and distribution patterns of spiders have been made for the Neotropical and a few other faunas, most other regions remain historically neglected.

The aim of this dissertation is to explore the systematics, diversity and distribution of spiders of Iran, a highly interesting region from a zoological and biogeographical point of view that unfortunately has been poorly investigated regarding its invertebrate fauna. For this purpose, I examined more than 9,000 specimens that were either collected during expeditions to numerous regions and ecosystems across the country or deposited in several natural history collections from around the world. As a result of these efforts, which were initiated in 2013 and mostly carried out in collaboration with researchers from various countries, a total of 11 genera and 147 species of Iranian spiders were described as new to science, and 419 taxa (i.e., 13 families, 87 genera and 319 species) were recorded in Iran for the first time. The total number of newly described and recorded species (i.e., 466 species) constitutes almost half (i.e., 49.83%) of the currently known Iranian species diversity of this group (i.e., 935 species). Amongst 147 species described, 137 are known only from Iran, representing 63.72% of all species currently considered endemic to this country (i.e., 215 species). These results were published in a total of 87 publications, 38 of which were published after the beginning of my doctoral studies at UTU in 2019. This dissertation, however, is primarily based on only nine taxonomic articles (i.e., I–IX), all published after 2019 and highlighting some of the more important findings.

Because of the newly obtained taxonomic information and an extensive database of all published records, it was possible to conduct a comprehensive review of spatial variation in the diversity patterns of spiders in Iran. This was the main objective of publication X, which also included an evaluation of the effect of sampling bias on the current understanding of the distribution of Iranian spiders. The analyses showed that the diversity of Iranian spiders remains inadequately studied and is heavily affected by the Linnean shortfall (i.e., gaps in taxonomic knowledge), despite a remarkable improvement in taxonomic research on this fauna since the beginning of the 21st century. There are 935 spider species in the 1,648,195 km² of Iran.

Comparing the number of species per area of 171 countries and other political regions indicated that Iran was in position 132, whereas many considerably smaller and less ecologically diverse countries were in lower positions. It was also found that this fauna clearly suffers from a severe Wallacean shortfall (i.e., lack of knowledge of species distributions), as approximately 85% of Iran lacks a single record of spiders. There is a highly uneven distribution of records throughout the country and its provinces and ecoregions, with most of the records situated near large cities. A high correlation was found between the number of records of spiders and the number of records of plants and other animals in Iran, indicating that the noted shortfalls are indeed corroborated by other taxa. Finally, it is suggested that to gain a more complete picture of the diversity of Iranian spiders, future collecting efforts should be primarily in the form of extensive systematic surveys instead of opportunistic sampling, and ideally targeting lesser sampled areas and ecoregions. Once a satisfactory amount of information regarding the taxonomy and distribution of species becomes available, it will be possible to properly assess the conservation status and risk factors that affect these species and to identify areas of higher conservation and management priority.

KEYWORDS: biodiversity, Linnean shortfall, Middle East, new species, taxonomy, Wallacean shortfall.

TURUN YLIOPISTO

Matemaattis-luonnontieteellinen tiedekunta

Biodiversiteettiyksikkö

ALIREZA ZAMANI: Spiders of Iran – Systematics, diversity and distribution

Väitöskirja, 385 s.

Biologian, maantieteen ja geologian tohtoriohjelman

Huhtikuu 2023

TIIVISTELMÄ

Hämähäkit (Araneae) ovat lajimäärältään hämähäkkieläinten suurin laho, ja kuudenneksi suurin eläinlahko. Lahkoon kuuluu yli 50 000 nykyisin elävää lajia ja yli 1400 lajia jotka tunnetaan fossiileista. Tästä valtavasta, arviolta 120 000–200 000 lajin monimuotoisuudesta huolimatta, on tietämys hämähäkkien systematiikasta ja levinneisyyksistä alkutekijöissään. Neotropiikin ja joidenkin muiden alueiden hämähäkkien monimuotoisuutta ja lajien levinneisyyksiä on yritetty selvittää, mutta useimmat muut alueet ovat jääneet huomiotta.

Tämän väitöskirjan tavoitteena on tutkia Iranin hämähäkkien systematiikkaa, monimuotoisuutta ja lajien levinneisyyksiä. Iran on eläintieteellisesti ja eliömaantieteellisesti kiinnostava alue, jonka selkärangattomien lajisto on jäänyt valitettavan vähälle huomiolle. Tarkastelin yli 9000 näytettä jotka oli joko kerätty tutkimusretkillä Iranissa lukuisilla alueilla ja lukuisissa ekosysteemeissä, tai jotka kuuluivat useisiin eri puolilla maailmaa sijaitseviin luonnontieteellisiin kokoelmiin. Tämä tarkastelu, joka alkoi 2013 ja toteutettiin useimmiten yhteistyössä muiden maiden tutkijoiden kanssa, johti 11 iranilaisen suvun ja 147 lajin kuvaamiseen tieteelle uusina. 419 taksonia (eli 13 heimoa, 87 sukua ja 319 lajia) havaittiin Iranissa ensimmäistä kertaa. Uudet lajit (yhteensä 466 lajia) muodostavat lähes puolet (49.83 %) Iranin tunnetusta lajistosta (935 lajia). Tulokset julkaistiin 87 julkaisussa, joista 38 julkaistiin aloitettuani jatko-opintoni Turun yliopistolla 2019. Väitöskirjani perustuu kuitenkin pääosin vain yhdeksään taksonomiseen julkaisuun (I–IX), jotka kaikki julkaistiin vuoden 2019 jälkeen, ja jotka tuovat esille osan tärkeimmistä havainnoista.

Uudet tiedot hämähäkkien taksonomiasta sekä kaikkien julkaistujen havaintojen sijoittaminen tietokantaan mahdollistivat kattavan katsauksen hämähäkkien monimuotoisuuden maantieteellisestä jakautumasta Iranissa. Tämä oli julkaisun X pääsisältö. Julkaisussa arvioitiin myös otantaharhan vaikutusta nykytietämykseen Iranin hämähäkkilajien levinneisyyksistä. Iranin hämähäkkien monimuotoisuus osoittautui puutteellisesti tutkituksi ja lajisto huonosti tunnetuksi, vaikka hämähäkkeihin kohdistuva taksonominen tutkimus on merkittävästi laajentunut sitten 2000-luvun alun. Iranissa on 935 hämähäkkilajia 1,648,195 km² pinta-alalla. Lajimäärän vertailu pinta-alaa kohti 171 valtiossa tai muulla hallinnollisella alueella sijoitti Iranin sijalle 132, huonompaan sijoitukseen kuin monet pienemmät ja muutoin lajistoltaan vähemmän monimuotoiset maat. Tietämys Iranin hämähäkkilajien levinneisyyksistä osoittautui myös äärimmäisen puutteelliseksi, sillä hämähäkkihavainnoja ei ole yhtäkään noin 85 %:ssa Irania. Havainnot

jakautuvat erittäin epätasaisesti koko maassa sekä sen provinseissa ja ekoalueilla, sijoittuen pääosin lähelle suuria kaupunkeja. Hämähäkkihavaintojen määrä korreloi vahvasti kasvihavaintojen ja muiden eläinten havaintojen kanssa, viitaten siihen että hämähäkkitietämyksen puutteet vastaavat muiden eliöryhmien tietämyksen puutteita. Lopuksi esitetään, että paremman kuvan saaminen Iranin hämähäkkilajistosta vaatii tulevilta keruutapahtumilta laajaa, systemaattista otostusta sattumanvaraisen ja pienimuotoisen otostuksen sijaan. Ideaalisesti otostus kohdistuisi vähemmän tutkittuihin alueisiin ja ekoalueisiin. Riittävän taksonomisen tiedon ja levinneisyystiedon saaminen tulee sallimaan sekä lajiston suojelutason että lajeihin kohdistuvien riskien arvioimisen, jolloin voidaan tunnistaa luonnonsuojelullisesti tärkeimmät alueet.

ASIASANAT: biodiversiteetti, puutteellinen taksonominen tietämys, Lähi-itä, uudet lajit, taksonomia, puutteellinen lajien levinneisyyden tietämys.

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List of Original Publications

This dissertation is based on the following original publications, which are referred to in the text by their Roman numerals:

- I Azarkina, G. N. & Zamani, A. (2019). The Aelurillina Simon, 1901 (Aranei: Salticidae) of Iran: a check-list and three new species of *Aelurillus* Simon, 1884 and *Proszynskiana* Logunov, 1996. *Arthropoda Selecta* 28(1): 83–97.
- II Zamani, A. & Marusik, Y. M. (2019). The spider genera *Azerithonica* and *Tegenaria* (Aranei: Agelenidae: Tegenariini) in Iran. *Arthropoda Selecta* 28(2): 291–303.
- III Zamani, A., Marusik, Y. M. & Šestáková, A. (2020). On *Araniella* and *Neoscona* (Araneae, Araneidae) of the Caucasus, Middle East and Central Asia. *ZooKeys* 906: 13–40.
- IV Zamani, A. & Marusik, Y. M. (2020). A review of Agelenini (Araneae: Agelenidae: Ageleninae) of Iran and Tajikistan, with descriptions of four new genera. *Arachnology* 18(4): 368–386.
- V Zamani, A. & Marusik, Y. M. (2020). A survey of Phrurolithidae (Arachnida: Araneae) in southern Caucasus, Iran and Central Asia. *Zootaxa* 4758(2): 311–329.
- VI Zamani, A., Mirshamsi, O. & Marusik, Y. M. (2021). 'Burning violin': the medically important spider genus *Loxosceles* (Araneae: Sicariidae) in Iran, Turkmenistan, and Afghanistan, with two new species. *Journal of Medical Entomology* 58(2): 666–675.
- VII Zamani, A. & Marusik, Y. M. (2021). Revision of the spider family Zodariidae (Arachnida, Araneae) in Iran and Turkmenistan, with seventeen new species. *ZooKeys* 1035: 145–193.
- VIII Zamani, A., Chatzaki, M., Esyunin, S. L. & Marusik, Y. M. (2021). One new genus and nineteen new species of ground spiders (Araneae: Gnaphosidae) from Iran, with other taxonomic considerations. *European Journal of Taxonomy* 751: 68–114.
- IX Zamani, A., Marusik, Y. M. & Szűts, T. (2023). A survey of the spider genus *Dysdera* Latreille, 1804 (Araneae, Dysderidae) in Iran, with fourteen new species and notes on two fossil genera. *ZooKeys* 1146: 43–86.

- X Zamani, A., Vahtera, V., Sääksjärvi, I. E. & Carvalho, L. S. (2023). The effect of sampling bias on evaluating the diversity and distribution patterns of Iranian spiders (Arachnida: Araneae). *Diversity* 15: 22.

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Author contributions

	I	II	III	IV	V	VI	VII	VIII	IX	X
Original idea	AZ, GA	AZ	AZ	AZ	AZ	AZ	AZ	AZ	AZ	AZ, LC, VV, IS
Material sorting	AZ, GA	AZ	AZ	AZ	AZ	AZ, OM	AZ	AZ, SE	AZ	-
Laboratory work	GA	AZ, YM	AZ, YM, AS	AZ, YM	AZ, YM	AZ, OM	AZ, YM	AZ, MC, SE, YM	AZ, TS	-
Data compilation	-	-	-	-	-	-	-	-	-	AZ
Analyses and interpretation of data	-	-	-	-	-	-	-	-	-	LC, AZ
Writing	GA, AZ	AZ, YM	AZ, YM, AS	AZ, YM	AZ, YM	AZ, OM, YM	AZ, YM	AZ, MC, SE, YM	AZ, YM	AZ, LC, VV, IS

Authors are listed in descending order of contribution for each publication.

Author abbreviations: AS = Anna Šestáková, AZ = Alireza Zamani, GA = Galina N. Azarkina, IS = Ilari Eerikki Sääksjärvi, LC = Leonardo S. Carvalho, MC = Maria Chatzaki, OM = Omid Mirshamsi, SE = Sergei L. Esyunin, TS = Tamás Szűts, VV = Varpu Vahtera, YM = Yuri M. Marusik.

Errata

Here, a list of errors in the original publications discovered after printing along with their corrections is provided:

Publication	Location	Error	Correction
I	Page 83, 2nd affiliation	Department of Biology	Biodiversity Unit
I	Page 84, Taxonomy, 2nd paragraph, line 7	Logunov [1996]	Logunov [1996b]
I	Page 87, Genus <i>Proszynskiana</i> Logunov, 1996, 1st paragraph, line 6	Logunov, 1996	Logunov, 1996a
I	Page 88, caption of Figs 27–34	the holotype <i>Proszynskiana izadii</i>	the holotype of <i>Proszynskiana izadii</i>
I	Page 92, diagnosis of <i>Proszynskiana logunovi</i> , lines 11–12	Logunov [1996]	Logunov [1996a]
I	Page 92, 'A check-list of the Aelurillina of Iran', line 8	complete reference lists of the taxonomic/faunistic records	complete reference lists of the taxonomic/faunistic records
II	Page 291, Introduction, line 15	we've had	we had
II	Page 300, line 11	type localities	listed localities
III	Page 18, line 15	type localities	listed localities
III	Page 23, line 2	type localities	listed localities
III	Throughout the text; Figures 12C–D, 13A–B	The record of <i>Neoscona theisi</i> (Walckenaer, 1841) from Georgia	This record was later attributed to <i>Neoscona spasskyi</i> (Brignoli, 1983)
V	Page 316, line 11	type localities	listed localities
V	Page 326, line 13	type localities	listed localities
VII	Page 172	Figs 18E–J, 21D–F, 23A–C, 26E, 29A, 30A–E, 33	Figs 18E–J, 21D–F, 23A–C, 26E, 27A–D, 29A, 30A–E, 33
VII	Page 182	Figs 26A–C, 27A–D, 32	Figs 26A–C, 32
VII	Page 183, caption of Figure 27	<i>Parazodarion raddei</i> (A–D)	<i>Acanthinozodium elburzicum</i> (A–D)

VIII	Page 69, Introduction, line 1	Gnaphosidae Pocock, 189	Gnaphosidae Banks, 1892
VIII	Page 70, Results	Family Gnaphosidae Pocock, 1898	Family Gnaphosidae Banks, 1892
VIII	Page 71, Diagnosis, line 1	all congeners	all of its congeners
VIII	Page 72, Diagnosis, line 1	all congeners	all of its congeners
VIII	Page 77, Diagnosis, line 4	their light color	its light color
VIII	Page 79, Diagnosis, line 1	from the congeners	from its congeners
VIII	Page 84, Diagnosis, line 1	all Palearctic congeners	all of its congeners in the Palearctic

1 Introduction

What amazing array of “endless forms most beautiful and most wonderful”¹ constitute the fascinating biodiversity of our planet. Officially defined at the 1992 United Nations Convention on Biological Diversity, the term ‘biodiversity’ indicates “the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.” The history of the modern way of documenting and classifying Earth’s biodiversity on the basis of a binomial nomenclature system dates back to 1753, when Carl Linnaeus published *Species Plantarum*. This diversity, however, remains so poorly studied that only about two million (Bánki et al. 2021) of the estimated nine million or more eukaryotic species (Mora et al. 2011) are currently documented (i.e., the Linnean shortfall). Taxonomists are in a race against time to describe the vast unknown diversity of Earth’s biota before it is extinct as a result of the Anthropocene mass extinction, especially considering that undescribed and newly described species appear to be more prone to extinction compared to those described in the past (Liu et al. 2022). The current rate at which species are described (*ca.* 18,000 new species descriptions per year) is objectively too low and estimated to be within or even lower than the extinction rate of species (Ceballos et al. 2015).

Although there is no shortage of undescribed species in natural history collections, there is an average ‘shelf life’ of 21 years between discovery and description of species, mostly due to a ‘taxonomic impediment’ or a shortage of taxonomic experts (Fontaine et al. 2012). The undocumented and unstudied material in museums comprise not only small, minute insects from hyperdiverse taxa, but also large, charismatic species of popular groups. For example, *Heteropoda maxima* Jäger, 2001 (Sparassidae), the largest spider in the world, was described in 2001 on the basis of material collected in early 1930s and found decades later in the Muséum national d’Histoire naturelle in Paris (Jäger 2001). Similarly, *Varanus nesterovi* Böhme, Ehrlich, Milto, Orlov & Scholz, 2015 (Squamata: Varanidae), a large monitor lizard with a total length of up to 120 cm, was described in 2015 based on

¹ From the closing statement of Charles Darwin’s 1859 book *On the Origin of Species*.

specimens that were collected in 1914 and 1964 and located in the Zoological Institute in Saint Petersburg and the United States National Museum, Washington D.C. (Böhme et al. 2015).

The knowledge deficiency caused by a severe lack of taxonomic information strongly affects or causes other shortfalls, in particular regarding species distribution (i.e., Wallacean shortfall), abundance and population dynamics (i.e., Prestonian shortfall), ecological interactions (i.e., Eltonian shortfall), and evolutionary patterns (i.e., Darwinian shortfall), all of which impede efficient conservation planning (Hortal et al. 2015; Walters et al. 2021). Unfortunately, modern attempts to accelerate the process of describing and naming species in hyperdiverse taxa (e.g., Sharkey et al. 2021) have been criticised for favouring mere speed and quantity over utility and quality, which in the long run risks hindering taxonomy to an even greater extent (Meier et al. 2021; Zamani et al. 2021d, 2022a).

Finally, although tropical invertebrate taxa constitute the vast majority of Earth's animal diversity, modern research in the past three decades has been found to be heavily and systematically biased towards more 'charismatic' but considerably less diverse vertebrate taxa (i.e., mammals and birds), particularly those from temperate regions (Titley et al. 2017). I aimed to address these shortfalls and biases in my almost-a-decade long research on Iranian spiders, by providing new taxonomic and distribution data on this megadiverse group of arthropods in a highly interesting region that unfortunately has been poorly studied regarding its invertebrate fauna. These data were obtained from both freshly collected specimens and material located in several natural history museums worldwide. A summary of these surveys and my main research findings are presented in this dissertation.

In the following sections of this introductory chapter, I provide a general review of the natural history, phylogeny and classification of spiders, geographical and ecological features of Iran, and a history of araneological studies in this country, including my own research on the topic.

1.1 The amazing, wonderful world of spiders

Spiders (Araneae), with more than 50,000 extant species (WSC 2023), are the largest arachnid order and the sixth most speciose order within the animal kingdom. It has been estimated that the global diversity of spiders may comprise at least 120,000–200,000 species (Agnarsson et al. 2013). Considering this immense diversity, it is not surprising that spiders vary greatly in size, lifestyle, ecology and behavioural patterns. For example, the smallest known species is *Patu digua* Forster & Platnick, 1977 (Symphytognathidae) from Colombia with a body length of less than 0.40 mm in males, while the largest one, *Heteropoda maxima* from Laos, may exceed 46 mm in body length and 300 mm in leg span. *Theraphosa blondi* (Latreille, 1804)

(Theraphosidae), although only slightly smaller than *H. maxima* in leg span, is the heaviest spider by a recorded maximum mass of around 170 grams (Mammola et al. 2017).

With over 1,400 currently recognized fossil species (Dunlop et al. 2020), spiders have a rich evolutionary history and a diverse fossil record (Figure 1). Although most spider fossils are from the Cretaceous onwards (Dunlop 2022), they also comprise a sparse fossil record from the Palaeozoic, with the oldest known species, i.e., a representative of *Arthrolycosa* Harger, 1874 (Arthrolycosidae), dating back to the late Carboniferous (*ca.* 315 Mya) (Selden 2021). Molecular estimates and the fossil record of other arachnids indicate that spiders most likely originated in the Devonian/Permian (Huang et al. 2018).



Figure 1. A female of an unidentified species of *Custodeia* Petrunkevitch, 1942 (Linyphiidae) in Baltic amber. Photo: Alireza Zamani.

1.1.1 External anatomy

Here, I present a brief general introduction to the external anatomy of spiders (Foelix 2011; Ramírez & Michalik 2019), as it is relevant to the topics discussed further in the text (Figures 2A–B).

A spider body consists of two parts, the cephalothorax (or prosoma) and the abdomen (or opisthosoma), connected by a narrow waist called the pedicel. The

cephalothorax is embryologically composed of six segments and has a dorsal and a ventral plate called the carapace and the sternum, respectively. In most spiders, the carapace has a median groove called the fovea, which is an invagination of the carapace that provides attachment sites for the stomach muscles. The eyes are all simple and located on the anterior part of the cephalothorax. Most spiders have eight eyes, although certain families and genera have fewer (e.g., six, four, or two), and many troglobitic species lack eyes altogether.

There are six pairs of appendages attached to the cephalothorax: a pair of chelicerae, a pair of pedipalps (commonly shortened to palps), and four pairs of legs. The chelicerae are two-segmented, composed of a basal segment and a curved fang. The palp consists of six segments, lacking the metatarsus. In adult male spiders, the most distal segment of the palp (i.e., the cymbium) is modified into a copulatory organ used for the indirect transfer of sperm to the female; the other segments may also be modified with different types of apophyses and outgrowths that may be used in copulation. The palps also have a sensorial function and are used during courtship and territorial displays, for prey capture and handling, and carrying egg sacs. The legs consist of seven segments: coxa (basal segment), trochanter, femur, patella, tibia, metatarsus and tarsus. The tarsus has either two or three claws. Some arachnologists consider the articulated, distal, claw-bearing portion of the tarsus as a separate segment (i.e., the pretarsus). A pair of maxillae, a labrum and a labium constitute the mouthparts.

The abdomen is composed of 12 segments, although an external segmentation is lacking in almost all spiders. Some species have scuta or sclerotized plates on the abdomen. The first segment forms the pedicel. The respiratory organs, in the form of booklungs, tracheae or a combination of them, are located ventrally on the second and third abdominal segments. The genital opening is at the epigastric furrow, a cuticular fold separating the second and third segments. In most spiders, the external genitalic area of the female is sclerotized and forms a plate called the epigyne. The spinning appendages, called the spinnerets, are on the fourth and fifth segments, and usually located posteriorly. In a few groups, the spinnerets are positioned more anterior, almost to the middle of the ventral abdominal area. Most species of Mesothelae have four pairs of spinnerets (see ‘Phylogeny and Classification’), and a few other groups have only one or two pairs. Most spiders, however, have three pairs of spinnerets, and the anterior median pair of the ancestral form, if not completely absent, is either modified into a silk spinning field called the cribellum or a vestigial bump called the colulus. The spinnerets bear thousands of tiny spigots at their tip, through which silk is extruded. Male spiders also bear epiandric spigots on the anterior margin of the epigastric furrow that are used to construct the sperm web (see ‘Life cycle’). The anal tubercle is located just posterior to the spinnerets, and bears the anus.

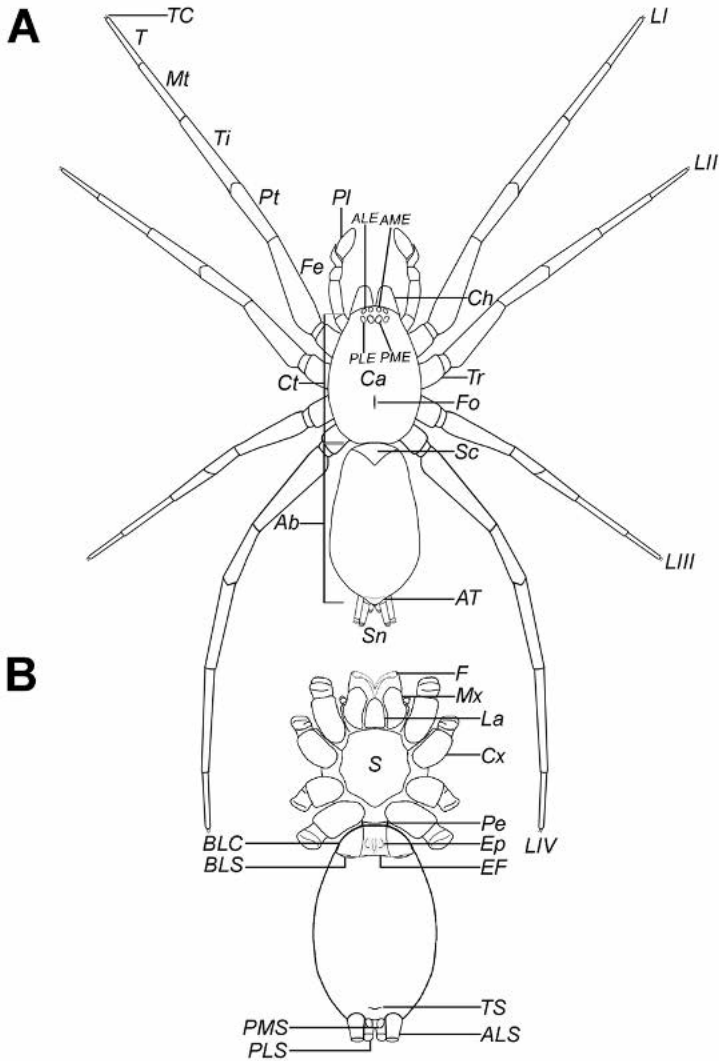


Figure 2. Basic spider external anatomy. **A.** Male, dorsal view. **B.** Female, ventral view. Abbreviations: *Ab* – abdomen, *ALE* – anterior lateral eye, *ALS* – anterior lateral spinneret, *AME* – anterior median eye, *AT* – anal tubercle, *BLC* – booklung cover, *BLS* – booklung slit, *Ca* – carapace, *Ch* – chelicera, *Ct* – cephalothorax, *Cx* – coxa, *EF* – epigastric furrow, *Ep* – epigyne, *F* – fang, *Fe* – femur, *Fo* – fovea, *La* – labium, *L1–LIV* – legs I–IV, *Mt* – metatarsus, *Mx* – maxilla, *Pe* – pedicel, *Pl* – palp, *PLE* – posterior lateral eye, *PLS* – posterior lateral spinneret, *PME* – posterior median eye, *PMS* – posterior median spinneret, *Pt* – patella, *S* – sternum, *Sc* – scutum, *Sn* – spinnerets, *T* – tarsus, *TC* – tarsal claws, *Ti* – tibia, *Tr* – trochanter, *TS* – tracheal spiracle. Illustrations: Mahla Pourcheraghi.

1.1.2 Life cycle

The life cycle of spiders can be divided into four main stages. The first is the embryonic period, comprising the period between egg fertilisation and the formation of typical

morphological features. Following is the larval period which is characterised by the dependency of the spider on the yolk reservoir. Then, there are several (typically 5–10) nymphal stages, before the spider finally becomes adult and develops functional sexual and copulatory organs (Foelix 2011). In some species, the adult individual differs from the nymphal stages also in coloration pattern, proportions of certain organs, and possession of certain structures (e.g., spurs and apophyses). All these stages are separated by moultings (Figure 3A). In arthropods, moulting (or ecdysis) is the periodic process of casting off the cuticle (i.e., the most fundamental of the two major layers of exoskeleton). Most spiders stop moulting after reaching maturity. Females of some groups with long lifespans continue to moult throughout their life.

All spiders, except for a few parthenogenetic species (Korenko et al. 2009), have separate sexes. Upon reaching adulthood, the male spider develops a unique palpal organ that is used to transfer the sperm to the female. For this purpose and (in part) using the epiandric spigots, the male weaves a thread of silk or a sperm web, on which he expels his seminal fluid to be absorbed by the palpal organ shortly afterwards. Once a female is located, most male spiders perform some sort of a courtship ritual that is species-specific in many groups (Girard et al. 2011). If the female is receptive, the male proceeds to mate with her (Figure 3B). During copulation, which can last for hours, the male inserts the intromittent sclerite (i.e., the embolus) of his palpal organ into the external copulatory/genital opening(s) of the female, discharging the sperm. The sperm is then usually kept in unique reservoirs (i.e., the spermathecae) until the female is ready to fertilise her eggs. Depending on the species, the female may lay anywhere between one to more than 3,000 eggs (Mammola et al. 2017), which in case of most species, are kept and protected in a silken sac (Figure 3C). Some spiders (e.g., Lycosidae, Pisauridae) carry and vigorously protect their egg sacs (Figure 3D).

Upon hatching and leaving the egg sac after a few moultings (Figure 3E), the spiderlings either disperse in the environment or stay with their mother for a period of time. In the case of many young and small spiders, especially those species with large distributions, the primary mode of dispersal is ballooning, for which the spider releases a thread of silk to be carried by the wind, with the spider still attached to it (Weyman 1993). The total lifespan of different species of spiders varies between less than six months to more than 40 years (Mammola et al. 2017).

It is noteworthy that spiders display a wide variety of interesting behavioural patterns, especially regarding their courtship, mating and parental care, that are often rarely documented in invertebrates or the whole animal kingdom. This makes them ideal models for studying certain aspects of evolutionary biology (e.g., sexual selection). Some examples include: nuptial gifts and male deception (Ghislandi et al. 2014), traumatic insemination (Řezáč 2009), genital mutilation, plugging and emasculation (Kuntner et al. 2015), remote copulation (Li et al. 2012), opportunistic

mating (Lubin 1986), mate-binding (Zhang et al. 2011), oral sex (Gregorič et al. 2016), sexual cannibalism (Schneider & Elgar 2001), prolonged ‘milk’ provisioning (Chen et al. 2018), matrophagy (Kim & Horel 1998), and infanticide (Schneider & Lubin 1997).



Figure 3. Various aspects of the life cycle of spiders. **A.** Female *Latrodectus tredecimguttatus* (Rossi, 1790) (Theridiidae), moulting. **B.** Male (top) and female *Latrodectus geometricus* C.L. Koch, 1841 (Theridiidae), mating. **C.** Female *Eusparassus mesopotamicus* Moradmand & Jäger, 2012 (Sparassidae), guarding an egg sac. **D.** Female *Pardosa tatarica* (Thorell, 1875) (Lycosidae), carrying an egg sac attached to her spinnerets. **E.** Juveniles of *Argiope trifasciata* (Forsskål, 1775) (Araneidae), shortly after leaving the egg sac. Photos: Anton A. Nadolny (**A, D**), Amir Weinstein (**B, E**) and Alireza Zamani (**C**). **A, D** from Zamani (2016b).

1.1.3 Biology and Ecology

As one of the most successful groups of organisms, spiders can be found in almost all terrestrial habitats and major land areas except for Antarctica (Foelix 2011). Additionally, spiders are one of the most common and abundant groups of predators, comprising a global biomass of approximately 25 million metric tons (Nyffeler & Birkhofer 2017), and may reach peak densities of up to 1,000 individuals per square metre of land (Ellenberg et al. 1986). The Atlantic Forest in South America, with an estimated spider diversity of 2,714–3,816 species, is the most diverse biome (Oliveira et al. 2017; Mammola et al. 2017). Several species have been reported from rather unusual habitats, including freshwater (Aakra & Dolmen 2003), intertidal zones (e.g., Zamani et al. 2016a), saline marshes (Crews et al. 2020b), altitudes as high as 6,700 metres on Mount Everest (Wanless 1975), extremely cold regions having an absolute minimal temperature as low as -71.2°C (Marusik et al. 2008), and extremely xeric deserts with a surface temperature as high as 80.83°C (Zamani & Marusik 2018c).

All spiders are carnivorous, predominantly feeding on arthropods and to a lesser degree other invertebrates and small vertebrates (Figures 4A–D). Some species have been reported to occasionally and/or indirectly feed on plant material (Suvák 2019), and one species, *Bagheera kiplingi* Peckham & Peckham, 1896 (Salticidae), is known to feed primarily on specialised leaf tips of acacias (Meehan et al. 2009).

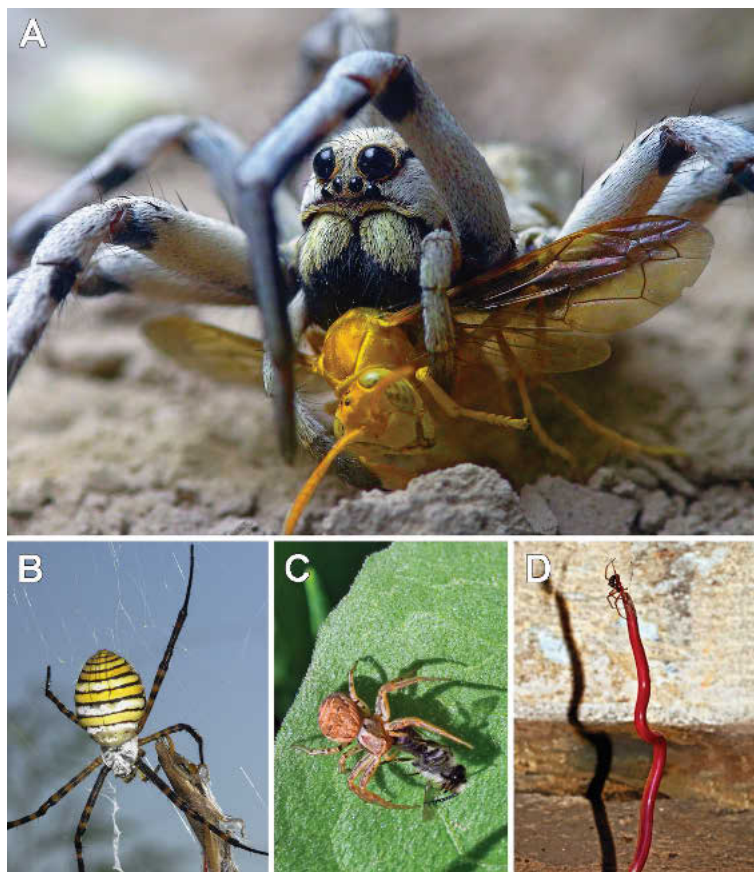


Figure 4. Spiders as predators. **A.** Female of an unidentified species of *Lycosa* Latreille, 1804 (Lycosidae), feeding on a female *Polistes watti* Cameron, 1900 (Hymenoptera: Vespidae). **B.** Female *Argiope trifasciata* (Forsskål, 1775) (Araneidae), preparing to feed on an unidentified short-horned grasshopper (Orthoptera: Acrididae). **C.** Female of an unidentified crab spider (Thomisidae), feeding on an unidentified wasp (Hymenoptera). **D.** Female of *Steatoda triangulosa* (Walckenaer, 1802) (Theridiidae), feeding on a Eurasian blind snake, *Xerotyphlops vermicularis* (Merrem, 1820) (Squamata: Typhlopidae). Photos: Seyyed Ali Mohtarami (**A**), Amir Weinstein (**B**), Alireza Zamani (**C**) and Seyyed Hamzeh Kalantari (**D**).

It has been estimated that the global spider community consumes 400–800 million metric tons of prey animals annually, with insects and collembolans constituting more than 90% of their captured prey (Nyffeler & Birkhofer 2017). Roughly 40% of spider species construct webs of different structures, shapes and properties, on which they depend for prey capture and immobilisation. The rest of them are wandering, burrowing or ambushing predators that hunt their prey using speed, force or an ability to camouflage (Foelix 2011). The fastest rotational strike in animals has been documented in selenopid spiders, which may reach an angular speed of 2000–3000 degrees per second while attacking their prey (Zeng & Crews 2018).

Spiders and their eggs are regularly preyed upon by many different groups of predatory arthropods, including other spiders. Members of all major groups of vertebrates are also known to hunt and feed on larger species of spiders. Many groups of nematodes, fungi, mites, protists, bacteria and viruses parasitize and infect spiders, and several groups of insects (particularly from Hymenoptera and Diptera) are parasitoids of spiders or their eggs (Figures 5A–D) (Durkin et al. 2021).

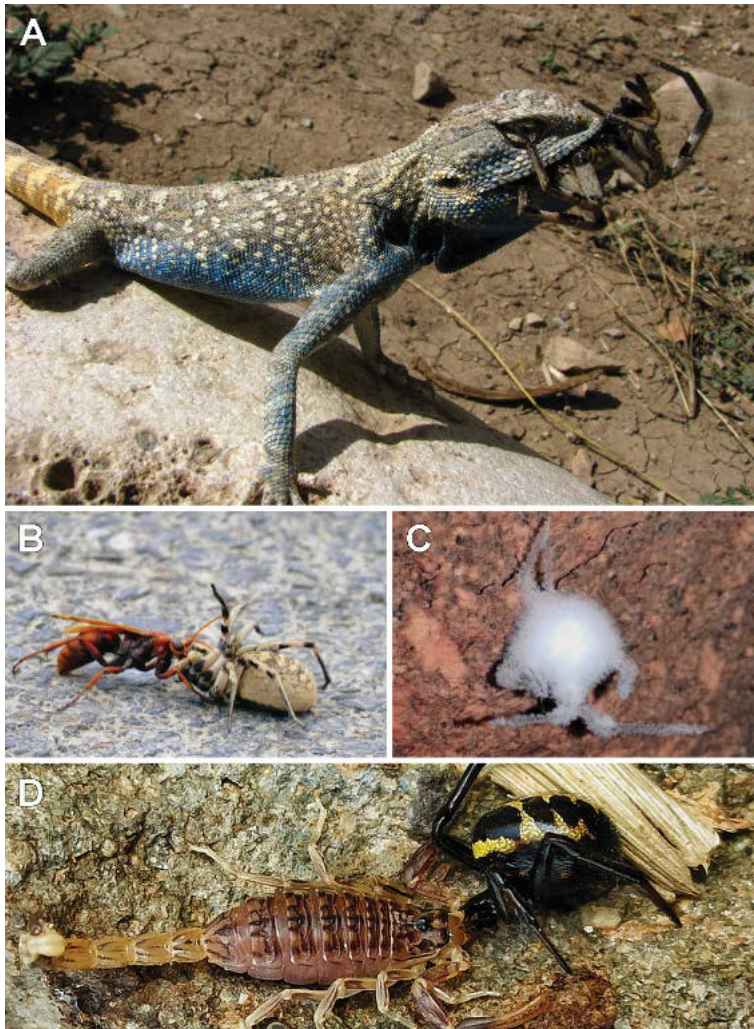


Figure 5. Various predators or parasites of spiders. **A.** Male *Trapelus ruderatus* (Olivier, 1804) (Squamata: Agamidae), feeding on a female *Lycosa praegrans* C.L. Koch, 1836 (Lycosidae). **B.** Female *Cryptocheilus rubellus* (Eversmann, 1846) (Hymenoptera: Pompilidae), dragging a paralyzed female *L. praegrans* into her burrow to lay an egg on. **C.** An unidentified cave-dwelling pholcid infected with fungal pathogens. **D.** Juvenile *Olivierus brutus* (Fet et al., 2018) (Scorpiones: Buthidae), feeding on a female *Steatoda paykulliana* (Walckenaer, 1806) (Theridiidae). Photos: Behzad Fathinia (**A**), Mandana Hazrati-Farid (**B**), Reza Donyadideh (**C**) and Ali Mokhtarian (**D**). **A** from Fathinia & Rastegar-Pouyani (2011).

Spiders use different mechanisms to defend themselves against predators and intruders, or to lower the probability of encountering them. Some examples include: fleeing at speeds as high as approximately two metres per second (Jäger 2014), diving (Swierk et al. 2022), gliding (Crews et al. 2020a), aposematism, displaying defence postures and biting (Foelix 2011), autotomy (Formanowicz 1990),

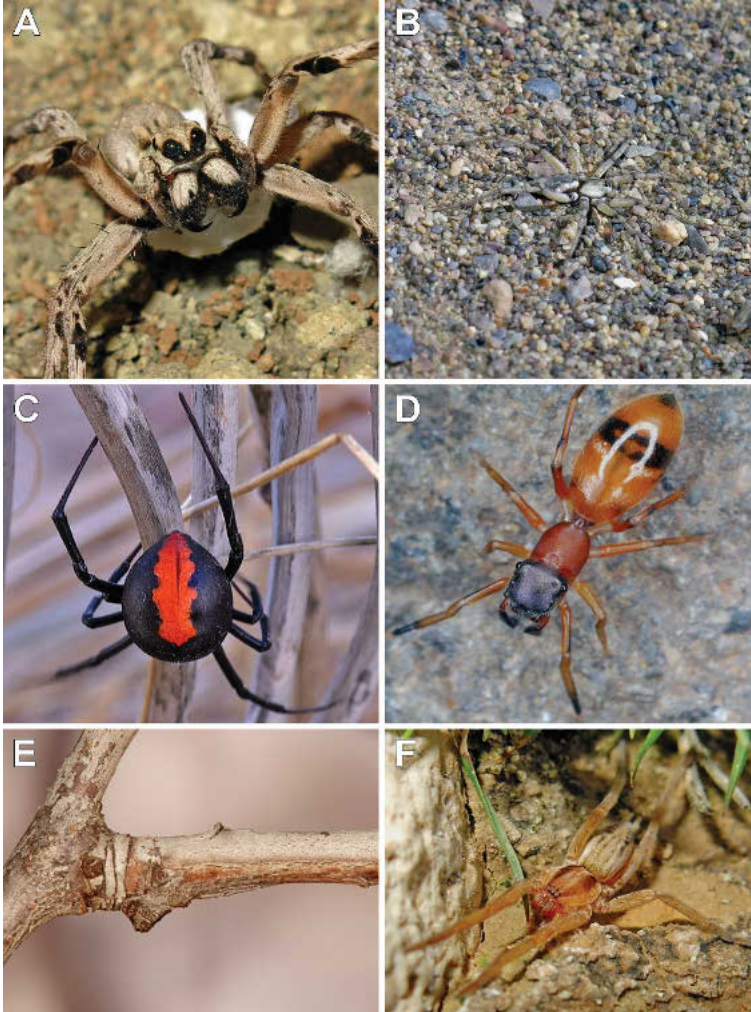


Figure 6. Some varieties of defence and avoidance mechanisms displayed by spiders. **A.** Female *Lycosa macrophthalma* Nadolny & Zamani, 2020 (Lycosidae), in defence posture. **B.** Female *Callipelis desertycola* Zamani & Marusik, 2017 (Gnaphosidae), well-camouflaged in its natural habitat. **C.** Female *Latrodectus cinctus* Blackwall, 1865 (Theridiidae), displaying the aposematic red abdominal stripe. **D.** Female *Myrmarachne formicaria* (De Geer, 1778) (Salticidae), a myrmecomorphic spider. **E.** Female *Tmarus piochardi* (Simon, 1866) (Thomisidae), a twig-mimicking spider. **F.** Female *Prochora lycosiformis* (O. Pickard-Cambridge, 1872) (Miturgidae), missing three legs that have been autotomized. Photos: Alireza Zamani (**A**, **B**, **F**), Seyyed Ali Mohtarami (**C**), Jørgen Lissner (**D**) and Amir Weinstein (**E**). **A** from Nadolny & Zamani (2020), **B** from Zamani et al. (2021a), **E** from Zamani (2016b).

stridulation (Líznarová et al. 2018), death-feigning, camouflaging (Théry & Casas 2002), mimicry (Shamble et al. 2017), constructing cryptic burrows sometimes bearing antipredatory decorations or additional escape routes (Williams et al. 2006), and rubbing off urticating setae (Kaderka et al. 2019) (Figures 6A–F).

Almost all spiders have a solitary and territorial lifestyle; a few groups, however, display different forms of sociality, ranging from a temporary aggregation of webs to dozens of individuals living in family-group territories within a communal nest, and cooperating in prey capture, feeding, brood care and web maintenance (Avilés & Guevara 2017) (Figure 7).



Figure 7. Juveniles of *Sahastata amethystina* Marusik & Zamani, 2016 (Filistatidae), cooperating in prey capture. Photo: Alireza Zamani.

1.1.4 Silk

One of the most characteristic features of spiders is their ability to produce silk from specialised abdominal glands that terminate into the spigots at the tip of their spinnerets (Figure 8). All silks are proteinaceous, and in the case of spiders, they are primarily comprised by a family of large, structural proteins called spidroins (Garb et al. 2010). Up to eight different types of silk glands have been recognized across the whole order, each leading to a particular pair of spinnerets and producing a specific type of silk with unique features (Foelix 2011). Silks are used for a variety of purposes, including web construction (Figures 9A–E) and moulting mats, lining

burrows, covering eggs, dispersal, navigation, safety, prey capture and immobilisation, courtship and mating (Durkin et al. 2021). Considering its high elasticity and tensile strength, low density, exceptional toughness outperforming Kevlar by a factor of seven (Hayashi et al. 2004; Foelix 2011), and biodegradability and antimicrobial properties (Franco et al. 2019), spider silk is one of the most remarkable biomaterials found in nature, with many potential applications in biomedicine and materials science and engineering.



Figure 8. Silk exuded from the spinnerets of a female *Meta menardi* (Latreille, 1804) (Tetragnathidae). Photo: Jørgen Lissner.

1.1.5 Venom

Almost all spiders are venomous. Their venom glands are either inside the basal segment of the chelicerae or in the cephalothorax, and open to the outside via a small hole near the tip of their fangs and connected to the gland by a duct (Foelix 2011). Only members of Uloboridae and *Holarchaea* Forster, 1955 (Anapidae) are known to lack venom glands (Kuhn-Nentwig et al. 2011). Spider venoms, although quite heterogeneous and complex in structure, mainly consist of a variety of peptides and proteins that affect different targets inside the body of the victim (Kuhn-Nentwig et al. 2011). Spiders primarily use their venoms to subdue prey, and to a lesser degree, for defence against large predators. Envenomation by only a few groups are

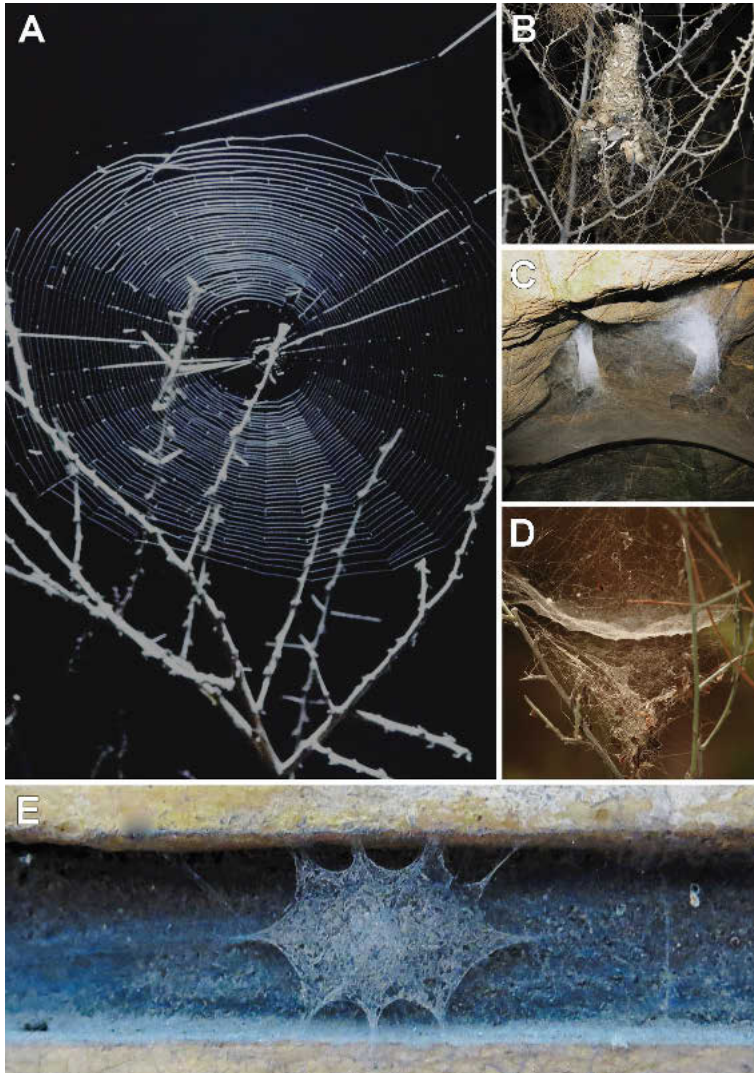


Figure 9. Some varieties of spider webs. **A.** Orb-web of an unidentified araneid. **B.** Retreat portion of the tangle-web of *Latrodectus pallidus* O. Pickard-Cambridge, 1872 (Theridiidae). **C.** Funnel-web of *Tegenaria zamani* Marusik & Omelko, 2014 (Agelenidae). **D.** Sheet-web of *Frontinellina frutetorum* (C.L. Koch, 1835) (Linyphiidae). **E.** Tent-web of *Oecobius putus* O. Pickard-Cambridge, 1876 (Oecobiidae). Photos: Seyyed Ali Mohtarami (**A**), Esam Al Ali (**B**), Alireza Zamani (**C**, **E**) and Amir Weinstein (**D**). **C**, **E** from Zamani (2016b).

considered dangerous to humans, most of which belong to the following genera: *Atrax* O. Pickard-Cambridge, 1877, *Hadronyche* L. Koch, 1873 (both Atracidae), *Latrodectus* Walckenaer, 1805 (Theridiidae) and *Phoneutria* Perty, 1833 (Ctenidae), which possess primarily neurotoxic venoms, and *Hexophthalma* Karsch, 1879, *Sicarius* Walckenaer, 1847 and *Loxosceles* Heineken & Lowe, 1832 (all Sicariidae), which have primarily cytotoxic venoms (Foelix 2011) (Figures 10A–B). Regardless,

and mostly due to the availability of effective antivenoms, the global number of human fatalities caused by spider bites is very low. Recent research has shown that spider venoms have promising applications as candidates for the development of several therapeutics, particularly against cancer and antibiotic resistant bacteria (Saez et al. 2010).



Figure 10. Representatives of the medically important genera of spiders in Iran. **A.** Female *Latrodectus tredecimguttatus* (Rossi, 1790) (Theridiidae). **B.** Male *Loxosceles rufescens* (Dufour, 1820) (Sicariidae). Photos: Amir Weinstein.

1.1.6 Phylogeny and Classification

Until recently, a male palp modified for sperm transfer and well-defined spinnerets were considered synapomorphies for Araneae (Wang et al. 2018). The recent discovery of Chimerarachnida, a remarkable arachnid lineage from mid-Cretaceous Burmese amber, has challenged this concept and our understanding of the evolutionary history and origin of spiders. Chimerarachnida is similar to Uraraneida, a spider-like fossil arachnid lineage, in possessing a segmented abdomen bearing spigots and a whip-like telson, but unlike Uraraneida and similar to Araneae, it displays multi-articulated spinnerets. Furthermore, Chimerarachnida is similar to Araneae in having a modified male palp. The condition of the mature male palp remains unknown in Uraraneida and other spider-like fossils, which provides additional challenges in proposing a concrete phylogeny (Dunlop 2022).

Chimerarachne yingi Wang et al., 2018 is the first genus and species of Chimerarachnida. It was described by Wang et al. (2018), who considered it as the sister to Araneae, with both groups forming a clade sister to Uraraneida. Huang et al. (2018) proposed a different phylogeny and considered *Chimerarachne* Wang et al., 2018 a member of Uraraneida, and Uraraneida as the sister group to Araneae. Wunderlich & Müller (2018) treated *Chimerarachne* as a member of an unnamed suborder of spiders. Wunderlich (2019) proposed Chimerarachnidae and the higher taxon Chimerarachnida to accommodate this genus and considered Araneae and Chimerarachnida as suborders of Araneida. This classification was followed and adopted by Selden (2021) and Dunlop (2022), with the latter considering a loss of the whip-like telson as the defining character for Araneae. A second genus and species of Chimerarachnida, *Parachimerarachne longiflagellum* Wunderlich, 2022, was described in Wunderlich & Müller (2022). Currently, there is no consensus in the arachnological community regarding the higher classification of Araneae and its relationship with Chimerarachnida and other spider-like fossil arachnids. Here, I consider Araneae in the traditional sense as a separate order.

The most widely accepted classification system considers Araneae to be comprised of two suborders (Platnick & Gertsch 1976): Mesothelae (Figure 11A), with two extant and several extinct families and more than 150 living species from East and Southeast Asia, displays plesiomorphic characters such as an externally segmented abdomen and retention of (at least vestiges of) all four pairs of spinnerets, which are located medioventrally. The rest of the families constitute Opisthothelae. They lack an external segmentation of the abdomen (except for a few with vestiges), and at most have three pairs of spinnerets, which are (usually) posteriorly located due to a suppression of the body segments 12–18 (Figure 13A) (Wheeler et al. 2017). Opisthothelae is further divided into two infraorders: Mygalomorphae (Figure 11B), which includes 30 extant families and more than 3,000 species, with (almost) paraxial chelicerae (Figure 12A), a simple silk spinning system and reduced

spinnerets (i.e., only two pairs present in most species) and two pairs of booklungs (Figure 13B–C) (Opatova et al. 2020). The rest of the families belong to Araneomorphae (Figures 11C–D), characterised by diaxial chelicerae (Figure 12B), modified spinning structures, unique pyriform silk glands, and (usually) one pair of booklungs coupled with a tracheal respiratory system (Figure 13D) (Wheeler et al. 2017).



Figure 11. Representatives of Mesothelae (A), Mygalomorphae (B) and Araneomorphae (C–D). **A.** Juvenile of an unidentified species of *Liphistius* Schiødte, 1849 (Liphistiidae). **B.** Female *Raveniola niedermeyeri* (Brignoli, 1972) (Nemesiidae). **C.** Female *Segestria senoculata* (Linnaeus, 1758) (Segestriidae). **D.** Male *Araniella villanii* Zamani, Marusik & Šestáková, 2020 (Araneidae). Photos: Alireza Zamani (A–B), Anton A. Nadolny (C) and Anatolij Ozerney (D).

Based on the absence or presence of a cribellum (Figure 14), Araneomorphae was traditionally divided into two groups, the Ecribellatae and Cribellatae. This has been refuted, as it is now generally agreed upon that the cribellum is a synapomorphy for Araneomorphae, albeit being secondarily lost in the majority of them (Wheeler et al. 2017).

Another traditional classification system divided Araneomorphae into two groups: Haplogynae, comprising families with ‘simple’ copulatory organs (i.e., bulb

usually simplified with fused sclerites and lacking basal haematodocha, female genitalia usually lacking sclerotization and bearing a single opening for the entrance of the sperm and the exit of the fertilised eggs), and Entelegynae, comprising families with ‘complex’ copulatory organs (i.e., male copulatory bulb complex and usually with multiple sclerites, female genitalia sclerotized and with separate ducts for copulation and fertilisation) (Figures 15A–E, 16A–D, 17A–B). Some recent phylogenies have not recovered Haplogynae as monophyletic, but weakly supported Entelegynae (Wheeler et al. 2017). Synspermiata, a non-typified group characterised by the fusion of several spermatids into one synspermium, comprises most families of the former Haplogynae (Michalik & Ramírez 2014; Wheeler et al. 2017).

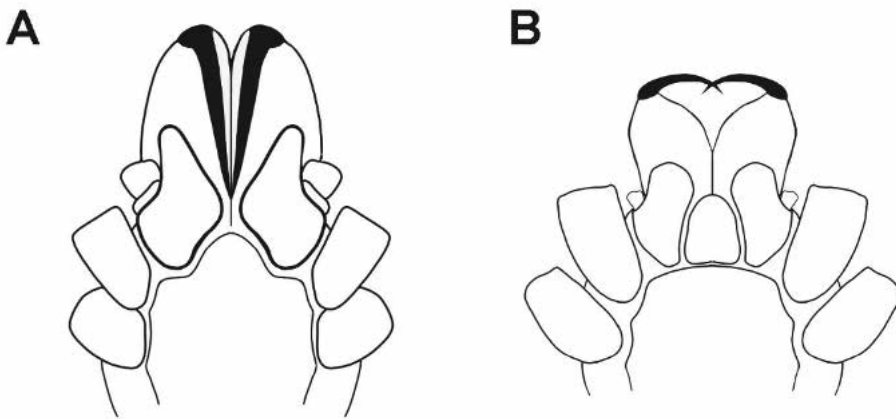


Figure 12. Comparison of chelicerae types. **A.** Paraxial chelicerae in Mygalomorphae. **B.** Diaxial chelicerae in Araneomorphae. Illustrations: Mahla Pourcheraghi.

On the basis of the number of tarsal claws, Entelegynae was traditionally divided into Dionycha (i.e., two claws) and Trionycha (i.e., three claws). Recent phylogenies support only the former group, albeit weakly. Together with several other families, Dionycha form the RTA clade, which is characterised by the presence of a retrolateral tibial apophysis on the male palp (though secondarily lost in some groups) that provides more stability during copulation (Wheeler et al. 2017) (Figure 15D).

There is no consensus within the arachnological community regarding the homology (or terminology) of the sclerites of the male palp across and within various groups of spiders. These sclerites are located on the bulb, which is attached (or rarely fused) to the cymbium (i.e., male palpal tarsus) and internally bears a tube containing the sperm called the spermophor.

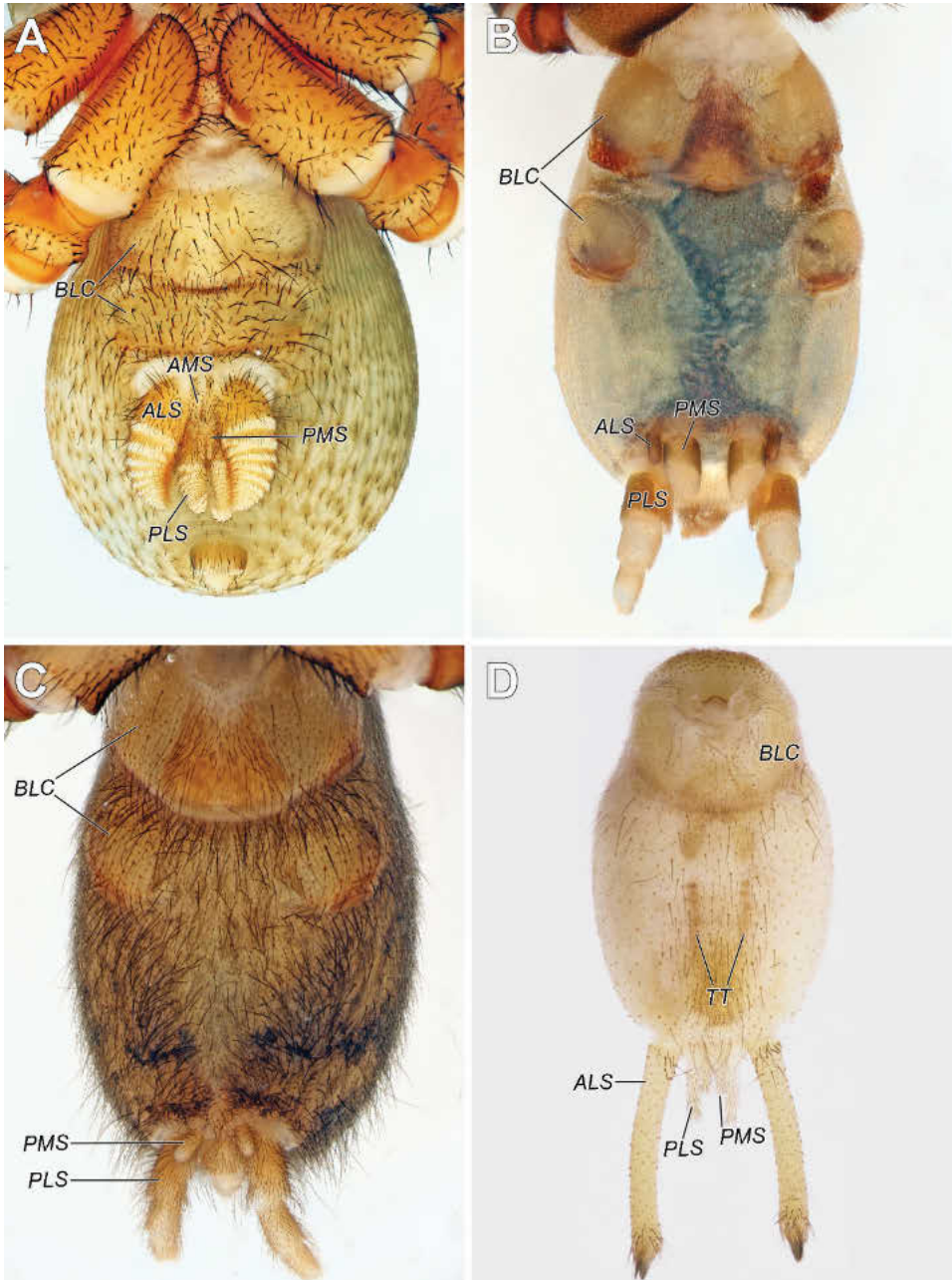


Figure 13. Comparison of the ventral view of the abdomen in representatives of Mesothelae (A), Mygalomorphae (B–C) and Araneomorphae (D). A. Juvenile of an unidentified species of *Liphistius* Schiødte, 1849 (Liphistiidae). B. Male *Atypus muralis* Bertkau, 1890 (Atypidae). C. Male *Raveniola niedermeyeri* (Brignoli, 1972) (Nemesiidae). D. Male *Pterotricha strandi* Spassky, 1936 (Gnaphosidae). Abbreviations: ALS – anterior lateral spinnerets, AMS – anterior median spinnerets, BLC – booklung cover, PLS – posterior lateral spinnerets, PMS – posterior median spinnerets, TT – tubular tracheae. Photos: Alireza Zamani. D from Zamani et al. (2018c).



Figure 14. Spinneret area of female *Sahastata sinuspersica* Marusik, Zamani & Mirshamsi, 2014 (Filistatidae). Abbreviation: Cr – cribellum. Photo: Yuri M. Marusik, from Marusik et al. (2014b).

In most groups of Entelegynae, the bulb is formed by three main divisions that are connected to each other and to the cymbium by inflatable membranous tissues called haematodochae. These three divisions are: the subtegulum (i.e., the basal division), the tegulum (i.e., the median division), and the embolic division. The subtegulum is connected to the cymbium and bears only the blind end of the spermophor, and the tegulum is the larger division that contains a larger portion of the spermophor and usually bears several sclerites. The embolic division is located distally and bears the embolus and occasionally other sclerites (Figure 15A–D).

Historically, the only sclerite with an uncontroversial homology assumed to be present in all spiders was the embolus, the intromittent sclerite containing the ejaculatory portion of the spermophor through which the sperm is injected into the female (Agnarsson & Coddington 2008). Recently, however, this was contradicted by the discovery of a remarkable sperm transfer system in a lineage of Australian

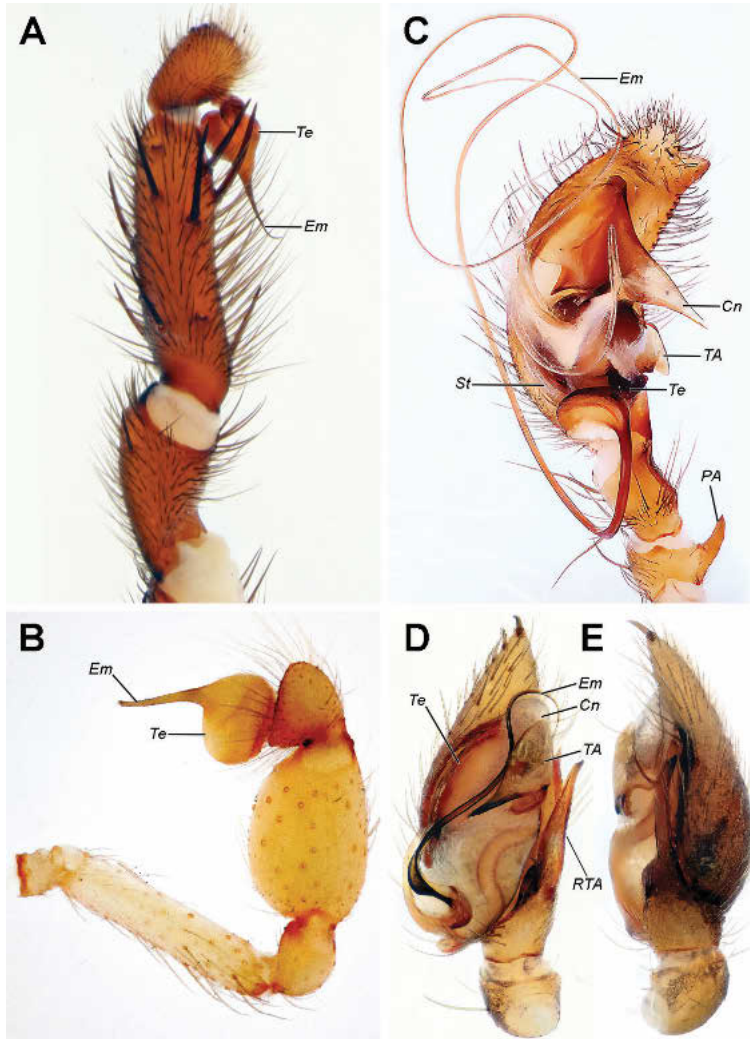


Figure 15. Comparison of male palps in representatives of Mygalomorphae (A), Synspermiata (B) and Entelegynae (C–E), in prolateral (A–B), ventral (C–D) and retrolateral (E) views. A. *Raveniola niedermeyeri* (Brignoli, 1972) (Nemesiidae). B. *Loxosceles rufescens* (Dufour, 1820) (Sicariidae). C. *Draconarius nathiagalicus* Zamani, 2021 (Agelenidae). D–E. *Parazodariion raddei* (Simon, 1889) (Zodariidae). Abbreviations: Cn – conductor, Em – embolus, PA – patellar apophysis, RTA – retrolateral tibial apophysis, St – subtegulum, TA – tegular apophysis, Te – tegulum. Photos: Alireza Zamani. C from Zamani (2021), D–E from Zamani & Marusik (2021b).

palpimanoids, consisting of a bifurcate spermophor bearing two ejaculatory ducts, each terminating within a distinct embolic sclerite (Rix et al. 2021). The most widespread sclerites on the tegulum are the conductor and the median apophysis, which may also be fused or lost in certain groups. There are additional sclerites occurring across different lineages (e.g., radix, theridiid tegular apophysis,

paramedian apophysis, terminal apophysis, suprategulum), the homology of which is even more controversial (Agnarsson & Coddington 2008). This lack of a unified hypothesis on the homology of these structures has led to the existence of different terminologies for sclerites that are more likely to be homologous. For example, the terms ‘median apophysis’ and ‘tegular apophysis’ refer to the same sclerite, with the former describing its position and the latter its origin.

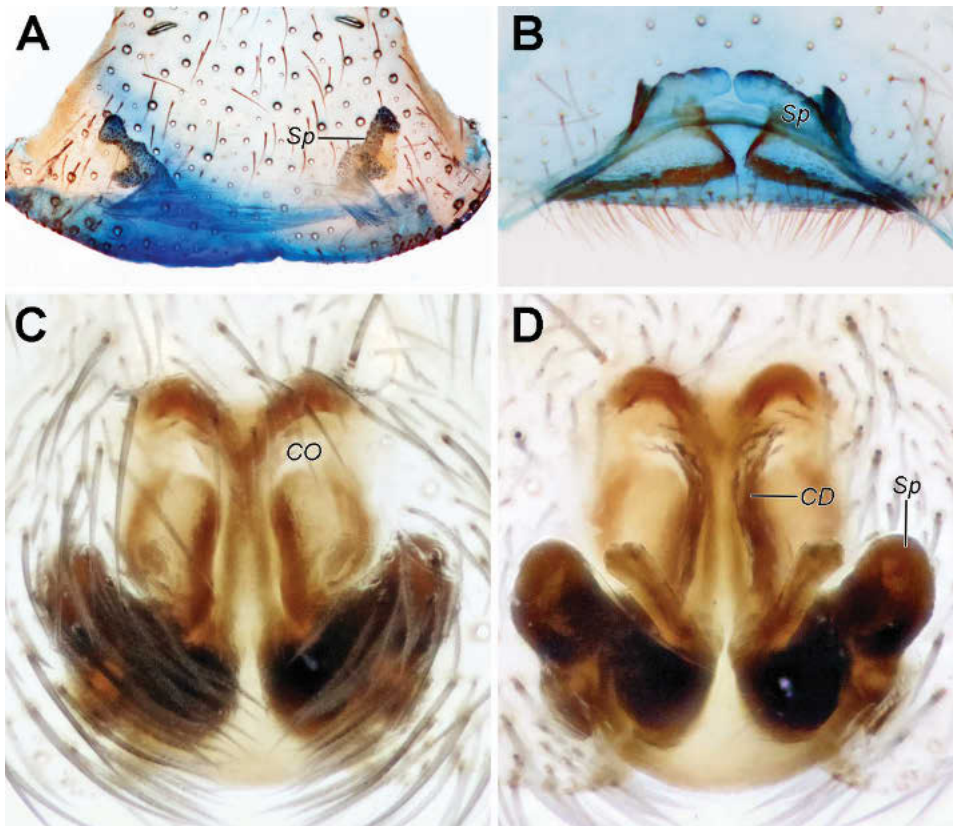


Figure 16. Comparison of female copulatory organs of Mygalomorphae (A), Synspermiata (B) and Entelegynae (C–D), in dorsal (A–B, D) and ventral (C) views. A. *Raveniola niedermeyeri* (Brignoli, 1972) (Nemesiidae). B. *Loxosceles rufescens* (Dufour, 1820) (Sicariidae). C–D. *Pterotricha strandi* Spassky, 1936 (Gnaphosidae). Abbreviations: CD – copulatory duct, CO – copulatory opening, Sp – spermatheca (i.e., receptacle). Photos: Alireza Zamani. C–D from Zamani et al. (2018c).

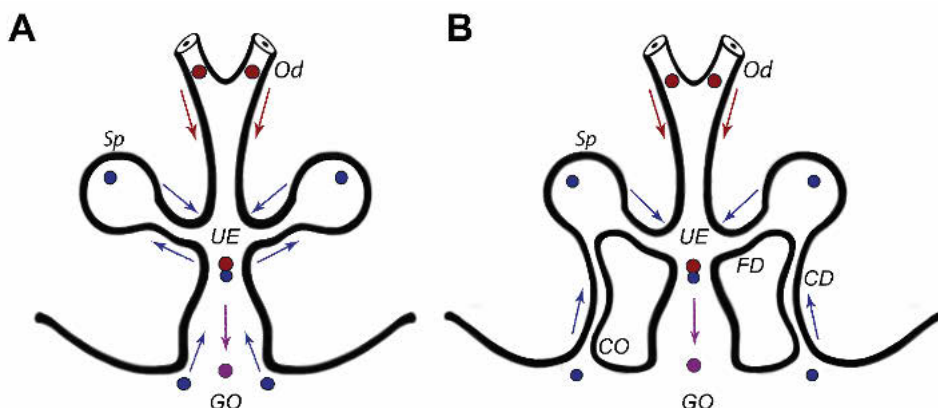


Figure 17. Schematic diagrams of the female reproductive anatomy of haplogyne (**A**) and entelegyne (**B**) spiders, showing the direction of transmission of the sperm (blue), eggs (red) leaving the ovaries and a fertilised egg (purple) being expelled from the genital opening. Abbreviations: *CD* – copulatory duct, *CO* – copulatory opening, *FD* – fertilisation duct, *GO* – genital opening, *Od* – oviduct, *Sp* – spermatheca, *UE* – uterus externus. Illustrations: Mahla Pourcheraghi.

1.1.7 Taxonomy and Identification

Based on a survey of spider taxonomic research published during 2008–2018 (i.e., a total of 2,083 publications with 8,433 new species descriptions), Bond et al. (2021) reported that the taxonomy of the group remains largely non-revisionary and non-integrative, without any clear conceptual framework. A species concept was found to be explicitly stated in only less than 4% of the publications, with almost half of the publications describing a single species, and more than one-third of the species descriptions based on singleton or doubleton specimens or only one sex. They also reported that integrative studies comprise only about 14% of the publications; molecular data, in particular, were found to be employed in only about 6% of all studies and represented in about 43% of the integrative ones.

As it is clear from these statistics, the taxonomy of spiders remains largely descriptive and morphologically oriented. The structure and conformation of the copulatory organs (i.e., adult male palp and female genitalia) are species-specific and generally show little to no intraspecific variations, making them the primary characters used in species descriptions and diagnoses. In taxonomic publications, spiders and their body parts are typically illustrated via drawings (Figure 18B), digital images (i.e., light microscopy, image stacking) (Figure 18A), scanning electron microscopy (Figure 18C) or micro computed tomography (Bond et al. 2021).

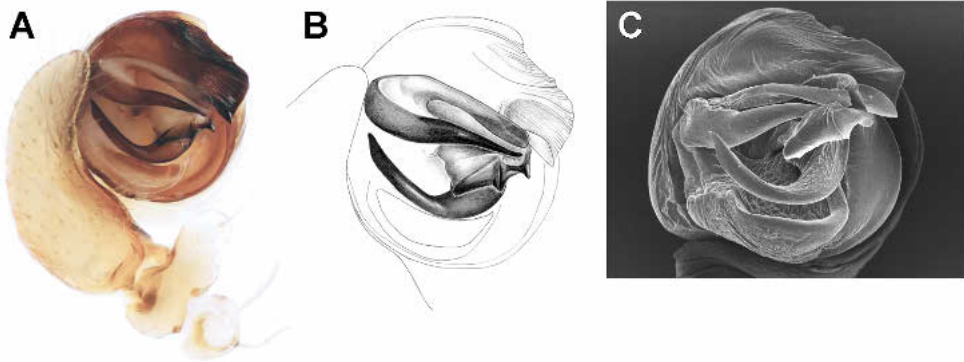


Figure 18. Male palp of *Araniella mithra* Zamani, Marusik & Šestáková, 2020 (Araneidae), illustrated via digital imaging (A), drawing (B) and scanning electron microscopy (C). Photos and Illustration: Alireza Zamani (A), Anna Šestáková (B) and Yuri M. Marusik (C). All from Zamani et al. (2020d), with modifications.

On average, more than 830 species of spiders have been described annually over the past decade, with an all-time high of 1,019 species in 2012 (WSC 2023) (Figure 19). This high productivity can partially be attributed to a relatively large number of collaborative research groups and their infrastructure and availability of financial support. Furthermore, the World Spider Catalog Association (WSCA), under the Natural History Museum of Bern (Switzerland) has collected all taxonomic spider literature (currently around 17,000 references) and made them freely accessible to its more than 5,000 members since 2014. WSCA is an association under the Swiss Civil Law, and since it is without commercial purpose and does not require membership fees, there are no restrictions concerning the availability of copyright protected material within this association. This initiative has significantly enhanced taxonomic research of spiders, as the database logs a daily average of more than 1,000 sessions and 600 downloads (data for 2020; W. Nentwig pers. comm.).

Finally, there are numerous identification resources available for different regions. The prime example for this is the ‘Spiders of Europe’ website, currently encompassing around 5,500 species for most of which dichotomous keys and taxonomic illustrations of the copulatory organs are included (Nentwig et al. 2023). This database is regularly used by experts and naturalists alike (i.e., reported to have an average of 500 daily visitors in May 2016) and has considerably facilitated the identification process of spiders in Europe, North Africa and the Middle East (pers. obs.). Further resources in the forms of field guides and identification manuals have also been published for different countries in North America (e.g., Bradley 2012; Ubick et al. 2017), Europe (e.g., Almquist 2005, 2006; Bee et al. 2017; Kůrka et al. 2015), Africa (e.g., Dippenaar-Schoeman 2014; Jocqué & Dippenaar-Schoeman

2006; Penney 2009), Asia (e.g., Koh & Bay 2019; Marusik & Kovblyuk 2011; Murphy & Murphy 2000; Ono 2009; Sebastian & Peter 2009; Song et al. 1999; Zamani 2016b) and Australasia (e.g., Forster & Forster 1999; Whyte & Anderson 2017).

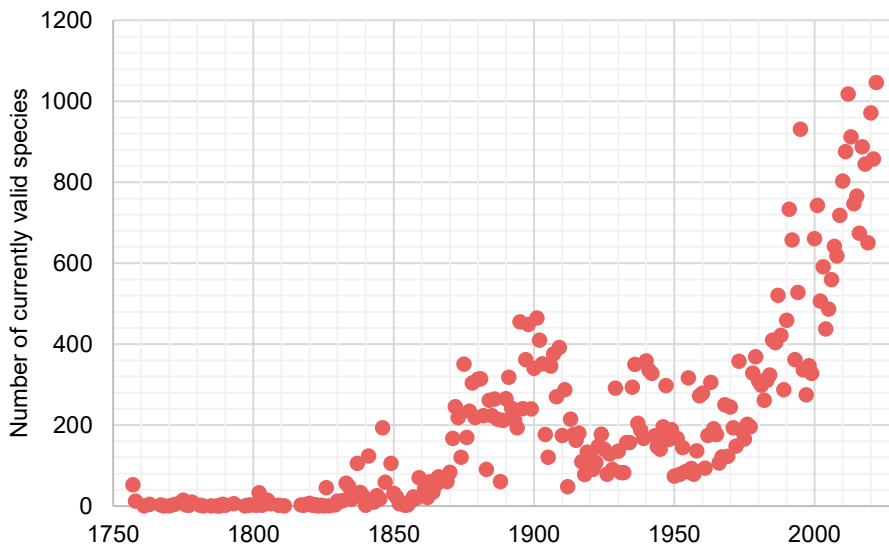


Figure 19. Numbers of currently valid species (as of January 15th, 2023) of spiders described per year (WSC 2023; D. Gloor, pers. comm.).

1.1.8 Distribution of records

The records of spiders, like most other taxonomic groups, are unevenly distributed on a global scale and often heavily affected by a biased sampling effort (Oliveira et al. 2017). This has resulted in vast geographic regions with few or no records of species, while smaller areas closer to main roads, larger cities, and research institutions comprise a considerably higher number of records (Santos et al. 2017). Acquiring such information and addressing the Wallacean shortfall is crucial for gaining a better understanding of the diversity and distribution patterns for any biological group. While attempts to explore such patterns and identifying areas affected by this shortfall have been made for the Neotropical spiders (Santos et al. 2017) and a few other faunas (e.g., Meng et al. 2008), most other regions have been historically neglected, even if not heavily affected by the Linnean shortfall (e.g., North America).

1.2 An overview of Iran and its geographical and ecological features

Iran, with an area of 1,648,195 km², is a vast Middle Eastern country that borders Armenia, Azerbaijan, Turkmenistan and the Caspian Sea in the north, Afghanistan and Pakistan in the east, Turkey and Iraq in the west, and the Persian Gulf and the Gulf of Oman in the south. The primary administrative divisions of Iran are its 31 provinces (Figure 20). Historically the country had been more commonly known as ‘Persia’ in the Western world, before ‘Iran’ became its officially universal title in 1935 (Baum & O’Gorman 2010).

Iran constitutes the greater part of the Iranian Plateau, a northwest–southeast-oriented geographical unit of mountainous highlands resulting from the collision of the Eurasian and Arabian tectonic plates during the Miocene (Mouthereau et al.

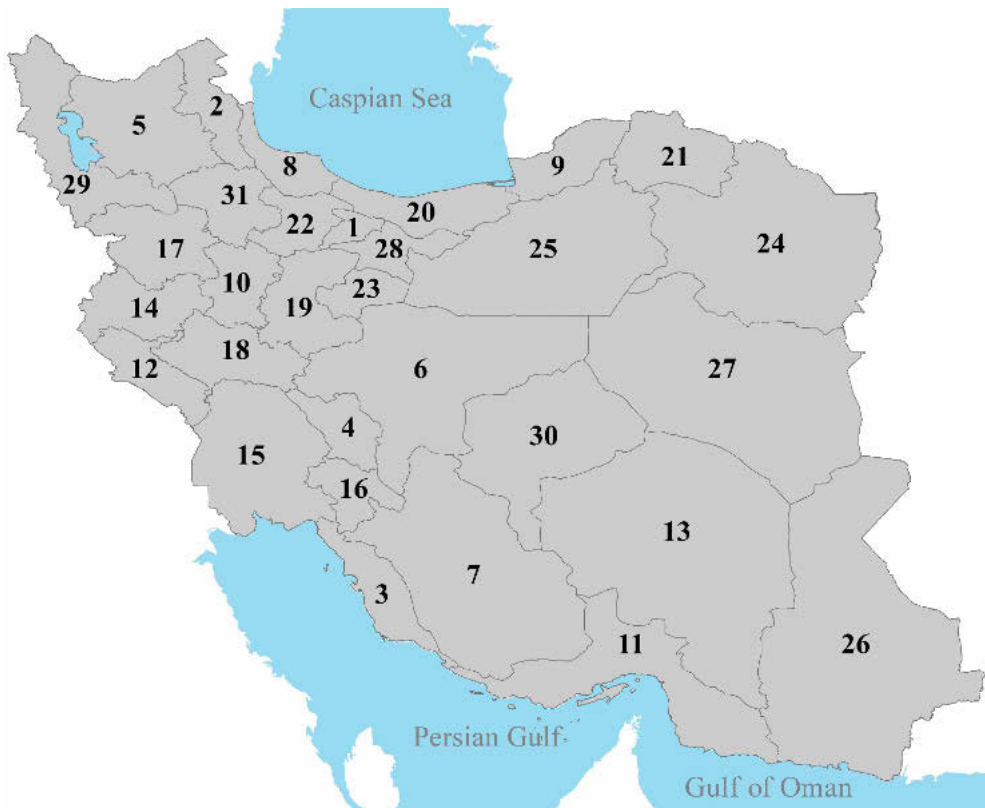


Figure 20. Provinces of Iran. 1. Alborz. 2. Ardabil. 3. Bushehr. 4. Chaharmahal & Bakhtiari. 5. East Azerbaijan. 6. Isfahan. 7. Fars. 8. Gilan. 9. Golestan. 10. Hamedan. 11. Hormozgan. 12. Ilam. 13. Kerman. 14. Kermanshah. 15. Khuzestan. 16. Kohgiluyeh & Boyer-Ahmad. 17. Kurdistan. 18. Lorestan. 19. Markazi. 20. Mazandaran. 21. North Khorasan. 22. Qazvin. 23. Qom. 24. Razavi Khorasan. 25. Semnan. 26. Sistan & Baluchistan. 27. South Khorasan. 28. Tehran. 29. West Azerbaijan. 30. Yazd. 31. Zanjan.

2012). Due to this collision, the Zagros Mountains (a part of the Alpine-Himalayan orogenic belt) were formed at the westernmost limits of the Iranian plateau, extending for a total length of 1,600 km in southeastern Turkey, northern Iraq and west to southern Iran. Several other mountain ranges and mountainous regions also occur within the modern boundaries of Iran: Qaradagh (=Arasbaran) Mountains in the northwest, the Alborz Range in the north, the Kopetdagh and Aladagh Ranges in the northeast, and the East and Central Iranian ranges. At an elevation of 5,671 m, Mount Damavand in the Alborz Range is the highest peak in Western Asia and the highest volcano in Asia. Iran is further characterised by seven desert plains and depressions, including the Lut Desert in the southeast, which has been dubbed the hottest desert and the ‘thermal pole’ of the Earth (Azarderakhsh et al. 2020). There are six main watersheds and more than 20 larger lakes in Iran, including the Urmia Lake in the northwest, which at its greatest extent was the world’s sixth largest saltwater lake (Zehzad et al. 2002).

Eighteen diverse terrestrial ecoregions are recognized in Iran (Olson et al. 2001) (Figure 21). Three comprise an arid to semi-arid region, covering around 55% of the area of the country: the central Persian desert basins (35.01%), the south Iran Nubio-Sindian desert and semi-desert (16.73%) and the Registan-North Pakistan sandy desert (2.91%). The most humid part of Iran is located in the Caspian-Hyrcanian mixed forests ecoregion (3.47%), along the coast of the Caspian Sea and the northern slopes of the Alborz Mountains. It receives 800–2,000 mm of annual rainfall (Zehzad et al. 2002).

Considering the diverse geology and topography of Iran and the transitional position of the country between the Palaearctic, Oriental and Afrotropical realms, a significant biogeographical diversity comprised of faunal and floral elements of all three noted regions can be observed in Iran, including more than 8,000 species of vascular plants and over 1,000 species of vertebrates (Serri & Frisch 2016; Jowkar et al. 2016; Noroozi et al. 2019). Furthermore, different regions of Iran underwent several glacial periods and Quaternary climatic oscillations, which significantly affected the diversity and distribution patterns of species (Kafash et al. 2020). The primary biodiversity hotspots in Iran and centres of origin for many endemic species are considered to be the Zagros and Alborz Mountain Ranges. Their uplift likely facilitated speciation by isolating populations of species and providing new, unoccupied habitats (Kafash et al. 2020). Also, both areas acted as refugia for different groups of species during the glacial periods (Veith et al. 2003; Ahmadzadeh et al. 2013; Parvizi et al. 2018; Kafash et al. 2020). Unfortunately, these areas remain poorly studied and insufficiently protected despite the high number of endemic and relic populations that they harbour.

Although there are more than 250 protected areas in Iran which roughly encompass 10% of the land surface of the country, the Iranian biodiversity suffers

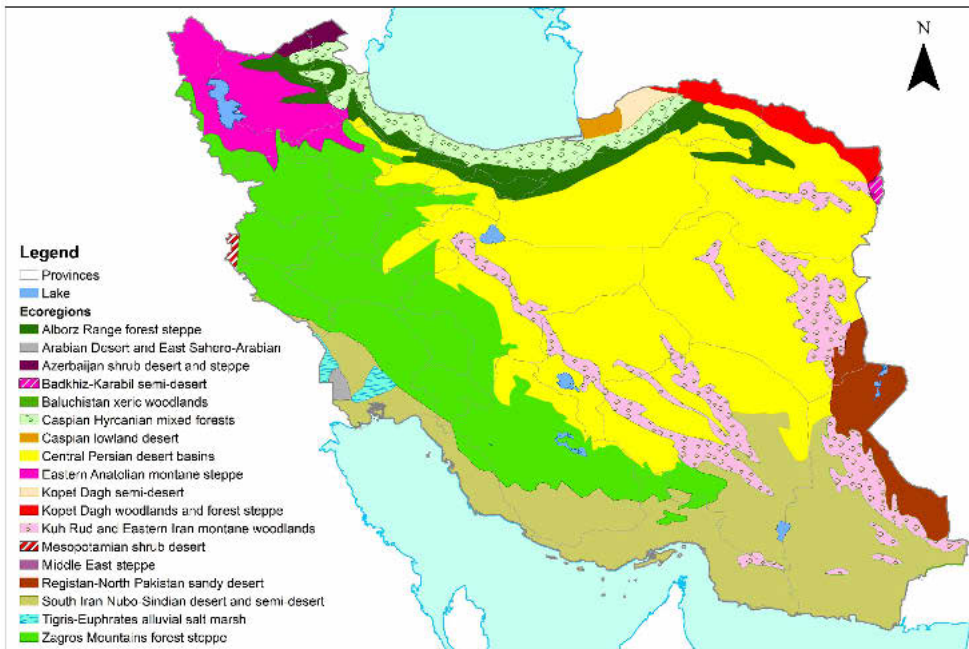


Figure 21. Terrestrial ecoregions of Iran, from Safaei-Mahroo et al. (2015) with modifications.

from serious threats primarily related to the large growth of the human population during the last six decades, as well as climate change, poaching and economic sanctions. According to the categories and criteria of the Red List of Threatened Species administered by the International Union for Conservation of Nature (IUCN 2012), there are more than 100 species of vertebrates in Iran that are classified as vulnerable, endangered or critically endangered. The local populations of the emblematic Asiatic lion and Caspian tiger have already been eradicated, and the two remaining species of large cats in Iran, the Asiatic cheetah and the Persian leopard, are currently classified as ‘Critically Endangered’ and ‘Endangered’, respectively (Jowkar et al. 2016). Unfortunately, scarcely any information exists on the conservation status of the local species or populations of invertebrates. Regardless, general trends of decline in their diversity or abundance have already been documented (e.g., Hodjat et al. 2019), and a few studies have evaluated the effects and impact of climate change on their distribution patterns (e.g., Solhjoui-Fard & Sarafrazi 2014; Ghasemi et al. 2021).

1.3 History of araneological research in Iran

The first known recorded observation of a spider from Iran was made by Olearius (1656), who reported the occurrence of ‘tarantulas’ in the vicinity of Kashan, central

Iran [from a translation by John Davies of 1662]: "... Kaschan [*sic*] is a place excellently well seated, but the air must be somewhat unwholesome, when they want fresh water thereabouts, and that it is here the tarantulas and the most dangerous scorpions of all Persia are most rife." Two years later, Schöngast (1668) reported a similar observation from Kerman in southeastern Iran, regarding a 'poisonous tarantula' that he termed 'Enkurek Persarum'. Both of these reports most likely refer to large-sized burrowing wolf spiders (Lycosidae) known in Medieval Latin as *tarantula* (Cokendolpher et al. 2019). The modern, international usage of the word 'tarantula' refers to members of Theraphosidae; although a few species of this family occur in the region, they are relatively rare, small (compared to their tropical relatives) and not of particular medical importance.

The first scientific collection of Iranian spiders was most likely the one made by Eugen von Keyserling and Theophil Bienert during 1859, the greater portion of which is currently housed in the Zoological Institute in Saint Petersburg (Russia). This collection has been partially studied by several researchers, and a few species have been described on the basis of its specimens (e.g., Logunov & Marusik 1999; Azarkina & Zamani 2019).

The Italian naturalists Giacomo Doria and Filippo de Filippi made the second collection of spiders in Iran from 1862 to 1863, the specimens of which are deposited in the Museo civico di Storia naturale di Genova (Italy) and Muséum national d'Histoire naturelle, Paris (France). The first two taxonomic publications in part including Iranian spiders were based on specimens collected by Doria and de Filippi in Tehran, and each involved the description of a new species: Simon (1874a) described *Sparassus doriae* (now in *Eusparassus* Simon, 1903) (Sparassidae), and Thorell (1881) described *Pholcus doriae* (now in *Artema* Walckenaer, 1837) (Pholcidae). Furthermore, two additional species, *Nurscia albosignata* Simon, 1874 (Titanocidae) and *Sparassus fontanieri* Simon, 1880, were described in this period based on material from unknown type localities that were assumed to be in Iran (Simon 1874b, 1880); for the latter, which is now a synonym of *Eusparassus walckenaeri* (Audouin, 1826), this (i.e., the type locality in Iran) was recently rejected by Zamani et al. (2022c).

In the late 19th and early 20th centuries, several contributions to the study of the arachnids of Iran (sometimes including the vicinity) were made by Pocock (1889, 1899, 1901, 1903) and Pickard-Cambridge (1902). These publications primarily reported new distribution records of species of *Argiope* Audouin, 1826 (Araneidae), *Latrodectus* and a few other genera, as well as the descriptions of three species, namely *Tarantula medica* Pocock, 1889 (now in *Karakumosa* Logunov & Ponomarev, 2020), *Lycosa guentheri* Pocock, 1899 (now a synonym of *Hogna radiata* (Latreille, 1817)) (both Lycosidae) and *Sparassus xerxes* Pocock, 1901 (now in *Eusparassus*). A few smaller contributions reporting (in part) on Iranian spiders

were later published by Reimoser (1913), Wiehle (1931), Werner (1936), Shulov (1940) and Pavlovsky (1942). Several expeditions were made to Iran by Russian, German and British naturalists during 1863–1916, including: Friedemann Adolph Goebel (in 1863 and 1867), William T. Blanford (in 1870s), Nikolai A. Zarudny (in 1899, 1903, 1904 and 1907), Frederick W. Townsend (in 1880s), Robert Gunther (in 1898), Andrei A. Matthiessen (in 1904), E.M. Filippovich (in 1905), Nikolai A. Solovkin (in 1913 and 1914), Oskar von Niedermayer (in 1913), Alexander N. Kirichenko (in 1914), Petr V. Nesterov (in 1914), Sergei N. von Wick (in 1914), P. Andrievskiy (in 1914) and Alexander N. Derzhavin (in 1916).

The first major publication on Iranian spiders was published in 1955 by the German arachnologist Carl Friedrich Roewer, who listed a total of 77 species (including 17 described as new) identified from the material collected in Iran by the Austrian naturalists Jens Hensen, Alfred Kaltenbach, Heinz Löffler and Ferdinand Starmühlner from 1949 to 1950 (Roewer 1955). The descriptions and illustrations are of poor quality, and most of the species are either misidentified or assigned to wrong genera or even families. For example, Roewer described different populations of *Trochosa hispanica* Simon, 1870 (Lycosidae) as three different species in three genera: *Arctosa nava* Roewer, 1955, *Geolycosa flavichelis* Roewer, 1955 and *Loculla austrocaspia* Roewer, 1955 (Marusik & Nadolny 2020). Subsequent re-examinations of this material by several authors have resulted in the synonymy of many species and a rejection of most of the records. Roewer reported two more species from Iran four years later (Roewer 1959), one of which was recently found to be misidentified in the wrong genus (Zamani et al. 2022c).

The first publication on spiders in Iranian literature was Zini (1958), who reported on the biology and distribution of the Mediterranean widow spider, *Latrodectus tredecimguttatus* (Rossi, 1790), in northeastern Iran. One year later, and in his revision of the genus, Levi (1959) provided a description of *Latrodectus dahli* Levi, 1959 based on material collected in southern Iran. During the 1950s–70s, several expeditions were made to Iran by American (e.g., Lee H. Herman in 1962; John W. Neal in 1964), Austrian (e.g., Franz Ressler in 1961; Gerhard Pretzmann in 1968, 1970 and 1974; Karl Bilek in 1970 and 1972; Hannes F. Paulus in 1971; Walter Gstader in 1976), Czechoslovak (e.g., Jaroslav Boháč in 1976; Bohumil Pražan in 1977), Finnish (e.g., Pekka Lehtinen in 1971), German (e.g., Jochen Martens and Harald Pieper in 1978), Italian (e.g., Valerio Sbordoni in 1966; Paolo M. Brignoli, Pier G. Bianco, Massimo di Rao and Sergio Zerunian in 1975 and 1976) and Swiss researchers, which provided new collections of material studied and reported over the following decades. The most comprehensive collection of Iranian spiders was made from 1973 to 1975 by the Swiss arachnologist Antoine Senglet, particularly in the northern and western parts of the country. This collection, now almost completely studied, is housed in the Muséum d'histoire naturelle, Genève

(Switzerland) and has provided an extensive amount of material treated in the regional revisions (Schwendinger & Monnerat 2022). The first paper published on the basis of this collection was Senglet (1974), which described four new species and reported one new record of *Pholcus* Walckenaer, 1805 (Pholcidae) from Iran.

The Italian arachnologist Paolo Brignoli published a series of articles from 1970 to 1982 that in part reported and described spider material collected in Iran, including several new species of Dysderidae, Filistatidae, Linyphiidae and Nemesiidae (Brignoli 1970, 1972, 1977, 1978, 1979, 1980, 1982). Until the end of the 20th century, further scattered material from Iran (including several new species and records) was reported by Baum (1972), Kraus & Baur (1974), Helsdingen et al. (1977), Thaler (1986), Wesołowska (1986), Kraus & Kraus (1989), Schwendinger (1990), Prószyński (1992), Ovtsharenko et al. (1994), Platnick & Gajbe (1994), Wunderlich (1995a, 1995b), Buchar & Thaler (1995), Saaristo & Tanasevitch (1996a, 1996b), Logunov (1997, 1998, 1999), Logunov & Marusik (1999, 2000), Logunov et al. (1999), Marusik et al. (2000) and Zonstein (2000). Several papers reporting new distribution records of Iranian spiders were published by local researchers during this period (Darvish & Mirshamsi 1999; Mirshamsi et al. 2000; Mozaffarian 2000; Mozaffarian et al. 2000). Additionally, Yuri. M. Marusik conducted an expedition to northern and south-central Iran in 2000, with his collected material reported in numerous publications over the years.

The beginning of the 21st century marked a turning point in araneological research in Iran, starting with the publication of the first national checklist by Mozaffarian & Marusik (2001), listing the occurrence of 141 species of 25 families of spiders in the country. An updated checklist of Iranian spiders was published by Ghavami (2006b), listing the occurrence of 244 species from 33 families; however, the list has several issues, e.g., 25 taxa not identified to species or even genus level, listing *Cheiracanthium mildei* L. Koch, 1864 (Cheiracanthiidae) once in Miturgidae and once (as *Clubiona mildei*) in Clubionidae, and not including the important publication of Ono & Martens (2005). Furthermore, the check list contains many spelling errors of taxon names, non-existent species and publications, and records of clearly misidentified taxa that do not occur in the region. The third checklist of Iranian spiders was published by Mirshamsi et al. (2015a), which listed 528 species of 230 genera and 45 families. Further versions of the checklist have since been published as an annually updated website (<<http://www.spiders.ir>>). The online checklist includes a complete bibliography and detailed list of provinces from which the species have been reported, as well as a list of rejected records and non-annotated checklists of other Iranian arachnids, except for Acari (Zamani et al. 2022b). A non-annotated checklist of Iranian spiders (and scorpions) is also included in “The Field Guide of Spiders and Scorpions of Iran,” which is the first field guide devoted to the arachnids of the Middle East (Zamani 2016b).

Several taxonomic contributions toward spiders of Iran have been published during the 21st century, many of them genus- or family-level regional revisions. Almost all of the new species descriptions were based on morphological data alone, with molecular data used only in the descriptions of two species (Tahami et al. 2017; Shafaie et al. 2018a). Publications from this period providing taxonomic and nomenclatural data on Iranian spiders, involving descriptions of new taxa and unknown sexes, redescriptions and proposal of synonymies, new combinations and other taxonomic acts are as follows:

Aharon et al. (2017), Azarkina (2002, 2004), Azarkina & Mirshamsi (2014), Azarkina & Zamani (2019, 2020), Blick & Ono (2021), Esyunin & Zamani (2019, 2020), Esyunin et al. (2011, 2017), Huber (2011, 2022), Kranz-Baltensperger et al. (2009), Logunov (2001a, 2001b, 2004, 2006, 2007, 2009, 2010, 2021, 2022), Logunov et al. (2002a, 2002b), Makhan & Ezzatpanah (2011), Malek Hosseini et al. (2015a), Marusik & Fet (2009), Marusik & Zamani (2015a, 2015b, 2015c, 2016), Marusik & Nadolny (2020, 2021), Marusik & Omelko (2018), Marusik et al. (2012, 2013a, 2013b, 2014a, 2014b), Mikhailov (2003), Mirshamsi (2018), Mirshamsi et al. (2013b, 2016), Moradmand (2013, 2017), Moradmand & Jäger (2011, 2012), Moradmand et al. (2016, 2019), Montemor et al. (2020), Mozaffarian & Marusik (2001), Nadolny & Zamani (2017, 2020), Ono & Martens (2005), Ovtchinnikov et al. (2009), Platnick et al. (2012), Schwendinger & Zamani (2018), Schwendinger & Zonstein (2011), Shafaie et al. (2018a, 2022a, 2022b), Senglet (2008, 2011, 2012, 2013), Szűts et al. (2023), Tahami et al. (2017), Tanasevitch (2008, 2009, 2011, 2017), Thaler (2002), Wunderlich (2011), Zakerzade et al. (2022), Zamani (2016c), Zamani & Bosselaers (2020), Zamani & Marusik (2016, 2017, 2018a, 2018b, 2018c, 2019, 2020a, 2020b, 2020c, 2020d, 2021a, 2021b, 2021c, 2021d, 2021e, 2021f, 2022a), Zamani et al. (2016a, 2017a, 2017b, 2017d, 2017e, 2018a, 2018c, 2020a, 2020b, 2020c, 2020d, 2021a, 2021b, 2021c, 2022c, 2022d, 2023a), Zonstein (2018), Zonstein & Marusik (2010, 2016, 2019), Zonstein et al. (2018).

A series of primarily faunistic papers entitled “New data on the spider fauna of Iran” aiming to report new distribution records on Iranian spiders was initiated in 2014. As a result of this series, with 10 parts to date, seven families, 56 genera and more than 260 species were reported in Iran for the first time, and hundreds of new and additional provincial records and occasional data on the fauna of other countries in the region were published. The series also included a few taxonomic contributions, such as the descriptions of four new species and the previously unknown male of one species, and the proposal of a new synonymy and a new combination (Zamani et al. 2014b, 2015, 2016b, 2017c, 2018b, 2019b, 2020b, 2021c, 2022c, 2022d). The latest instalment of the series includes an updated list of misidentified taxa and rejected records.

Other publications from the 21st century that either wholly or in part provide distribution records of Iranian spiders are as follows:

Abbasi et al. (2019), Aharon et al. (2017), Alimohammadi & Moradmand (2021), Amooghli-Tabari & Ghahari (2021), Azarkina (2004), Azarkina & Mirshamsi (2014), Azarkina & Zamani (2020), Bidabadi et al. (2022), Boukan et al. (2018), Burger et al. (2003), Caleb et al. (2020), Dadpour et al. (2021), Esyunin & Sozontov (2015), Esyunin & Zamani (2019), Esyunin et al. (2017), Ghahari (2020), Ghahari & Marusik (2009), Ghahari & Tabari (2012), Ghavami (2006a, 2007, 2008a, 2008b), Ghavami & Amooz (2008), Ghavami et al. (2007a, 2007b, 2008), Gündüz et al. (2022), Henriques et al. (2018), Hosseini et al. (2014), Hosseinpour et al. (2019, 2022), Jäger (2012), Jäger & Gromov (2011), Kakhki (2005a, 2005b, 2006), Kakhki & Darvish (2002), Kashefi et al. (2013), Khodashenas et al. (2012), Khoobdel et al. (2019), Kiany et al. (2017), Knoflach et al. (2009), Komposch (2002), Logunov (2001a, 2001b, 2006, 2009, 2010, 2011, 2015, 2020, 2021), Logunov & Huseynov (2008), Logunov & Koponen (2002), Logunov & Kronestedt (2003), Logunov & Ponomarev (2020), Logunov & Zamanpoore (2005), Logunov et al. (2002a, 2002b, 2007, 2013), Luo & Li (2015), Malek Hosseini & Zamani (2017), Malek Hosseini et al. (2015b), Marusik (2010), Marusik & Guseinov (2003), Marusik & Nadolny (2020, 2021), Marusik & Zamani (2015a, 2015c), Marusik & Zonstein (2014), Marusik et al. (2009a, 2009b, 2012, 2013a, 2013b, 2014a, 2018), Mikhailov (2003, 2015), Mirshamsi & Darvish (2005), Mirshamsi et al. (2013a, 2013b, 2013c, 2015b, 2016), Mirzaee et al. (2021), Mohammadi Bavani et al. (2021), Mollaiizadeh et al. (2017), Moradi et al. (2016), Moradmand et al. (2014, 2015), Muster & Thaler (2004), Nadolny et al. (2022), Namaghi et al. (2014, 2016), Nejati et al. (2022), Nikdel (2015), Ono & Martens (2005), Ovtchinnikov et al. (2009), Özkütük et al. (2013, 2017), Rafinejad et al. (2007), Rahmani et al. (2014), Rostami et al. (2018), H. Sadeghi et al. (2016), S. Sadeghi et al. (2017), Sanaei-Zadeh (2017), Schwendinger & Zonstein (2011), Senglet (2008, 2011, 2012), Šestáková et al. (2014), Shafaie et al. (2018b, 2022a, 2022b), Shahi et al. (2011, 2015), Soufi et al. (2013), Tabrizi et al. (2014, 2015), Tanasevitch (2008, 2009), Teimouri et al. (2020), Torabi et al. (2019), Zamani (2014a, 2014b, 2014c, 2015, 2016a, 2016b), Zamani & André (2017), Zamani & Bosselaers (2020), Zamani & Crews (2019), Zamani & Marusik (2016, 2018a, 2018c, 2019, 2020a, 2020b, 2021b, 2021c), Zamani & Mozaffarian (2017), Zamani & Rafinejad (2014), Zamani et al. (2014a, 2017b, 2017d, 2018c, 2019a, 2020c, 2020d, 2021a, 2021b, 2022e), Zonstein & Marusik (2010, 2019), Zonstein et al. (2018).

In addition to systematic and faunistic publications, there have been several papers primarily dealing with other aspects of araneology in Iran. Most of these articles report cases of latrodectism and loxoscelism from different regions of the country, some also including the medical procedure that was used to treat the patients (Afshari et al. 2009;

Alizadeh et al. 2018; Ansari & Salehi 2008; Baniardalani et al. 2020; Dadpour et al. 2021; Dehghani et al. 2017; Khadem-Rezaiyan et al. 2018; Mirshamsi et al. 2013; Nejati et al. 2022; Rafinejad et al. 2007; Rahmani et al. 2014; Sanaei-Zadeh 2017; Shahi et al. 2014; Teimouri et al. 2020). There are a few publications evaluating the venoms of widow spiders, the effectivity of the antivenoms and the proposal of a clinical index for measuring the severity of the envenomation cases (Akbari et al. 2013; Monzavi & Afshari 2014; Mousavi et al. 2019; Valikhanfard-Zanjani et al. 2016, 2017). Also, based on specimens collected in Iran, Keimasi et al. (2022) reported on the effects of lycotoxin purified from the venom of *Lycosa praegrandis* C.L. Koch, 1836 on memory deficits of a rat model with glutamate-induced excitotoxicity. Some research has also been done on spider silk and its antibacterial and wound dressing properties (Roozbahani et al. 2014; Setooni et al. 2018).

Mozaffarian & Tirgari (2000) reported on the life cycle and some behavioural aspects of 12 species of spiders from northern Iran. Ghavami (2008a) explored the role of spiders as potential biological control agents against pests of cotton in Tehran. Nikdel (2015) reported *Araneus diadematus* Clerck, 1757 (Araneidae) and *Cheiracanthium punctorium* (Villers, 1789) (Cheiracanthiidae) amongst the natural predators of the gypsy moth, *Lymantria dispar* (Linnaeus, 1758) (Lepidoptera: Erebiidae) in northwestern Iran. Rostami et al. (2018) reported the predation of the lynx spider *Oxyopes lineatus* Latreille, 1806 (Oxyopidae) on the tomato leaf miner, *Tuta absoluta* (Meyrick, 1917) (Lepidoptera: Gelechiidae) from Hamedan. Several cases of teratological deformities in wolf spiders were reported by Nadolny et al. (2022), including three from Iran. Zamani (2014c) reported a case of parasitism by a mermithid nematode for the crab spider *Heriades spinipalpus* Loerbroks, 1983 (Thomisidae), and a case of predation on *Cyrtopodion scabrum* (Heyden, 1827) (Squamata: Gekkonidae) by *Steatoda paykulliana* (Walckenaer, 1806) (Theridiidae) was reported by Zamani (2016a). Doberski (1973) reported an observation of a spotted flycatcher, *Muscicapa striata* (Pallas, 1764) (Passeriformes: Muscicapidae), caught in a spider web in Miankaleh, northern Iran. Finally, Zamani et al. (2023b) reported on the effects of sampling bias on evaluating the diversity and distribution patterns of Iranian spiders. For a chart illustrating the annual numbers of publications involving Iranian spiders see Figure 22.

In addition to “The Field Guide of Spiders and Scorpions of Iran” (Zamani 2016b), there are a few other books published on the spiders in Iran, of which three are noteworthy: “The World of Spiders”, which is a Persian translation of the “Spiders of the World” by Preston-Mafham & Preston-Mafham (1984) (Mozaffarian 2004), a list of Iranian arachnids (Mohammadian 2008), and a book on the general biology, medical importance and toxicology of spiders (Goudarzi 2015).

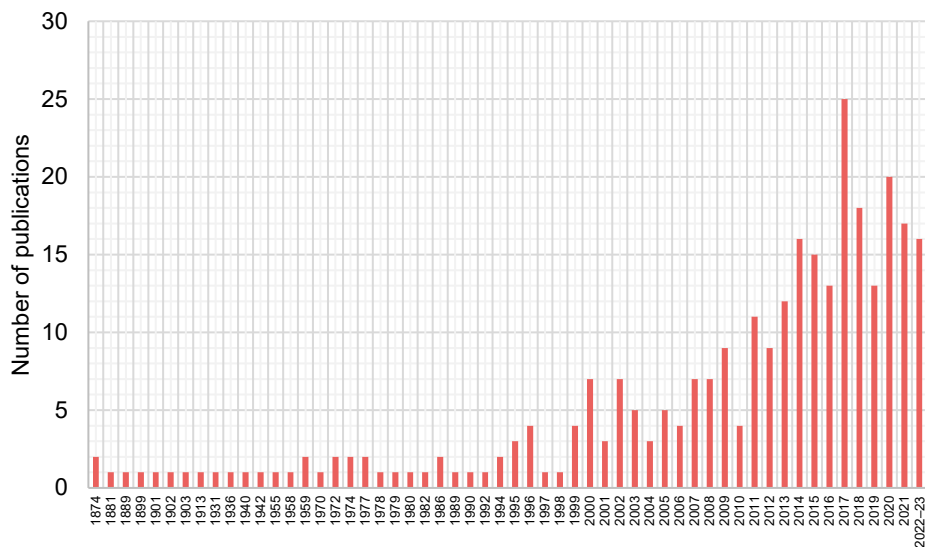


Figure 22. Numbers of scientific publications involving Iranian spiders per year. Papers published in 2023 (three, until February 10th) are counted with those of 2022.

Some species of Iranian endemic spiders display interesting ecological preferences and distributional patterns. *Iraponia scutata* Kranz-Baltensperger, Platnick & Dupérré, 2009 (Caponiidae) from southwestern Iran and the sole species of its genus, is the only caponiid known from Eurasia besides two other species occurring in Laos, China and Vietnam (WSC 2023). *Trilacuna qarzi* Grismado & Malek-Hosseini, 2015 (Oonopidae) described from Gakal Cave in southwestern Iran (Malek Hosseini et al. 2015a), is the only known Iranian spider that displays troglomorphic characters (i.e., lack of eyes, depigmentation, and relative elongation of appendages). *Paratheuma enigmatica* Zamani, Marusik & Berry, 2016 (Dictynidae) (Figure 23A), inhabiting the intertidal zone of the Persian Gulf and the Gulf of Oman, is distributed more than 6,000 km away from the closest recorded occurrence of the genus, which is otherwise known from North America, Hawaii, Far East Asia, Australia and islands in the Pacific Ocean (Zamani et al. 2016a). *Pseudomicrommata mokranica* Moradmand, Zamani & Jäger, 2019 (Sparassidae) (Figure 23B) from southeastern Iran is distributed more than 4,000 km away from the closest recorded occurrence of the genus in Kenya (Moradmand et al. 2019). *Iranotricha lutensis* Zamani & Marusik, 2018 (Gnaphosidae) (Figure 23C) and *Proszynskiana izadii* Azarkina & Zamani, 2019 (Salticidae) (Figure 23D) inhabit the hottest place on earth in southeastern Iran, where the surface temperature has been recorded as high as 80.83°C (Zamani et al. 2018c; Azarkina & Zamani 2019). The smallest spider recorded from Iran appears to be *Theridion hermonense* Levy, 1991 (Theridiidae), a species known only from females and otherwise known from Tunisia

and Israel, with a body length of only 1.1–1.3 mm (Levy 1991). The largest species in the Middle East (by leg span) is *Spariolenus iranomaximus* Moradmand & Jäger, 2011 (Figure 23E) known from Khoffash Cave in western Iran. The females of this species have been recorded to reach a body length of 31 mm and a leg span of approximately 15 cm (Moradmand & Jäger 2011).

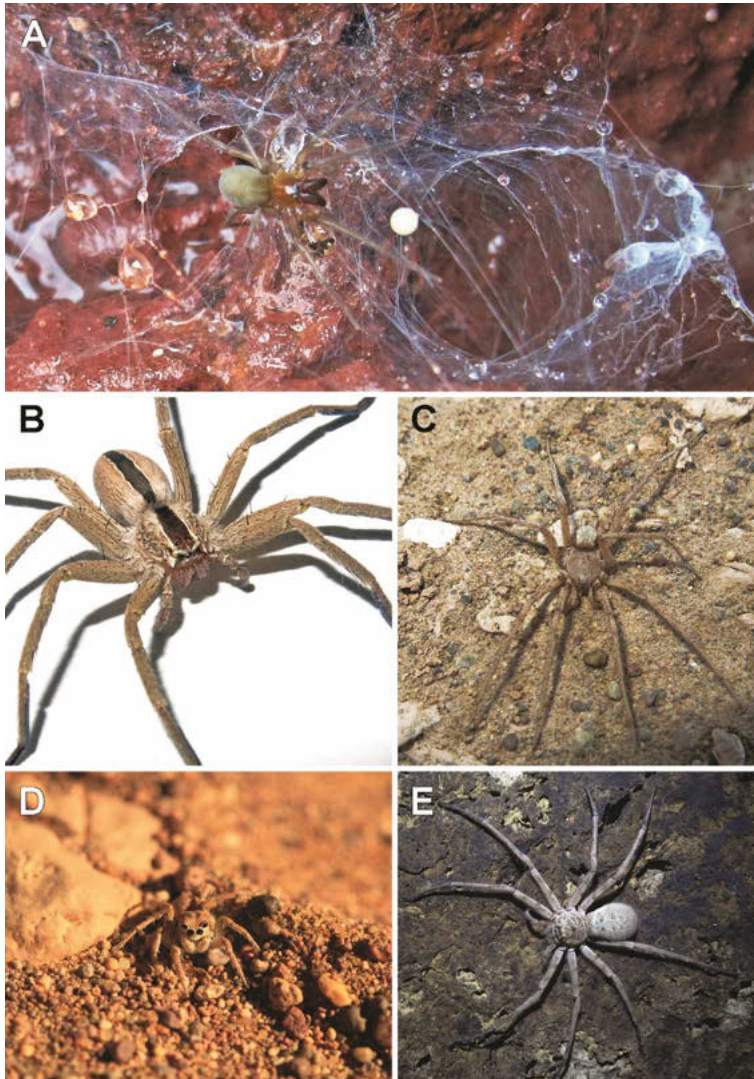


Figure 23. Various species of Iranian spiders. **A.** Female *Paratheuma enigmatica* Zamani, Marusik & Berry, 2016 (Dictynidae). **B.** Female *Pseudomicrommata mokranica* Moradmand, Zamani & Jäger, 2019 (Sparassidae). **C.** Male *Iranotricha lutensis* Zamani & Marusik, 2018 (Gnaphosidae). **D.** Female *Proszynskiana izadii* Azarkina & Zamani, 2019 (Salticidae). **E.** Female *Spariolenus iranomaximus* Moradmand & Jäger, 2011 (Sparassidae). Photos: Nasser Pourvali (**A**), Alireza Zamani (**B–C**), Bahman Izadi (**D**) and Behzad Zadhoush (**E**). **C** from Zamani et al. (2018c), **E** from Mirshamsi et al. (2015a).

There are several popularly known and iconic species of spiders described from Iran that their discovery and naming gained the attention of the media and public: *Filistata maguirei* Marusik & Zamani, 2015 and *Pritha garfieldi* Marusik & Zamani, 2015 (both Filistatidae) (Figures 24C–D), named after Tobey Maguire and Andrew Garfield, the actors who played the role of ‘Spider-Man’ (Marusik & Zamani 2015b),

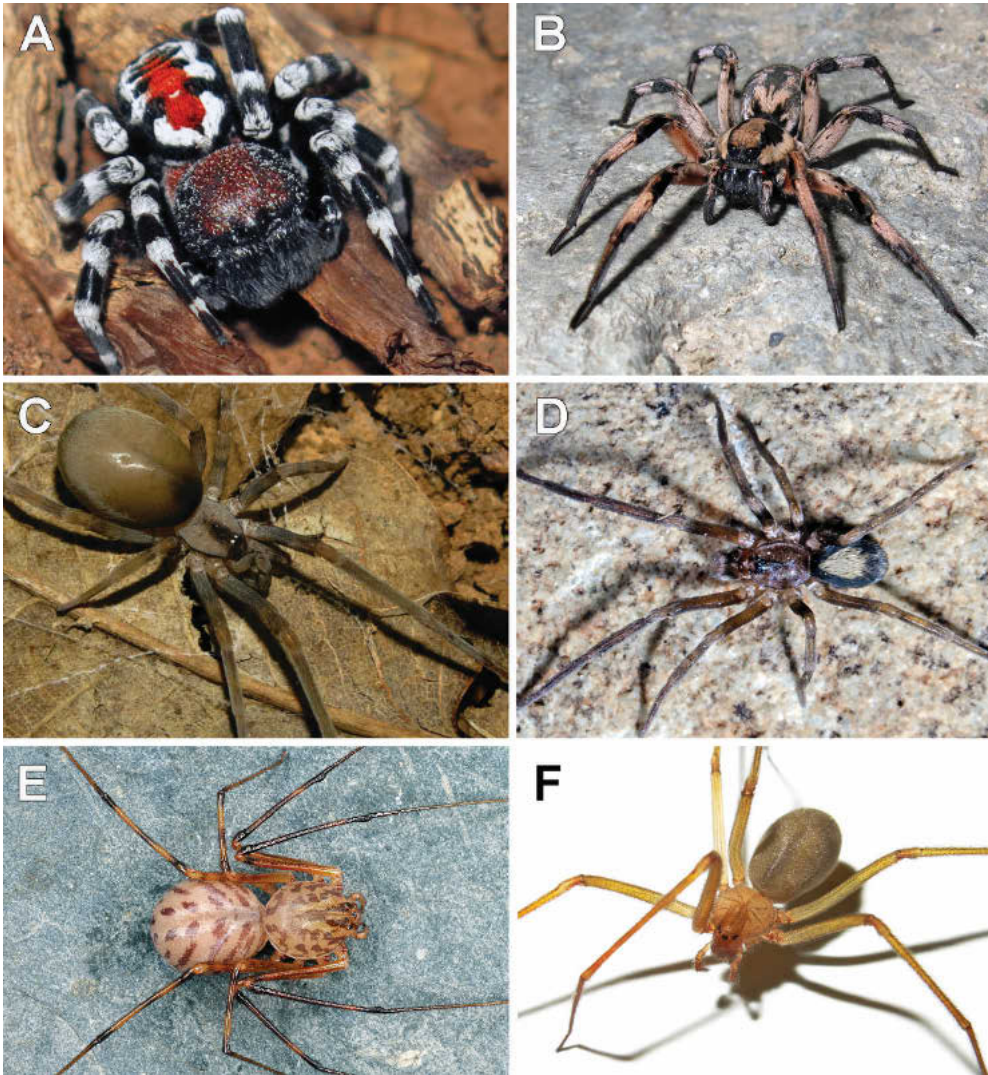


Figure 24. Various species of Iranian spiders. **A.** Male *Loureedia phoenixi* Zamani & Marusik, 2020 (Eresidae). **B.** Female *Lycosa aragogi* Nadolny & Zamani, 2017 (Lycosidae). **C.** Female *Filistata maguirei* Marusik & Zamani, 2015 (Filistatidae). **D.** Male *Pritha garfieldi* Marusik & Zamani, 2015 (Filistatidae). **E.** Female *Scytodes kumonga* Zamani & Marusik, 2020 (Scytodidae). **F.** Female *Loxosceles coheni* Zamani, Mirshamsi & Marusik, 2021 (Sicariidae). Photos: Alireza Zamani (**A–C, F**), Ali Mohajeran (**D**) and Mark Stockmann (**E**). **D** from Marusik & Zamani (2015b).

Lycosa aragogi Nadolny & Zamani, 2017 (Lycosidae) (Figure 24B), named after Aragog, the fictional spider from the 'Harry Potter' franchise, due to its resemblance to the animatronic version of this character used in the film adaptation of 'Harry Potter and the Chamber of Secrets' (Nadolny & Zamani 2017), *Loureedia phoenixi* Zamani & Marusik, 2020 (Eresidae) (Figure 24A), named after the actor Joaquin Phoenix who played the titular character in the 2019 movie 'Joker', due to a resemblance between the abdominal colour pattern of the male spider and the facial makeup of Joker (Zamani & Marusik 2020c), *Scytodes kumonga* Zamani & Marusik, 2020 (Scytodidae) (Figure 24E), named after Kumonga, a spider monster from the 'Godzilla' franchise, due to their similar coloration pattern and hunting strategy (Zamani & Marusik 2020d), and *Loxosceles coheni* Zamani, Mirshamsi & Marusik, 2021 (Sicariidae) (Figure 24F), named after the singer-songwriter, poet and novelist Leonard Cohen (Zamani et al. 2021b). Using such popular epithets for naming newly discovered species have proven to be very helpful in generating a public interest in taxonomy, which may occasionally lead to obtaining additional records and natural history data or even finding of closely related new species by citizen scientists (A. Zamani, pers. obs.).

There are 935 species of 324 genera and 55 families of spiders known from Iran, including eight genera and 215 species currently known only from this country (Figures 25, 26). Although these numbers are relatively high (especially in comparison to almost all other countries in the regions), the spider fauna of Iran is far from being properly documented as vast areas of the country remain completely unexplored, with every expedition yielding an additional number of new species and records.

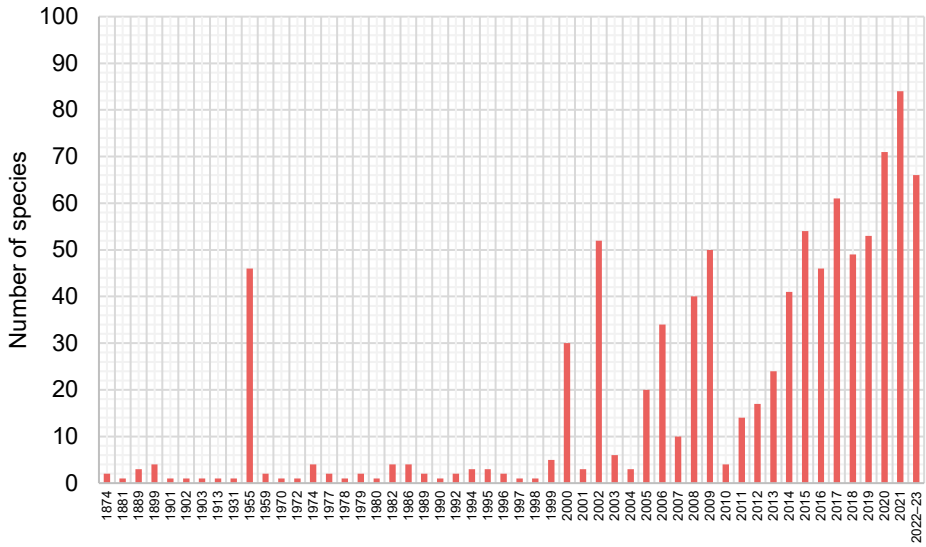


Figure 25. Numbers of species reported and described from Iran per year, excluding those rejected from the checklist. Data for 2023 (14 species, until February 10th) are grouped with those of 2022.

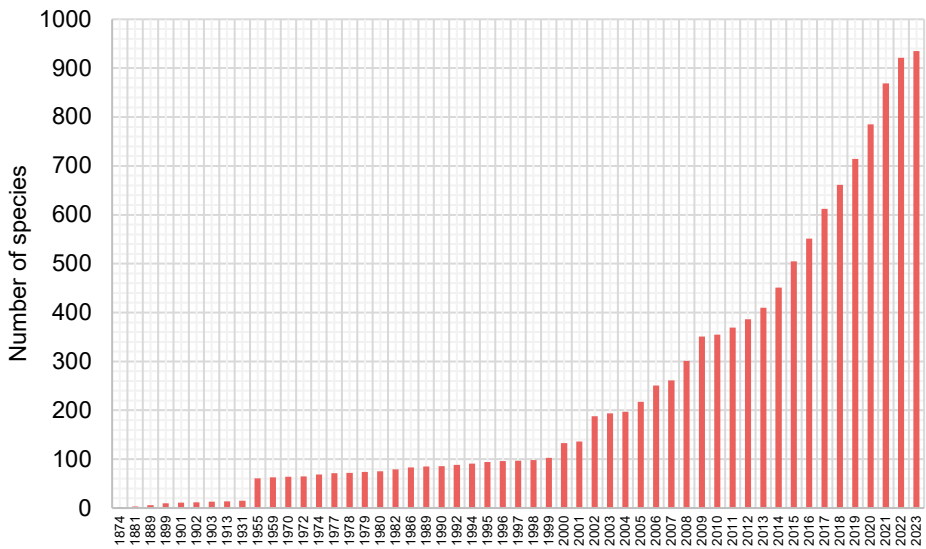


Figure 26. Cumulative numbers of species reported and described from Iran per year (until February 10th, 2023), excluding those rejected from the checklist.

1.4 Aims of the dissertation

In 2013, when I initiated my research on Iranian spiders, the araneofauna of Iran was known to comprise around 400 species, an objectively low number for such a large and ecologically diverse country, especially when accounting for the number of species known at that time for much smaller countries in the region (e.g., approximately 600 and 700 species from Azerbaijan and Turkey, respectively). It was evident by the scarcity of taxonomic and faunistic studies that the low number of documented species did not reflect the true species composition of this megadiverse group in Iran, and highlighted the Linnean and Wallacean shortfalls, indicating a taxonomic impediment. Ghahari & Marusik (2009) had already anticipated that the true diversity of spiders in Iran should be no less than 900 species from over 40 families.

Therefore, the primary objective of my research was to tackle these shortfalls through the publication of regional systematic revisions, smaller taxonomic contributions and large-scale faunistic surveys. This was done on the basis of the material newly collected in numerous expeditions conducted by myself and my colleagues in different regions of Iran, as well as those housed in both local and foreign institutional collections. This taxonomic and faunistic information formed the necessary backbone to conduct the second objective of the dissertation.

For the second objective, I aimed to explore the diversity and distribution patterns of Iranian spiders and evaluate how they are affected by sampling biases. Furthermore, I intended to investigate if there is a correlation between the number of records and species of spiders and the number of records of plants and other animals in Iran. Finally, I aimed to identify areas and ecoregions of Iran that remain particularly poorly sampled or completely unsampled; this will guide future researchers in their collecting efforts and taxonomic surveys more effectively towards less explored regions.

2 Materials and Methods

2.1 Fieldwork

During 2013–2019, I conducted numerous expeditions to different regions of Iran, particularly in the Alborz Mountains in the north, and Zagros Mountains in the west, southwest and southern Iran. Additional sampling was done in various localities in the central and southeastern parts of the country. A wide variety of habitats were sampled in these surveys, including mountains, forests, woodlands, steppes, deserts, salt marshes, intertidal zones and caves (Figures 27A–H, 28A–H). The specimens were collected using various methods, including direct sampling with an aspirator, sifting, pitfall trapping and sweep netting. Once collected, the specimens were preserved in 75% ethyl alcohol and accompanied by a label bearing information on the collection locality and date. Material collected in surveys conducted by other researchers was also examined.

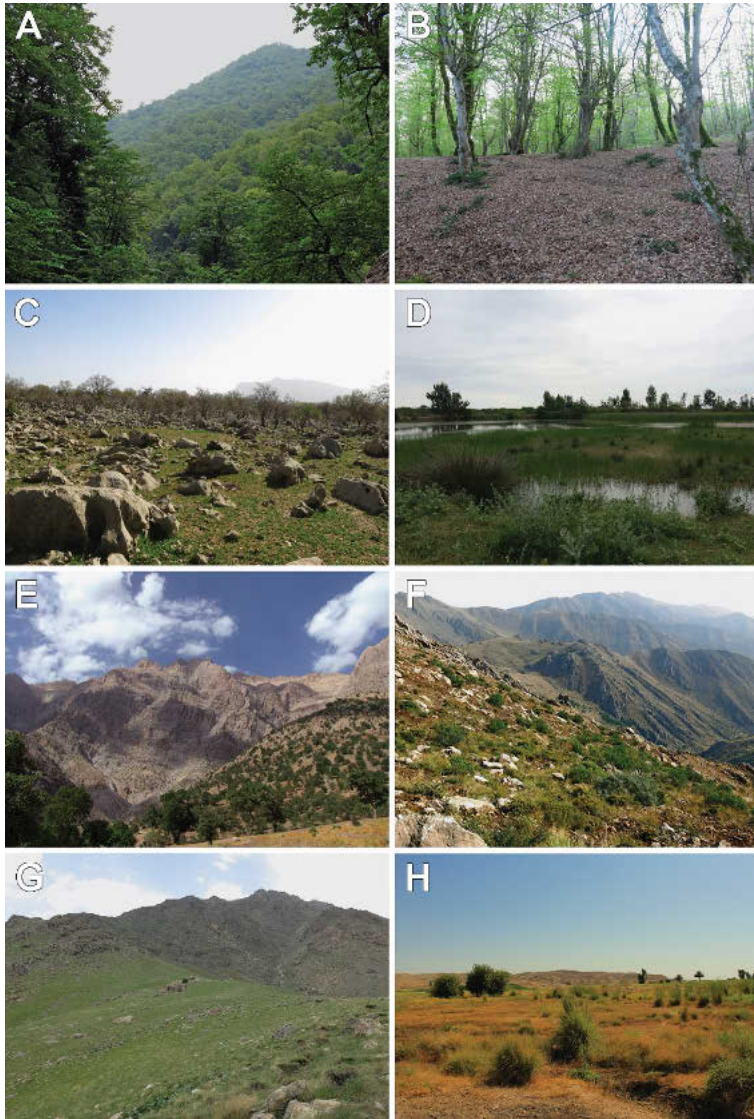


Figure 27. Various Iranian ecoregions. **A.** Caspian Hyrcanian mixed forest, Shirabad, Golestan Province. **B.** Caspian Hyrcanian mixed forest, Sari, Mazandaran Province. **C.** Zagros Mountains forest steppe, Dezful, Khuzestan Province. **D.** Caspian Hyrcanian mixed forest, Miankaleh, Mazandaran Province. **E.** Zagros Mountains forest steppe, Mount Dena, Kohgiluyeh & Boyer-Ahmad Province. **F.** Zagros Mountains forest steppe, Marivan, Kurdistan. **G.** Alborz Range forest steppe, Tehran, Tehran Province. **H.** Mesopotamian shrub desert, Qasr-e Shirin, Kermanshah Province. Photos: Alireza Zamani (**A–D, F–G**) and Barbod Safaei-Mahroo (**E, H**). **A** from Zonstein et al. (2018).

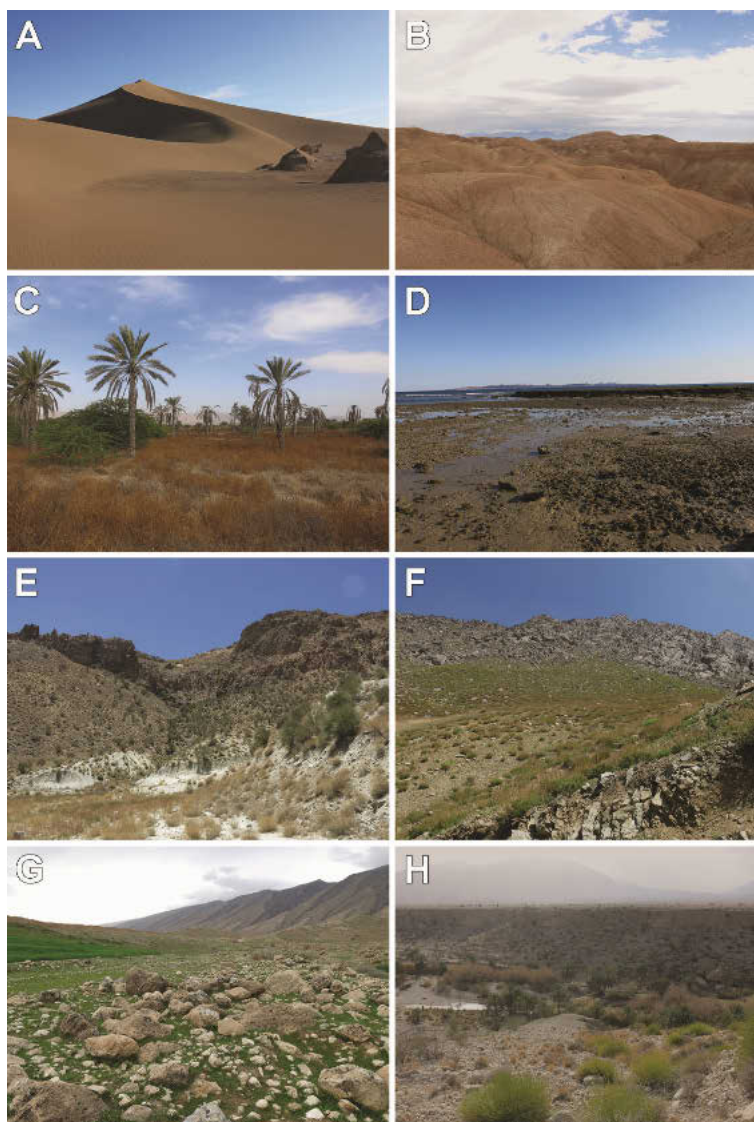


Figure 28. Various Iranian ecoregions. **A.** Central Persian desert basins, Lut desert, Kerman Province. **B.** Central Persian desert basins, vicinity of Karaj, Alborz Province. **C.** South Iran Nubo-Sindian desert and semi-desert, Parsian, Hormozgan Province. **D.** Intertidal zone, Qeshm island, Persian Gulf. **E.** Kuh Rud and Eastern Iran montane woodlands, vicinity of Mount Taftan, Sistan & Baluchistan Province. **F.** Kuh Rud and Eastern Iran montane woodlands, Lalehzar, Kerman Province. **G.** Zagros Mountains forest steppe, Pol Dokhtar, Lorestan Province. **H.** South Iran Nubo-Sindian desert and semi-desert, Siahu, Hormozgan Province. Photos: Alireza Zamani. **A** from Zamani et al. (2018c).

2.2 Museum collections

The following is a list of museums and institutions with studied collections of Iranian spiders, as well as those in which the newly collected specimens were deposited:

AMNH – the American Museum of Natural History, New York, USA.

AZMI – the Zoological Museum of the Iranian Research Institute of Plant Protection, Tehran, Iran.

CRBA-UB – Centre de Recursos de Biologia Animal, Universitat de Barcelona, Barcelona, Spain.

EM-SUMS – the Entomological Museum of Shiraz University of Medical Sciences, Shiraz, Iran.

IBSP – the Arachnid Collection of Butantan Institute, São Paulo, Brazil.

ISEA – the Institute of Systematics and Ecology of Animals, Novosibirsk, Russia.

JAZM – the Jalal Afshar Zoological Museum of the University of Tehran, Karaj, Iran.

MCSN – Museo Civico di Storia Naturale di Verona, Verona, Italy.

MHNG – Muséum d'histoire naturelle de la Ville de Genève, Geneva, Switzerland.

MMTT – the National Museum of Natural History of Iran, Tehran, Iran.

MMUE – the Manchester Museum of the University of Manchester, UK.

NHMW – Naturhistorisches Museum Wien, Vienna, Austria.

NMB – Naturhistorisches Museum Basel, Basel, Switzerland.

NMNHS – National Museum of Natural History, Sofia, Bulgaria.

NMP – the National Museum in Prague, Prague, Czech Republic.

PSU – the Zoological Museum of the Perm State University, Perm, Russia.

SMF – Naturmuseum Senckenberg, Frankfurt am Main, Germany.

TNU – National Arachnological Collection in the V.I. Vernadsky Taurida National University, Simferopol, Ukraine.

ZISP – the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia.

ZM-CBSU – the Zoological Museum of the Department of Biology, Shiraz University, Shiraz, Iran.

ZMFUM – the Zoological Museum of the Ferdowsi University of Mashhad, Mashhad, Iran.

ZMMU – the Zoological Museum of the Moscow State University, Moscow, Russia.

ZMUI – the Zoological Museum of the University of Isfahan, Isfahan, Iran.

ZMUT – the Zoological Museum of the University of Turku, Turku, Finland.

ZUTC – the Zoological Museum of the University of Tehran, Tehran, Iran.

2.3 Morphological analyses

In total, more than 9,000 specimens were examined. The primary set of equipment used to examine, measure and illustrate the specimens include an Olympus Camedia E-520 camera attached either to an Olympus SZX16 stereomicroscope or to the eyepiece of an Olympus BH2 transmission microscope, and a JEOL JSM-5200 scanning electron microscope at the Zoological Museum of the University of Turku. The acquired digital images were stacked and edited using the software packages CombineZP, Zerene Stacker and Adobe Photoshop. The illustrations of the internal genitalia were made after clearing them in a 10% KOH aqueous solution or other similar solutions, and if needed, a few minutes of treatment in an alcohol/water solution of Chlorazol Black.

2.4 Biogeographical analyses

A database of distribution records for all species of Iranian spiders was created using information from more than 300 publications as well as some unpublished data, totalling 4,434 non-duplicated records. A review of the literature with the goal of locating primary sources that either list the species or mention the known species richness for each country was done in order to compare the species diversity of Iran with that of other countries. In the absence of such sources, the WSC (2023) database was filtered to obtain a total count of the number of valid species with a distribution that explicitly listed the names of each country.

Parts of Iran with no spider records were approximated by calculating the percentage of total country area occupied by two buffers with different radii surrounding the points of occurrences: 5 km (a more realistic estimate) and 10 km (a more conservative estimate). To take into account the coordinates' imprecision, two different ranges were used. The functions "Sampling Effort" (search radius = 50,000 m) and "Species Richness" (hexagon size = 0.5; minimum number of samples = 10; Lambda smoothing factor of spline = 40) in the package BioDinamica, developed for the Dinamica EGO 7 software, were used, respectively, to access the spatial variation in the density of records and species (Oliveira et al. 2019). Using data from the Global Biodiversity Information Facility (GBIF 2022), all specimen-based Iranian records of plants and animals were retrieved in order to compare the diversity and distribution patterns of Iranian spiders with those of other taxa. Duplicate records and those flagged as suspicious were removed from the dataset. The density of records for all taxa (plants and animals) ($n = 17,762$), all animals ($n = 7,954$), and arthropods ($n = 2,523$) were calculated using the same methods and parameters as for spiders. Finally, using the function 'beta.pair' from the 'betapart' package for R, a

pairwise Jaccard dissimilarity index was calculated for the Iranian ecoregions that include at least 50 records of spiders (Baselga et al. 2022).

2.5 Species concept

Species delineation was based on the morphological species concept (Mayr 2000; Bond & Godwin 2013), in a way that species were considered as populations (or groups of populations) with qualitative morphological features that distinctly differentiate them from other populations or groups.

3 Results and Discussion

The main results of my research on the Iranian spider fauna are the taxonomic and faunistic contributions that were published in my articles, most of them in collaboration with other researchers.

An important clarification to be made is that although I started my doctoral studies at UTU in January of 2019, my research on Iranian spiders began in 2013. Because my articles on this subject published before 2019 (i.e., 49 publications) are in line with those published after my enrolment at UTU (i.e., 38 publications), I have also included those taxonomic and faunistic findings that were published in my pre-2019 articles within the overall results of this dissertation (a list of all my publications on Iranian spiders is included in Appendix 1). Regardless, I must emphasise that the main taxonomic and faunistic publications on which this dissertation is based must be considered those published in 2019 and afterwards, with UTU listed as my affiliation. Since it is not practical to include all the aforementioned 38 articles published during 2019–2023 in this dissertation, only nine taxonomic articles (i.e., original publications **I–IX**) highlighting some of the more important findings are included as examples, in addition to the final article (i.e., original publication **X**) which involves the patterns of diversity and distribution of Iranian spiders.

Either solely or in collaboration with other researchers, I described 11 genera and 147 species of Iranian spiders as new to science. A list of these newly described taxa is included in Appendix 2.

A total of 419 taxa were recorded in Iran for the first time in publications that I authored or co-authored, including 13 families, 87 genera and 319 species. Additionally, several hundred new provincial and distribution records were published, considerably expanding the known ranges of many spider species in Iran. The total number of newly described and recorded species (i.e., 466 species) constitutes almost half (i.e., 49.83%) of the currently known species diversity of spiders in Iran (i.e., 935 species). Amongst 147 species described, 137 are known only from Iran, representing 63.72% of all species currently considered endemic to this country (i.e., 215 species). An up-to-date, non-annotated checklist of Iranian spiders is included in Appendix 3.

Here, I briefly review the main findings reported in the nine taxonomic publications that are included as the ‘Original Publications I–IX’:

3.1 The Aelurillina Simon, 1901 (Aranei: Salticidae) of Iran: a check-list and three new species of *Aelurillus* Simon, 1884 and *Proszynskiana* Logunov, 1996

In this paper, the taxonomy and distribution of Aelurillina (Salticidae: Salticinae: Aelurillini) in Iran were reviewed. This subtribe comprises nine genera and 293 species (Maddison 2015; Logunov & Azarkina 2018), which with the exception of *Phlegra hentzi* (Marx, 1890), are all known exclusively from the Old World (WSC 2023).

Three species, *Aelurillus westi* Azarkina & Zamani, 2019, *Proszynskiana izadii* Azarkina & Zamani, 2019 and *P. logunovi* Azarkina & Zamani, 2019, were described as new to science. The latter two represented the first records of *Proszynskiana* in the Middle East, extending the known range of this genus approximately 700 km to the south. A checklist of all species of this subtribe occurring in Iran (i.e., 19 species in six genera), as well as a map of their distribution records were also provided.

The preserved specimens of *P. logunovi* were located in ZISP, amongst the material of the first collection of Iranian spiders conducted by Eugen von Keyserling and Theophil Bienert in 1859. The discovery of the other species, *P. izadii*, is interesting because the type specimens were collected in the Lut Desert, the hottest desert on Earth (Azarderakhsh et al. 2020). The surface temperature of the type locality of *P. izadii*, which is also shared with *Iranotricha lutensis* (Zamani et al. 2018c), has been recorded as high as 80.83 °C. The natural history and potential adaptations of these desert-dwelling species should be a topic worthy of further investigation.

3.2 The spider genera *Azerithonica* and *Tegenaria* (Aranei: Agelenidae: Tegenariini) in Iran

This paper was the first of two concerning a taxonomic revision of the family Agelenidae in Iran. The tribe Tegenariini and the genera *Azerithonica* Guseinov, Marusik & Koponen, 2005 and *Tegenaria* Latreille, 1804 were the focus of this publication. The distribution records of all 14 species known from Iran were mapped, and with the exception of the widely distributed *T. domestica* (Clerck, 1757) and *T. pagana* C.L. Koch, 1840, the remaining species were illustrated.

Seven species of both genera were described as new to science: *A. sagartia* Zamani & Marusik, 2019, *T. arsacia* Zamani & Marusik, 2019, *T. daylamanica* Zamani & Marusik, 2019, *T. eros* Zamani & Marusik, 2019, *T. guseinovi* Zamani & Marusik, 2019, *T. rahnamayi* Zamani & Marusik, 2019 and *T. shirin* Zamani & Marusik, 2019. Two species previously known only from Azerbaijan, *A. hyrcanica* Guseinov, Marusik & Koponen, 2005 and *T. halidi* Guseinov, Marusik & Koponen, 2005, were recorded in Iran for the first time, and additional distribution records were provided for *T. domestica*, *T. lenkoranica* Guseinov, Marusik & Koponen, 2005 and *T. pagana*. Prior to this publication, *Azerithonica* comprised only one species. The discovery of a second species of this genus from Iran made a revision of its diagnosis possible.

With the exception of *T. domestica* and *T. pagana*, two cosmopolitan species often found in and around human dwellings, the remaining species of Tegenariini are either endemic or subendemic to Iran, and known from localities in the Hyrcanian forests and the mountain ranges of Alborz and Zagros, the primary biodiversity hotspots in Iran. It is likely that the Iranian diversity of this group, particularly regarding *Tegenaria*, should be much higher. *Tegenaria* species are common inhabitants of subterranean ecosystems, the spider fauna of which remain very poorly documented in Iran.

3.3 On *Araniella* and *Neoscona* (Araneae, Araneidae) of the Caucasus, Middle East and Central Asia

In this publication and on the basis of species occurring in the Caucasus, Middle East and Central Asia, new taxonomic information on the araneid genera *Araniella* Chamberlin & Ivie, 1942 and *Neoscona* Simon, 1864 were provided, and the distribution records of all treated species were mapped.

Three species, *A. mithra* Zamani, Marusik & Šestáková, 2020 (Iran), *A. villanii* Zamani, Marusik & Šestáková, 2020 (Iran, Kazakhstan and India), and *N. isatis* Zamani, Marusik & Šestáková, 2020 (Iran), were described as new to science. *Neoscona theisi* (Walckenaer, 1841) was recorded in Iran, Georgia and Russia for the first time, although the Georgian record was later rejected by Zamani et al. (2022c) and attributed to *N. spasskyi* (Brignoli, 1983). Two new combinations, two new synonymies and a resurrection from synonymy were also proposed.

The discovery of *A. villanii* was quite interesting as the known range of the species encompasses a very large area, from southwestern Iran in the west to northern India in the south and eastern Kazakhstan in the north. It is surprising that this species was not discovered earlier, especially bearing in mind the relatively high regional abundance exhibited by most *Araniella* species.

3.4 A review of Agelenini (Araneae: Agelenidae: Ageleninae) of Iran and Tajikistan, with descriptions of four new genera

This paper was the second part of a regional taxonomic revision of Agelenidae in Iran, focussing on the tribe Agelenini. The fauna of the poorly studied Tajikistan was also considered.

Four genera (i.e., *Asiascape* Zamani & Marusik, 2020; *Gorbiscape* Zamani & Marusik, 2020; *Persilena* Zamani & Marusik, 2020; *Persiscape* Zamani & Marusik, 2020) and seven species (i.e., *A. parthica* Zamani & Marusik, 2020; *G. gorbachevi* Zamani & Marusik, 2020; *Persilena sengleti* Zamani & Marusik, 2020; *Persiscape caspica* Zamani & Marusik, 2020; *P. ecbatana* Zamani & Marusik, 2020; *P. nassirkhanii* Zamani & Marusik, 2020; *P. zagrosensis* Zamani & Marusik, 2020) were described as new to science. Except for *G. gorbachevi* from Tajikistan, the remaining noted species are endemic to Iran. Further taxonomic considerations, including four new combinations and two new synonymies, were also proposed. An extreme level of variation in the conformation of the female copulatory organs of the species of *Persiscape* was documented.

Agelescape Levy, 1996 was redefined to include only two species, *A. livida* (Simon, 1875) and *A. affinis* (Kulczyński, 1911); all other species previously considered in this genus were transferred to *Persiscape*. Interestingly, both species appear to have an identical male palp, but show clear differences in the female genitalia, which is an extremely rare condition in the taxonomy of spiders. The situation becomes more complicated when considering that the illustration provided by Levy (1996) for the male of *A. livida* shows differences compared to those provided by the other authors. We considered this to be a mistake in the drawings. Unfortunately, we were not able to examine the type material to reach a more solid conclusion, and no new taxonomic considerations were proposed. It is possible that the two names in fact represent the same species with a high variation in the female genitalia, even though no clinal variations or intermediate forms were detected in our extensive material. Employing integrative methods, particularly molecular ones, should be helpful in resolving this issue.

3.5 A survey of Phrurolithidae (Arachnida: Araneae) in southern Caucasus, Iran and Central Asia

In this publication, the taxonomy of the family Phrurolithidae was revised based on the faunas of Azerbaijan, Iran and Tajikistan. The genus *Bosselaerius* Zamani & Marusik, 2020 and three species were described as new to science: *B. hyrcanicus* Zamani & Marusik, 2020 (Azerbaijan and Iran), *B. tajikistanicus* Zamani & Marusik,

2020 (Tajikistan) and *Phrurolithus azarkinae* Zamani & Marusik, 2020 (Azerbaijan and Iran). The previously unknown female of *P. luppovae* Spassky, 1941 from Tajikistan was described for the first time and a redescription was provided for the male, and *P. pullatus* Kulczyński, 1897 was newly recorded in Iran. *Phrurolithus azarkinae* was shortly afterwards reported from Armenia, Turkey and Cyprus (Lecigne 2021; Zarikian et al. 2022; R. Bosmans, pers. comm.).

New combinations were proposed for 28 East Asian species previously classified in *Phrurolithus*. Except for one species that was transferred to *Bosselaerius*, the rest were transferred to *Otacilia* Thorell, 1897. Out of these 27 species, seven were later transferred to four newly established genera (Liu et al. 2020, 2022; Kamura 2021).

3.6 ‘Burning violin’: the medically important spider genus *Loxosceles* (Araneae: Sicariidae) in Iran, Turkmenistan, and Afghanistan, with two new species

The taxonomy and distribution of the genus *Loxosceles* was revised and surveyed in this publication based on the faunas of Iran, Turkmenistan and Afghanistan. Two species were described as new to science: *L. coheni* Zamani, Mirshamsi & Marusik, 2021 (southwestern Iran) and *L. turanensis* Zamani, Mirshamsi & Marusik, 2021 (southern Turkmenistan and eastern Iran). The distribution records of all species occurring in the region were mapped. Additionally, a new synonymy was proposed for a species described from Peru.

The taxonomy of *Loxosceles* is notoriously difficult due to the overall simplicity of the copulatory organs and genital structures in this group. For example, one of the interesting aspects of this study was the close similarity of the male palp of *L. turanensis* with that of *L. mrazig* Ribera & Planas, 2009, a species known from Algeria and Tunisia. This is most likely due to a convergence resulting from the noted simplicity of structures (Ribera & Planas 2009), as there are no historical biogeographic patterns between the areas of distribution of the two species. Another Iranian endemic species, *L. persica* Ribera & Zamani, 2017, is also morphologically similar to and phylogenetically associated with *L. mrazig* and *L. foutadjalloni* Millot, 1941, a species known from Guinea (Tahami et al. 2017). Another potential reason for these observed similarities and affinities is a lack of comprehensive sampling south of the Atlas Mountain range and towards the Middle East (i.e., Darwinian shortfall). This results in other potential closely related species occurring between the noted regions to remain undiscovered. Before the publication of Tahami et al. (2017), the only species of *Loxosceles* known from Western Asia was the cosmopolitan *L. rufescens*. The recent findings indicate that the entire region and the Zagros Mountains in particular are very likely to harbour a relatively high diversity

of these spiders, and more sampling is needed, especially in isolated habitats (e.g., caves).

In *Loxosceles*, unlike most groups of spiders, generally the structure of the female genitalia is more diagnostic than the male palp, even though it could still show relatively high levels of variation. We documented a high variability in the structure of the vulva amongst the specimens that we identified as *L. rufescens* from various localities in Iran, Turkey and Afghanistan. It is very likely that they represent a complex of various cryptic species, rather than different populations of a widely distributed species (e.g., Duncan et al. 2010). Although molecular data are frequently used in species delineation of *Loxosceles* (e.g., Navarro-Rodríguez & Valdez-Mondragón 2020), these data are not always helpful for confirming taxonomy. For example, the material of *L. persica* reported in the paper describing the species were collected in three caves separated from one another by 165 and 450 km in a straight line (Tahami et al. 2017). Regarding COI, the authors reported an average evolutionary divergence (i.e., p-distance) of 16.2% amongst the three populations, which is considerably higher than what has been reported for *L. rufescens* in the Mediterranean (i.e., 7.8%; Planas et al. 2014), although similar to what has been observed in lineages occurring in three localities southwest of the Atlas range in Morocco (i.e., >7% within each lineage and as high as 12.7% amongst neighbouring lineages; Tahami et al. 2017). Such patterns have also been reported in other groups of spiders that have similar limited dispersal abilities, such as Mygalomorphae (Satler et al. 2013) and Filistatidae (Magalhaes et al. 2020). For example, intraspecific genetic distance as high as 15% and an interspecific distance of up to 22% was reported for *Sahastata* Benoit, 1968 (Filistatidae) by Magalhaes et al. (2020) based on COI data. These high levels of divergence can be linked to a number of potential causes. One explanation is that these distant populations in fact represent morphologically cryptic species. This is likely for *L. persica* because the male and female were only collected together at a single locality, and the assignment of populations from the other caves to this species was tentative. Another explanation is that these populations are conspecific but have highly structured populations due to their occurrence in mountainous regions, which when coupled with their limited dispersal abilities and potential microhabitat preferences, result in geographical isolation and a lack of gene flow (Tahami et al. 2017).

Finally, *Loxosceles* is one of the few groups of spiders whose envenomation is of clinical relevance. All species of *Loxosceles* examined so far have phospholipase D as their main venom component, which is capable of causing tissue necrosis and haemolysis in some incidents, a condition known as loxoscelism (Malaque et al. 2022). In this publication, we also reviewed all reported cases of loxoscelism from Iran. The medical relevance of *Loxosceles* further highlights the need for more well-founded taxonomic and faunistic surveys of this genus, especially in less explored

regions. The other group of medically important spiders in Iran is the genus *Latrodectus*, which is also severely in need of a regional revision based on integrative approaches.

3.7 Revision of the spider family Zodariidae (Arachnida, Araneae) in Iran and Turkmenistan, with seventeen new species

A taxonomic revision of the family Zodariidae based on the faunas of Iran and Turkmenistan was provided in this paper. Seventeen species were described as new to science: *Acanthinozodium armita* Zamani & Marusik, 2021, *A. atrisa* Zamani & Marusik, 2021, *A. diara* Zamani & Marusik, 2021, *A. dorsa* Zamani & Marusik, 2021, *A. elburzicum* Zamani & Marusik, 2021, *A. kiana* Zamani & Marusik, 2021, *A. masa* Zamani & Marusik, 2021, *A. niusha* Zamani & Marusik, 2021, *A. ovtchinnikovi* Zamani & Marusik, 2021, *A. parmida* Zamani & Marusik, 2021, *A. parysatis* Zamani & Marusik, 2021, *A. sorani* Zamani & Marusik, 2021, *Lachesana kavirensis* Zamani & Marusik, 2021, *L. perseus* Zamani & Marusik, 2021, *Pax ellipita* Zamani & Marusik, 2021, *P. leila* Zamani & Marusik, 2021 and *Trygetus susianus* Zamani & Marusik, 2021. With the exception of *A. ovtchinnikovi* from Turkmenistan, the rest of the species were described from Iran. The genera *Acanthinozodium* Denis, 1966, *Pax* Levy, 1990 and *Zodariellum* Andreeva & Tyshchenko, 1968, and the species *Z. prozynskii* Nenilin & Fet, 1985 were recorded in Iran for the first time, with *Acanthinozodium* also newly reported from Turkmenistan. *Zodariellum*, which at the time comprised only its type species, was redefined, and 13 species were transferred to it. Additional taxonomic considerations on this genus (including new species, combinations and synonymies) were proposed by Zamani & Marusik (2022b), resulting in a total of 21 species. A new Iranian species of *Trygetus* Simon, 1882 and the male of *T. susianus* were later described by Zamani & Marusik (2022a).

Jocqué & Henrard (2015) redefined *Acanthinozodium* and considered the presence of a dorsal circular pit at the base of the cymbium as a diagnostic character for the genus, despite that the male of the type species, *A. spinulosum* Denis, 1966, remains undescribed. This pit is the outlet of a gland that produces substances used to plug the epigyne after copulation. A similar character was previously documented in the *lutipes* species-group of *Zodarion* Walckenaer, 1826 (as ‘sulcus’) by Bosmans (2009), and later reported for *Zodarion ovatum* Zhang & Zhang, 2019 and all *Zodariellum* species (as ‘cymbial diverticulum’) by Zamani & Marusik (2022b). In this publication, we followed Jocqué & Henrard (2015) and described 12 species bearing this structure (termed ‘cymbial groove’) in *Acanthinozodium*, despite the presence of numerous differences in the overall configuration of the male palp. It is

now known that this groove (or pit) is slightly variable and present in other zodariid genera, and thus cannot be used as a major differential character (or a synapomorphy) for *Acanthinozodium*. Therefore, it is very likely that at least some of the 12 species that we described in this genus should be transferred to other genera; this matter should be addressed in a large-scale revision of the group, preferably using integrative approaches.

Zodariids are interesting from several aspects other than purely taxonomic ones. Many species display different forms of defensive (primarily Batesian) or aggressive mimicry, and most are assumed to be myrmecophagous or termitophagous specialists often found around or within the ant and termite colonies (Pekár & Král 2002). For this reason, zodariids are somewhat popular subjects in studies dealing with spider behaviour. Furthermore, the venom of at least one species of *Lachesana* Strand, 1932 has been found to contain peptides with antimicrobial and cytolytic activities that could potentially be useful in anticancer treatments (Dubovskii et al. 2015). It is possible this feature exists in other species of the genus (including two that we described from Iran), a topic that is worthy of further investigation.

3.8 One new genus and nineteen new species of ground spiders (Araneae: Gnaphosidae) from Iran, with other taxonomic considerations

In this publication, the genus *Zagrotus* Zamani, Chatzaki, Esyunin & Marusik, 2021 and nineteen species of Gnaphosidae (and Prodidomidae, see below) from Iran were described as new to science: *Berinda bifurcata* Zamani et al., 2021, *B. hoerwegi* Zamani et al., 2021, *Berlandina artaxerxes* Zamani et al., 2021, *Cryptodrassus iranicus* Zamani et al., 2021, *Drassodes persianus* Zamani et al., 2021, *Echemus caspicus* Zamani et al., 2021, *Gnaphosa qamsarica* Zamani et al., 2021, *Haplodrassus medes* Zamani et al., 2021, *H. qashqai* Zamani et al., 2021, *Marinarozelotes achaemenes* Zamani et al., 2021, *Marjanus isfahanicus* Zamani et al., 2021, *Nomisia ameretatae* Zamani et al., 2021, *Prodidomus inexpectatus* Zamani et al., 2021, *Scotophaeus anahita* Zamani et al., 2021, *S. elburzensis* Zamani et al., 2021, *Sosticus montanus* Zamani et al., 2021, *Synaphosus martinezi* Zamani et al., 2021, *Zagrotus apophysalis* Zamani et al., 2021 and *Zelotes hyrcanus* Zamani et al., 2021. At the time of publication, the family Prodidomidae (type genus: *Prodidomus* Hentz, 1847) was considered a synonym of Gnaphosidae, with its genera forming the subfamily Prodidominae, but it was later reinstated to the family-level by Azevedo et al. (2022). Three additional species of *Zagrotus* were later described by Zamani & Marusik (2021d), which allowed a revision of the diagnosis of the genus and led to *B. bifurcata* to also be transferred to *Zagrotus*.

This publication also provided the first Iranian records of the genera *Berinda* Roewer, 1928, *Echemus* Simon, 1878 and *Marjanus* Chatzaki, 2018, and the species *Berlandina mesopotamica* Al-Khazali, 2020. The female of the desert dwelling Iranian endemic *Callipelis deserticola* Zamani & Marusik, 2017 was described for the first time. A new synonymy and a new combination were also proposed.

With 134 species in 38 genera known from Iran, including 26 endemic and six subendemic species, Gnaphosidae is currently the most species-rich family of spiders in this country (Zamani et al. 2022b), albeit ranking as the sixth largest spider family (WSC 2023). This may be because of the generally high diversity and abundance of gnaphosids in hot and arid environments (Lubin et al. 2020), further exemplified by the fact that it is the most species rich family also in Turkey (Danışman et al. 2022) and Israel (Zonstein & Marusik 2013). Another possibility responsible for its diversity could be attributed to a lack of comprehensive regional taxonomic surveys on other families that have a higher global diversity. The Gnaphosidae of Iran comprise three endemic genera, which is also the highest described for any family. Two of these genera (i.e., *Callipelis* Zamani & Marusik, 2017 and *Iranotricha* Zamani & Marusik, 2018) are monotypic and exclusively found in xeric sand dunes of the Central Persian desert basins (Zamani et al. 2018c).

Most of the data on the Gnaphosidae of Iran were published in the faunistic series “New data on the spider fauna of Iran” (Zamani et al., 2014b, 2015, 2016b, 2017c, 2018b, 2019b, 2020b, 2021c, 2022c, 2022d). Considering that most of the material reported in all of these publications was primarily sampled by direct collecting by hand, and also the presence of vast areas of arid and semi-arid environments in Iran which remain particularly poorly surveyed (Zamani et al. 2023b), a much higher diversity of Gnaphosidae can be expected in this country. This diversity can be better explored once further systematic surveys are conducted across the country and especially its xeric ecosystems, and by employing sampling techniques that specifically target epigeal arthropods (e.g., pitfall and ramp trapping).

3.9 A survey of the spider genus *Dysdera* Latreille, 1804 (Araneae, Dysderidae) in Iran, with fourteen new species and notes on two fossil genera

This publication is a taxonomic revision of *Dysdera* (Dysderidae) in Iran. Prior to this, the genus was known in Iran from a single record that was initially identified as *D. concinna* L. Koch, 1878 by Pocock (1889), but was later attributed to *D. pococki* Dunin, 1985 by Deeleman-Reinhold & Deeleman (1988).

The following 14 species were described as new to science, with their distribution records mapped: *D. achaemenes* Zamani, Marusik & Szűts, 2023, *D.*

bakhtiari Zamani, Marusik & Szűts, 2023, *D. damavandica* Zamani, Marusik & Szűts, 2023, *D. genoensis* Zamani, Marusik & Szűts, 2023, *D. hormuzensis* Zamani, Marusik & Szűts, 2023, *D. iranica* Zamani, Marusik & Szűts, 2023, *D. isfahanica* Zamani, Marusik & Szűts, 2023, *D. mazeruni* Zamani, Marusik & Szűts, 2023, *D. medes* Zamani, Marusik & Szűts, 2023, *D. persica* Zamani, Marusik & Szűts, 2023, *D. sagartia* Zamani, Marusik & Szűts, 2023, *D. tapuria* Zamani, Marusik & Szűts, 2023, *D. verkana* Zamani, Marusik & Szűts, 2023 and *D. xerxesi* Zamani, Marusik & Szűts, 2023. Additionally, taxonomic notes were provided on *Mistura* Petrunkevitch, 1971 and *Segistriites* Straus, 1967, two monotypic Neogene fossil genera, with the latter transferred from Dysderidae to Segestriidae.

Most species of *Dysdera* occur in the Mediterranean region, where they comprise one of the most speciose spider genera. The genus is known to comprise complexes of sibling species that not only exhibit very small morphological differences but may also have overlapping ranges, resulting in their very complicated taxonomy. Almost all species of *Dysdera* have small ranges, with one of the few exceptions being the cosmopolitan *D. crocata* C.L. Koch, 1838. This species has been anthropogenically introduced to almost all continents (Řezáč et al. 2018), although it remains unrecorded from Iran. These spiders have unique morphological characters congruent with them being specialist predators that almost exclusively feed on woodlice (Řezáč et al. 2008).

The material of the newly described species was primarily collected in northern and southern Iran. Considering the results of this publication, there are 15 species of *Dysdera* known to occur in Iran. This should be considered only the first step towards the documentation of the Iranian diversity of this genus. Based on personal estimates there may be up to 40 species of *Dysdera* in Iran. Turkey (Danışman et al. 2022) and the Caucasus (Otto 2022) each have roughly 30 species of *Dysdera*. It is suspected that there are dozens of closely related, undescribed species with narrow distributions across the Alborz and Zagros Mountains.

All the newly obtained taxonomic data and distribution records, coupled with an extensive review of the records published in the literature, enabled us to conduct a comprehensive review of spatial variation in the diversity patterns of Iranian spiders, and further evaluate the effects of sampling biases on the results, which are dealt with in the last publication of this dissertation:

3.10 The effect of sampling bias on evaluating the diversity and distribution patterns of Iranian spiders (Arachnida: Araneae)

In this publication, a comprehensive review of spatial variation in the diversity patterns of Iranian spiders was provided, and the effect of sampling bias on the

results were evaluated. This study was the second of its type in the world (i.e., only the Brazilian fauna has been described in such detail before; see Santos et al. 2017 and Oliveira et al. 2016, 2017).

Of 935 species of spiders known from Iran, 215 species (i.e., 22.99%) are endemic to (or currently only known from) Iran, 38 species (i.e., 4.06%) are known only from the Middle East, 36 species (i.e., 3.85%) are known only from the Middle East and Caucasus, 60 species (i.e., 6.41%) are known only from the Middle East and Central Asia, 23 species (i.e., 2.45%) are known only from the Caucasus, Middle East and Central Asia, 455 species (i.e., 48.66%) are known only from the Old World, and 108 species (i.e., 11.55%) are known from both the Old and New World. Out of 55 families of spiders known from Iran, only the four most diverse families (i.e., Gnaphosidae, Linyphiidae, Lycosidae and Salticidae) were found to be known from more than four hundred records, while six families (i.e., Caponiidae, Cyrtaucheniidae, Mysmenidae, Nesticidae, Synsphyridae and Zoropsidae) were found to be known only from a single record. Only nine species (i.e., three lycosids, six linyphiids) were found to be known from more than 40 records. Furthermore, 522 species (i.e., 55.82%) were found to be represented by only one or two records, including 176 of 215 endemic species (i.e., 81.86%).

Despite a considerable increase in the number of taxonomic and faunistic surveys conducted in Iran during the past 20 years, the records of spiders were found to be highly unevenly distributed throughout the country and its 18 terrestrial ecoregions. The majority of records were near the most populated cities, and approximately 85% of the country remains without a single record of spiders, both suggesting a tremendous Wallacean shortfall. On one hand, the three largest Iranian ecoregions (i.e., Central Persian desert basins, South Iran Nubo-Sindian desert and semi-desert, and Zagros Mountains forest steppe) comprise only 52.1% of the records, despite encompassing about 73% of the area of Iran. On the other hand, the Alborz Range forest steppe and the Caspian Hyrcanian mixed forests comprise 10.33% and 22.72% of the records, respectively, despite together encompassing only 7.78% of the area of Iran. A high mean dissimilarity (56–76%) in spider communities was found between the Iranian ecoregions.

A similar trend is also observed in the number of species reported from each province: Mazandaran comprises the highest number of reported species for any province (i.e., 307 species), while comprising only 1.44% of the area of Iran. There are 94 species reported from Kerman, the largest province, which covers 11.12% of the country's area, while 107 species have been reported from Alborz, the smallest province comprising only 0.35% of the area of Iran. Although the lowest number of species (i.e., 11 species) have been reported from Qom, the second smallest province, the least studied Iranian provinces should be considered Sistan & Baluchistan (i.e., 29 species) and South Khorasan (i.e., 30 species), despite being the second and third

largest provinces and comprising 10.96% and 9.21% of the country's area, respectively (Figure 29).

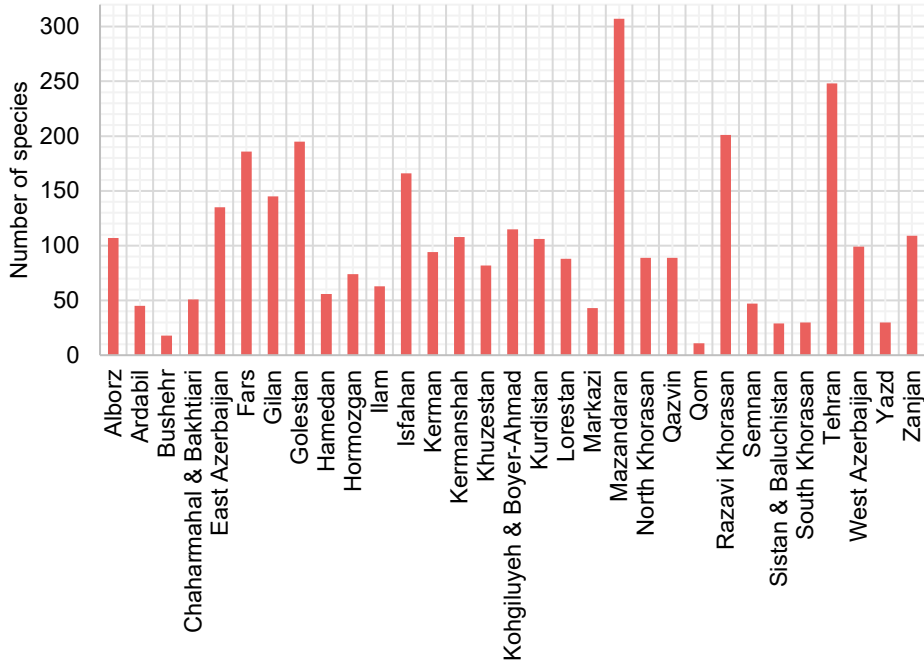


Figure 29. Numbers of species reported from each Iranian province.

The number of spider species known from Iran is disproportionately low (mean 0.00058 species/km²) compared to smaller and less ecologically diverse countries in the Caucasus, Middle East, North Africa and Central Asia, suggesting a large Linnean shortfall: Turkey (13 terrestrial ecoregions, 1,251 species; 0.00160 species/km²), Azerbaijan (four terrestrial ecoregions, 710 species; 0.00827 species/km²), Israel (five terrestrial ecoregions, 631 species; 0.03037 species/km²), Morocco (six terrestrial ecoregions, 487 species; 0.00121 species/km²), Turkmenistan (seven terrestrial ecoregions, 416 species; 0.00088 species/km²), and Armenia (three terrestrial ecoregions, 231 species; 0.00773 species/km²). Among the 171 countries compared in this research, Iran was ranked in the 132nd position regarding the mean number of species per area.

Overall, a higher level of endemism was found for recently described species and Iranian endemics, suggesting that either most of the recent taxonomic research on Iranian spiders has primarily focused on narrowly distributed species that are known only from one or a few sites, or a tremendous Wallacean shortfall caused by

the rarity of large-scale surveys. The relatively high number of endemic species (i.e., 215) in Iran is likely to be biased by more severe biodiversity shortfalls in most of the neighbouring and nearby countries: Pakistan (308 species; 0.00035 species/km²), Afghanistan (167 species; 0.00026 species/km²), Oman (143 species; 0.00046 species/km²), Iraq (104 species; 0.00024 species/km²), Kuwait (three species; 0.00016 species/km²). It is very possible that further taxonomic and faunistic surveys in these countries will result in many of these species being reported outside of the Iranian borders.

Finally, a high correlation (0.99) was found between the distribution of records of spiders and the spatial variation in species richness. The distribution pattern of records of Iranian spiders was found to be highly correlated to those of all arthropods (0.54), all animals (0.58) and all plants and animals (0.61) in Iran, suggesting that the biodiversity shortfalls described for spiders also exist for other taxa.

3.11 How many species of spiders are expected to occur in Iran?

It is difficult to provide a reliable assessment of the potential true diversity of Iranian spiders. Regardless, considering that vast areas of the country remain unsampled (particularly in the southeast and the whole Dasht-e Kavir desert in central Iran), with new records and species regularly found in every expedition to any part of the country, a much higher diversity than what is currently known can be expected. Indeed, most of the better-studied groups of animals in Iran are known to comprise almost the same number of species that has been reported from the whole of continental Europe (numbers of European species in parentheses, from de Jong et al. 2014): >100 species (Schneider et al. 2018) of dragonflies and damselflies (*vs. ca.* 140 species), *ca.* 450 species (Tshikolovets et al. 2014) of butterflies (*vs.* >480 species), *ca.* 260 species (Safaei-Mahroo et al. 2015) of reptiles (*vs.* >150 species), >550 species (Khaleghizadeh et al. 2017) of birds (*vs. ca.* 500 species), and *ca.* 200 species (Yusefi et al. 2019) of mammals (*vs. ca.* 260 species). Considering that there are more than 4,500 species of spiders known from Europe, it is safe to assume that at least some 2,000–3,000 species are likely to occur in Iran.

According to the most recent checklist, there are 55 families of spiders known from Iran. At least one other family, Stenochilidae, is expected to occur in this country, as it has been reported from Iraq and an area close to the Iranian border (Al-Khazali 2021). Four other families, namely Anapidae, Ctenizidae, Phyxelididae and Macrothelidae, are known from the western parts of the neighbouring Turkey; their occurrence in Iran is unlikely, considering that their distribution in the region is limited to the Mediterranean. Finally, Synaphridae is not known from Iran, although the family is included in the checklist based on the type locality of *Synaphris*

orientalis Marusik & Lehtinen, 2003, situated only a few kilometres away from the Iranian border in Turkmenistan (Marusik & Lehtinen 2003). Additionally, four species, namely *Karakumosa medica* (Pocock, 1889) (Lycosidae), *Leptonetela caucasica* Dunin, 1990 (Leptonetidae), *Olios stimulator* (Simon, 1897) (Sparassidae) and *Proszynskiana iranica* Logunov, 1996 (Salticidae) are included in the checklist only on the basis of borderland records.

3.12 Conservation

Despite their high diversity and ecological importance, spiders remain globally poorly studied regarding their conservation biology. Currently, there are only 389 species of spiders listed in the IUCN Red List of Threatened Species, of which eight are extinct, 66 are critically endangered, 98 are endangered, 65 are vulnerable, 17 are near threatened, and 89 and 46 are categorised as ‘least concern’ and ‘data deficient’, respectively. The list includes only 91 European species, an objectively low number in comparison to groups such as butterflies and dragonflies, for which extinction risks of 97% of European species have been assessed (Kalkman et al. 2010; van Swaay et al. 2011; Milano et al. 2021). Habitat loss and degradation, climate change, environmental pollution, agroforestry and illegal wildlife trade are some of the major threats affecting spiders (Branco & Cardoso 2020).

Unfortunately, the extinction risks of no Iranian spiders have been evaluated so far. However, it is expected that many species with narrow habitat tolerances (e.g., species of the sparassid genus *Spariolenus* Simon, 1880) are prone to multiple threats (e.g., drought, climate change), and may already have a decreasing population trend. Further taxonomic and faunistic surveys are necessary to assess the effects of these threats on different populations and to identify areas of higher diversity, for which new conservation and management policies can later be proposed.

4 Conclusions

The results of an almost a decade long taxonomic and faunistic survey on spiders of Iran were summarised in this dissertation. These surveys were conducted based on both freshly collected material and thousands of specimens deposited in institutional collections around the world, often in collaboration with researchers from various countries. Despite a significant improvement in the quality and quantity of such research during the past two decades resulting in almost all families receiving some level of taxonomic treatment, the Iranian spider fauna remains insufficiently studied (i.e., Linnean shortfall) and heavily affected by sampling bias, which is evidenced by a highly heterogeneous distribution of records throughout the country and its ecoregions (i.e., Wallacean shortfall). Most of the highly sampled areas are near large and populous cities, and vast areas particularly in central and southeastern parts of the country remain completely unsampled. To gain a better understanding of the spider diversity in this country and to reduce the effects of the aforementioned shortfalls, it is suggested that future researchers conduct their studies in the form of extensive systematic surveys based on various sampling methods (particularly pitfall trapping and sifting), and actively focus their collecting efforts on lesser sampled areas and ecoregions. Furthermore, there still remain several unstudied collections of Iranian spiders in institutes and universities both inside and outside of Iran that should be documented for publication. Hopefully, these efforts will form a robust backbone that will enable an assessment of the conservation status of and threat factors to Iranian spiders, as well as aid in the prioritization of areas for conservation and management.

Acknowledgements

Similar to many naturalists, my interest in biological diversity started at an early age. I remember spending most of my childhood observing and collecting animals that I could find in our backyard in Tehran. Amongst the various kinds of critters that I came upon, spiders were those that amazed me the most. Fortunately, I pursued my passion for these eight-legged wonders by continuing to collect and study them, which resulted in a growing admiration for their huge diversity and versatility.

A major turning point in my arachnological journey happened when I collected a specimen of recluse spider during high school. Keen to identify and document the presence of this medically important group of spiders in my country and motivated by my biology teacher, I decided to study animal biology at the University of Tehran. Shortly after my enrolment at the university, I managed to identify this specimen as *Loxosceles rufescens*, and reported its occurrence in Iran in my first scientific publication in 2013. Today, almost a decade later, I am still studying spiders, and consider myself fortunate to be able to present the research to which I devoted my whole adult life within a doctoral dissertation.

It has been quite a long journey, and many people have positively affected the trajectory of my career. First of all, I wish to thank my mentor and the primary co-author in most of my publications, **Yuri M. Marusik**, for responding to my first email to him on May 31, 2013, encouraging me to pursue arachnological research from the very beginning, and the wonderful pilaffs that he prepares for the after-sauna parties. Second, I wish to thank my supervisors, **Varpu Vahtera** and **Ilari E. Sääksjärvi**, for their continuous support and help during my doctoral studies. I also wish to thank all the people of the **Biodiversity Unit**, and especially those from the **Zoological Museum**, with whom I have had the great pleasure of working since 2019. Special thanks to **Seppo** and **Heli** for their hospitality and the nice and relaxing occasional gatherings on weekends and holidays.

I have been extremely fortunate to receive inspiration from numerous people: the documentaries of the Canadian arachnologist **Rick C. West** motivated me at a young age to pursue a life studying spiders, my high school biology teacher, **Omid Rahnamay**, encouraged me to study animal biology at the University of Tehran, and as a child, **George C. McGavin's** *Insects, Spiders and Other Terrestrial Arthropods*

was one of my favourite books that helped to expand my interest in the wonderful lives of these beautiful animals.

It would have been extremely difficult to complete this project without financial support. Here, I want to acknowledge an **EDUFI Fellowship** received from the **Finnish National Agency for Education**, the funded doctoral researcher position granted by the **University of Turku Graduate School**, and the additional support that I received from the Director of the Biodiversity Unit, **Ilari E. Sääksjärvi**.

I had the pleasure of working with almost 200 co-authors from more than 50 countries, to whom I am grateful for making the publication of over a hundred scientific papers possible. Special thanks belong to my top co-authors – **Yuri M. Marusik, Omid Mirshamsi, Sergei L. Esyunin, Majid Moradmand** and **Anton A. Nadolny** – for their knowledge and collaborative spirit. I also wish to acknowledge the collaboration of **Galina N. Azarkina, Leonardo S. Carvalho, Maria Chatzaki, Anna Šestáková** and **Tamás Szűts** in the papers included in this dissertation. I am deeply indebted to my good friend **Sarah Crews**, for the time and effort that she spent proofreading the English of many of my publications, including this dissertation. Additionally, I wish to acknowledge the invaluable contributions of **Dmitri V. Logunov, Andrei V. Tanasevitch** and the late **Antoine Senglet** to the taxonomy of Iranian spiders, which greatly benefitted my own research on this topic.

The vast majority of the specimens that I studied during my doctoral research were from various natural history collections in Europe. The support of the following curators (and their assistants) in accessing this material is greatly acknowledged: **Peter J. Schwendinger** and **Lionel Monod** (MHNG), **Christoph Hörweg** (NHMW), **Peter Jäger** and **Julia Altmann** (SMF), **Dmitri V. Logunov** (MMUE) and **Maria Tavano** (MCSN).

A portion of the studied material was collected during several expeditions to numerous regions of Iran, either by myself or my colleagues and friends. Although it is not possible to mention all individuals who provided me with some sort of assistance and support during these trips, I wish to particularly highlight the great efforts of **Amir Hossein Aghaei, Parham Beyhaghi, Mojtaba Ezazi, Alireza Naderi, Barbod Safaei-Mahroo** and **Soheyl Sami**.

I wish to extend my gratitude to all those who provided me with illustrations and photographs used in this dissertation: **Esam Al Ali, Reza Donyadideh, Behzad Fathinia, Mandana Hazrati-Farid, Bahman Izadi, Seyyed Hamzeh Kalantari, Jørgen Lissner, Yuri M. Marusik, Ali Mohajeran, Seyyed Ali Mohtarami, Ali Mokhtarian, Anton A. Nadolny, Anatoliy Ozernoy, Mahla Pourcheraghi, Nasser Pourvali, Barbod Safaei-Mahroo, Anna Šestáková, Mark Stockmann, Amir Weinstein** and **Behzad Zadhoush**. Special thanks goes to **Tapani Hopkins** for providing a Finnish translation of the abstract, and **Hamidreza Mirzadeh** for his help with the layout.

I would like to express my sincere gratitude to the pre-examiners of this thesis, **Francesco Ballarin** and **Christian Kropf** for their insightful feedback and constructive comments.

Finally, I wish to thank my family for their continued and ever-present support. I have also been blessed to find many wonderful friends along this journey, to all of whom I am grateful for making my life more colourful by being a part of it.

February 2023
Alireza Zamani

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Appendices

Appendix 1: List of my publications involving Iranian spiders, as of February 9th, 2023.

<https://doi.org/10.5281/zenodo.7625171>

Appendix 2: List of spider taxa that I described/co-described based on material from Iran, either in part or in whole. The known distributions are mentioned in brackets, with type localities of species underlined.

<https://doi.org/10.5281/zenodo.7625196>

Appendix 3: A non-annotated checklist of Iranian spiders (i.e., 935 species, 324 genera, 55 families), excluding unpublished data, records of doubtful species previously rejected from the checklist of Iranian spiders, and those not identified to the species-level. The species that are known only from records in border areas are accompanied with a question mark. The order of listed families is based on their currently accepted evolutionary relationships. Within each family, species are listed alphabetically.

<https://doi.org/10.5281/zenodo.7625216>



**TURUN
YLIOPISTO**
UNIVERSITY
OF TURKU

ISBN 978-951-29-9252-2 (PRINT)
ISBN 978-951-29-9253-9 (PDF)
ISSN 0082-6979 (Print)
ISSN 2343-3183 (Online)