



**HAL**  
open science

## **Lycosa Latreille, 1804 (Araneae, Lycosidae) of Israel, with a note on Geolycosa Montgomery, 1904**

Igor Armiach Steinpress, Mira Cohen, Julien Pétillon, Ariel D Chipman, Efrat Gavish-Regev

### ► To cite this version:

Igor Armiach Steinpress, Mira Cohen, Julien Pétillon, Ariel D Chipman, Efrat Gavish-Regev. *Lycosa Latreille, 1804 (Araneae, Lycosidae) of Israel, with a note on Geolycosa Montgomery, 1904*. *European Journal of Taxonomy*, 2022, 832, pp.1-54. <10.5852/ejt.2022.832.1877>. <hal-03931438>

**HAL Id: hal-03931438**

**<https://hal.science/hal-03931438v1>**

Submitted on 12 Jan 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons CC BY 4.0 - Attribution - International License



This work is licensed under a Creative Commons Attribution License (CC BY 4.0).

## Monograph

[urn:lsid:zoobank.org:pub:6AD25640-2B25-458D-942D-22ED24D177BD](https://zoobank.org/pub:6AD25640-2B25-458D-942D-22ED24D177BD)

# *Lycosa* Latreille, 1804 (Araneae, Lycosidae) of Israel, with a note on *Geolycosa* Montgomery, 1904

Igor ARMIACH STEINPRESS<sup>1,\*</sup>, Mira COHEN<sup>2</sup>, Julien PÉTILLON<sup>3</sup>,  
Ariel D. CHIPMAN<sup>4</sup> & Efrat GAVISH-REGEV<sup>5</sup>

<sup>1,5</sup>The Arachnid National Natural History Collection, The Hebrew University of Jerusalem,  
Edmond J. Safra Campus, Giv'at Ram, Jerusalem, Israel.

<sup>1,2,4</sup>The Department of Ecology, Evolution and Behavior, The Hebrew University of Jerusalem,  
Edmond J. Safra Campus, Giv'at Ram, Jerusalem, Israel.

<sup>3</sup>University of Rennes, Rennes, France.

<sup>3</sup>Nelson Mandela University, Port Elizabeth, South Africa.

\* Corresponding author: [bomtombadil@gmail.com](mailto:bomtombadil@gmail.com)

<sup>2</sup>Email: [mira.cohen@mail.huji.ac.il](mailto:mira.cohen@mail.huji.ac.il)

<sup>3</sup>Email: [julien.petillon@univ-rennes1.fr](mailto:julien.petillon@univ-rennes1.fr)

<sup>4</sup>Email: [ariel.chipman@huji.ac.il](mailto:ariel.chipman@huji.ac.il)

<sup>5</sup>Email: [efrat.gavish-regev@mail.huji.ac.il](mailto:efrat.gavish-regev@mail.huji.ac.il)

<sup>1</sup>[urn:lsid:zoobank.org:author:380129F9-96AC-4F19-A30E-3FB65AA39076](https://zoobank.org/author:380129F9-96AC-4F19-A30E-3FB65AA39076)

<sup>2</sup>[urn:lsid:zoobank.org:author:0FE66053-001F-44F1-A0EC-36DDAF791AE2](https://zoobank.org/author:0FE66053-001F-44F1-A0EC-36DDAF791AE2)

<sup>3</sup>[urn:lsid:zoobank.org:author:9A91C3B1-C4C5-485D-ACC5-E831EA5E7EA2](https://zoobank.org/author:9A91C3B1-C4C5-485D-ACC5-E831EA5E7EA2)

<sup>4</sup>[urn:lsid:zoobank.org:author:C7A32B57-33D0-4A35-BB05-62C919137F53](https://zoobank.org/author:C7A32B57-33D0-4A35-BB05-62C919137F53)

<sup>5</sup>[urn:lsid:zoobank.org:author:FC073F19-2202-4C89-8B43-CEA4CC5E2D50](https://zoobank.org/author:FC073F19-2202-4C89-8B43-CEA4CC5E2D50)

**Abstract.** *Lycosa* (Araneae, Lycosidae) is a wolf spider genus typical of subtropical latitudes in the western Palearctic. Despite being erected over 200 years ago, the taxonomy of *Lycosa* is still unclear. Many species formerly ascribed to it are currently being moved to other genera, while new species are still being described. The species of *Lycosa* of the western Mediterranean basin are relatively well known, yet the Levantine region, the easternmost part of the Mediterranean basin, has not received much attention since the early 20<sup>th</sup> century. Here, we study *Lycosa* from the southern Levant using morphological, molecular and behavioral characteristics, to delimit the species found in this region. We describe two new species: *L. hyraculus* sp. nov. and *L. gesserit* sp. nov. We re-describe the widespread and polymorphic species, *Lycosa piochardi* Simon, 1876. *Lycosa piochardi infraclara* Strand, 1913 is synonymized with *Lycosa piochardi*. By adding novel data to the molecular phylogeny of *Lycosa* created by Planas *et al.* (2013) and re-analyzing it, we explore the relationship of the Levantine species to other Mediterranean species of *Lycosa*. We discuss habitat preferences of the two species of *Lycosa*. Additionally, we report the burrowing species *Geolycosa vultuosa* (C.L. Koch, 1838) as a new record to Israel, thus extending the distribution of this species and genus into the Levant.

**Keywords.** Integrative taxonomy, key, Levant, molecular phylogeny, wolf-spiders.

Armiach Steinpress I., Cohen M., Pétilion J., Chipman A.D. & Gavish-Regev E. 2022. *Lycosa* Latreille, 1804 (Araneae, Lycosidae) of Israel, with a note on *Geolycosa* Montgomery, 1904. *European Journal of Taxonomy* 832: 1–54. <https://doi.org/10.5852/ejt.2022.832.1877>

## Introduction

Lycosidae Sundevall, 1833 is a family of medium-sized to large entelegyne spiders, easily recognized by a combination of characters: three-row eye-arrangement, lack of an RTA (retrolateral tibial apophysis, in males), carrying the egg sac attached to the spinnerets and carrying hatchlings on the body (in females) (Dippenaar-Schoeman & Jocqué 1997). Lycosids inhabit most terrestrial habitats, especially open habitats and habitat patches, from the Arctic Circle to the tropics and from deserts to rainforests (Silva 1996; Dippenaar-Schoeman & Jocqué 1997; Bowden & Buddle 2012). With some exceptions, lycosids are ground-dwelling, active hunters, either vagrant or burrowing (Dippenaar-Schoeman & Jocqué 1997).

Lycosidae is the sixth most species-rich family of spiders, with over 2400 described species in 126 genera (World Spider Catalog 2022). Although the family is well defined by morphological synapomorphies, there are still many lycosid genera with unclear morphological species boundaries; therefore, an integration of morphology and molecular data is needed for species delimitation. Recent molecular work recognized nine subfamilies in Lycosidae (Piacentini & Ramírez 2019). Of these, Lycosinae Simon, 1898 is the most species rich, with 60–70 genera and over 1500 species (Piacentini & Ramírez 2019; World Spider Catalog 2022). It includes some of the largest lycosids, and all the large lycosids found in the Levant, belonging to *Geolycosa* Montgomery, 1904, *Hogna* Simon, 1885 and *Lycosa* Latreille, 1804. We have noticed that, perhaps due to their physical similarity, and because of significant changes in genus delimitations, *Lycosa*, *Geolycosa* and *Hogna* often tend to be confused. For this reason, we discuss *Geolycosa* and *Hogna* briefly in this paper.

*Geolycosa* Montgomery, 1904, includes 71 accepted species distributed across all continents (except Antarctica) and some islands, such as Timor and Bioko (World Spider Catalog 2022). These are large lycosids, characterized by adaptations to burrowing (Mcheidze 1997). Their genitalia are largely plesiomorphic, resembling the genitalia of *Hogna* Simon, 1885 and *Trochosa* C.L. Koch, 1847. The genus is in need of revision and as it is a large, cosmopolitan taxon, it might be found to be polyphyletic (Breitling 2019). *Geolycosa iaffa* (Strand, 1913) and *Geolycosa urbana* (O. Pickard-Cambridge, 1876) were previously reported from Israel (Zonstein & Marusik 2013), yet they have been transferred to *Hogna effera* (O. Pickard-Cambridge, 1872) and *Trochosa urbana* O. Pickard-Cambridge, 1876, respectively (Zonstein *et al.* 2015).

*Hogna* Simon 1885, the genus with the smallest body size of the region's large lycosids (with body length of 12–16 mm), is represented in the southern Levant by at least three species: *Hogna effera* (O. Pickard-Cambridge, 1872) (Eastern Mediterranean basin, Middle East); *Hogna* (cf.) *graeca* (Israel and Palestine (if conspecific with *Hogna graeca* (Roewer, 1951), also Greece, Turkey)); and *Hogna sinaia* (Roewer, 1959) (Sinai peninsula) (Armiach *et al.* 2016; Logunov 2020; World Spider Catalog 2022). It will not be discussed in this paper, as its taxonomy was already partly resolved by Logunov (2020) and in part would need, to our assessment, a separate study to be addressed adequately. As we could not procure any type material of *Hogna graeca*, the local specimens are referred to as *Hogna* (cf.) *graeca* in this paper.

*Lycosa* Latreille, 1804 is the type genus of Lycosidae, as well as of Lycosinae. It has a long taxonomic history, with the type species, *Lycosa tarantula* (Linnaeus, 1758) erected as *Aranea tarantula* in *Systema Naturae*, in which, following Baglivi (1695), it is falsely claimed to be a medically significant species, causing tarantism (a medical condition, sometimes ascribed to *Latrodectus tredecimguttatus* Rossi,

1790) that can be cured by music (Linnaeus 1758). *Lycosa* comprises 224 species, second in number within Lycosidae, only to *Pardosa* C.L. Koch, 1847 (World Spider Catalog 2022). This high number of species is at least partially the result of the genus being used as a wastebasket taxon for two centuries (Framenau & Vink 2001). Species in the genus *Lycosa* are characterized by relatively short, strong legs with black markings on the ventral side, an elevated cephalothorax and relatively large posterior eyes. Contrary to many other genera in Lycosinae, the genitalia of *Lycosa* s. str. are highly derived and are useful for circumscribing the genus (Piacentini & Ramírez 2019), but not always for assessing species boundaries. Many species live in burrows, usually with a modification (turret or door) at the burrow entrance (Planas *et al.* 2013). The species of *Lycosa* s. lat. (as listed in World Spider Catalog 2022) are distributed across all continents (except Antarctica) as well as on many islands, such as Madagascar, New Guinea and Taiwan. Due to the sheer size and distribution of the genus, it may take many years until there is a full revision of *Lycosa*. Such a task is not in our power. However, we can work with some confidence on ‘*Lycosa sensu stricto*’: the species most closely related and geographically adjacent to the type species, *Lycosa tarantula* (Linnaeus, 1758). The distribution of *Lycosa* s. str. lies around the Mediterranean Sea, Eastern Europe, the Middle East and central Asia, with *Lycosa pia* (Bösenberg & Strand, 1906) as an outlier, endemic to Japan (World Spider Catalog 2022).

A phylogeny of 12 western Mediterranean species (Planas *et al.* 2013) found four main lineages (*tarantula* group, *oculata* group, *baulnyi* group and *fasciiventris* group) of north-west African origin. Each lineage was found to have a different burrow-constructing behavior: the *tarantula* and *baulnyi* groups construct burrows with turrets, the *oculata* group constructs burrows with doors, and the *fasciiventris* group does not construct burrows. Many regions in the study of Planas *et al.* (2013) were inhabited by more than one species, with species in a given locality belonging to different lineages. All the species mentioned in Planas *et al.* (2013) are found in Africa, or both Africa and Europe, except *Lycosa tarantula* (Linnaeus, 1758) that is found only in Europe. All *Lycosa* found in western Europe are assumed by the authors to have originated in Africa, with some speciation occurring post dispersal (Planas *et al.* 2013).

The Levant is the name denoting the countries in the easternmost part of the Mediterranean Sea (Israel, Jordan, Lebanon, Palestine, Syria, parts of Turkey and sometimes adjacent areas, such as the Sinai Peninsula and the island of Cyprus). It is geographically and climatically diverse, and lies wholly in the Palearctic biogeographical realm. As with the rest of the Mediterranean region, endemism is relatively high (Yom-Tov & Tchernov 1988). Several species that were originally described as *Lycosa* have been historically recorded from the Levant: *Allocosa cambridgei* (Simon, 1876) (Syria, Turkey), *Allocosa deserticola* (Simon, 1898) (Egypt), *Allocosa olivieri* (Simon, 1876) (Israel, Syria), *Lycosa articulata* Costa, 1875 (Israel), *Lycosa cingara* (C.L. Koch, 1847) (Egypt), *Lycosa cretacea* Simon, 1898 (Egypt), *Lycosa nilotica* Audouin, 1826 (Egypt), *Lycosa piochardi* Simon, 1876 (Israel), *Lycosa praegrans* C.L. Koch, 1836 (Turkey), and *Lycosa tarantula* (Linnaeus, 1758) (Egypt, Turkey). Not much information exists about most of these species. In cases such as *Lycosa nilotica* Audouin, 1826 and *Allocosa deserticola* (Simon, 1898) (illustrated in Roewer 1959) the illustrations accompanying the descriptions present a spider that, in all likelihood, would not be considered as belonging to *Lycosa* by its modern definition, as outlined by Zyuzin & Logunov (2000). The description of *Lycosa articulata* Costa, 1875, is very incomplete, but the mention of a “biramous median band” (Costa 1875) in the original description would suggest a species of *Hogna* Simon, 1885 rather than a species of *Lycosa*.

In this study we aimed at uncovering the diversity of large lycosids found in the southern Levant (mainly Israel and Palestine) using different sets of characters for species delimitation (morphology, molecular data and behavior (burrow-construction)). The diversity of the somatic and genital morphology of *Lycosa* together with their distribution along a climatic gradient from the mesic habitats in the north of Israel to the arid habitats of the Negev (Israel) and Sinai (Egypt), led us to hypothesize that there are several (four to six) species of *Lycosa*. The burrow-construction behavior of individuals collected

**Table 1.** Species of *Lycosa* Latreille, 1804 delimitation hypotheses.

Character set	Number of species	Character	Distribution
Somatic morphology	four to six	Ventral abdomen coloration and patch size (Fig. 15)	One species throughout the region, one to three in northern Israel, one throughout southern Israel, and one in the Negev high mountains and the Arava valley.
Genital morphology	three (according to each character separately) to five (if combined)	male: Tegular apophysis tip bent proximally or not bent proximally. Crest of tegular apophysis serrated or smooth (Figs 13, 19–20)  female: Septal pedicel present or absent. Septum triangular or trapezoidal (Fig. 9). Spermatheca spiral-shaped or bent dorso-ventrally. Head of spermatheca narrow or bulbous (Fig. 10).	Two species along Israel from the Hermon to the Negev, one in the loess plains of the Negev, one in the Negev high mountains, and one in the Arava valley.
Burrow building behavior	two	Door- or turret-building (Fig. 22)	One species throughout the southern Levant, in all habitat types. Another species in the desert habitats of the south of Israel.

by us led us to hypothesize that there are only two species of *Lycosa* in the southern Levant: a door-building and a turret-building *Lycosa* (Table 1). Integrating these data could indicate the existence of several sympatric, or vicariant species, or, conversely, a few wide-ranging species with variability in their genital and somatic morphology – or a combination of the two. We tested these hypotheses using a third set of characters – molecular sequence data, for those populations for which we had freshly collected material. Regarding sympatry, we aimed to investigate possible mechanisms of coexistence, such as niche partitioning.

In addition, we aimed at testing the phylogenetic relationships of these putative species, especially in relation to the western Mediterranean species. There are several possible scenarios for the origin of the southern Levantine *Lycosa* in relation to the previously studied western Mediterranean species. The species of *Lycosa* of the southern Levant, studied here, could have originated within one or more of the western north African *Lycosa* lineages reported in Planas *et al.* (2013) and migrated eastward. In this case, the migration of *Lycosa* to the Levant could have taken a southern route, directly from Africa, or a northern route, originating in the groups that had colonized Europe prior to the dispersal eastward. If the split is older, and the southern Levantine species are nested deep in the western Mediterranean group before its radiation into the four current lineages, dispersal would be expected to take place directly from north Africa, where the taxon is supposed to have originally diversified. An additional scenario is that the southern Levantine species of *Lycosa* do not belong to the western Mediterranean clade at all and would be recovered in the phylogeny as its sister taxa. Under this scenario, no information could be gleaned on the origin of these species, as genetic material of most of the non-Mediterranean species has not been sequenced yet. More elaborate dispersal scenarios can be suggested beyond these routes, but the phylogenetic position of the Levantine clades should provide a strong hint as to the most parsimonious possibility.

In order to differentiate among these scenarios, and test our species hypotheses, we used fresh material from Israel and Palestine as well as historical material collected from Israel, Jordan, Lebanon, Palestine and the Sinai Peninsula, and examined the identities, distributions and relatedness of species of *Lycosa* and *Geolycosa* of the southern Levant. A short ecological survey was performed, to assess the habitat preferences and niche partitioning of two of the species found to be distributed sympatrically in the Negev desert.

## Material and methods

This synopsis is based on material deposited at the Israel Arachnid National Collection, the National Natural History Collections (NNHC), the Hebrew University of Jerusalem (HUJ), Senckenberg Naturmuseum (SMF), National Museum of Natural History, Paris (MNHN) and Natural History Museum in London (NHM). Four hundred and forty-one specimens from ~160 localities were examined (Fig. 1), 348 of which were freshly collected by the authors, or by collaborators. The samples were preserved in 70% ethanol in room temperature (for morphology only), or absolute ethanol in -80°C (for DNA extraction) and identified using relevant literature (Koch 1836; Simon 1876; Strand 1915), and comparison with paratype specimens. Specimen lists created according to Magalhaes (2019).

## Repositories

HUJ INV-AR	=	The Hebrew University of Jerusalem, Israel
MNHN	=	Muséum national d'histoire naturelle, Paris, France
NHM	=	Natural History Museum, London, UK
SMF	=	Senckenberg Naturmuseum, Frankfurt, Germany

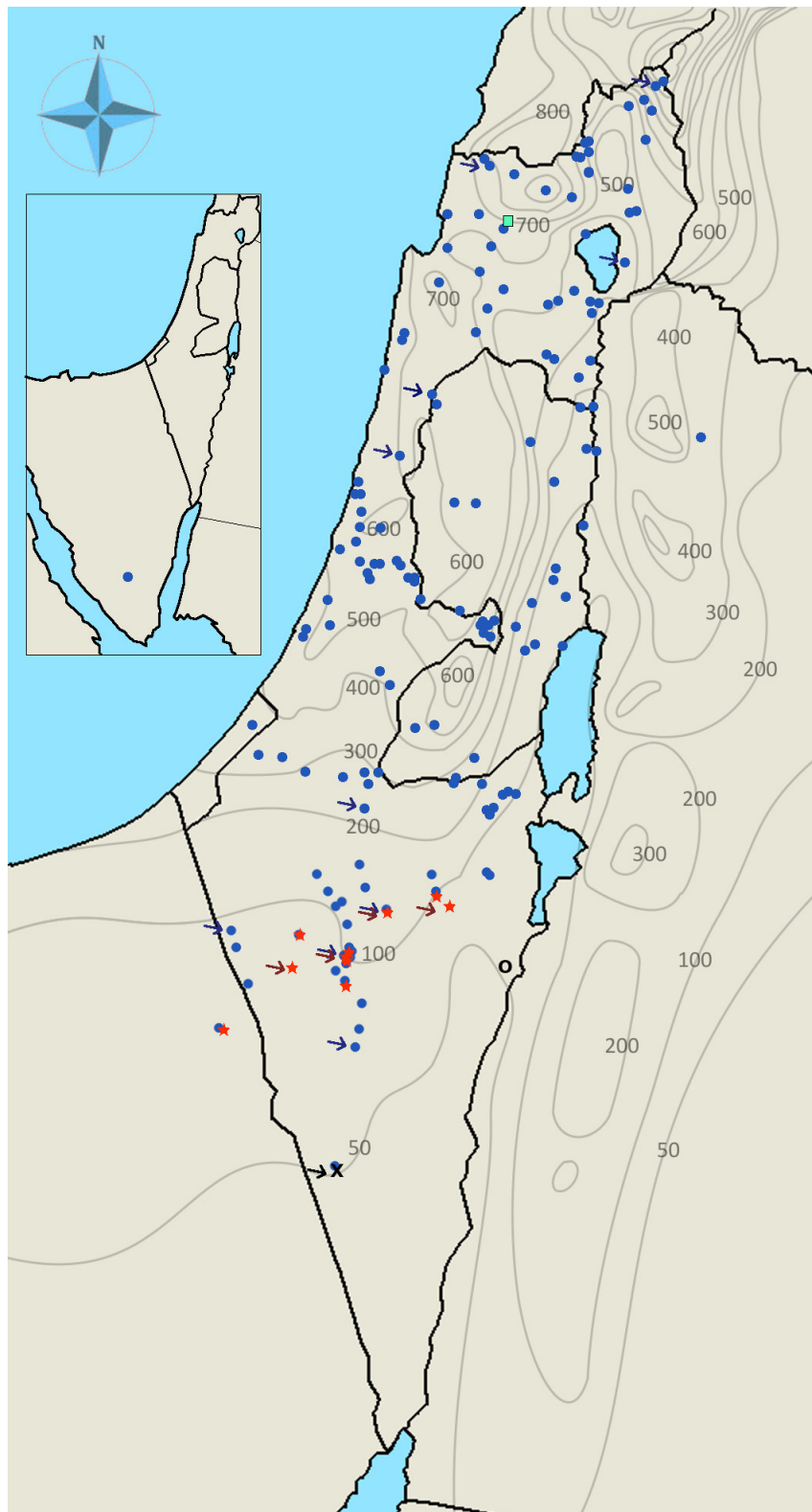
## Distribution and morphology

The distribution map was generated with Google Maps and edited in GIMP ver. 2.10.24. Transliterated names of the localities in Israel and Palestine follow the 'Israel Touring Map' (1:250 000) and 'List of Settlements', published by the Israel Survey, Ministry of Labor. Coordinates are given in decimal degrees (DD). Coordinates estimated from Google maps by the locality name are in '()', coordinates taken in situ with a GPS are in '[]'.

Measurements are in mm. Epigynes were detached and temporarily cleared with clove oil. Specimens were examined and measured using a Nikon SMZ25 stereo microscope. Digital microscope images were taken using NIS-elements imaging system with Nikon DS Fi2 digital camera mounted on a Nikon SMZ25 stereo microscope. Habitus images were taken with Nikon B500. Images were edited using GIMP ver. 2.10.24.

## Anatomical abbreviations used in text and figures

A	=	atrium
AER	=	anterior eye row
ALE	=	anterior lateral eyes
AME	=	anterior median eyes
C	=	conductor
CT	=	conductor tip
CTA	=	crest of tegular apophysis
CY	=	cymbium
E	=	embolus
ET	=	embolus tip
FD	=	fertilization duct
Fe	=	femur



**Fig. 1.** Collecting localities for this study (small map points to a locality in southern Sinai). ■: *Geolycosa vultuosa* C.L. Koch, 1838. x: *Lycosa gesserit* sp. nov. o: *Lycosa* sp. ★: *Lycosa hyraculus* sp. nov. ●: *Lycosa piochardi* Simon, 1876. Isohyets represent mean annual precipitation in mm. Arrows point to localities represented in molecular phylogeny.

HS	=	head of spermatheca
Mt	=	metatarsus
Pa	=	patella
PME	=	posterior median eyes
PP	=	posterior probability
S	=	septum
SA	=	spermatheca
SD	=	sperm duct
SE	=	synembolus
SEL	=	synemolus lobe
SET	=	synembolus tip
ST	=	subtegulum
T	=	tegulum
TA	=	tegular apophysis
TAT	=	tegular apophysis tip
Ti	=	tibia
Tr	=	tarsus

### Molecular analysis

DNA was extracted from the legs of 16 specimens (Table 2) of three species of *Lycosa*. The method chosen was Minicolumn Purification, using the BioVision Insect Genomic DNA Kit (Catalog #: K1412), following the protocol provided with the product (except that the samples were incubated in proteinase K overnight, rather than 30 minutes). Two genetic markers were amplified by PCR using general primers (Table 3) and sequenced bidirectionally with Sanger sequencing. We retrieved a ~650 bp long fragment of mitochondrial cytochrome c oxidase I (COI) and a ~650 bp long fragment of nuclear 28S ribosomal RNA (28S).

All sequences are deposited in GenBank (Table 2). To these, we added the corresponding COI and 28S fragments from 18 species retrieved from GenBank (Table 2), mostly from the material used by Planas *et al.* (2013). These two markers were selected for their proven utility in lycosid phylogeny (Piacentini & Ramírez 2019). The sequences were trimmed and aligned using MEGA 10 (Kumar *et al.* 2018). We performed a Bayesian analysis, using BEAUti ver. 1.10.4 and BEAST ver. 1.10.4 (Suchard *et al.* 2018) and constructed a phylogeny using TreeAnnotator ver. 1.10.4 (Drummond & Rambaut 2007). Tree prior used in BEAUti was ‘Speciation: Yule Process’ (Yule 1925; Gernhard 2008). The rest of the parameters were left at default: substitution model: HKY, base frequencies: estimated, site heterogeneity model: none, MCMC length of chain: 10 000 000, thread pool size: automatic, prefer use of: CPU, prefer precision: double, rescaling scheme: default. Visualization was done with FigTree ver. 1.4.4 (Rambaut 2018) and GIMP ver. 2.10.24.

### Ecological survey

A short-term and small-spatial scale ecological survey was performed during the nights of 13–14 September 2020, at two localities in the Negev desert: Midreshet Ben-Gurion and Yeruham Park. Both localities, set about 18 km apart, are home to the two native species of *Lycosa* and are of similar environmental conditions (Midreshet Ben-Gurion: average altitude 480 m a.s.l. (above sea level), average precipitation 93 mm; Yeruham park: average altitude 460 m a.s.l., average precipitation 100 mm; both with loess soil and limestone bedrock). A total of 47 spiders were recorded (detailed in the supplementary material). A 1 × 1 meter square of ground in the vicinity of each specimen was photographed for further examination. In each locality the habitat was recorded (plain, hill), the incline of the surface (>10°, <10°), the direction of the incline (north, east, south, west), relative vegetation cover (negligible, sparse, abundant), percentage of stones on surface, and the distance to the nearest shrub were measured. Percentage of

**Table 2** (continued on next page). Sequences used in molecular phylogeny.

Species	Specimen ID	GenBank accession	Source
<i>Arctosa alluaudi</i> Guy, 1966	CRBA-LC1440	KC550815	Planas <i>et al.</i> 2013
<i>Hogna radiata</i> (Latreille, 1817)	CRBA-LC1315	KC550816	Planas <i>et al.</i> 2013
<i>Lycosa</i> aff. <i>oculata</i> 1	CRBA-LC1403	KC550679	Planas <i>et al.</i> 2013
<i>Lycosa</i> aff. <i>oculata</i> 1	CRBA-LC1413	KC550680	Planas <i>et al.</i> 2013
<i>Lycosa</i> aff. <i>oculata</i> 1	CRBA-LC1414	KC550681	Planas <i>et al.</i> 2013
<i>Lycosa</i> aff. <i>oculata</i> 1	CRBA-LC1415	KC550682	Planas <i>et al.</i> 2013
<i>Lycosa</i> aff. <i>oculata</i> 2	CRBA-LC1603	KC550684	Planas <i>et al.</i> 2013
<i>Lycosa</i> aff. <i>oculata</i> 2	CRBA-LC1598	KC550683	Planas <i>et al.</i> 2013
<i>Lycosa</i> aff. <i>suboculata</i>	CRBA-LC1154	KC550695	Planas <i>et al.</i> 2013
<i>Lycosa</i> aff. <i>suboculata</i>	CRBA-LC1167	KC550692	Planas <i>et al.</i> 2013
<i>Lycosa</i> aff. <i>suboculata</i>	CRBA-LC1169	KC550693	Planas <i>et al.</i> 2013
<i>Lycosa</i> aff. <i>suboculata</i>	CRBA-LC1171	KC550694	Planas <i>et al.</i> 2013
<i>Lycosa</i> aff. <i>suboculata</i>	CRBA-LC1362	KC550687	Planas <i>et al.</i> 2013
<i>Lycosa baulnyi</i> Simon, 1876	CRBA-LC1152	KC550802	Planas <i>et al.</i> 2013
<i>Lycosa baulnyi</i> Simon, 1876	CRBA-LC1095	KC550782	Planas <i>et al.</i> 2013
<i>Lycosa baulnyi</i> Simon, 1876	CRBA-LC1097	KC550796	Planas <i>et al.</i> 2013
<i>Lycosa baulnyi</i> Simon, 1876	CRBA-LC1104	KC550783	Planas <i>et al.</i> 2013
<i>Lycosa baulnyi</i> Simon, 1876	CRBA-LC1158	KC550807	Planas <i>et al.</i> 2013
<i>Lycosa bedeli</i> Simon, 1876	CRBA-LC1002	KC550713	Planas <i>et al.</i> 2013
<i>Lycosa bedeli</i> Simon, 1876	CRBA-LC1022	KC550714	Planas <i>et al.</i> 2013
<i>Lycosa bedeli</i> Simon, 1876	CRBA-LC1068	KC550715	Planas <i>et al.</i> 2013
<i>Lycosa bedeli</i> Simon, 1876	CRBA-LC1398	KC550716	Planas <i>et al.</i> 2013
<i>Lycosa bedeli</i> Simon, 1876	CRBA-LC1402	KC550719	Planas <i>et al.</i> 2013
<i>Lycosa fasciiventris</i> Dufour, 1835	CRBA-AL1187	KC550720	Planas <i>et al.</i> 2013
<i>Lycosa fasciiventris</i> Dufour, 1835	CRBA-AL1189	KC550728	Planas <i>et al.</i> 2013
<i>Lycosa fasciiventris</i> Dufour, 1835	CRBA-AL1201	KC550736	Planas <i>et al.</i> 2013
<i>Lycosa fasciiventris</i> Dufour, 1835	CRBA-AL1209	KC550734	Planas <i>et al.</i> 2013
<i>Lycosa fasciiventris</i> Dufour, 1835	CRBA-AL9907	KC550721	Planas <i>et al.</i> 2013
<i>Lycosa gesserit</i> sp. nov.	HUJ INV-AR20631	OK044018	This study
<i>Lycosa hispanica</i> (Walckenaer, 1837)	CRBA-LC1115	KC550661	Planas <i>et al.</i> 2013
<i>Lycosa hispanica</i> (Walckenaer, 1837)	CRBA-AL1182	KC550639	Planas <i>et al.</i> 2013
<i>Lycosa hispanica</i> (Walckenaer, 1837)	CRBA-AL1184	KC550640	Planas <i>et al.</i> 2013
<i>Lycosa hispanica</i> (Walckenaer, 1837)	CRBA-AL9921	KC550641	Planas <i>et al.</i> 2013
<i>Lycosa hispanica</i> (Walckenaer, 1837)	CRBA-CO0086	KC550646	Planas <i>et al.</i> 2013
<i>Lycosa hyraculus</i> sp. nov.	HUJ INV-AR20553	OK044021	This study
<i>Lycosa hyraculus</i> sp. nov.	HUJ INV-AR20835	OK044020	This study
<i>Lycosa hyraculus</i> sp. nov.	HUJ INV-ARINVAr 20318	OK044019	This study
<i>Lycosa hyraculus</i> sp. nov.	HUJ INV-AR20757	OK044022	This study
<i>Lycosa muniери</i> Simon, 1876	CRBA-LCMENO	KC550768	Planas <i>et al.</i> 2013
<i>Lycosa muniери</i> Simon, 1876	CRBA-LC1001	KC550749	Planas <i>et al.</i> 2013

**Table 2** (continued). Sequences used in molecular phylogeny.

Species	Specimen ID	GenBank accession	Source
<i>Lycosa muniere</i> Simon, 1876	CRBA-LC1003	KC550750	Planas <i>et al.</i> 2013
<i>Lycosa muniere</i> Simon, 1876	CRBA-LC1041	KC550753	Planas <i>et al.</i> 2013
<i>Lycosa muniere</i> Simon, 1876	CRBA-LC1056	KC550751	Planas <i>et al.</i> 2013
<i>Lycosa oculata</i> (Simon, 1876)	CRBA-LC1000	KC550670	Planas <i>et al.</i> 2013
<i>Lycosa oculata</i> (Simon, 1876)	CRBA-LC1012	KC550671	Planas <i>et al.</i> 2013
<i>Lycosa oculata</i> (Simon, 1876)	CRBA-LC1013	KC550674	Planas <i>et al.</i> 2013
<i>Lycosa oculata</i> (Simon, 1876)	CRBA-LC1018	KC550672	Planas <i>et al.</i> 2013
<i>Lycosa oculata</i> (Simon, 1876)	CRBA-LC1019	KC550673	Planas <i>et al.</i> 2013
<i>Lycosa piochari</i> Simon, 1876	HUJ INV-AR20559	OK044011	This study
<i>Lycosa piochari</i> Simon, 1876	HUJ INV-AR20583	OK044014	This study
<i>Lycosa piochari</i> Simon, 1876	HUJ INV-AR20873	OK044007	This study
<i>Lycosa piochari</i> Simon, 1876	HUJ INV-AR20963	OK044012	This study
<i>Lycosa piochari</i> Simon, 1876	HUJ INV-AR20763	OK044017	This study
<i>Lycosa piochari</i> Simon, 1876	HUJ INV-AR20709	OK044009	This study
<i>Lycosa piochari</i> Simon, 1876	HUJ INV-AR20606	OK044008	This study
<i>Lycosa piochari</i> Simon, 1876	HUJ INV-AR20912	OK044015	This study
<i>Lycosa piochari</i> Simon, 1876	HUJ INV-AR20548	OK044016	This study
<i>Lycosa piochari</i> Simon, 1876	HUJ INV-AR20607	OK044013	This study
<i>Lycosa piochari</i> Simon, 1876	HUJ INV-AR20893	OK044010	This study
<i>Lycosa praegrandis</i> C.L. Koch, 1836	P6A 7055	MH763772	Just <i>et al.</i> 2019
<i>Lycosa suboculata</i> Guy, 1966	CRBA-LC1383	KC550702	Planas <i>et al.</i> 2013
<i>Lycosa suboculata</i> Guy, 1966	CRBA-LC1224	KC550696	Planas <i>et al.</i> 2013
<i>Lycosa suboculata</i> Guy, 1966	CRBA-LC1358	KC550697	Planas <i>et al.</i> 2013
<i>Lycosa suboculata</i> Guy, 1966	CRBA-LC1360	KC550699	Planas <i>et al.</i> 2013
<i>Lycosa suboculata</i> Guy, 1966	CRBA-LC1427	KC550703	Planas <i>et al.</i> 2013
<i>Lycosa tarantula</i> (Linnaeus, 1758)	CRBA-LCFRA6	KC550663	Planas <i>et al.</i> 2013
<i>Lycosa tarantula</i> (Linnaeus, 1758)	CRBA-LC1088	KC550669	Planas <i>et al.</i> 2013
<i>Lycosa tarantula</i> (Linnaeus, 1758)	CRBA-LC1090	KC550667	Planas <i>et al.</i> 2013
<i>Lycosa tarantula</i> (Linnaeus, 1758)	CRBA-LC1089	KC550666	Planas <i>et al.</i> 2013
<i>Lycosa tarantula</i> (Linnaeus, 1758)	CRBA-LC1091	KC550668	Planas <i>et al.</i> 2013
<i>Lycosa vachoni</i> Guy, 1966	CRBA-LC1008	KC550775	Planas <i>et al.</i> 2013
<i>Lycosa vachoni</i> Guy, 1966	CRBA-LC1007	KC550773	Planas <i>et al.</i> 2013
<i>Lycosa vachoni</i> Guy, 1966	CRBA-LC1017	KC550779	Planas <i>et al.</i> 2013
<i>Lycosa vachoni</i> Guy, 1966	CRBA-LC1065	KC550778	Planas <i>et al.</i> 2013
<i>Lycosa vachoni</i> Guy, 1966	CRBA-LC1609	KC550774	Planas <i>et al.</i> 2013
<i>Pirata piraticus</i> (Clerck, 1757)	BIOUG06991-A10	KM839375	Hebert <i>et al.</i> 2016
<i>Pisaura mirabilis</i> (Clerck, 1757)	CRBA-LC1468	KC550814	Planas <i>et al.</i> 2013
<i>Xerolycosa miniata</i> (C.L. Koch, 1834)	ZFMK-DNA-100425649	KY270253	Astrin <i>et al.</i> 2016*

\* Astrin J., Hoefler H., Spelda J., Holstein J., Bayer S., Hendrich L., Huber B.A., Kielhorn K.-H., Krammer H.-J., Lemke M., Monje J.C., Moriniere J., Rulik B., Petersen M., Janssen H. and Muster C. Direct submission to GenBank

**Table 3.** Primers used in molecular phylogeny.

name	sequence	gene	direction	source
LCOI	GGTCAACAAATCATAAAGATATTGG	COI	F	Folmer <i>et al.</i> 1994
HCOI	CCCGGTAAAATTAATAAATAAACTTC	COI	R	Folmer <i>et al.</i> 1994
MT6	CCCGGTAAAATTAATAAATAAACTTC	COI	F	Simon <i>et al.</i> 1994
NANCY	CCCGGTAAAATTAATAAATAAACTTC	COI	R	Simon <i>et al.</i> 1994
JERRY	CAACATTTATTTTGATTTTTTGG	COI	F	Simon <i>et al.</i> 1994
MAGGIE	GGATAATCAGAATATCGTCGAGG	COI	R	Hedin & Maddison 2001
Lyc28SFa	GGAAGTAAGAGTAGGGCTTCCC	28S	F	Planas <i>et al.</i> 2013
Lyc28SRa	ATGGTTCGATTAGTCTTTCGCCCC	28S	R	Planas <i>et al.</i> 2013

stones was calculated using the Trainable Weka Segmentation plugin (Arganda-Carreras *et al.* 2017) in Fiji (Schindelin *et al.* 2012). A comparison between the parameters in sites with the different species of *Lycosa* was done with the aid of JMP package (JMP®. SAS Institute Inc., Cary, NC, 1989–2021).

## Results

We reject our hypotheses of four to six (morphology) or two (burrow construction behavior) species of *Lycosa* in Israel and Palestine. By using integrative taxonomy, we conclude that three species can be identified using morphology, behavior and molecular data, from Israel and Palestine. We therefore describe (see below) two new species of *Lycosa* from Israel and redescribe the widespread species *Lycosa piochari* Simon, 1876. We additionally document one female specimen that might represent an additional species of *Lycosa*, yet we did not have males or material for molecular analysis to test this hypothesis. We here present a key to the species of large lycosids (*Geolycosa*, *Hogna*, *Lycosa*) in Israel and Palestine. We added to the key the northern Levant species, *Lycosa praegrandis* C.L. Koch, 1836, that might exist in the north of Israel.

### *Key to large lycosids (Geolycosa, Hogna, Lycosa) of Israel and Palestine*

1. First eye row as wide as second eye row (PME). Second eye row narrower than half of front of the carapace. Posterior eyes arranged in trapezoid ..... 2
  - First eye row narrower than second eye row (PME). Second eye row wider than half of front of carapace. Posterior eyes arranged in rectangle ..... 3
2. Base of epigyne septum as wide as half of length of pedicel. Terminal apophysis with prolateral spur that is longer than half of width of bulb (incl. spur) .....
  - ..... *Geolycosa vultuosa* (C.L. Koch, 1838) Figs 2A, 3A, 4A, 5A, 6A, 7A, 8A
  - Base of epigyne septum as wide as length of pedicel. Terminal apophysis with prolateral spur that is shorter than half of width of bulb (incl. spur) .....
    - ..... *Hogna effera* (O. Pickard-Cambridge, 1872) Fig. 8F
3. Epigyne septum hammer-shaped, pedicel long. Terminal apophysis with prolateral spur .....
  - ..... *Hogna* (cf.) *graeca* (Roewer, 1951) Fig. 8E
  - Epigyne septum trapezoid, pedicel greatly reduced to absent. Terminal apophysis without prolateral spur ..... *Lycosa* Latreille, 1804 ...4

4. Ocular area less than one third of length of carapace. Tegular apophysis tip curving posteriorly at  $\sim 90^\circ$ . Left spermatheca not twisting clockwise ..... 5
  - Ocular area longer than one third of length of carapace. Tegular apophysis tip directed retrolaterally and not curving posteriorly. Left spermatheca twisting clockwise ..... 6
5. Crest of tegular apophysis  $\frac{1}{2}$  width of tegular apophysis. Conductor tip acute. Base of spermathecae parallel or subparallel, not helical ..... *Lycosa piochardi* Simon, 1876  
 Figs 2D, 3D, 4D, 5D, 6D, G, 7D, G, 9C–L, 10C–L, 11E–F, 12C, 13–18
  - Crest of tegular apophysis  $> \frac{1}{2}$  width of tegular apophysis. Conductor tip blunt. Base of spermathecae helical, twisting counterclockwise ... *Lycosa praegrans* C.L. Koch, 1836 Figs 2E, 9M, 10M, 12A  
 (Not yet known from the southern Levant. May be present in nearby areas)
6. Tegular apophysis tip and crest of tegular apophysis distinct from one another. Septal pedicel present. Atria of epigyne visible .....
  - ..... *Lycosa hyraculus* sp. nov. Figs 2C, 3C, 4C, 5C, 6C, F, 7C, F, 8C–D, 9B, 10B, 11C–D, 12C, 19
  - Tegular apophysis tip indistinct from the crest and continuing line of crest of tegular apophysis .....  
 ..... *Lycosa gesserit* sp. nov. Figs 2B, 3B, 4B, 5B, 6B, 7B, 8B, 12B, 20
  - Septal pedicel absent. Atria of epigyne not visible ..... *Lycosa* sp. Figs 6E, 7E, 9A, 10A, 12A–B

### Taxonomy

Class Arachnida Cuvier, 1812  
 Order Araneae Clerck, 1757  
 Family Lycosidae Sundevall, 1833  
 Genus *Geolycosa* Montgomery, 1904

### Type species

*Geolycosa latifrons* Montgomery, 1904.

### Diagnosis

Large lycosids; carapace elevated anteriorly; PME and ALE forming rectangle; septal pedicel on epigyne and spur on TA long (Zyuzin & Logunov 2000).

### Description

Leg I strongest, nearly as long as IV, with thick scopulae on three terminal joints. Chelicerae large. Cephalic region of cephalothorax raised. 1<sup>st</sup> eye row as wide as 2<sup>nd</sup> eye row (PME). Otherwise, similar to *Lycosa* (Montgomery 1904). The type species with elongated epigynal septum and elongated palpal TA (Wallace 1942).

### Natural history

Burrowing lycosids, not venturing far from their burrow (except mature males) (Wallace 1942).

### Distribution

In its current composition *Geolycosa* is nearly cosmopolitan, recorded in all continents, except Antarctica, in tropical to temperate latitudes.

### Relationships

*Geolycosa* is a polyphyletic genus, as shown by Picentini *et al.* (2019). The morphology is possibly a convergence across Lycosinae, due to adaptation to a digging lifestyle. The type species is from North America, and it might not be related to the Old-World species.

## Composition

72 species are recorded in the World Spider Catalog (2022).

### *Geolycosa vultuosa* (C.L. Koch, 1838)

Figs 1, 2A, 3A, 4A, 5A, 6A, 7A, 8A, 21A, 22A

*Lycosa vultuosa* C.L. Koch, 1838: 102, figs 407–408 (D♂♀).

*Lycosa infernalis* Motschulsky, 1849: 289, pl. 2 figs 1–2 (D♂; N.B.: considered a nomen dubium by Zyuzin & Logunov 2000: 309).

*Trochosa infernalis* Thorell, 1875: 172 (D♀).

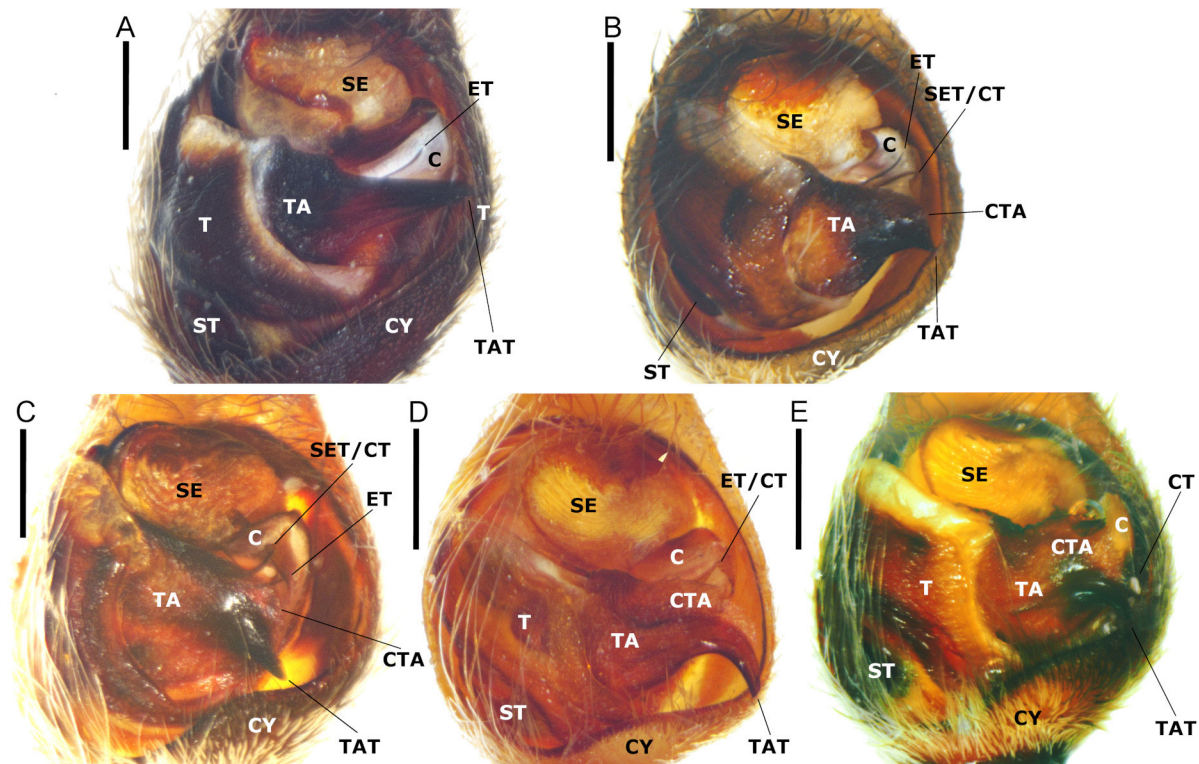
*Arctosa vultuosa* – Simon 1864: 346.

*Trochosa infernalis* – Lendl 1887: 37, 51, figs 1–15 (♂♀).

*Mimohogna vultuosa* – Roewer 1955: 279.

*Lycosa vultuosa* – Fuhn & Niculescu-Burlacu 1971: 202, figs 98a–b, 99a–f (♂♀). — Miller 1971: 154, pl. xxiii fig. 24, pl. xxiv fig. 5 (♂♀). — Loksa 1972: 51, figs 44c, 46c–d (♂♀). — Mcheidze 1997: 226, figs 474–475 (♂♀).

*Geolycosa vultuosa* – Zyuzin & Logunov 2000: 308, figs 5–6, 10 (T♂♀ from *Lycosa*). — Kovblyuk *et al.* 2012: 246, figs 8, 11, 14, 18, 21, 27, 30, 36, 39, 43 (♂♀).



**Fig. 2.** ♂♂ Pedipalps, ventral view. **A.** *Geolycosa vultuosa* C.L. Koch, 1838 (HUJ INV-AR20960). **B.** *Lycosa gesserit* sp. nov., holotype (HUJ INV-AR20631). **C.** *Lycosa hyraculus* sp. nov., holotype (HUJ INV-AR20818). **D.** *Lycosa piochari* Simon, 1876 (HUJ INV-AR20948). **E.** *Lycosa praegrandis* C.L. Koch, 1836 (Veles, North Macedonia; 1 Jun. 2002; courtesy of Marjan Komnenov). Scale bars = 0.5 mm. Photos by I. Armiach Steinpress.

### Diagnosis

Large lycosids (carapace > 5 mm). 1<sup>st</sup> eye row as wide as 2<sup>nd</sup> eye row (PME). Front of cephalothorax square from above. 1<sup>st</sup> eye row < 0.5 width of front of carapace. Epigyne septum hammer-shaped, pedicel twice as long as than width of septum base. Terminal apophysis (TA) with prolateral spur. TA (incl. spur) > 0.5 width of bulb. The only species of *Geolycosa* in the Levantine region (Figs 1A, 2A, 3A, 4A, 5A, 6A).

The only species in the Levant with a similar habitus is *Hogna effera* (O. Pickard-Cambridge, 1872). It is generally smaller, with septal pedicel as long as width of septum base, TA smaller than 0.5 width of bulb.

### Material examined

ISRAEL – Galilee • 2 ♂♂; Karmiel; [32.9168° N, 35.2946° E]; 30 Dec. 2016; I. Armiach Steinpress leg.; HUJ INV-AR20960, HUJ INV-AR20961.

### Natural history

This is a burrowing species, found mainly in open, herbaceous habitats (Mcheidze 1997). Hibernation takes place in the burrow (at least in the north of its range) (Mcheidze 1997), juveniles emerge in springtime. Maturation takes about a year (Mcheidze 1997). The species is preyed upon by pompiliids, scorpions and centipedes, and the eggs are subject to mite infestations (Mcheidze 1997). The specimens examined in this study were found active in daytime in an urban meadow: one on the surface, the other in a burrow with a turret made of soil (Figs 7A, 19A, 21A, 22, Table 4).

### Distribution

AZERBAIJAN, BULGARIA, GEORGIA, HUNGARY, IRAN, RUSSIA, TURKEY, UKRAINE (World Spider Catalog 2022), ISRAEL. According to Mcheidze (1997), also SYRIA.

### Records

ISRAEL: Galilee (Karmiel) (Fig. 1).

### Relationships

*Geolycosa vultuosa* is related to *Geolycosa charitonovi* (Mcheidze, 1997) and *Geolycosa dunini* Zyuzin & Logunov, 2000 (Zyuzin & Logunov 2000). The type species of *Geolycosa* (*G. latifrons* Montgomery, 1904) is of Nearctic distribution. It may not be congeneric with the Palearctic species ascribed to *Geolycosa*. As the revision work needed to find the correct phylogenetic placement of *G. vultuosa* is widely beyond the scope of this work, we refrained from moving *G. vultuosa* to a different genus.

Genus *Lycosa* Latreille, 1804

### Type species

*Lycosa tarantula* (Linnaeus, 1758).

### Diagnosis

Large lycosids; anterior eye row clearly shorter than PME; epigyne septum tongue-shaped or rhomboid, confined to posterior half of epigyne; septal pedicel reduced or absent; TA wide and flat, ending with a distal process (TAT) directed retrolaterally to posteriorly (Zyuzin & Logunov 2000).

### Description

Large lycosids (body length over 12 mm). Carapace sloping posterior to ocular area. Carapace margins with thick pubescence (Zyuzin 1990). Chelicerae with three retromarginal teeth. AER recurved. PME

**Table 4.** Documented activity of *Lycosa* Latreille, 1804 and *Geolycosa* Montgomery, 1904 in Israel (by month). Females with egg-sacs marked by ‘o’. Grey squares without a sex sign denote juveniles only.

Species \ Month	1	2	3	4	5	6	7	8	9	10	11	12
<i>Geolycosa vultuosa</i> (C.L. Koch, 1838)												♂
<i>Lycosa gesserit</i> sp. nov.									■			
<i>Lycosa</i> sp.											♀	
<i>Lycosa hyraculus</i> sp. nov.	■			■	■	♀♂		♀♂		■	♂	
<i>Lycosa piochardi</i> Simon, 1876	o♀	♀	♀	o♀♂	♀	o♀	♀♂	♀♂	o♀♂	o♀♂	o♀	o♀♂

wider than AER. Abdomen venter usually with black markings. Sexual dimorphism weak. Posterior part of epigynal septum widened and clearly outlined. Septal pedicle fused with genital groove or wholly absent. This contrasts with other large Lycosinae (*Hogna*, *Geolycosa*), having a clearly outlined pedicle. Cymbium asymmetrical. Tegular apophysis wide and flat, with an elongated distal process, directed retrolaterally to posteriorly. Embolus thin, long, with narrow epiconductor.

### Natural history

Generalist predators, typical of open habitats. Most species are burrowing, but some seem to be vagrant (Planas *et al.* 2013). The burrow entrance is usually modified with a door or a turret (an elevated structure made of silk and vegetation, surrounding the entrance). Activity is mostly nocturnal. Reproductive season recorded in the summer and autumn.

### Distribution

Known from the Mediterranean Basin, eastern Europe, Middle East, central Asia and Japan (World Spider Catalog 2022).

### Relationships

*Lycosa* s. str. is related to *Hogna* Simon 1885 (Piacentini & Ramírez 2019). According to Zyuzin & Logunov (2000), *Lycosa* is closely allied with *Alopecosa pictilis* (Emerton, 1885), *A. sibirica* (Kulczyn'ski, 1908), *A. solivaga* (Kulczyn'ski, 1901) and *A. hirtipes* (Kulczyn'ski, 1908).

#### *Lycosa gesserit* sp. nov.

[urn:lsid:zoobank.org:act:A5A1F6AD-14B4-488F-BC74-A2B5E240A86B](https://zoobank.org/act:A5A1F6AD-14B4-488F-BC74-A2B5E240A86B)

Figs 1, 2B, 3B, 4B, 5B, 6B, 7B, 8B, 12B, 23–24

### Diagnosis

#### Male

Recognized by pedipalp structure: TAT not bent posteriorly, directed retrolaterally. Contrasts with *L. hyraculus* sp. nov. by having TAT shorter than TAC (TAT as long as TAC in *L. hyraculus* sp. nov.). Contrasts with all other known males of *Lycosa*, with TAT bent posteriorly (Figs 2B, 3B, 4B, 5B, 6B, 7B, 8B).

#### Female

Unknown.

### Etymology

Species named after the order of *Bene Gesserit*, from Frank Herbert's 1965 novel, *Dune*.

### Type material

#### Holotype

ISRAEL – Negev • ♂; Har Karkom; [30.28° N, 34.74° E]; 7 Sep. 2017; E. Gavish-Regev; col. sub.; collected at night; HUI INV-AR20631.

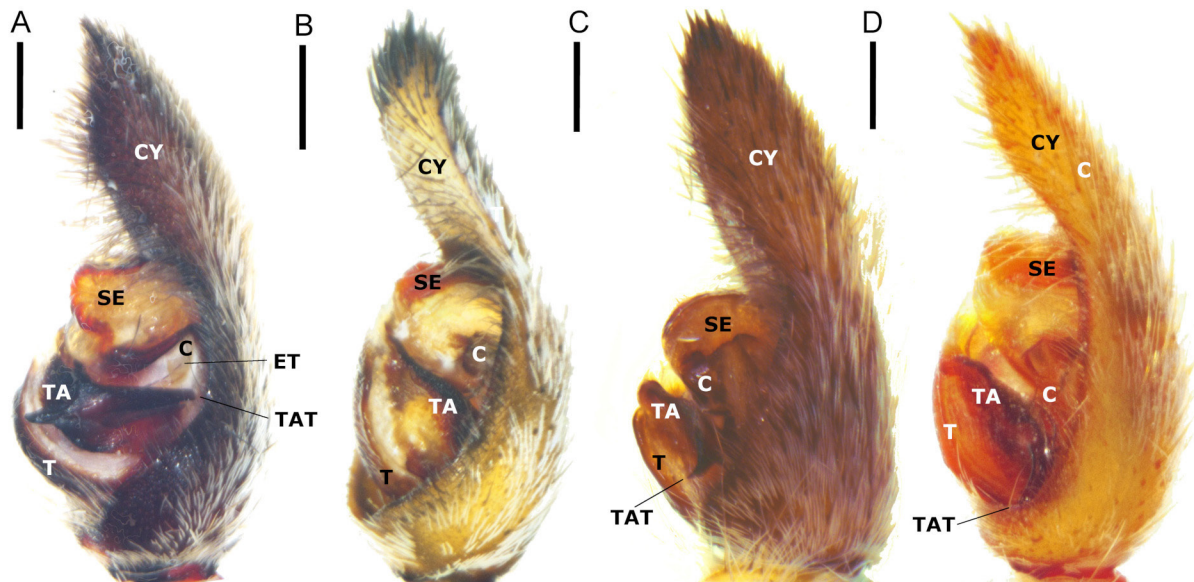
### Description

#### Male

HOLOTYPE MEASUREMENTS. AME diameter: 0.2; ALE diameter: 0.18; PME diameter: 0.8; PLE diameter: 0.7; carapace length: 6.6; carapace width: 4.8; carapace maximal height: 2.1; abdomen length: 5.2; leg I (Fe, Pa, Ti, Mt, Tr): 5.5, 2.5, 4.9, 5.5, 2.8; leg II: 5.1, 2.3, 4.6, 5.3, 2.9; leg III: 4.9, 2.4, 4.1, 5.9, 2.3; leg IV: 6, 2.6, 5.5, 8.2, 3.4.

CARAPACE. Ocular area  $> \frac{1}{3}$  length of carapace, distinctly raised, making the carapace between PLE and fovea appear slightly concave in profile.

COLOR. Carapace cream colored, with dark brown median bands, darker on margins, connecting to dark ocular area. Perimeter light brown. Sternum grey. Chelicerae reddish-brown. Abdomen yellow infused with light brown dorsad, cardiac mark brown, darker on margins. Abdomen venter with black patch surrounding epigastric fold, connecting to two parallel black bars stretching towards spinnerets (II shaped patch). Spinnerets brown. Legs cream colored, infused with brown dorsad, yellow-grey ventrad, to reddish-brown distad, with two black bands on tibia. Coxae dark grey, trochanters brown. Pedipalps yellow, to dark brown distad (Figs 6B, 7B, 8B).



**Fig. 3.** Male pedipalps, prolateral view. **A.** *Geolycosa vultuosa* C.L. Koch, 1838 (HUI INV-AR20960). **B.** *Lycosa gesserit* sp. nov., holotype (HUI INV-AR20631). **C.** *Lycosa hyraculus* sp. nov., holotype (HUI INV-AR20818). **D.** *Lycosa piochardi* Simon, 1876 (HUI INV-AR20948). Scale bars = 0.5 mm. Photos by I. Armiach Steinpress.

**GENITALIA.** Genital opening sclerotized, similar to subadult epigyne. Cymbium reddish-brown. Tegular apophysis (TA) lying flat on bulb, oriented retrolaterally. TAT highly sclerotized, dark brown, not bent posteriorly (unlike most other species of *Lycosa*), but slightly bent ventrad. Crest of TA (CTA) with smooth edge, and abrupt, rounded end at base of TAT. TAT shorter than width of CTA. Tip of conductor membranous, triangular, with smooth edges. Synembolus with large, slightly sclerotized lobe (SEL), on retrolateral edge (Figs 2B, 3B, 4B, 5B, 12B).

**LEGS.** Metatarsus I ventral spination: 2 pairs + apical triplet. Tibia I ventral spination: 2 pairs + apical pair. Tarsus with scopula.

### Natural history

This species is nocturnal. A single juvenile male was collected at night, in September, at 650 m a.s.l., in a stony plain near Har Karkom, a secluded tableland in the hyperarid desert (annual precipitation < 75 mm) (Fig. 1, Table 4). The specimen was mature after two molts in captivity, in August 2018. Like the closely related *L. hyraculus* sp. nov., it makes a burrow with a trapdoor. Shares habitat with *L. piochardi*. Reproductive season unknown.

### Distribution

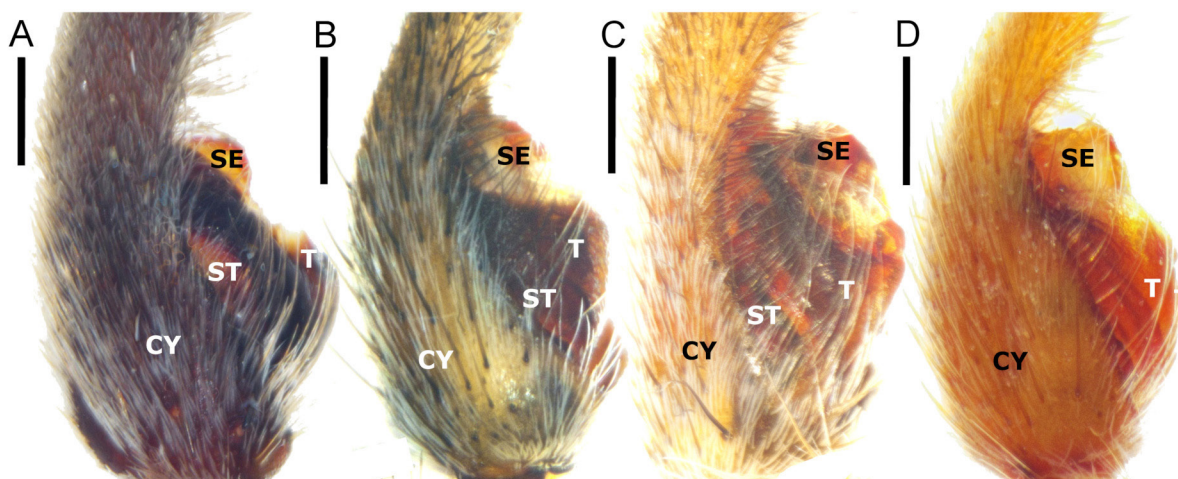
ISRAEL. Possibly endemic to the Har Karkom tableland or found throughout hyperarid zone.

### Records

ISRAEL: Negev (Har Karkom) (Fig. 1).

### Relationships

According to our molecular phylogeny, this species is the sister taxon of *Lycosa hyraculus* sp. nov., and closely related to *Lycosa oculata*, *Lycosa* aff. *oculata* 1 and *Lycosa* aff. *oculata* 2 (Figs 21–24). Cephalothorax is similar to *Lycosa macrophthalma* Nadolny & Zamani, 2020 and it might be related to it as well.



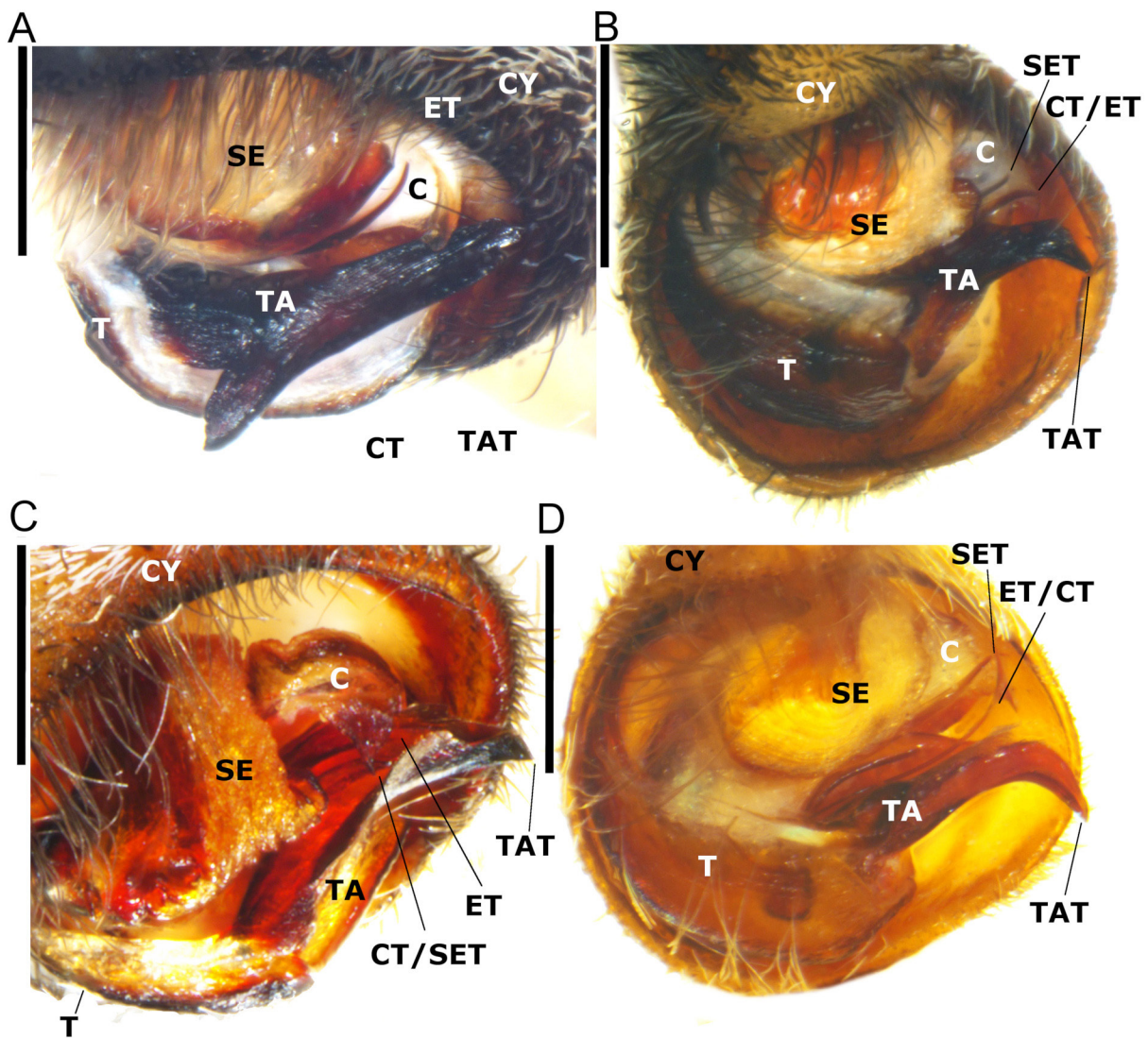
**Fig. 4.** Male pedipalps retrolateral view. **A.** *Geolycosa vultuosa* C.L. Koch, 1838 (HUJ INV-AR20960). **B.** *Lycosa gesserit* sp. nov., holotype (HUJ INV-AR20631). **C.** *Lycosa hyraculus* sp. nov., holotype (HUJ INV-AR20818). **D.** *Lycosa piochardi* Simon, 1876 (HUJ INV-AR20948). Scale bars = 0.5 mm. Photos by I. Armiach Steinpress.

The single known male specimen was raised in the laboratory for two molts. This has probably affected the size of the adult spider. Even though we have observed an aberrant morphology in the genitalia of females grown in lab conditions, we have not observed the same in males, either of *L. piochardi* or of *L. hyraculus* sp. nov. We consider it highly probable that the diagnostic characters in the male's pedipalp were not affected by the laboratory conditions.

Although genitalia of other males of *Lycosa* grown in our laboratory did not show distortions (see discussion about distortions of female genitalia), we cannot dismiss the possibility that the pedipalps of specimens in the wild are somewhat different to the type specimen, which was raised in the laboratory.

**Notes**

The locality where the type was found is a remote and not easily reachable nature reserve, encircled by army training areas, that are closed to the public most of the year. There are only few occasions every



**Fig. 5.** Male pedipalps, distal view. **A.** *Geolycosa vultuosa* C.L. Koch, 1838 (HUJ INV-AR20960). **B.** *Lycosa gesserit* sp. nov., holotype (HUJ INV-AR20631). **C.** *Lycosa hyraculus* sp. nov., holotype (HUJ INV-AR20818). **D.** *Lycosa piochardi* Simon, 1876 (HUJ INV-AR20948). Scale bars = 0.5 mm. Photos by I. Armiach Steinpress.

year that access to the public is possible. As of the writing of this paper, we have not succeeded in collecting additional specimens.

*Lycosa hyraculus* sp. nov.

[urn:lsid:zoobank.org:act:8BA7C78F-E972-41B9-B7AC-C65ECA9B67E2](https://doi.org/10.21203/rs.3.rs-1234567)

Figs 1, 2C, 3C, 4C, 5C, 6C, F, 7B, F, 8B–D, 9B, 10B, 11C–D, 12C, 19, 21B, 22B, 23–24

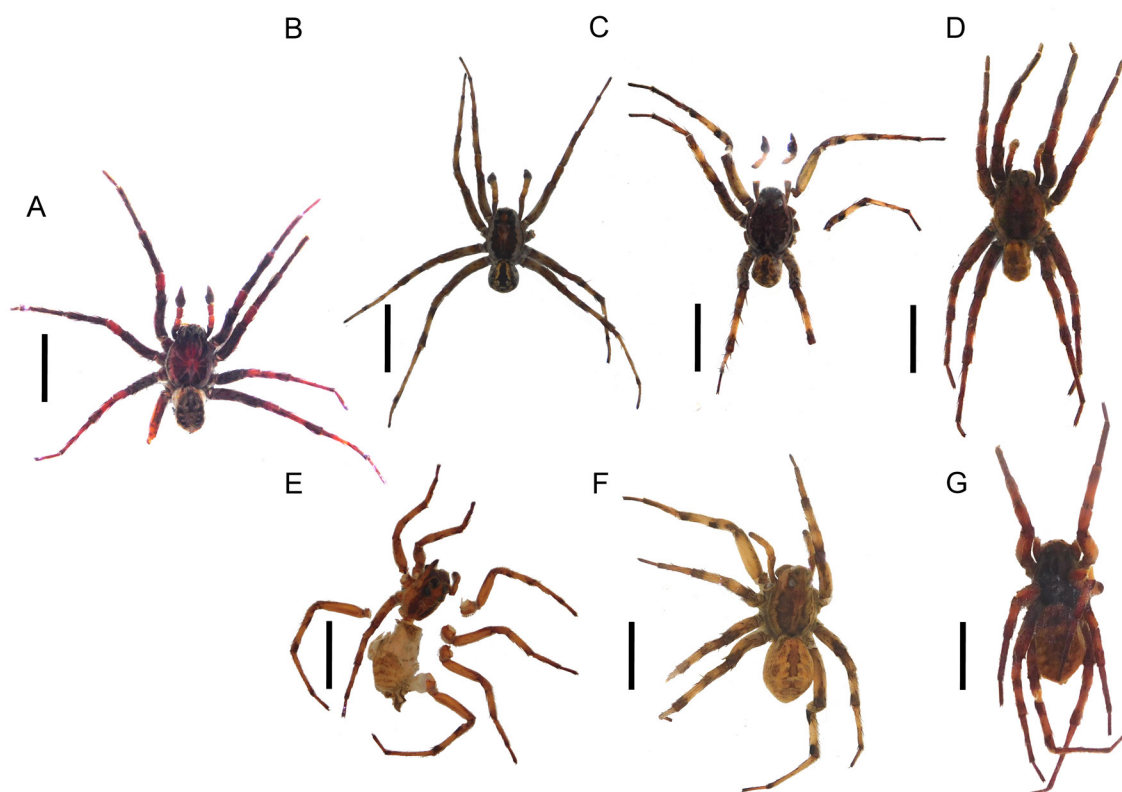
**Diagnosis**

**Male**

TER not bent posteriorly, directed retrolaterally. Contrasts with *L. gesserit* sp. nov. by having TAT as long as CTA (TAT as shorter than CTA in *L. gesserit*). Contrasts with all other known males of *Lycosa*, with TER bent posteriorly (Figs 2C, 3C, 4C, 5C, 6C, F, 7C, 19).

**Female**

Recognized by combination of characters: ocular area:  $> \frac{1}{3}$  length of carapace, distinctly raised, making the carapace between PLE and fovea appear slightly concave in profile. Epigyne: septal pedicel reduced, septum trapezoidal, broader proximally, wider than long. Copulatory openings narrow, at anterior end of septum. Carapace resembles *L. oculata*, *L. suboculata*, and *L. macrophthalma*, but in these species the septum is longer than wide. Carapace also resembles *Lycosa* sp., but in this species the copulatory



**Fig. 6.** Habitus, dorsal view. **A.** *Geolycosa vultuosa* C.L. Koch, 1838, ♂ (HUJ INV-AR20961). **B.** *Lycosa gesserit* sp. nov., holotype, ♂ (HUJ INV-AR20631). **C.** *Lycosa hyraculus* sp. nov., holotype, ♂ (HUJ INV-AR20818). **D.** *Lycosa piochardi* Simon, 1876, ♂ (HUJ INV-AR20597). **E.** *Lycosa* sp., ♀ (HUJ INV-AR20573). **F.** *Lycosa hyraculus* sp. nov., paratype, ♀ (HUJ INV-AR20817). **G.** *Lycosa piochardi* Simon, 1876, ♀ (SMFD11934). Scale bars = 10 mm. Photos by I. Armiach Steinpress.

openings are not visible in ventral view. Epigyne similar to *L. piochardi* and *L. baulnyi*, but in these species the ocular area is not distinctly raised, and is  $< \frac{1}{3}$  length of carapace (Figs 6C, F, 7C, F, 9B, 10B, 11C–D).

### Etymology

Species name from *Hyrax*. This species often leaves the entrance to its burrow open. This behavior reminded the authors of an Israeli nursery rhyme, in which “the little hyrax forgot to close the door”.

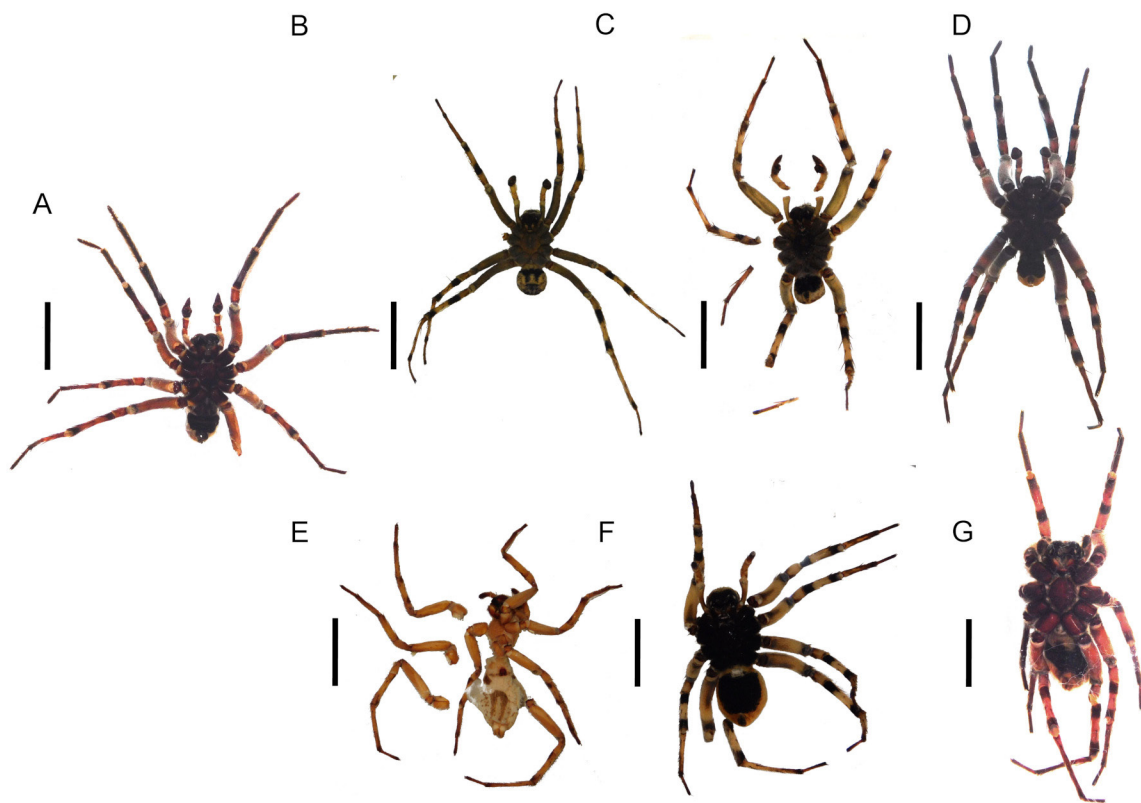
### Type material

#### Holotype

ISRAEL – Negev • ♂; Sede Zin; [30.854° N, 34.773° E]; 13 Aug. 2016; I. Steves leg.; HUI INV-AR20818.

#### Paratype

ISRAEL – Negev • ♀; same collection data as for holotype; HUI INV-AR20817.



**Fig. 7.** Habitus, ventral view. **A.** *Geolycosa vultuosa* C.L. Koch, 1838, ♂ (HUI INV-AR20961). **B.** *Lycosa gesserit* sp. nov., holotype, ♂ (HUI INV-AR20631). **C.** *Lycosa hyraculus* sp. nov., holotype, ♂ (HUI INV-AR20818). **D.** *Lycosa piochardi* Simon, 1876, ♂ (HUI INV-AR20597). **E.** *Lycosa* sp., ♀ (HUI INV-AR20573). **F.** *Lycosa hyraculus* sp. nov., paratype, ♀ (HUI INV-AR20817). **G.** *Lycosa piochardi* Simon, 1876, ♀ (SMFD11934). Scale bars = 10 mm. Photos by I. Armiach Steinpress.

### Other material examined

EGYPT – **Sinai** • 1 juv.; Al-Qusaymah (Kadesh Barnea); [30.668° N, 34.366° E]; 13 Nov. 1967; P. Amitai leg.; HUI INV-AR20840 •

ISRAEL – **Negev** • 1 ♀; Ha-Ro'a Campsite; [30.876° N, 34.784° E]; 14 Jun. 2015; E. Gavish-Regev leg.; HUI INV-AR20658 • 1 ♂; Haluqim ridge; [30.86° N, 34.77° E]; 24 Jul. 2018; E. Gavish-Regev leg.; col. sub.; HUI INV-AR20663 • 1 juv.; Hawat Even Ari; [30.786° N, 34.77° E]; 3 Jan. 2018; col. sub.; HUI INV-AR20942 • 1 ♂; Mamshit; 7 Nov. 2017; A. Uzan leg.; HUI INV-AR20553 • 1 juv.; Midreshet Ben-Gurion; [30.854° N, 34.773° E]; 22 Oct. 2018; I. Armiach Steinpress leg.; HUI INV-AR20737 • 1 juv.; same collection data as for preceding; HUI INV-AR20738 • 1 juv.; same collection data as for preceding; HUI INV-AR20739 • 1 juv.; same collection data as for preceding; col. juv.; HUI INV-AR20740 • 1 juv.; same collection data as for preceding; col. juv.; HUI INV-AR20741 • 1 juv.; same collection data as for preceding; col. juv.; HUI INV-AR20742 • 1 juv.; same collection data as for preceding; col. juv.; HUI INV-AR20743 • 1 juv.; same collection data as for preceding; col. juv.; HUI INV-AR20744 • 1 juv.; same collection data as for preceding; col. juv.; HUI INV-AR20745 • 1 juv.; same collection data as for preceding; col. juv.; HUI INV-AR20746 • 1 juv.; same collection data as for preceding; col. juv.; HUI INV-AR20747 • 1 juv.; same collection data as for preceding; col. juv.; HUI INV-AR20748 • 1 ♀; same collection data as for preceding; col. juv.; HUI INV-AR20749 • 1 juv.; same collection data as for preceding; col. juv.; HUI INV-AR20750 • 1 ♂; same collection data as for preceding; col. juv.; HUI INV-AR20757 • 1 ♂; Mishor Yamin; [31.003° N, 35.1° E]; 11 May 2014; S. Aharon leg.; col. sub.; HUI INV-AR20855 • 1 ♂; Shivta camp; [30.9245° N, 34.6244° E]; 22 Oct. 2018; O. Erlichman leg.; col. juv.; HUI INV-AR20835 • 1 juv.; Tel Jaulan, Yeruham; [30.985° N, 34.904° E]; 10 Oct. 1962; P. Amitai leg.; HUI INV-AR20836 • 1 ♀; Yeruham; [30.985° N, 34.9° E]; 1 Apr. 2017; A. Novikova leg.; col. sub.; HUI INV-AR 20523 • 1 juv.; same locality as for preceding; 29 Jul. 2018; E. Gavish-Regev leg.; col. juv.; HUI INV-AR20616 • 1 juv.; same collection data as for preceding; HUI INV-AR20620 • 1 ♂; same collection data as for preceding; col. sub.; HUI INV-AR20617 • 1 ♂; same collection data as for preceding; col. sub.; HUI INV-AR20618 • 1 ♂; same collection data as for preceding; col. sub.; HUI INV-AR20619 • 1 ♀; same locality as for preceding; 2 Jun. 2016; E. Zvik; col. sub.; HUI INV-AR20665 • 1 juv.; same locality as for preceding; 19 Jul. 2019; Y. Zvik leg.; col. sub.; HUI INV-AR20868 • 1 ♂; Yeruham Park; 2 Jun. 2016; Y. Zvik leg.; HUI INV-AR20874 • 1 juv.; same collection data as for preceding; HUI INV-AR20875.

### Description

#### Male

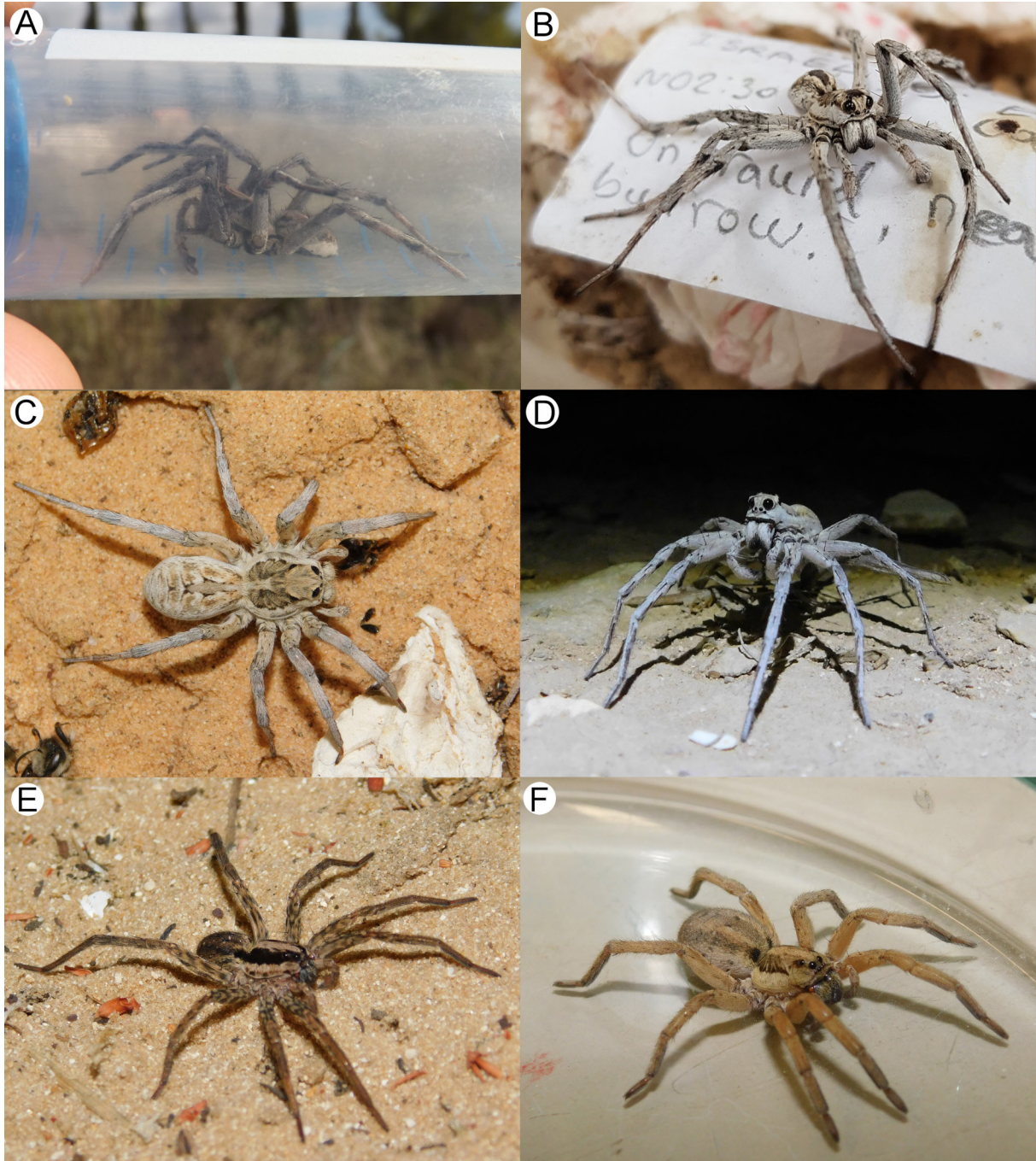
HOLOTYPE MEASUREMENTS. AME diameter: 0.4; ALE diameter: 0.35; PME diameter: 1.25; PLE diameter: 0.99; carapace length: 9.71; carapace width: 7.28; carapace maximal height: 3.59; abdomen length: 6.9; leg I (Fe, Pa, Ti, Mt, Tr): 7.9, 3.54, 6.45, 6.48, 3.67; leg II: 7.31, 3.7, 5.58, 6.93, 3.76; leg III: (missing), 2.88, 5.03, 6.82, 3.57; leg IV: 8.99, 3.56, 7.14, 9.35, 4.07.

VARIATION IN MALES COLLECTED AS ADULTS (n = 2, all other male adults collected as juveniles). AME diameter: 0.28–0.44; PME diameter: 0.9–1.19; carapace length: 0.78–10.03; carapace width: 0.59–7.75; carapace maximal height: 2.78–3.36; abdomen length: 5.9–6.5; leg I (Fe, Pa, Ti, Mt, Tr): 6.44–7.7, 3.02–3.68, 5.5–6.7, 5.84–7.3, 3–3.23; leg II: 6.19–8.2, 2.7–3.6, 5–6.36, 5.66–7.36, 3.1–3.8; leg III: 5.85–7.66, 2.4–3.36, 4.5–5.72, 6.2–7.58, 2.8–3.43; leg IV: 7.5–9.42, 2.8–3.59, 6.06–10, 8.03–10.33, 4.03–4.26.

CARAPACE. Ocular area > 1/3 length of carapace, distinctly raised, making the carapace between PLE and fovea appear slightly concave in profile.

COLOR. Carapace cream colored, with light brown median bands, radiated and darker on margins, connecting to dark ocular area. Perimeter light brown. Sternum black. Chelicerae reddish-brown.

Abdomen yellow infused with light brown dorsad, cardiac mark brown, darker on margins. Abdomen venter black posterior to epigastric fold. Genital opening brown. Spinnerets black. Legs cream colored, infused with brown dorsad, yellowish ventrad, to reddish-brown distad, with two black bands on tibia. Coxae dark grey, trochanters brown. Pedipalps yellow, to dark brown distad (Figs 6C, 7C, 8C–D).

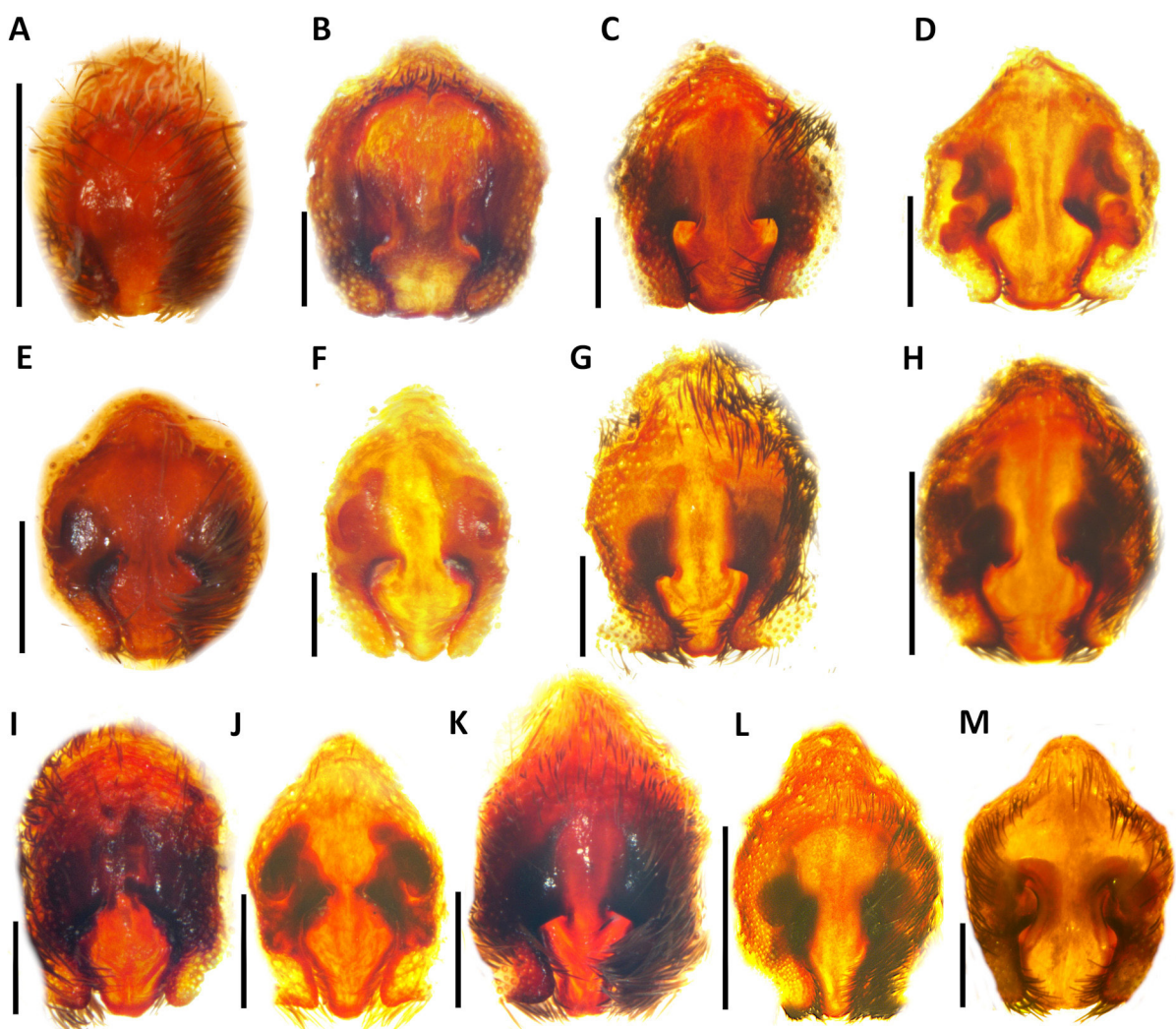


**Fig. 8.** Live specimens. **A.** *Geolycosa vultuosa* C.L. Koch, 1838. **B.** *Lycosa gesserit* sp. nov., holotype, ♂ (HUJ INV-AR20631) **C.** *Lycosa hyraculus* sp. nov., juveniles. **D.** *Lycosa hyraculus* sp. nov., ♂ (specimen not collected). **E.** *Hogna* (cf.) *graeca* (specimen not collected). **F.** *Hogna effera* (O. Pickard-Cambridge, 1872). Photos by I. Armiach Steinpress.

COLOR VARIATION IN MALES (n = 5). Abdominal black patch sometimes trapezoidal, narrow distad; sometimes short, not reaching spinnerets. Spinnerets sometimes grey, brown or yellow.

GENITALIA. Genital opening sclerotized, similar to subadult female epigyne. Cymbium reddish-brown. Tegular apophysis (TA) lying flat on bulb, oriented retrolaterally. TAT highly sclerotized, dark brown, not bent posteriorly (unlike most other species of *Lycosa*), slightly bent ventrad. CTA with smooth edge, and abrupt, rounded end at base of TAT. Tip of conductor membranous, triangular, with smooth edges. Synembolus with small, slightly sclerotized lobe (SEL), on retrolateral edge (Figs 2C, 3C, 4C, 5C, 19).

LEGS. Metatarsus I ventral spination: 2 pairs + apical pair. Tibia I ventral spination: 2 pairs + apical pair. Tarsus with scopula.



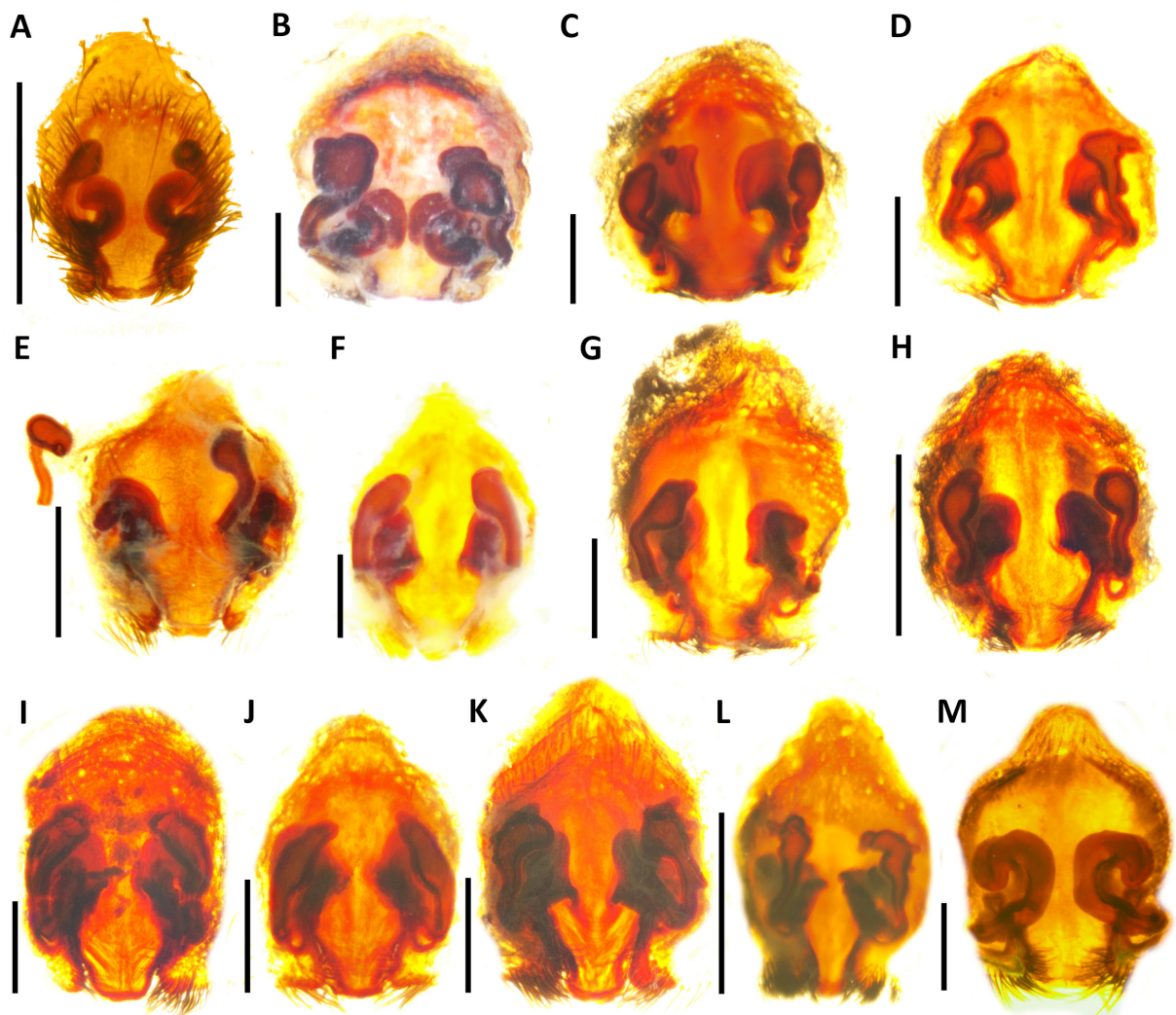
**Fig. 9.** Epigynes, ventral view. **A.** *Lycosa* sp. (HUJ INV-AR20573). **B.** *Lycosa hyraculus* sp. nov., paratype (HUJ INV-AR20817). **C–L.** *Lycosa piochardi* Simon, 1876. **C.** HUJ INV-AR20607. **D.** HUJ INV-AR20912. **E.** HUJ INV-AR20671. **F.** SMFD2184. **G.** HUJ INV-AR20963. **H.** HUJ INV-AR20709. **I.** HUJ INV-AR20897. **J.** HUJ INV-AR20530. **K.** HUJ INV-AR20860. **L.** HUJ INV-AR20758. **M.** *Lycosa praegrandis* C.L. Koch, 1836 (Veles, North Macedonia, 1 Jun. 2002; courtesy of Marjan Komnenov). Scale bars = 0.5 mm. Photos by I. Armiach Steinpress.

**Female**

PARATYPE MEASUREMENTS. AME diameter: 0.44; PME diameter: 1.6; carapace length: 10.97; carapace width: 7.96; carapace maximal height: 3.96; abdomen length: 10.88; leg I (Fe, Pa, Ti, Mt, Tr): 8.18, 3.75, 6.07, 5.62, 3.1; leg II: 7.56, 3.7, 5.56, 6.03, 3.1; leg III: 6.34, 3.28, 5, 6.72, 3.29; leg IV: 8.25, 3.66, 6.84, 8.66, 3.75.

VARIATION OF AN ADDITIONAL FEMALE COLLECTED AS ADULT (n = 1, all other female adults collected as juveniles). AME diameter: 0.55; PME diameter: 1.35; carapace length: 10.7; carapace width: 8.2; carapace maximal height: 4.02; abdomen length: 9.98; leg I (Fe, Pa, Ti, Mt, Tr): 8, 3.9, 6.3, 5.5, 3.17; leg II: 8.06, 4, 5.87, 6.26, 3.6; leg III: 7.45, 3.6, 5.56, 6.94, 3.53; leg IV: 9.64, 3.7, 7.46, 10.2, 4.23.

CARAPACE. Similar to male.



**Fig. 10.** Epigynes, dorsal view. **A.** *Lycosa* sp. (HUJ INV-AR20573). **B.** *Lycosa hyraculus* sp. nov., paratype (HUJ INV-AR20817). **C–L.** *Lycosa piochardi* Simon, 1876 (HUJ INV-AR20607). **D.** HUJ INV-AR20912. **E.** HUJ INV-AR20671. **F.** SMFD2184. **G.** HUJ INV-AR20963. **H.** HUJ INV-AR20709. **I.** HUJ INV-AR20897. **J.** HUJ INV-AR20530. **K.** HUJ INV-AR20860. **L.** HUJ INV-AR20758. **M.** *Lycosa praegrandis* C.L. Koch, 1836 (Veles, North Macedonia, 1 Jun. 2002; courtesy of Marjan Komnenov). Scale bars = 0.5 mm. Photos by I. Armiach Steinpress.

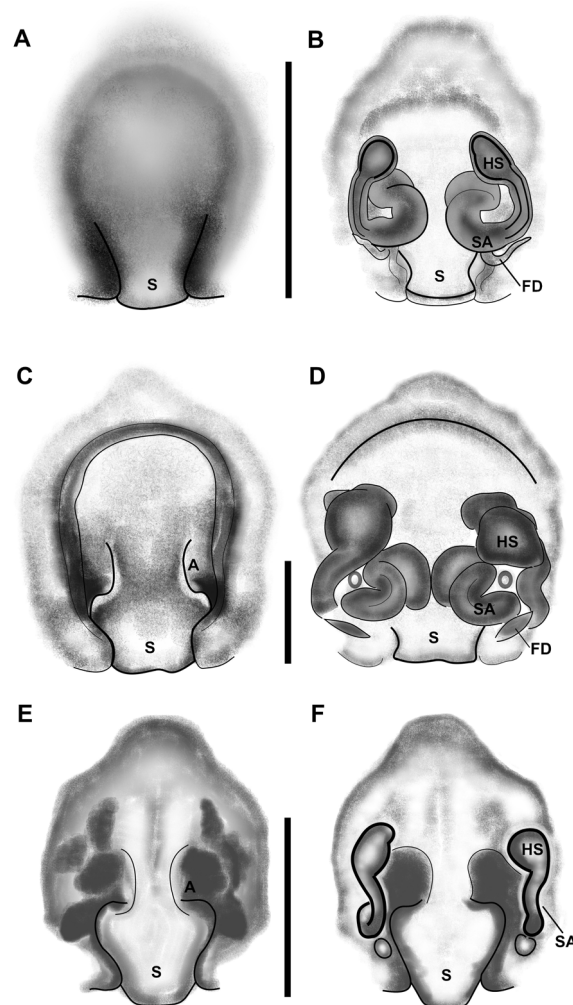
COLOR. Similar to male. No significant variation observed (Figs 6F, 7F, 8C).

GENITALIA. Epigyne longer than wide. Septal pedicel reduced, narrower than septum. Septum trapezoidal, wider proximally, about as long as proximal part of epigyne. Copulatory openings narrow, flanking septal pedicel. Spermatheca dark brown, compact, distal part arching laterally. Head of spermatheca distinctly wider than sperm duct, subcircular, positioned anterior to copulatory opening (Figs 9B, 10B, 11C–D).

LEGS. Similar to male.

### Natural history

This species is nocturnal. Females were collected March, June, August and September. Males collected June, August and September. Subadult females were collected April and June. Subadult males were



**Fig. 11.** *Lycosa* female epigyne, line drawings. **A–B.** *Lycosa* sp. (HUI INV-AR20573). **A.** Ventral view. **B.** Dorsal view. **C–D.** *Lycosa hyraculus* sp. nov., paratype (HUI INV-AR20817). **C.** Ventral view. **D.** Dorsal view. **E–F.** *Lycosa piochardi* Simon, 1876 (HUI INV-AR20709). **E.** Ventral view. **F.** Dorsal view. Scale bars = 0.5 mm. Drawings by I. Armiach Steinpress.

collected May, July and September. Juveniles were collected January, June, July and October (Table 4). Reproductive season unknown. This species inhabits loess soils in arid desert environments (annual precipitation 75–200 mm). The burrow usually with a modification in the form of a thin, flexible door made of silk and soil, and hinged to the entrance with silk. Rarely an object such as a piece of soil crust or a flat stone can be used as a door. The door is often left open. The spiders are usually found at night, standing near the burrow, rarely on rocks or vegetation. Captive specimens accept a wide variety of insects, similar to other species of *Lycosa* (Steves *et al.* 2017) (Figs 8C–D, 21B, 22B).

### Distribution

EGYPT, ISRAEL.

### Records

EGYPT: Sinai (Al-Qusaymah (Kadesh Barnea)). ISRAEL: Negev (Ha-Ro'a Campsite, Haluqim ridge, Hawat Even Ari, Mamshit, Midreshet Ben-Gurion, Mishor Yamin, Sede Zin, Shivta camp, Yeruham) (Fig. 1).

### Relationships

According to our molecular phylogeny, this species is the sister taxon of *Lycosa gesserit* sp. nov., and closely related to *Lycosa oculata*, *Lycosa* aff. *oculata* 1 and *Lycosa* aff. *oculata* 2. The cephalothorax is morphologically similar to *Lycosa macrophthalma* Nadolny & Zamani, 2020 and the species might be related to it as well (Figs 23–24).

### *Lycosa* sp.

Figs 1, 6E, 7E, 9A, 10A, 11A–B

### Diagnosis

#### Female

Epigyne: septal pedicel absent, septum trapezoidal, broader proximally, as wide as long. Copulatory openings not visible in ventral view (only *Lycosa* in the Levant without visible copulatory openings!) (Figs 6E, 7E, 9A, 10A, 11A–B).

#### Male

Unknown.

### Material examined

ISRAEL – **Arava Valley** • ♀; Nahal Amatsyahu; [30.835° N, 35.275° E]; 13 Nov. 1988; B. Shalmon leg.; HUU INV-AR20573.

### Description

#### Female

FEMALE MEASUREMENTS. AME diameter: 0.45; ALE diameter: 0.3; PME diameter: 1.1; PLE diameter: 1; carapace length: 7.1; carapace width: 5.2; carapace maximal height: 3; abdomen length: 10.7; leg I (Fe, Pa, Ti, Mt, Tr): 5.7, 2.7, 4.2, 3.7, 2.4; leg II: 5.4, 2.7, 4, 3.9, 2.3; leg III: 5.1, 2.5, 3.7, 4.9, 2.4; leg IV: 6.6, 2.4, 5.2, 7, 2.9.

CARAPACE. Ocular area  $> \frac{1}{3}$  length of carapace, distinctly raised, making the carapace between PLE and fovea appear slightly concave in profile.

**COLOR.** Carapace cream colored, darker on margins, with chocolate brown median bands, connecting to dark ocular area. Sternum yellow. Chelicerae reddish-brown. Abdomen cream colored with light brown chevrons dorsad. Abdomen venter with black patch posterior to epigastric fold, connecting to two parallel black bars stretching towards spinnerets (Π shaped patch). Spinnerets yellow. Legs yellow, infused with brown dorsad, yellow ventrad with two black bands on tibia, to reddish-brown distad, Coxae and trochanters yellow. Pedipalps yellow, to dark brown distad (Figs 6E, 7E).

**GENITALIA.** Epigyne longer than wide. Septal pedicel absent, septum connects directly to epigyne. Septum trapezoidal, wider proximally, about as long as proximal part of epigyne. Copulatory openings not seen in ventral view. Spermatheca spiral-shaped, distal part arching laterally. Head of spermatheca slightly wider than sperm duct, oval, positioned anterior to copulatory opening (Figs 9A, 10A, 11A–B).

**LEGS.** Metatarsus I ventral spination: 2 pairs + apical triplet. Tibia I ventral spination: 2 pairs + apical pair. Tarsus with scopula.

### Natural history

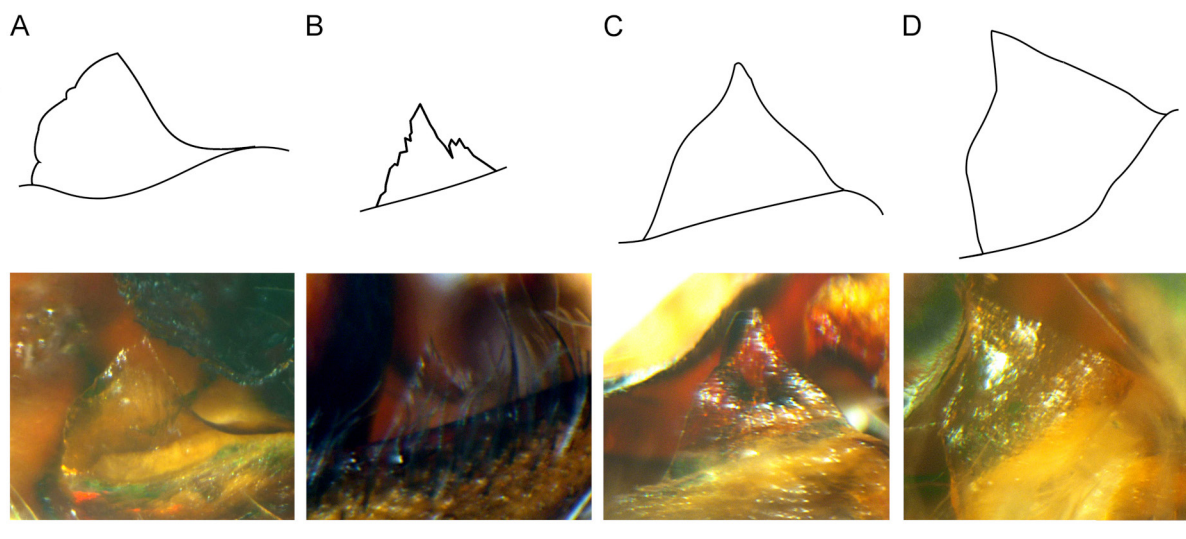
A single female was collected in the hyperarid desert (annual precipitation <75 mm) of the ‘Arava valley, ~200 m below sea level (Fig. 1, Table 4). No ecological data is available.

### Records

ISRAEL: ‘Arava Valley (Nahal Amatsyahu).

### Relationships

As of the writing of this paper, we have not succeeded in collecting fresh specimens, and therefore we could not test its relationship using molecular methods. Somatically, it resembles *L. gesseri* sp. nov. and *L. hyraculus* sp. nov. Additionally, it is the only other specimen in our dataset, apart from the *L. gesseri*



**Fig. 12.** *Lycosa* ♂♂, conductor tip, photograph and outline. **A.** *Lycosa praegrans* C.L. Koch, 1836. **B.** *Lycosa gesseri* sp. nov., holotype (HUJ INV-AR20631). **C.** *Lycosa hyraculus* sp. nov., holotype (HUJ INV-AR20818). **D.** *Lycosa piochardi* Simon, 1876 (HUJ INV-AR20855). Scale bar = 0.5 mm. Photos and drawings by I. Armiach Steinpress.

male, to exhibit a ventral patch on the abdomen shaped like the letter Π. As we could not know whether this is a new species or the female of *L. gesserit*, it is described here as *Lycosa* sp. only.

## Notes

We executed at least five field trips to the locality where this specimen was collected, at different dates, and couldn't find a single specimen of *Lycosa* any more. Since 1988, when the specimen was collected, intensive agriculture has changed the area, and this might have eradicated the habitat of this species.

### *Lycosa piochardi* Simon, 1876

Figs 1, 2D, 3D, 4D, 5D, 6D, G, 7D, G, 9C–L, 10C–L, 11E–F, 12D, 13–18, 21C–D, 22C–D, 23–27

*Lycosa piochardi* Simon, 1876: 72, pl. 3 figs 8–9 (♂♀, Syria).

*Tarentula piochardi infraclara* Strand, 1915: 167 (♀, Israel). **Syn. nov.**

*Tarentula piochardi* – Kulczyński 1911: 51, pl. 2 figs 60–61 (♀, Lebanon).

*Lycosa piochardi infraclara* – Roewer 1955: 269.

*Lycosa piochardi* – Nentwig *et al.* 2019: 40, fig. 6a–b (♀). — Nadolny & Zamani 2020: 209, fig. 19 (♀).

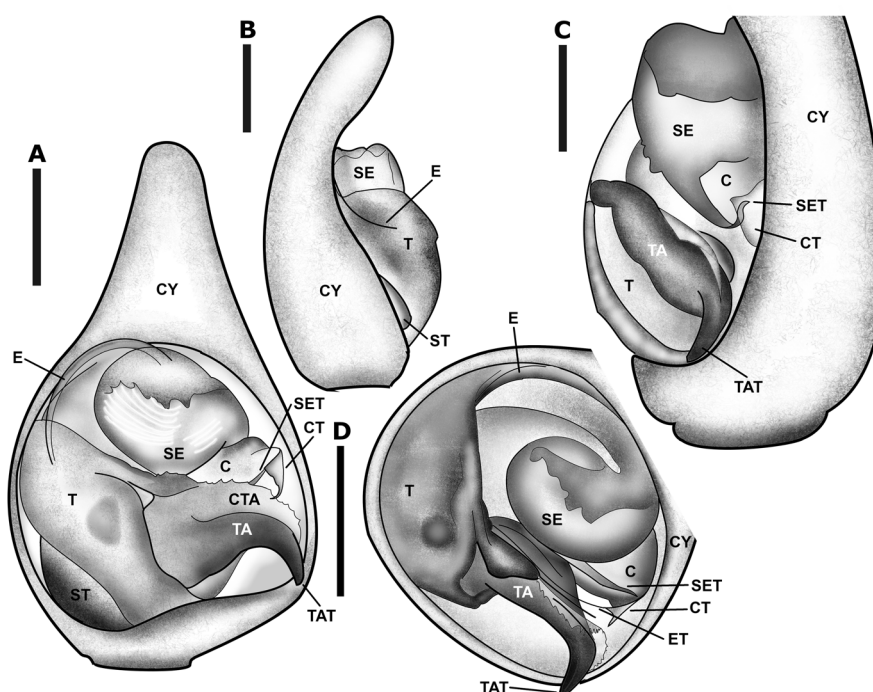
— Zamani *et al.* 2021: 284, figs 7a–f, 8a–o (♀, Iran).

*Lycosa piochardi infraclara* – Nentwig *et al.* 2019: 40, fig. 6c–e (♀, subspecies inquirenda).

## Diagnosis

### Male

Tegular apophysis tip (TAT) bent posteriorly at ~90° (in *L. hyraculus* sp. nov. TA unbent posteriorly). CTA (Fig. 2D) serrated (in *L. hyraculus* CTA smooth-edged), not wider than TA (in *L. praegrandis*,



**Fig. 13.** *Lycosa piochardi* Simon, 1876, ♂ (HUJ INV-AR20948) right pedipalp (flipped) line drawings. A. Ventral view. B. Prolateral view. C. Retrolateral view. D. Distal view. Scale bars = 0.5 mm. Drawings by I. Armiach Steinpress.

Fig. 2E, CTA wider than TA). Tip of conductor membranous, triangular, smooth-edged (in the similar *L. praegrans* it is semicircular and unevenly toothed) (Figs 2D, 3D, 4D, 5D, 6D, 7D, 12D, 13).

### Female

Epigyne: septal pedicel reduced, septum subtriangular to trapezoidal, proportions vary greatly! Copulatory openings narrow, at anterior end of septum. Distal part of spermatheca (Fig. 10C–L) bent dorso-ventrally (in the similar *L. praegrans* it is bent distally, so that the left spermatheca twists counterclockwise, Fig. 10M). Head of spermatheca elongated, not much wider than spermatheca. Both sexes distinguished from other levantine *Lycosa* by habitus: ocular area  $< \frac{1}{3}$  length of carapace, not raised (Figs 6G, 7G, 9C–L, 10C–L, 11E–F).

### Type material

#### Holotype

SYRIA • ♀; 1876; M.Ch. Piochard de la Brûlerie leg.; MNHN 2076 (not examined).

#### Paratypes

SYRIA • 5 ♀♀; same collection data as for holotype; MNHN 1266 (examined)

### Other material examined

EGYPT – **Sinai** • 1 ♀; Al-Qusaymah (Kadesh Barnea); [30.668° N, 34.366° E]; 13 Nov. 1967; P. Amitai leg.; HUI INV-AR20838 • 1 juv.; same collection data as for preceding; HUI INV-AR20839 • 1 ♀; Mt. Catherine; [28.56° N, 33.95° E]; 16 Aug. 1968; Tsabar leg.; HUI INV-AR20860 • 1 ♂; same collection data as for preceding; 17 Jul. 1968; HUI INV-AR20862 • 1 ♂; same collection data as for preceding; 16 Aug. 1968; HUI INV-AR20861



**Fig. 14.** *Lycosa piochardi* Simon, 1876, size comparison of largest and smallest ♀♀ in the dataset. **A.** HUI INV-AR20671. **B.** HUI INV-AR20897. Scale bar = 5 mm. Photo by I. Armiaich Steinpress.

ISRAEL and PALESTINE – **Coastal Plain** • 1 ♂; Ashdod sands; [31.763° N, 35.633° E]; 19 Jun. 2020; I. Armiach Steinpress leg.; col. sub.; HUI INV-AR20734 • 1 ♂; Be'eri; [31.42° N, 34.48° E]; 22 Sep. 2011; HUI INV-AR20923 • 1 ♀; east Holon (near Yamit 2000); [32° N, 34.793° E]; 20 Jul. 2017; I. Armiach Steinpress leg.; HUI INV-AR20735 • 1 ♀; same collection data as for preceding; 28 Jul. 2018; HUI INV-AR20782 • 1 juv.; ETSEL memorial monument, Lod; [31.9404° N, 34.8658° E]; 28 May 2014; I. Armiach Steinpress leg.; HUI INV-AR20779 • 1 juv.; same collection data as for preceding; HUI INV-AR20780 • 1 ♀; Gaza area; [31.5° N, 34.46° E]; 1942; HUI INV-AR20895 • 1 ♂; grove near Drezner st., Tel Aviv; [32.1295° N, 34.808° E]; 18 Jun. 2019; I. Armiach Steinpress leg.; col. juv.; HUI INV-AR20730 • 1 ♀; same collection data as for preceding; col. sub.; HUI INV-AR20731 • 1 ♂; same collection data as for preceding; col. sub.; HUI INV-AR20732 • 1 ♂; same collection data as for preceding; col. sub.; HUI INV-AR20733 • 1 ♀; Hadera sands; [32.461° N, 34.885° E]; 23 Aug. 2018; I. Armiach Steinpress leg.; HUI INV-AR20759 • 1 ♂; same collection data as for preceding; HUI INV-AR20760 • 1 ♂; same collection data as for preceding; col. sub.; HUI INV-AR20761 • 1 ♂; same collection data as for preceding; 4 Jul. 2019; col. sub.; HUI INV-AR20787 • 1 ♀; Hatsor; [31.77° N, 34.71° E]; 2008; HUI INV-AR20897 • 1 ♂; same collection data as for preceding; HUI INV-AR20898 • 1 ♂; same collection data as for preceding; HUI INV-AR20899 • 1 ♀; Jaffa-Rehoboth; [31.95° N, 34.78° E]; May 1913; I. Aharoni leg.; SMFD2184 • 1 ♀; Kfar Bialik; [32.82° N, 35.087° E]; 17 Sep. 2018; HUI INV-AR20913 • 1 ♀; same collection data as for preceding; 7 Sep. 2018; with eggsac; HUI INV-AR20950 • 1 ♀; Mavo Ashdod; [31.84° N, 34.7° E]; 24 Aug. 2015; HUI INV-AR20926 • 1 ♂; Nitzanim; [31.739° N, 34.623° E]; 11 Jul. 2017; I. Armiach Steinpress leg.; col. juv.; HUI INV-AR20683 • 1 ♂; Nitzanim sands; 7 Aug. 2017; B. Shacham leg.; HUI INV-AR20572 • 1 ♀; Oranim boarding School, Rishon LeTsiyon; [31.944° N, 34.805° E]; 24 Aug. 2013; I. Armiach Steinpress leg.; HUI INV-AR20762 • 1 ♀; Ramat-Gan; [32.08° N, 34.81° E]; 1947; A. Shulov leg.; HUI INV-AR 20526 • 1 ♂; Rehovot; [31.8992° N, 34.8363° E]; 5 Sep. 2019; I. Armiach Steinpress leg.; HUI INV-AR20788 • 1 ♀; Savyon; [32.04° N, 34.87° E]; 29 Sep. 1972; HUI INV-AR20937 • 1 ♀; Superland, Rishon LeTsiyon; [31.9748° N, 34.74235° E]; 6 Sep. 2018; I. Armiach Steinpress leg.; HUI INV-AR20790 • 1 ♀; Talmei Menashe; [31.941° N, 34.853° E]; 28 May 2014; I. Armiach Steinpress leg.; col. sub.; HUI INV-AR20781 • 1 juv.; Tel Akko; [32.9212° N, 35.0877° E]; 20 Aug. 2018; I. Armiach Steinpress leg.; HUI INV-AR20736 • 1 ♀; Tel Baruch, Tel Aviv; [32.13° N, 34.789° E]; 22 Aug. 2020; D. Simon leg.; HUI INV-AR20584 • 1 ♀; Tel Kofer, Tel Aviv; [32.04° N, 34.807° E]; 12 Oct. 2018; I. Armiach Steinpress leg.; HUI INV-AR20685 • 1 ♀; same collection data as for preceding; HUI INV-AR20686 • 1 ♀; same collection data as for preceding; HUI INV-AR20687 • 1 ♀; same collection data as for preceding; HUI INV-AR20688 • 1 ♀; same collection data as for preceding; HUI INV-AR20689 • 1 ♀; same collection data as for preceding; HUI INV-AR20690 • 1 ♀; same collection data as for preceding; HUI INV-AR20691 • 1 ♀; same collection data as for preceding; HUI INV-AR20692 • 1 ♀; same collection data as for preceding; HUI INV-AR20693 • 1 ♀; same collection data as for preceding; HUI INV-AR20694 • 1 ♀; same collection data as for preceding; HUI INV-AR20695 • 1 ♀; same collection data as for preceding; HUI INV-AR20696 • 1 ♀; same collection data as for preceding; HUI INV-AR20697 • 1 ♀; same collection data as for preceding; HUI INV-AR20698 • ♀; same collection data as for preceding; HUI INV-AR20699 • 1 ♀; same collection data as for preceding; HUI INV-AR20700 • 1 ♀; same collection data as for preceding; with eggsac; HUI INV-AR20701 • 1 ♀; same collection data as for preceding; with eggsac; HUI INV-AR20702 • 1 ♀; same collection data as for preceding; with eggsac; HUI INV-AR20703 • 1 ♀; same collection data as for preceding; with eggsac; HUI INV-AR20704 • 1 ♂; same collection data as for preceding; HUI INV-AR20705 • 1 ♀; Tel Michal, Herzlia; [32.162° N, 34.8° E]; 16 Jun. 2017; I. Armiach Steinpress leg.; col. sub.; HUI INV-AR20716 • 1 ♀; Tira; [32.234° N, 34.934° E]; 17 Jun. 2019; A. Topper leg.; col. sub.; HUI INV-AR20548 • 1 juv.; Yashresh nature reserve, Rehovot; [31.9155° N, 34.8304° E]; 9 Mar. 2018; I. Armiach Steinpress leg.; HUI INV-AR20813. – **Dead Sea Area** • 1 ♀; Ein Feshkha; [31.716° N, 35.451° E]; 15 May 1935; A. Shulov leg.; HUI INV-AR20530 • 1 ♀; Hawat Einot Kedem; [31.928° N, 35.4301° E]; 2 Jun. 2019; E. Gavish-Regev leg.; col. juv.; HUI INV-AR20621 • 1 ♀; same collection data as for preceding; col. juv.; HUI INV-AR20622 • 1 ♀; same collection data as for preceding; col. sub.; HUI INV-AR20623 • 1 ♀; Jericho; [31.85° N, 35.46° E]; 12 Dec. 1987; P. Amitai leg.; HUI INV-AR20837

• 1 ♀; same collection data as for preceding; 10 Nov. 1971; with juv.; HUI INV-AR20904. – **Galilee** • 1 ♀; Adamit; [33.081° N, 35.21° E]; 10 Aug. 1964; HUI INV-AR20903 • 1 ♀; Ahihud forest; [32.92° N, 35.19° E]; 10 Oct. 2017; B. Shacham leg.; HUI INV-AR20556 • 1 ♀; Biq'at Qedesh; [33.13° N, 35.54° E]; 13 May 2015; E. Gavish-Regev leg.; HUI INV-AR20588 • 1 ♂; Dishon; [33.085° N, 35.519° E]; 14 Aug. 2014; E. Gavish-Regev leg.; HUI INV-AR20589 • 1 ♂; same collection data as for preceding; HUI INV-AR20590 • 1 ♂; same collection data as for preceding; HUI INV-AR20591 • ♂; same collection data as for preceding; HUI INV-AR20592 • 1 ♀; Eilon; [33.059° N, 35.224° E]; 24 Jul. 2018; I. Armiach Steinpress leg.; col. juv.; HUI INV-AR20763 • 1 juv.; same collection data as for preceding; HUI INV-AR20764 • 1 juv.; same collection data as for preceding; HUI INV-AR20765 • 1 ♀; same collection data as for preceding; col. sub.; HUI INV-AR20766 • 1 ♀; same collection data as for preceding; col. sub.; HUI INV-AR20767 • 1 ♀; same collection data as for preceding; col. sub.; HUI INV-AR20768 • 1 ♂; same collection data as for preceding; col. sub.; HUI INV-AR20769 • 1 ♂; same collection data as for preceding; col. sub.; HUI INV-AR20770 • 1 ♂; same collection data as for preceding; col. sub.; HUI INV-AR20771 • 1 ♂; Har Eliezer; [33.044° N, 35.55° E]; Sep. 1995; HUI INV-AR20955 • 1 ♀; Kfar HaHoresh; [32.7° N, 35.27° E]; 9 Oct. 1968; Gershoni leg.; HUI INV-AR20679 • 1 ♂; Kfar Kisch; [32.67° N, 35.45° E]; 19 Aug. 2008; HUI INV-AR20917 • 1 ♀; Moreshet; [32.825° N, 35.232° E]; 23 Sep. 2018; with eggsac; HUI INV-AR20924 • 1 juv.; Mt. Meron; [32.99° N, 35.41° E]; 9 Apr. 1967; Pener leg.; sub. female; HUI INV-AR20853 • 1 ♂; Nahal Snir; [33.235° N, 35.676° E]; 9 Jul. 1992; R. Kasher leg.; HUI INV-AR20854 • 1 ♀; Nahal Tzippori; [32.75° N, 35.19° E]; 30 Apr. 2018; D. Ben Natan leg.; col. juv.; HUI INV-AR20576 • 1 ♀; same collection data as for preceding; HUI INV-AR20577 • 1 ♂; same collection data as for preceding; I. Tesler leg.; HUI INV-AR20821 • 1 ♀; north Yiftah; [33.134° N, 35.548° E]; 9–17 Sep. 2015; E. Gavish-Regev leg.; HUI INV-AR20633 • 1 juv.; Ramot Naftali; [33.1° N, 35.547° E]; 13 May 2014; sub. female.; HUI INV-AR20905 • 1 ♀; Safed; [32.966° N, 35.491° E]; 2 Oct. 1967; Blondheim leg.; HUI INV-AR20574 • 1 ♀; Yavne'el; [32.697° N, 35.5° E]; 1 Aug. 2019; Y. Zvik leg.; col. juv.; HUI INV-AR20869 • 1 ♂; same collection data as for preceding; HUI INV-AR20870 • 1 ♂; Yuvalim; [32.877° N, 35.27° E]; 3 Aug. 2018; I. Armiach Steinpress leg.; HUI INV-AR20785 • 1 ♀; same collection data as for preceding; 30 Apr. 2017; col. juv.; HUI INV-AR20783 • 1 juv.; same collection data as for preceding; 3 Aug. 2018; HUI INV-AR20786 • 1 ♂; same collection data as for preceding; 30 Apr. 2017; col. sub.; HUI INV-AR20784 • 1 ♂; Zar'it; [33.085° N, 35.51° E]; 9–18 Aug. 2014; E. Gavish-Regev leg.; HUI INV-AR20634 • 1 ♂; same collection data as for preceding; 18 Aug. 2014; HUI INV-AR20594 • 1 ♂; Zavit cave; [33.038° N, 35.306° E]; 23 Aug. 2018; E. Gavish-Regev leg.; HUI INV-AR20598. – **Golan Heights** • 1 ♀; Horvat Susita; [32.777° N, 35.663° E]; 26 Jul. 2018; E. Gavish-Regev leg.; HUI INV-AR20607 • 1 ♀; same collection data as for preceding; HUI INV-AR20608 • ♀; same collection data as for preceding; col. juv.; HUI INV-AR20609 • 1 ♀; same collection data as for preceding; col. sub.; HUI INV-AR20610 • 1 ♀; same collection data as for preceding; col. sub.; HUI INV-AR20611 • 1 ♀; same collection data as for preceding; col. sub.; HUI INV-AR20612 • 1 ♀; same collection data as for preceding; col. sub.; HUI INV-AR20613 • 1 juv.; same collection data as for preceding; sub. female; HUI INV-AR20614 • 1 ♂; same collection data as for preceding; col. sub.; HUI INV-AR20615 • 1 ♀; same collection data as for preceding; HUI INV-AR20664 • 1 ♀; Nahal Yehudiya; [32.926° N, 35.7003° E]; 24 May 2015; B. Shacham leg.; HUI INV-AR20567 • 1 ♀; same collection data as for preceding; [32.9221° N, 35.678° E]; 3 Jun. 2015; HUI INV-AR20569 • 1 juv.; Odem Forest; [33.22° N, 35.75° E]; 14 Jun. 1972; P. Amitai leg.; sub. female; HUI INV-AR20841 • 1 ♀; Qatsrin; [32.988° N, 35.677° E]; 7 Oct. 2018; I. Armiach Steinpress leg.; HUI INV-AR20791 • 1 ♀; same collection data as for preceding; HUI INV-AR20792 • 1 ♀; same collection data as for preceding; HUI INV-AR20793 • 1 ♀; same collection data as for preceding; HUI INV-AR20794 • 1 ♀; same collection data as for preceding; HUI INV-AR20795 • 1 ♀; same collection data as for preceding; HUI INV-AR20796 • 1 ♀; same collection data as for preceding; with eggsac; HUI INV-AR20797 • 1 ♀; same collection data as for preceding; HUI INV-AR20798 • 1 ♀; same collection data as for preceding; HUI INV-AR20799 • 1 ♀; same collection data as for preceding; HUI INV-AR20800 • 1 ♀; same collection data as for preceding; HUI INV-AR20801 • 1 ♀; same collection data as for preceding; HUI INV-AR20802 • 1 ♀; same collection data as for preceding; HUI INV-AR20803 • 1 ♀; same collection data

as for preceding; with eggsac; HUI INV-AR20804 • 1 ♀; same collection data as for preceding; HUI INV-AR20805 • 1 ♀; same collection data as for preceding; with eggsac; HUI INV-AR20806 • 1 ♀; same collection data as for preceding; with eggsac; HUI INV-AR20807 • 1 ♀; same collection data as for preceding; with eggsac; HUI INV-AR20808 • 1 ♀; same collection data as for preceding; with eggsac; HUI INV-AR20809 • 1 ♀; same collection data as for preceding; with eggsac; HUI INV-AR20810 • 1 ♂; Waset (Wassit); [33.139° N, 35.733° E]; 19 Jul. 1970; HUI INV-AR20918. – **Hermon** • 1 juv.; Hermon; [33.3° N, 35.78° E]; 23 Jun. 2017; N. Givon leg.; HUI INV-AR20834 • 1 juv.; same collection data as for preceding; [33.28° N, 35.75° E]; 6 Apr. 1967; P. Amitai leg.; sub. female; HUI INV-AR20847 • 1 ♀; Hermon; [33.29° N, 35.759° E]; 1400 m a.s.l.; 2 Jun. 2017; A. Uzan leg.; col. juv.; HUI INV-AR20549 • 1 juv.; same collection data as for preceding; [33.28° N, 35.75° E]; 6 Apr. 1971; HUI INV-AR20949 • 1 juv.; Hermon; [33.3043° N, 35.7882° E]; 2000 m a.s.l.; 9 Sep. 1971; Lebovits leg.; dolina; HUI INV-AR20832 • 1 juv.; Hermon (dolina near peak 2072); 23 Jun. 2017; N. Givon leg.; HUI INV-AR20833 • 1 ♀; Hermon (near upper chairlift station); [33.306° N, 35.784° E]; 9 Jun. 2019; D. David leg.; HUI INV-AR20583 • 1 ♀; same collection data as for preceding; [33.3061° N, 35.7851° E]; 14 Jul. 2019; EGR, MC; HUI INV-AR20674 • 1 ♀; same collection data as for preceding; [33.304° N, 35.789° E]; 23 Jun. 2017; I. Armiach Steinpress leg.; HUI INV-AR20758 • 1 ♀; Nabi Hazuri; [33.251° N, 35.729° E]; 24 Aug. 2018; I. Armiach Steinpress leg.; HUI INV-AR20772 • 1 ♀; same collection data as for preceding; HUI INV-AR20773 • 1 ♂; same collection data as for preceding; HUI INV-AR20774 • 1 ♂; same collection data as for preceding; HUI INV-AR20775 • 1 ♂; same collection data as for preceding; HUI INV-AR20776. – **Emeq Yizra'el** • 1 ♀; Kfar Baruh Reservoir; [32.643° N, 35.218° E]; 16 Sep. 2019; I. Armiach Steinpress leg.; HUI INV-AR20710 • 1 ♀; same collection data as for preceding; HUI INV-AR20711 • 1 ♀; same collection data as for preceding; HUI INV-AR20712 • 1 ♀; same collection data as for preceding; HUI INV-AR20713 • 1 ♀; same collection data as for preceding; HUI INV-AR20714 • 1 ♀; same collection data as for preceding; HUI INV-AR20715 • 1 juv.; same collection data as for preceding; [32.641° N, 35.219° E]; 6 Feb. 2018; HUI INV-AR20789 • 1 juv.; Sarid; [32.6674° N, 35.229° E]; 22 Jun. 2020; Y. Zvik leg.; sub. female; HUI INV-AR20962. – **Jordan Valley** • 1 ♀; Ashdot Ya'akov; [32.66° N, 35.578° E]; 5 Aug. 1972; Zevi leg.; HUI INV-AR20894 • 1 ♀; same collection data as for preceding; Oct. 1971; with eggsac; HUI INV-AR20957 • 1 ♂; same collection data as for preceding; HUI INV-AR20958 • 1 ♀; Ein Sukkot; [32.365° N, 35.547° E]; 11 May 2017; B. Shacham leg.; col. juv.; HUI INV-AR20557 • 1 ♀; Karei Deshe; [32.862° N, 35.536° E]; 16 Sep. 2013; HUI INV-AR20910 • 1 ♀; Maoz Haim; [32.4935° N, 35.5517° E]; 30 Jan. 1943; A. Shulov leg.; HUI INV-AR20534 • 1 ♀; Menahemia; [32.664° N, 35.5538° E]; 22 Sep. 2019; Y. Zvik leg.; HUI INV-AR20871 • 1 juv.; same collection data as for preceding; 24 May 2017; sub. female; HUI INV-AR20927 • 1 ♂; Nahal Hagal; [32.631° N, 35.554° E]; 21 Jun. 2015; col. sub.; HUI INV-AR20921 • 1 ♀; Sde Eliyahu; [32.441° N, 35.514° E]; 23 Jun. 2019; Y. Zvik leg.; col. sub.; HUI INV-AR20872 • 1 ♀; Southern Jordan Valley; [32.2471° N, 35.5588° E]; 23 Apr. 2017; B. Shacham leg.; col. juv.; HUI INV-AR20564 • 1 juv.; same collection data as for preceding; [32.0446° N, 35.5166° E]; 24 Apr. 2017; HUI INV-AR20566. – **Judea** • 1 juv.; `Ayn ad Duyuk (near Jericho); [31.8959° N, 35.4222° E]; 8 Jun. 1978; P. Amitai leg.; sub. female; HUI INV-AR20848 • 1 ♀; Alon; [31.833° N, 35.352° E]; Jan. 2016; D. Waysman leg.; HUI INV-AR20585 • 1 ♀; Arad; [31.26° N, 35.21° E]; 9 Dec. 2015; HUI INV-AR20953 • 1 ♀; Arad Cemetery; [31.273° N, 35.229° E]; 31 Jul. 2018; J. Ballesteros Chaves leg.; HUI INV-AR20822 • 1 ♀; same collection data as for preceding; HUI INV-AR20823 • 1 ♀; same collection data as for preceding; HUI INV-AR20824 • 1 ♀; same collection data as for preceding; HUI INV-AR20825 • 1 ♀; same collection data as for preceding; HUI INV-AR20826 • 1 ♂; same collection data as for preceding; HUI INV-AR20827 • 1 ♂; same collection data as for preceding; HUI INV-AR20828 • 1 ♂; same collection data as for preceding; HUI INV-AR20829 • 1 ♂; same collection data as for preceding; HUI INV-AR20830 • 1 ♀; Beit Guvrin; [31.61° N, 34.9° E]; 4 Apr. 2015; A. Uzan leg.; col. juv.; HUI INV-AR20552 • 1 ♀; Beit Nir; [31.65° N, 34.868° E]; 31 Jan. 2015; HUI INV-AR20941 • 1 ♀; Ben Shemen; [31.95° N, 34.92° E]; 21 May 2017; B. Shacham leg.; col. sub.; HUI INV-AR20563 • 1 juv.; same collection data as for preceding; 18 Jul. 1956; J. Machlis leg.; HUI INV-AR20831 • 1 juv.; Bet Yatir; [31.357° N, 35.11° E]; 17 Apr. 2018; HUI INV-AR20911 • 1 ♀; Biq'at Qanna'im; [31.316° N, 35.276° E]; 5 Aug. 2019; Y. Zvik leg.; HUI INV-AR20880 • 1 ♀; Bor `Atin;

[31.3125° N, 35.26° E]; 3 May 2018; Y. Zvik leg.; col. sub.; HUI INV-AR20878 • 1 ♀; same collection data as for preceding; col. sub.; HUI INV-AR20879 • 1 juv.; Canada Park; [34.9954° N, 31.8427° E]; 13 Jun. 2018; I. Armiach Steinpress leg.; sub. male; HUI INV-AR20707 • 1 ♀; Gazelle Valley; [31.759° N, 35.196° E]; 25 May 2018; I. Armiach Steinpress leg.; col. juv.; HUI INV-AR20777 • 1 ♀; Givat Ram, Jerusalem; [31.777° N, 35.197° E]; 28 Dec. 2014; HUI INV-AR20936 • 1 ♂; Har Amasa; [31.343° N, 35.103° E]; 17 Apr. 2018; B. Shacham leg.; HUI INV-AR20562 • 1 juv.; Har Hardon; [31.339° N, 35.191° E]; 8 May 2018; D. Ben-Natan leg.; HUI INV-AR20580 • 1 ♂; same collection data as for preceding; col. sub.; HUI INV-AR20581 • 1 juv.; Holyland hotel, Jerusalem; [31.784° N, 35.233° E]; 24 Apr. 1975; faunistics course leg.; HUI INV-AR20676 • 1 ♀; same collection data as for preceding; 15 Apr. 1980; HUI INV-AR20909 • 1 ♂; Horkanya valley; [31.719° N, 35.364° E]; 14 Mar. 2016; B. Shacham leg.; col. sub; HUI INV-AR20560 • 1 ♀; Jerusalem; [31.75° N, 35.2° E]; 30 Sep. 1935; A. Shulov leg.; HUI INV-AR20537 • 1 ♀; same collection data as for preceding; 1 Mar. 1935; HUI INV-AR20531 • 1 ♀; same collection data as for preceding; Summer 1938; HUI INV-AR20547 • 1 ♀; same collection data as for preceding; 23 Oct. 1929; HUI INV-AR20532 • 1 ♀; same collection data as for preceding; 30 Apr. 1953; HUI INV-AR20535 • 1 ♀; same collection data as for preceding; 30 Sep. 1937; HUI INV-AR20538 • 1 ♀; 10 Dec. 1951; with juv.; HUI INV-AR 20528 • 1 juv.; same collection data as for preceding; [31.76° N, 35.18° E]; 31 Oct. 1953; HUI INV-AR20540 • 1 juv.; same collection data as for preceding; 5 Jun. 1954; HUI INV-AR20544 • 1 juv.; same collection data as for preceding; 7 Apr. 1953; HUI INV-AR20545 • 1 ♀; same collection data as for preceding; [31.75° N, 35.2° E]; 4 Oct. 1958; Golani leg.; HUI INV-AR20680 • 1 ♀; same collection data as for preceding; 1948; HUI INV-AR20896 • 1 ♀; same collection data as for preceding; HUI INV-AR20900 • 1 ♂; same collection data as for preceding; HUI INV-AR20901 • 1 ♂; Judean Desert (road 3199); [31.314° N, 35.299° E]; 25 Aug. 2017; A. Uzan leg.; HUI INV-AR20551 • 1 ♀; Kfar Daniel; [31.9342° N, 34.9372° E]; 3 Oct. 2017; B. Shacham leg.; HUI INV-AR20570 • 1 ♀; Kiryat Anavim; [31.81° N, 35.12° E]; 10 Oct. 1937; A. Shulov leg.; HUI INV-AR 20527 • 1 ♀; same collection data as for preceding; 1936; HUI INV-AR 20525 • 1 ♂; same collection data as for preceding; 5 Sep. 1938; HUI INV-AR20948 • 1 ♀; Kiryat Shmuel, Jerusalem; [31.769° N, 35.211° E]; 28 Oct. 1940; with eggsac; HUI INV-AR20935 • 1 juv.; Ma'ale Adumim; [31.77° N, 35.3° E]; 3 May 1977; Broza leg.; HUI INV-AR20575 • 1 juv.; same collection data as for preceding; 9 Jun. 1974; Tsabar leg.; sub. female; HUI INV-AR20864 • 1 juv.; same collection data as for preceding; sub. male; HUI INV-AR20865 • 1 ♀; same collection data as for preceding; 19 Aug. 1973; HUI INV-AR20916 • 1 ♀; same collection data as for preceding; 25 Oct. 1972; HUI INV-AR20931 • 1 juv.; same collection data as for preceding; Mar. 2018; sub. male, col. juv.; HUI INV-AR20954 • 1 ♀; Maon ridge; [31.41° N, 35.17° E]; 23 May 2017; B. Shacham leg.; col. sub.; HUI INV-AR20565 • 1 juv.; Mar Saba; [31.705° N, 35.331° E]; 7 Jul. 1967; A. Shulov leg.; sub. male; HUI INV-AR20546 • 1 ♂; same collection data as for preceding; HUI INV-AR20951 • 1 juv.; Matsleva cave; [31.772° N, 35.206° E]; 1 Aug. 2018; HUI INV-AR20919 • 1 ♀; Modi'in; [31.89° N, 34.978° E]; 10 Oct. 2012; E. Gavish-Regev leg.; HUI INV-AR20587 • 1 ♂; same collection data as for preceding; [31.9° N, 34.98° E]; 20 Aug. 2013; HUI INV-AR20595 • 1 ♂; same collection data as for preceding; HUI INV-AR20596 • 1 ♀; same collection data as for preceding; [31.89° N, 34.978° E]; 11–20 Apr. 2012; I. Bernstein leg.; HUI INV-AR20967 • 1 juv.; same collection data as for preceding; [31.9° N, 34.96° E]; Apr. 2012; HUI INV-AR20814 • 1 ♂; Modi'in (near Pa'ate Modi'in train station); [31.897° N, 34.964° E]; 20 Aug. 2013; E. Gavish-Regev leg.; HUI INV-AR20597 • 1 ♀; Negohot; [31.493° N, 34.983° E]; 2 Jun. 2019; B. Shacham; leg. col. juv.; HUI INV-AR20568 • 1 juv.; Ramat Rachel; [31.74° N, 35.22° E]; 29 Apr. 1980; faunistics course leg.; HUI INV-AR20677 • 1 juv.; South Hebron Mountains; [31.5° N, 35.04° E]; 14 May 2018; B. Shacham leg.; sub. female, col. juv.; HUI INV-AR20561 • 1 ♀; Valley of the Cross; [31.772° N, 35.206° E]; 15 Oct. 2012; E. Gavish-Regev leg.; HUI INV-AR20593 • 1 ♀; same collection data as for preceding; 15 Oct. 2018; I. Armiach Steinpress leg.; HUI INV-AR20708. – **Karmel** • 1 ♂; Isfiya; [32.72° N, 35.06° E]; 26 Aug. 1971; HUI INV-AR20933 • 1 juv.; Mt. Carmel; [32.56° N, 34.95° E]; 15 Jul. 1955; P. Amitai leg.; HUI INV-AR20842 • 1 ♀; Ramat Hanadiv; [32.72° N, 35.06° E]; 5 Oct. 2012; E. Gavish-Regev and R. Raven leg.; HUI INV-AR20669 • 1 ♀; same collection data as for preceding; HUI INV-AR20670 • 1 ♀; same collection data as for preceding; HUI INV-AR20671 • 1 ♀;

same collection data as for preceding; with eggsac; HUI INV-AR20672 • 1 ♀; same collection data as for preceding; with eggsac; HUI INV-AR20673 • 1 ♀; same collection data as for preceding; 5–6 Oct. 2012; with eggsac; TAUZMar50544 • 1 ♀; same collection data as for preceding; [32.552° N, 34.944° E]; 14 Dec. 2017; with eggsac; HUI INV-AR20906 • 1 juv.; same collection data as for preceding; hatched in capt.; HUI INV-AR20907 • 1 juv.; same collection data as for preceding; hatched in capt.; HUI INV-AR20908 • 1 ♀; Zikhron Ya'akov; [32.57° N, 34.95° E]; 4 Dec. 1937; A. Shulov leg.; HUI INV-AR20541 • 1 ♀; same collection data as for preceding; HUI INV-AR20542. – **Negev** • 1 juv.; Arad; [31.269° N, 35.208° E]; 30 May 1968; A. Shulov leg.; HUI INV-AR20539 • 1 ♀; same collection data as for preceding; [31.256° N, 35.218° E]; 15 Mar. 2018; D. David leg.; HUI INV-AR20582 • 1 juv.; same collection data as for preceding; [31.26° N, 35.2° E]; 15 Jun. 1969; faunistics course leg.; HUI INV-AR20675 • 1 juv.; same collection data as for preceding; [31.269° N, 35.208° E]; 30 May 1968; HUI INV-AR20678 • 1 ♀; same collection data as for preceding; [31.256° N, 35.218° E]; 15 Mar. 2018; I. Tesler leg.; col. juv.; HUI INV-AR20820 • 1 juv.; same collection data as for preceding; [31.269° N, 35.208° E]; 20 Dec. 1962; P. Amitai leg.; HUI INV-AR20845 • 1 ♀; same collection data as for preceding; [31.26° N, 35.21° E]; 23 Oct. 1968; Tsabar leg.; with juv.; HUI INV-AR20863 • 1 ♀; same collection data as for preceding; 24 Aug. 1964; HUI INV-AR20928 • ♀; same collection data as for preceding; HUI INV-AR20929 • 1 ♀; Ariel Sharon Camp; [31.053° N, 34.837° E]; 5 Aug. 2018; E. Gavish-Regev leg.; HUI INV-AR20628 • 1 ♂; same collection data as for preceding; HUI INV-AR20629 • 1 ♀; same collection data as for preceding; 9 Jan. 2018; I. Armiach Steinpress leg.; HUI INV-AR20811 • 1 ♂; same collection data as for preceding; col. sub.; HUI INV-AR20812 • 1 juv.; Avdat; [30.79° N, 34.77° E]; 30 Apr. 1957; Pener leg.; HUI INV-AR20852 • 1 ♀; same collection data as for preceding; [30.794° N, 34.772° E]; 4 Jul. 2016; col. sub.; HUI INV-AR20946 • 1 ♀; Be'er Mash'abim; [31.015° N, 34.76° E]; 15 Jan. 1946; A. Shulov leg.; HUI INV-AR20529 • 1 juv.; same collection data as for preceding; 26 Dec. 1956; Pener leg.; HUI INV-AR20849 • 1 ♀; Be'er Milka; [30.935° N, 34.408° E]; 4 Aug. 2018; E. Gavish-Regev leg.; HUI INV-AR20667 • 1 ♀; same collection data as for preceding; HUI INV-AR20668 • 1 juv.; same collection data as for preceding; 26 Jun. 2017; INV-AR20932 • 1 ♀; same collection data as for preceding; 4 Aug. 2018; with juv.; HUI INV-AR20947 • 1 ♀; Be'er Sheva; [31.271° N, 34.817° E]; 15 Nov. 2017; I. Armiach Steinpress leg.; with juv.; HUI INV-AR20709 • 1 juv.; Brosh; [31.37° N, 34.63° E]; 29 Jun. 1967; Pener leg.; HUI INV-AR20851 • 1 ♀; Dimona ridge; [31.08746° N, 35.04686° E]; 31 Apr. 2019; E. Gavish-Regev leg.; col. juv.; HUI INV-AR20624 • 1 ♀; Ezuz; [34.46041° N, 30.78654° E]; 21 Jan. 2020; D. Ben-Natan leg.; with juv.; HUI INV-AR20578 • 1 ♂; Giv'ot Bar; [31.358° N, 34.753° E]; 10 Apr. 2018; co. sub. died molting; HUI INV-AR20902 • 1 ♀; same collection data as for preceding; 8 May 2018; co. sub. died molting; HUI INV-AR20952 • 1 ♀; Gvaot Goral; [31.34° N, 34.83° E]; 4 Apr. 2018; B. Shacham leg.; col. juv.; HUI INV-AR20571 • 1 ♀; Ha-Ro'a Campsite; [30.876° N, 34.784° E]; 5 Aug. 2018; E. Gavish-Regev leg.; HUI INV-AR20627 • 1 ♀; same collection data as for preceding; HUI INV-AR20630 • 1 juv.; same collection data as for preceding; 11 Jun. 2018; HUI INV-AR20649 • 1 ♀; same collection data as for preceding; col. sub.; HUI INV-AR20650 • 1 ♂; same collection data as for preceding; col. sub.; HUI INV-AR20652 • 1 ♀; Haluqim ridge (near Midreshet Ben-Gurion); [30.854° N, 34.768° E]; 22 Oct. 2018; I. Armiach Steinpress leg.; col. juv.; HUI INV-AR20752 • 1 ♀; same collection data as for preceding; col. juv.; HUI INV-AR20753 • 1 ♂; same collection data as for preceding; col. juv.; HUI INV-AR20754 • 1 juv.; Har Karkom; [30.28° N, 34.74° E]; 7 Oct. 2017; E. Gavish-Regev leg.; HUI INV-AR20632 • 1 ♀; Hawat Even Ari; [30.786° N, 34.77° E]; 11 Jun. 2018; E. Gavish-Regev leg.; col. sub.; HUI INV-AR20651 • 1 juv.; Hirbet Rimon; [31.3712° N, 34.8646° E]; 24 Mar. 2018; HUI INV-AR20925 • 1 ♀; Holot `Agur; [30.93° N, 34.408° E]; 17 Sep. 2017; HUI INV-AR20912 • 1 juv.; Irus HaNegev; [31.0854° N, 34.6809° E]; 3 Mar. 2018; HUI INV-AR20944 • 1 juv.; same collection data as for preceding; HUI INV-AR20945 • 1 ♀; Lehavim; [31.37° N, 34.82° E]; 28 Jun. 2017; E. Gavish-Regev leg.; col. sub.; HUI INV-AR20666 • 1 ♀; Lipa Gal lookout; [30.822° N, 34.741° E]; 21 Mar. 2018; D. Ben-Natan leg.; col. sub.; HUI INV-AR20579 • 1 ♀; Mamshit; [31.03° N, 35.06° E]; 24 Mar. 1954; A. Shulov leg.; HUI INV-AR20533 • 1 juv.; Mamshit; [31.03° N, 35.06° E]; 11 Apr. 2018; A. Uzan leg.; HUI INV-AR20550 • 1 ♀; Mash'abim dunes; [31.015° N, 34.76° E]; 23 Feb. 2020; I. Magalhaes leg.; HUI INV-AR20816 • 1 ♂; same collection data as for preceding; [31.002° N, 34.74° E]; Aug. 2020; col. sub.; HUI INV-

AR20956 • 1 juv.; Merhav Am (near Har Qatum); [30.8543° N, 34.7688° E]; 29 Jun. 2020; sub. male; HUI INV-AR20938 • 1 ♂; Midreshet Ben-Gurion; [30.85° N, 34.78° E]; 26 Jul. 2017; E. Gavish-Regev leg.; HUI INV-AR20606 • 1 ♂; same collection data as for preceding; Apr. 2013; col. juv.; HUI INV-AR20636 • 1 juv.; same collection data as for preceding; Mar. 2013; sub. female; HUI INV-AR20635 • 1 ♀; same collection data as for preceding; [30.874° N, 34.79° E]; 21 Jul. 2018; HUI INV-AR20963 • 1 ♂; same collection data as for preceding; HUI INV-AR20964 • 1 ♀; same collection data as for preceding; 17 May 2016; col. sub.; HUI INV-AR20660 • 1 juv.; same collection data as for preceding; [30.8543° N, 34.7688° E]; 22 Oct. 2018; I. Armiach Steinpress leg.; HUI INV-AR20751 • 1 juv.; same collection data as for preceding; sub. female; HUI INV-AR20756 • 1 ♂; Mitzpe Ramon; [30.6632° N, 34.8157° E]; 13 Jun. 2019; B. Shacham leg.; col. sub.; HUI INV-AR20559 • 1 ♀; same collection data as for preceding; [30.6128° N, 34.8039° E]; 25 Jun. 2015; with eggsac; HUI INV-AR20930 • 1 ♀; Nahal Dumiya, Arad; [31.256° N, 35.219° E]; 4 Apr. 2019; E. Gavish-Regev leg.; col. juv.; HUI INV-AR20626 • 1 ♀; Nahal Gmalim; [31.088° N, 35.225° E]; 24 Sep. 2019; A. Uzan leg.; HUI INV-AR20555 • 1 ♀; same collection data as for preceding; 12 Sep. 2018; B. Shacham leg.; col. juv.; HUI INV-AR20558 • 1 ♀; same collection data as for preceding; E. Gavish-Regev leg.; with eggsac; HUI INV-AR20656 • 1 ♀; same collection data as for preceding; with eggsac; HUI INV-AR20657 • 1 ♀; same collection data as for preceding; 11 Mar. 2018; col. juv.; HUI INV-AR20637 • 1 juv.; same collection data as for preceding; 11 Apr. 2018; HUI INV-AR20638 • 1 juv.; same collection data as for preceding; HUI INV-AR20639 • 1 juv.; same collection data as for preceding; HUI INV-AR20640 • 1 juv.; same collection data as for preceding; HUI INV-AR20641 • 1 juv.; same collection data as for preceding; HUI INV-AR20642 • 1 juv.; same collection data as for preceding; HUI INV-AR20643 • 1 juv.; same collection data as for preceding; HUI INV-AR20644 • 1 ♂; same collection data as for preceding; col. juv.; HUI INV-AR20645 • 1 ♂; same collection data as for preceding; col. sub.; HUI INV-AR20647 • 1 ♀; same collection data as for preceding; I. Armiach Steinpress leg.; col. juv.; HUI INV-AR20681 • 1 ♂; same collection data as for preceding; 12 Dec. 2019; col. juv.; HUI INV-AR20706 • 1 ♀; same collection data as for preceding; 28 Apr. 2019; col. juv.; HUI INV-AR20778 • 1 ♀; same collection data as for preceding; 24 Sep. 2019; S. Aharon leg.; HUI INV-AR20857 • 1 ♀; same collection data as for preceding; HUI INV-AR20858 • 1 ♀; Nahal Hamarmar; [31.087° N, 35.234° E]; 11 Apr. 2018; E. Gavish-Regev leg.; col. juv.; HUI INV-AR20646 • 1 ♀; same collection data as for preceding; col. juv.; HUI INV-AR20648 • 1 ♀; same collection data as for preceding; I. Armiach Steinpress leg.; col. juv.; HUI INV-AR20682 • 1 ♂; Nahal Nafha; [30.733° N, 34.824° E]; 30 Apr. 1959; A. Shulov leg.; HUI INV-AR20536 • 1 ♀; Nahal Revivim; [31.044° N, 34.717° E]; 28 Jun. 2018; col. sub.; HUI INV-AR20934 • 1 ♀; Nahal Tavia; [31.256° N, 35.218° E]; 15 Mar. 2018; E. Gavish-Regev leg.; HUI INV-AR20659 • 1 ♀; Nitzana; [30.887° N, 34.423° E]; 29 Aug.; HUI INV-AR20939 • 1 juv.; 30 May 1957; HUI INV-AR20940 • 1 juv.; Park Yeruham; [30.985° N, 34.9° E]; 6 Apr. 2018; Y. Zvik leg.; HUI INV-AR20881 • 1 juv.; Reches Boker (Boker ridge), near road 40; [30.9502° N, 34.7792° E]; 3 Jan. 2020; E. Gavish-Regev leg.; HUI INV-AR20625 • 1 juv.; Sand Dunes 15 km S of Be'er Sheva; [31.114° N, 34.815° E]; 29 May 1980; Pener leg.; HUI INV-AR20850 • 1 ♀; Sede Zin; [30.854° N, 34.773° E]; 1 Aug. 2016; I. Steves leg.; HUI INV-AR20819 • 1 juv.; Shivta camp; [30.9245° N, 34.6244° E]; 22 Oct. 2018; I. Armiach Steinpress leg.; HUI INV-AR20755 • 1 ♀; upper Nahal Ashalim; [31.079° N, 35.225° E]; 11 Apr. 2018; Alon leg.; col. juv.; HUI INV-AR20554 • 1 juv.; same collection data as for preceding; 12 Apr. 2018; E. Gavish-Regev leg.; HUI INV-AR20653 • 1 juv.; same collection data as for preceding; HUI INV-AR20654 • 1 ♀; same collection data as for preceding; HUI INV-AR20655 • 1 ♂; same collection data as for preceding; [31.088° N, 35.225° E]; 12 Sep. 2018; I. Armiach Steinpress leg.; col. juv.; HUI INV-AR20684 • 1 ♂; same collection data as for preceding; [31.079° N, 35.225° E]; S. Aharon leg.; col. juv.; HUI INV-AR20856 • 1 ♀; West of Netivot; [31.414° N, 34.557° E]; 17 Sep. 2019; I. Armiach Steinpress leg.; HUI INV-AR20717 • 1 ♀; same collection data as for preceding; HUI INV-AR20718 • ♀; same collection data as for preceding; HUI INV-AR20719 • 1 ♀; same collection data as for preceding; HUI INV-AR20720 • 1 ♀; same collection data as for preceding; HUI INV-AR20721 • 1 ♀; same collection data as for preceding; HUI INV-AR20722 • 1 ♀; same collection data as for preceding; HUI INV-AR20723 • 1 ♀; same collection data as for preceding; HUI INV-AR20724 • 1 ♀; same collection data as for preceding;

HUJ INV-AR20725 • 1 ♀; same collection data as for preceding; HUI INV-AR20726 • 1 ♂; same collection data as for preceding; HUI INV-AR20727 • 1 ♂; same collection data as for preceding; HUI INV-AR20728 • 1 ♂; same collection data as for preceding; HUI INV-AR20729 • 1 juv.; Yeruham; [30.985° N, 34.9° E]; 5 Jun. 1954; A. Shulov leg.; HUI INV-AR20543 • 1 ♀; same collection data as for preceding; [30.985° N, 34.904° E]; 10 Apr. 2019; E. Gavish-Regev leg.; HUI INV-AR20586 • 1 juv.; same collection data as for preceding; 17 Apr. 1967; P. Amitai leg.; HUI INV-AR20843 • 1 juv.; same collection data as for preceding; HUI INV-AR20844 • 1 ♂; same collection data as for preceding; [30.985° N, 34.9° E]; 2 Jun. 2017; Y. Zvik leg.; col. juv.; HUI INV-AR20876 • 1 ♀; same collection data as for preceding; [30.985° N, 34.904° E]; 28 May 2017; col. sub.; HUI INV-AR20873 • 1 juv.; Yeruham Park (near ruins); [30.985° N, 34.899° E]; 30 Mar. 2017; Y. Zvik leg.; HUI INV-AR20877. – **Samaría** • 1 ♀; Ari'el; [32.103° N, 35.173° E]; 20 Jan. 2015; HUI INV-AR20920 • 1 ♀; same collection data as for preceding; Oct. 2014; with eggsac; HUI INV-AR20959 • 1 ♀; Barkan; [32.108° N, 35.105° E]; 28 Nov. 2011; Z.Ganem leg.; HUI INV-AR20891 • 1 juv.; Ein Dor; [32.655° N, 35.416° E]; 3 May 2018; HUI INV-AR20945 • 1 ♀; Gilboa; [32.51° N, 35.41° E]; 22 Sep. 1976; HUI INV-AR20922 • 1 ♀; Hemdat, Umm Zoka; [N32.25°, E35.525°]; 14 Mar. 2018; A. Schmida leg.; HUI INV-AR 20524 • 1 ♀; Ibthan; [32.369° N, 35.048° E]; 26 Mar. 2018; Z.Ganem leg.; HUI INV-AR20890 • 1 ♀; same collection data as for preceding; 12 Oct. 2019; HUI INV-AR20883 • 1 ♀; same collection data as for preceding; 30 Aug. 2019; HUI INV-AR20893 • 1 ♀; same collection data as for preceding; 2 Dec. 2017; with eggsac; HUI INV-AR20892 • 1 ♀; same collection data as for preceding; 12 Oct. 2019; with eggsac (hatched 28 Oct. 2019); HUI INV-AR20884 • 1 ♀; same collection data as for preceding; 23 Dec. 2017; with juv.; HUI INV-AR20889 • 1 ♂; same collection data as for preceding; 12 Aug. 2018; HUI INV-AR20882 • 1 ♀; same collection data as for preceding; 14 Jul. 2018; col. sub.; HUI INV-AR20885 • 1 ♀; same collection data as for preceding; 18 Jul. 2019; col. sub.; HUI INV-AR20886 • 1 ♂; same collection data as for preceding; col. sub.; HUI INV-AR20887 • 1 juv.; Jatt; [32.397° N, 35.036° E]; 19 May 2018; Z.Ganem leg.; col. sub.; HUI INV-AR20888 • 1 juv.; Lower Nahal Yitspor; [32.495° N, 35.433° E]; 24 Jun. 2019; E. Gavish-Regev leg.; HUI INV-AR620599 • 1 ♀; same collection data as for preceding; [32.49578° N, 35.43363° E]; col. juv.; HUI INV-AR20600 • 1 ♀; same collection data as for preceding; [32.4945° N, 35.4336° E]; col. juv.; HUI INV-AR20601 • 1 ♀; same collection data as for preceding; [32.49521° N, 35.43121° E]; col. juv.; HUI INV-AR20602 • 1 ♂; same collection data as for preceding; [32.49495° N, 35.43307° E]; col. juv.; HUI INV-AR20603 • 1 ♂; same collection data as for preceding; [32.49494° N, 35.43307° E]; col. juv.; HUI INV-AR20604 • 1 ♂; same collection data as for preceding; [32.495° N, 35.433° E]; col. sub.; HUI INV-AR20605 • 1 ♂; Megiddo; [32.578° N, 35.179° E]; 27 Jul. 1959; P. Amitai leg.; HUI INV-AR20846 • 1 ♀; Mehola; [32.364° N, 35.515° E]; 6 Oct. 2020; Y. Zvik leg.; HUI INV-AR20965 • 1 ♀; same collection data as for preceding; HUI INV-AR20966 • 1 ♂; same collection data



**Fig. 15.** *Lycosa piochardi* Simon, 1876, ♀♀, common ventral abdominal coloration morphs. **A.** Black patch reaches posterior tip (HUI INV-AR20735). **B.** Black patch does not reach posterior tip (HUI INV-AR20626). **C.** Black patch with shallow notch (HUI INV-AR20763). **D.** Black patch with deep notch (HUI INV-AR20913). **E.** Black patch divided (HUI INV-AR20671). **F.** No black patch (HUI INV-AR20803). Scale bars = 10 mm. Photos by I. Armiach Steinpress.

as for preceding; [32.36318° N, 35.507° E]; 10 Jun. 2018; col. juv.; HUI INV-AR20866 • 1 juv.; same collection data as for preceding; [32.364° N, 35.515° E]; 10 Oct. 2018; sub. female, col. juv.; HUI INV-AR20867 • 1 ♀; Mehora; [32.164° N, 35.423° E]; 12 May 2018; I. Ihia leg.; col. sub.; HUI INV-AR20815 • 1 juv.; Wadi Al-Far'a; [32.27° N, 35.35° E]; 12 May 1972; Tsabar leg.; HUI INV-AR20859.

JORDAN • 1 ♀; Jerash; [32.28° N, 35.89° E]; 17 Nov. 1945; HUI INV-AR20914 • 1 ♀; same collection data as for preceding; with juv.; HUI INV-AR20915.

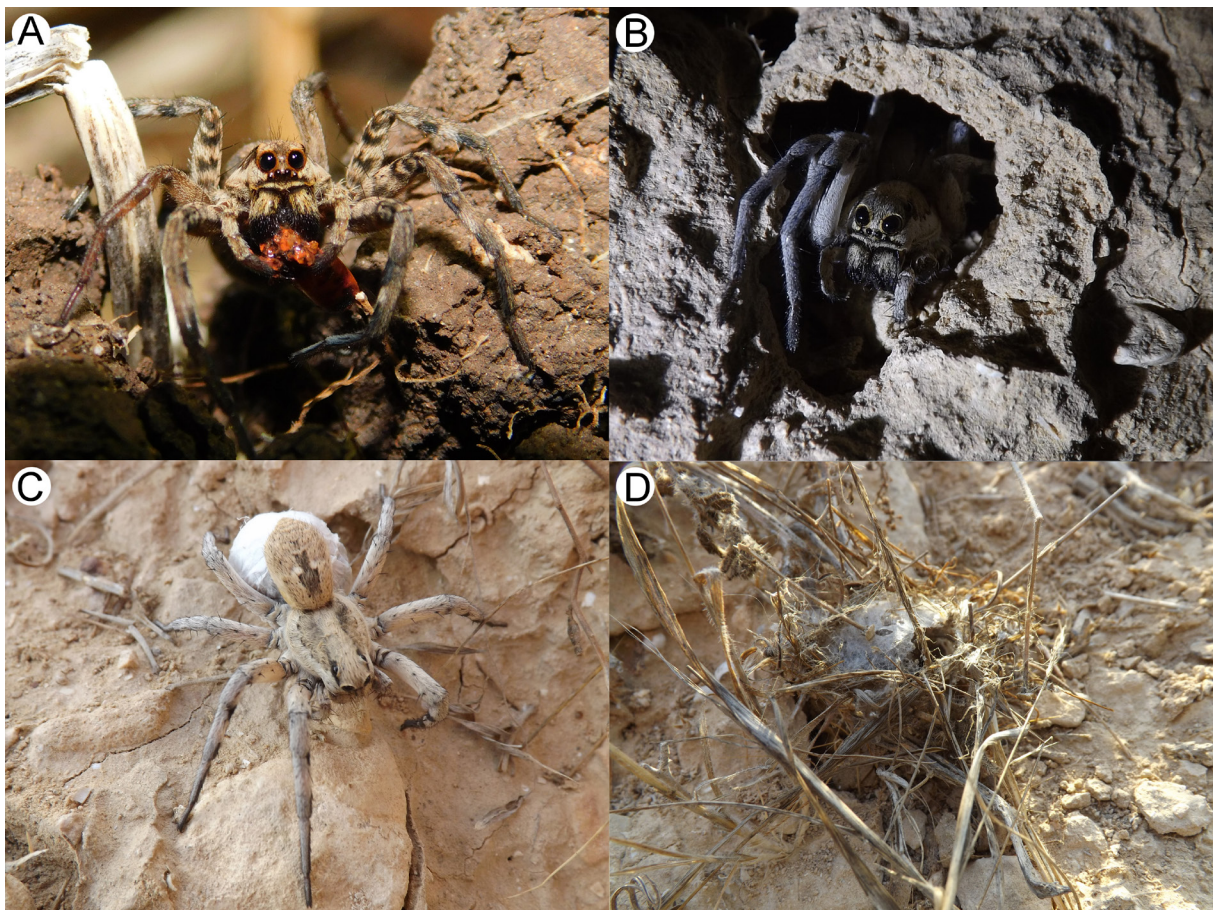
LEBANON • 1 ♀; Lebanon; “???”; Kulchinsky leg.; SMFD11934, jar 834.

## Description

### Male

VARIATION IN MALES (n = 54). ALE diameter: 0.3–0.39; AME diameter: 0.25–0.45; PLE diameter: 0.67–0.73; PME diameter: 0.84–1.19; carapace length: 6.6–11.71; carapace width: 5–8.96; carapace maximum height: 2.5–3.19; abdomen length: 5.2–9.18; leg I (Fe, Pa, Ti, Mt, Tr): 5.56–9.07, 2.8–4.56, 5.3–7.91, 5.65–8.85, 2.95–4.38; leg II: 5.4–8.94, 2.8–4.39, 5–7.53, 5.36–8.96, 3.23–4.22; leg III: 5.42–7.78, 2.27–3.56, 4.4–6.6, 5.34–8.81, 2.99–4.13; leg IV: 6.79–9.83, 2.73–4.19, 5.88–8.77, 8.19–12.56, 4.99–4.79.

CARAPACE. Low, gently sloping posteriorly. Ocular area < 1/3 length of carapace.



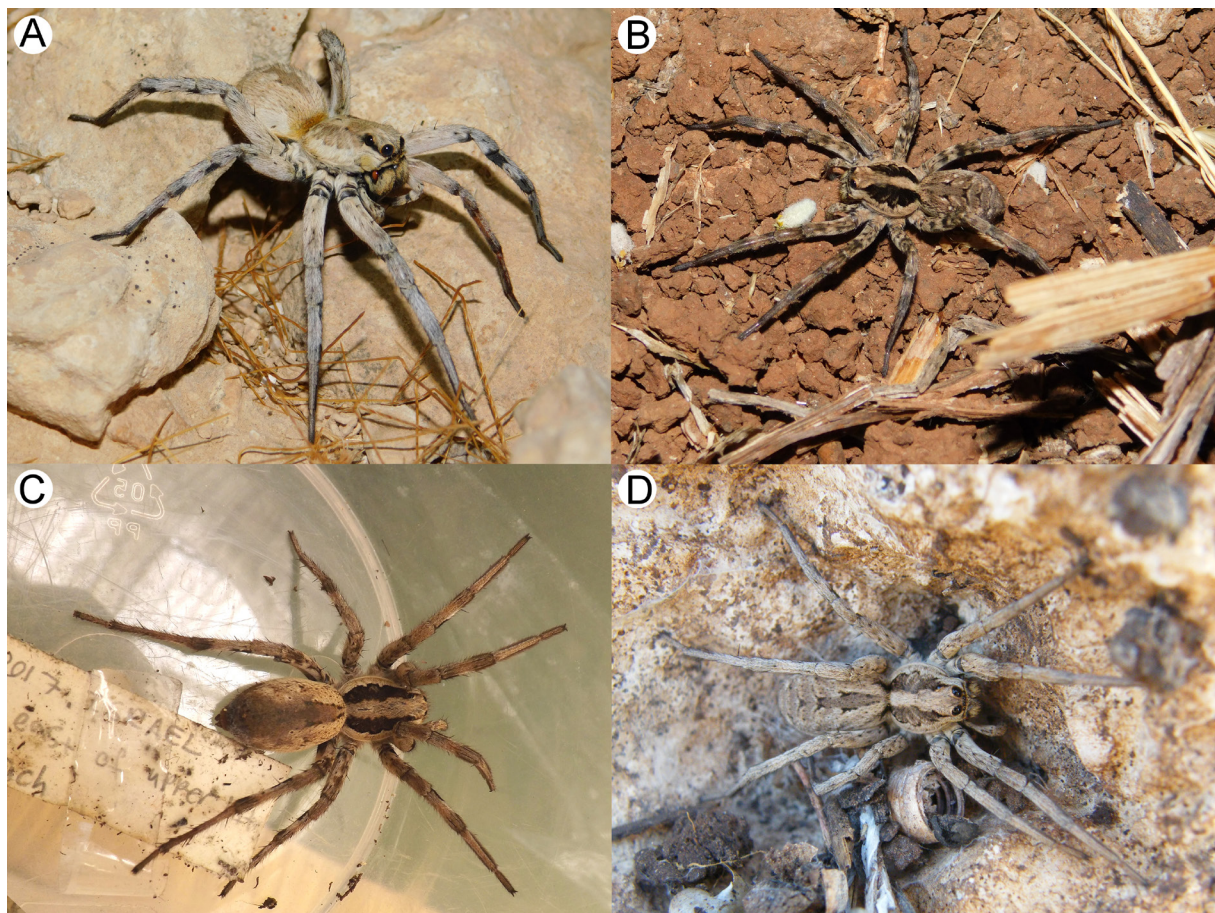
**Fig. 16.** *Lycosa piochardi* Simon, 1876, natural history. **A.** Feeding on *Pyrrhocoris apterus* (Linnaeus, 1758), Mt. Gilboa. **B.** At the opening of a turretless burrow, central Negev. **C.** Female with egg sac, Midreshet Ben-Gurion. **D.** Turreted burrow sealed with silk, Midreshet Ben-Gurion. Photos by I. Armiach Steinpress.

**COLOR.** Carapace light brown, with dark brown median bands, connecting to dark ocular area. Perimeter dark brown. Sternum black. Chelicerae reddish-brown. Abdomen yellow infused with light brown dorsad, cardiac mark brown. Abdomen venter with black patch, orange on margins. Spinnerets brown. Legs light brown, greyish ventrad, to dark brown distad, with two black bands on tibiae. Coxae and trochanters black. Pedipalps light brown (Figs 6D, 7D, 16–17).

**COLOR VARIATION IN MALES (n =52).** Coloration varies greatly. General coloration may be sand-yellow (almost as light as *Lycosa hyraculus* sp. nov.), grey, light brown, reddish-brown and dark brown (Fig. 17). The lighter specimens usually found in arid environments. Black patch on abdomen may be covering the whole ventral side, a part of it (this is the most common condition) or, in rare cases, be altogether absent.

**GENITALIA.** Cymbium reddish-brown, asymmetrical. Tegular apophysis (TA) lying flat on bulb, oriented retrolaterally. TAT highly sclerotized, dark brown, bent posteriorly at  $\sim 90^\circ$ . Crest of TA with unevenly serrated edge, tapering towards TAT. Tip of conductor membranous, triangular, with smooth edges. Synsymbolus with an indistinct, unsclerotized retrolateral edge (Figs 2D, 3D, 4D, 5D, 6D, 7D, 12D, 13).

**LEGS.** Metatarsus I ventral spination: 2 pairs + apical pair. Tibia I ventral spination: 2 pairs + apical pair. Tarsus and metatarsus with scopula.



**Fig. 17.** *Lycosa piochardi* Simon, 1876, live females demonstrating common dorsal coloration morphs. **A.** Sandy morph, Midreshet Ben-Gurion. **B.** Dark brown morph, Mt. Gilboa. **C.** Light brown with dark brown median bands, Mt. Hermon. **D.** Light brown morph, Modi'in. Photos by I. Armiach Steinpress.

### Female

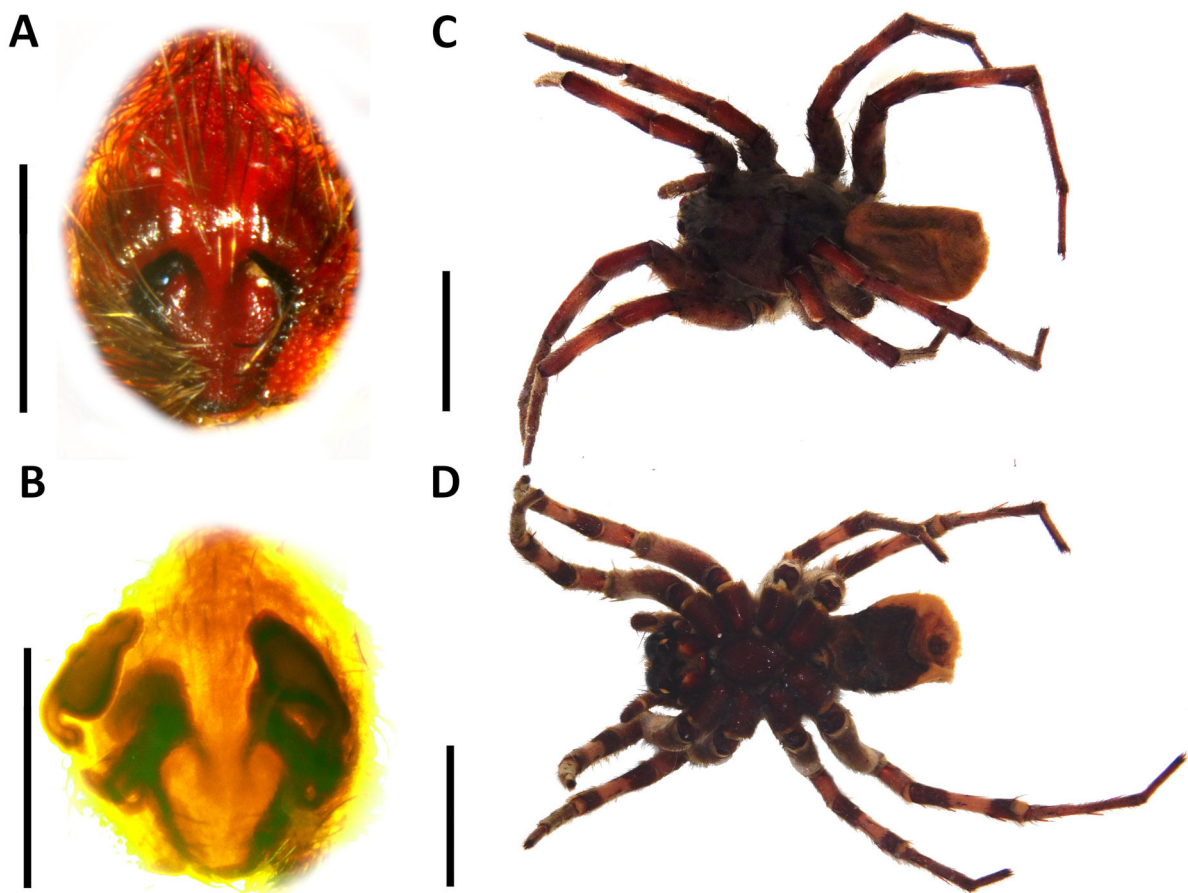
FEMALE PARATYPE (MNHN 1266) MEASUREMENTS. ALE diameter: 0.4; AME diameter: 0.5; PLE diameter: 0.95; PME diameter: 1.2; carapace length: 11.7; carapace width: 8.9; carapace maximum height: 3.6; abdomen length: 10; leg I (Fe, Pa, Ti, Mt, Tr): 8.2, 4.8, 6.6, 6.8, 3.8; leg II: 7.8, 4.2, 6.4, 6.5, 3.7; leg III: 7, 3.8, 5.7, 7.5, 3.6; leg IV: 9.5, 4.3, 7.9, 11, 4.3.

VARIATION IN FEMALES (n = 172). ALE diameter: 0.32–0.44; AME diameter: 0.32–0.53; PLE diameter: 0.68–1.05; PME diameter: 0.82–1.3; carapace length: 6.26–14.29; carapace width: 4.61–10.89; carapace maximum height: 2.37–4.08; abdomen length: 7.51–11.73; leg I (Fe, Pa, Ti, Mt, Tr): 4.99–9.44, 2.61–5, 3.91–7.93, 3.58–7.79, 2.13–3.91; leg II: 4.88–8.85, 2.2–4.9, 4.07–7.14, 3.9–7.49, 2.21–3.94; leg III: 4.43–8.48, 2.17–4.19, 3.68–6.6, 4.06–8.26, 2.24–3.63; leg IV: 5.87–x, 2.53–4.8, 4.8–8.9, 6.41–12.26, 2.82–4.54.

CARAPACE. As in male.

COLOR. As in male (Figs 6G, 7G, 14, 16–17).

GENITALIA. Epigyne: oval, longer than wide, anterior tip pinched, merging with background. Septal pedicel reduced. Septum less than  $\frac{1}{2}$  epigyne length, subtriangular, as long as wide, slightly constricted



**Fig. 18.** *Lycosa piochardi* Simon, 1876, paratype, ♀ (MNHN 1266, vial 2076). **A.** Epigyne, ventral view. **B.** Epigyne, dorsal view. **C.** Habitus, dorsal view. **D.** Habitus, ventral view. Scale bars A–B = 0.5 mm; C–D = 10 mm. Photos by I. Armiach Steinpress.

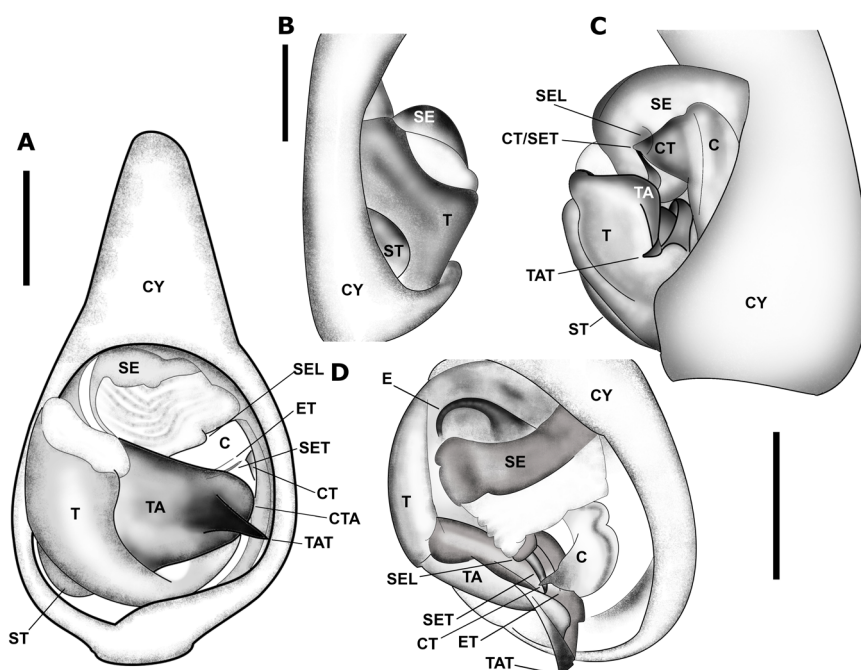
posteriorly, tips rounded. Atria reduced to slits, slightly widening posteriorly. Copulatory openings narrow, at anterior end of septum. Two low, parallel ridges anterior to copulatory openings. Vulva: distal part of spermathecae narrow, oriented dorso-ventrally (parallel). Head of spermatheca elongated, conical, not much wider than spermatheca, oriented ventrad, positioned anteriorly to copulatory opening (Figs 6G, 7G, 9C–L, 10C–L, 11E–F).

VARIATION IN FEMALE GENITALIA (n = 241). Epigyne: proportions vary greatly! General shape of epigyne oval to pentagonal; as long as wide to much longer than wide; sometimes asymmetrical in relation to septum. Septum triangular to trapezoidal, almost rectangular, wider than long to longer than wide. Copulatory openings, usually reduced to slits, but rarely a little wider. Wide copulatory openings sometimes appear in laboratory-raised specimens (not found in the wild, Fig. 27). Anterior edges of atria aligned or prolaterally slanting, wider or narrower than septal pedicel. Ridges anterior to copulatory openings sometimes accentuated with dark color. Vulva: head of spermatheca often with protrusions ('warts') in random places. Distal part of spermatheca sometimes slightly undulating (Figs 9–10).

LEGS. As in male.

### Natural history

The species is mostly nocturnal, but diurnal activity in winter is suspected. Females were collected throughout the year. Females carrying eggs or juveniles were collected September through January, with a single specimen from June. 79% of adult females (167 specimens) were collected July–October. Males were collected in April, July–October and December. 86% of the males (45 specimens) were collected in July–September. Subadult females were collected in March–July and October. Subadult males were collected in January and March–August. Juveniles were collected throughout the year (Table 4). Twenty seven of the specimens kept in the laboratory lived for more than a year. Specimen HUI INV-



**Fig. 19.** *Lycosa hyraculus* sp. nov., holotype, ♂ (HUI INV-AR20818), left pedipalp line drawings. A. Ventral view. B. Prolateral view. C. Retrolateral view. D. Distal view. Scale bars = 0.5 mm. Drawings by I. Armiach Steinpress.

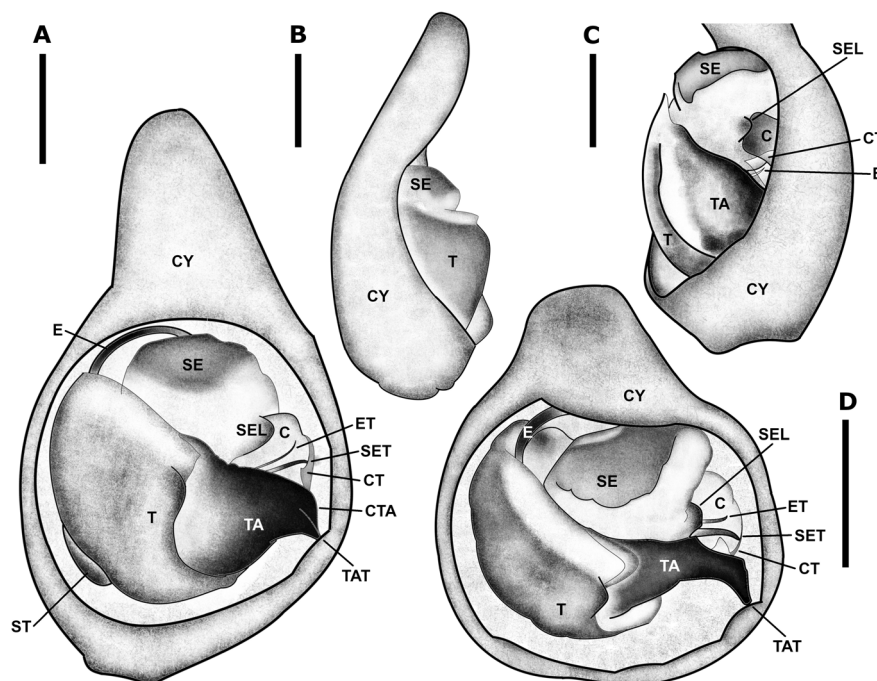
AR20813 was collected as a young juvenile, lived for 26 months and moulted ten times, before dying as a subadult (Fig. 26). *Lycosa piochardi* is found in a wide range of climates: dry summer continental climate, Mediterranean, steppe, arid desert and hyperarid desert, spanning altitudes of 380 m b.s.l. to 2400 m a.s.l., and average precipitations of 21 mm to 1150 mm. It is most commonly found in low scrub, grasslands and habitats with bare ground. *Lycosa piochardi* is abundant in natural and agricultural areas, but is very uncommon in urban environments. The burrow is built in open ground, in a great variety of soil types: from stabilized sand to alluvial clay soils and rocky regosols. The burrow opening is usually modified, with a short turret, made of vegetation held together with silk. Yet, it is not rare to find turretless entrances. Some turrets are found sealed with silk in autumn. One burrow (specimen HUI INV-AR20912) found in a sandy substrate had a full silk lining. In rare cases *L. piochardi* is found in a retreat under a stone. *Lycosa piochardi* is a generalist predator, feeding on a wide variety of prey species. Captive specimens readily accept crickets, cockroaches, honeybees, flies, butterflies, pholcid spiders and other soft-bodied arthropods (personal observation). Beetles and bugs were usually rejected, yet wild specimens were observed feeding on *Pyrrhocoris apterus* (Linnaeus, 1758) (Figs 16–17, 21C–D, 22C–D, 25–26).

### Distribution

EGYPT, IRAN, ISRAEL, LEBANON, PALESTINE, SYRIA, TURKEY.

### Records

EGYPT: Sinai (Al-Qusaymah (Kadesh Barnea), Mt. Catherine). ISRAEL and PALESTINE: Coastal Plain (Akko, Ashdod, Be'eri, Gaza, Hadera, Hatsor, Herzlia, Holon, Kfar Bialik, Lod, Nitzanim, Ramat-Gan, Rehovot, Rishon LeTsiyon, Savyon, Talmei Menashe, Tel Aviv, Tira), Dead Sea Area (Ein Feshkha, Hawat Einot Kedem, Jericho), Galilee (Adamit, Ahihud forest, Biq'at Qedesh, Dishon, Eilon,

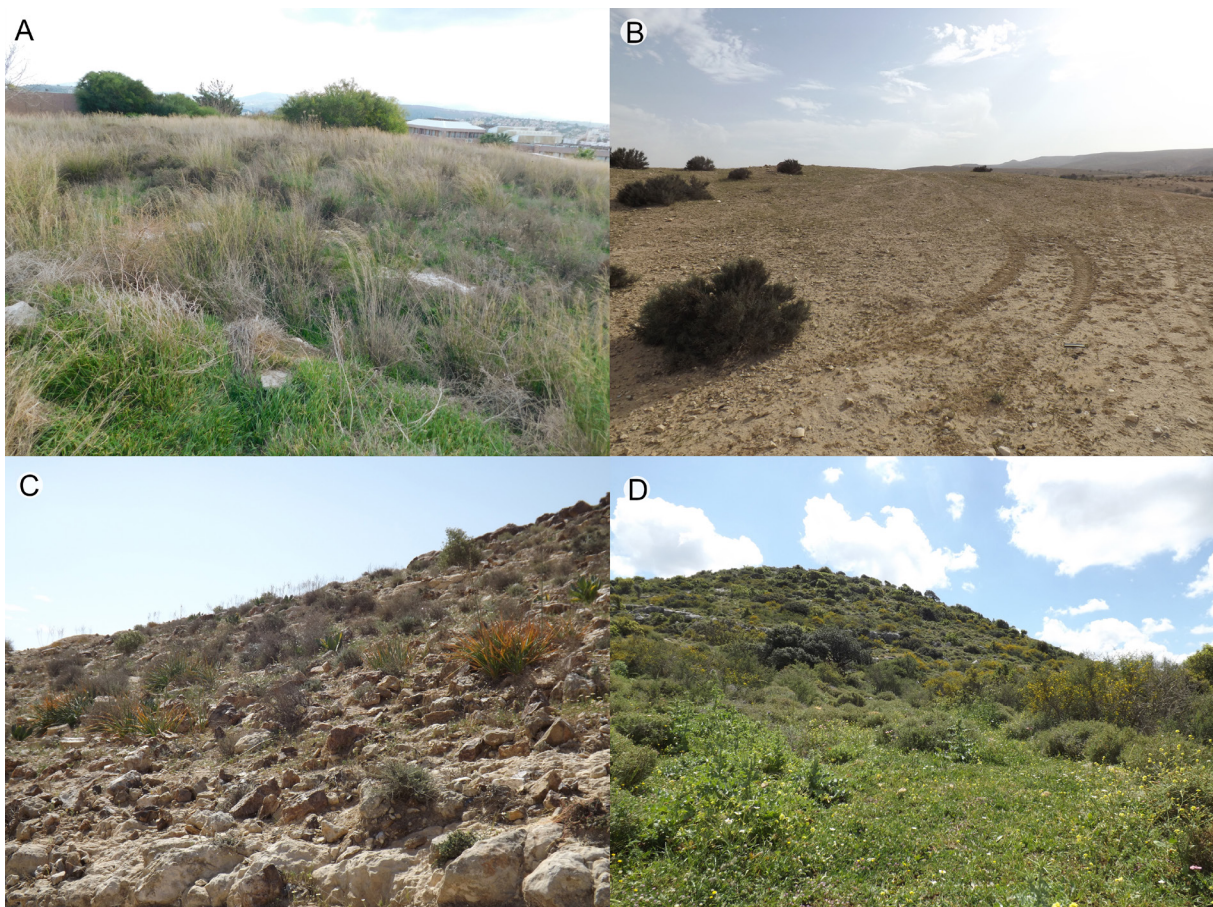


**Fig. 20.** *Lycosa gesserit* sp. nov., holotype, ♂ (HUI INV-AR20631), left pedipalp line drawings. **A.** Ventral view. **B.** Prolateral view. **C.** Retrolateral view. **D.** Distal view. Scale bars = 0.5 mm. Drawings by I. Armiach Steinpress.

Her Eliezer, Kfar HaHoresh, Kfar Kisch, Moreshet, Mt. Meron, Nahal Tzippori, Ramot Naftali, Snir, Yavne'el, Yiftah, Yuvalim, Zar'it, Zavit cave), Golan Heights (Horvat Susita, Nahal Yehudiya, Odem forest, Qatsrin, Waset), Hermon (Givon, Nabi Hazuri, upper chairlift station), Emeq Yizra'el (Kfar Baruh, Sarid), Jordan Valley (Ashdot Ya'akov, Ein Sukkot, Karei Deshe, Maoz Haim, Menahemia, Nahal Hagal, Sde Eliyahu, Southern Jordan Valley), Judea (Ayn ad Duyuk, Alon, Arad, Beit Guvrin, Beit Nir, Ben Shemen, Bet Yatir, Biq'at Qanna'im, Bor `Atin, Canada Park, Har Amasa, Har Hardon, Horkanya valley, Jerusalem, Kfar Daniel, Kiryat Anavim, Kiryat Shmuel, Ma'ale Adumim, Maon ridge, Mar Saba, Modi'in, Negohot, Ramat Rachel, South Hebron Mountains), Karmel (Isfiya, Ramat Hanadiv, Zikhron Ya'akov), Negev (Ariel Sharon camp, Avdat, Be'er Mash'abim, Be'er Milka, Be'er Sheva, Brosh, Dimona ridge, Ezuz, Giv'ot Bar, Gvaot Goral, Haluqim ridge, Har Karkom, Hirbet Rimon, Holot 'Agur, Irus HaNegev, Lehavim, Lipa Gal lookout, Mamshit, Merhav Am, Midreshet Ben-Gurion, Mitzpe Ramon, Nahal Gmalim, Nahal Hamarmar, Nahal Ashalim, Nahal Nafha, Nahal Revivim, Netivot, Nitzana, Yeruham, Shivta camp), Samaria (Ari'el, Barkan, Ein Dor, Gilboa, Hemedat, Ibthan, Jatt, Megiddo, Mehola, Mehora, Wadi Al-Far'a). JORDAN: Jerash. SYRIA (Fig. 1)

### Relationships

According to our molecular phylogeny, this species is closely related to *Lycosa baulnyi* (Figs 23–24).



**Fig. 21.** Typical habitats. **A.** Mediterranean grassland, Karmiel. **B.** Desert loess plain, Yeruham. **C.** Desert rocky slope, Yeruham. **D.** Mediterranean dwarf scrub (batha), Yodfat. Photos by I. Armiach Steinpress.

## Notes

We could not locate the holotype of *Lycosa piochardi* Simon, 1876, either in its original repository in the MNHN or in other collections. For the identification we used a paratype (MNHN 1266, Fig. 18) that was collected with the holotype and identified by Simon.

We examined the holotype of *Lycosa piochardi infraclara* Strand, 1915 (SMFD2184). We synonymize it with *L. piochardi*, as its morphology (Figs 9F, 10F) falls within the normal range of *L. piochardi* morphology and is described from the typical area of distribution for this species.

We could not locate the holotype of *Allocosa olivieri* (Simon, 1876), but judging from the locality (the Jordan Valley) and the shape of the epigyne in the illustration (Simon 1876: pl. 3 fig. 10), it should probably be synonymized with *L. piochardi*.

A male specimen (BMNH 742) collected by Koch in Sardarapat (Armenia) was originally identified as *L. piochardi*. Our examination shows it to be *L. praegrandis*, with a characteristic semicircular conductor, rather than a triangular one.



**Fig. 22.** Retreats. **A.** *Geolycosa vultuosa* C.L. Koch, 1838, burrow with turret made of soil. **B.** *Lycosa hyraculus* sp. nov., burrow with door, Midreshet Ben-Gurion. **C–E.** *Lycosa piochardi* Simon, 1876. **C.** Burrow with turret made of plant material, Midreshet Ben-Gurion. **D.** Burrow without turret, Tel Kofer. **E.** Retreat under stone, Ariel Sharon camp. Photos by I. Armiach Steinpress.

*Lycosa piochardi* was recently recorded by Zamani *et al.* (2021) from Iran. The epigynes and spermathecae presented in the paper (Zamani *et al.* 2021: fig. 8) bear great resemblance to the material examined by us. However, the Iranian specimens differ by having stouter spermathecae with bulbous heads (unlike the elongated heads in our material). A molecular phylogeny may help to decide whether the specimens are indeed *L. piochardi*, or represent a closely related, but separate species.

### **Phylogenetic relationships based on COI**

The 28S segments we recovered proved to be too conservative for this study and were omitted from the phylogenetic analysis. Bayesian analysis of COI was performed for 78 specimens (16 original) spanning 20 species: *Arctosa alluaudi* Guy, 1966, *Hogna radiata* (Latreille, 1817), *Pisaura mirabilis* (Clerck, 1757), *Pirata piraticus* (Clerck, 1757), and *Xerolycosa miniata* (C.L. Koch, 1834) as outgroup taxa, and *Lycosa* aff. *oculata* 1 Planas, 2013, *Lycosa* aff. *oculata* 2 Planas, 2013, *Lycosa* aff. *suboculata* Planas 2013, *Lycosa baulnyi* Simon, 1876, *Lycosa bedeli* Simon, 1876, *Lycosa fasciiventris* Dufour, 1836, *Lycosa hispanica* (Walckenaer, 1837), *Lycosa hyraculus* sp. nov., *Lycosa munieri* Simon, 1876, *Lycosa gesserit* sp. nov., *Lycosa oculata* Simon, 1876, *Lycosa piochardi* Simon, 1966, *Lycosa praegrans* C.L. Koch, *Lycosa suboculata* Guy, 1966, *Lycosa tarantula* (Linnaeus, 1758), and *Lycosa vachoni* Guy, 1966 as ingroup taxa. The cladogram topology recovered *Lycosa* s. str. as monophyletic (posterior probability (PP) = 1), with a topology largely congruent with that found by Planas *et al.* (2013). *Lycosa hyraculus* sp. nov. came out as monophyletic (PP = 1), and as a sister taxon of *L. gesserit* sp. nov. (PP = 0.92). The two species formed a sister taxon to *L. oculata* + *L. aff. oculata* 1 + *L. aff. oculata* 2 clade (PP = 0.74). *Lycosa piochardi* came out as monophyletic (PP = 0.9) and as a sister species to *L. baulnyi* (PP = 1). (Figs 23–24).

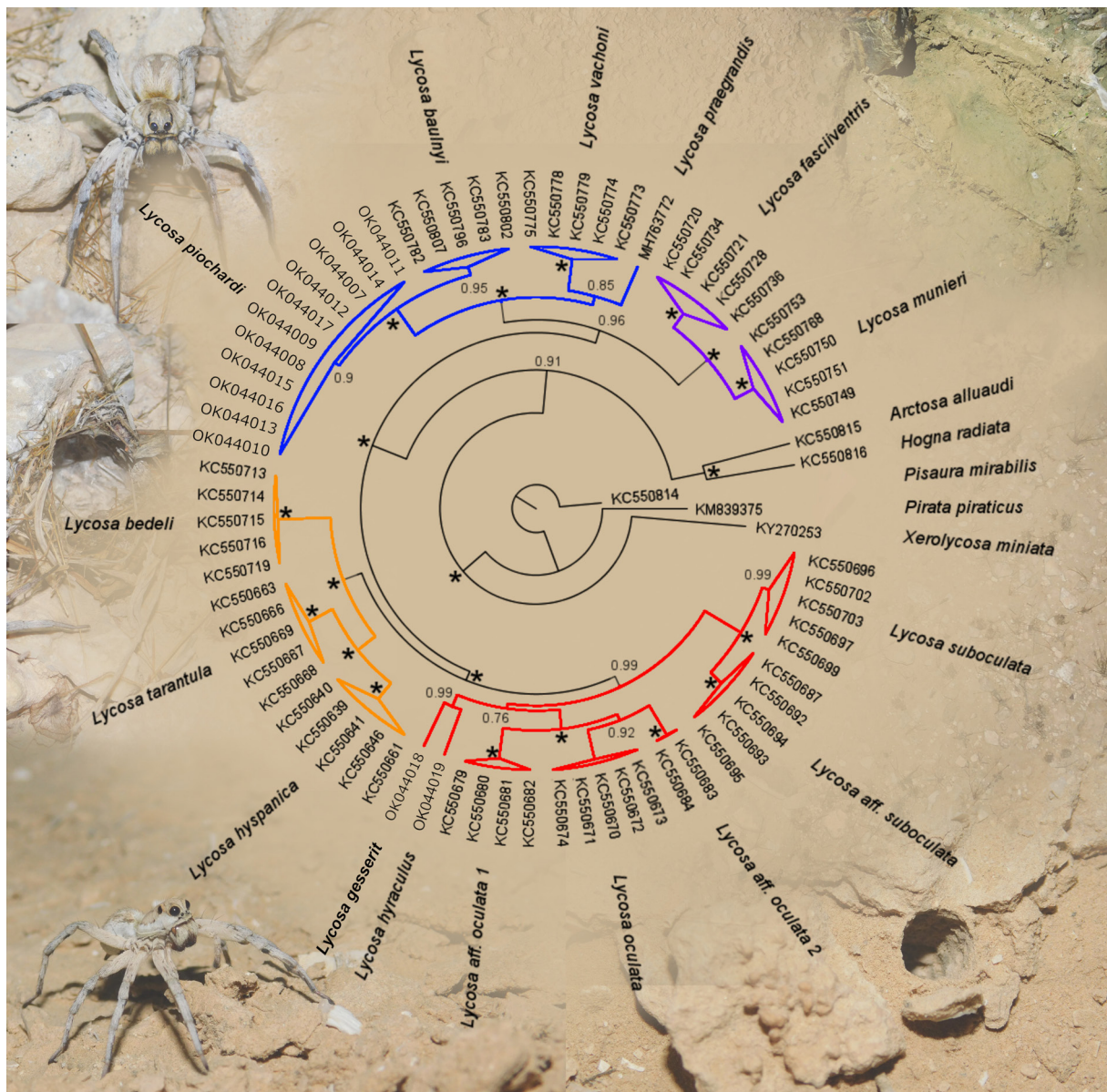
### **Ecological survey**

A total of 47 individuals of the genus *Lycosa* were recorded (30 in Midreshet Ben-Gurion, 17 in Yeruham park), of these 31 were *L. hyraculus* sp. nov. and 16 *L. piochardi*. The micro-habitats of the two species were found to be significantly different in all parameters (Table 5). The abundance of *Lycosa hyraculus* sp. nov. was positively correlated with a plain habitat, with a surface incline smaller than 10°, east and north facing slopes, distance from shrubs (0–9 m), low percentage of stones on surface (0.3–77%) and localities with sparse vegetation. The abundance of *Lycosa piochardi* was positively correlated with a hill habitat with a surface incline greater than 10°, south facing slopes, short distance from shrubs (0–1.06 m) and high percentage of stones on the surface (8.9–99.8%). But the habitat category ‘hill’ was significantly positively correlated with the degree of incline (likelihood ratio = 0.0002, Pearson = 0.0002) and distance from nearest shrub (two-tailed T test,  $p = 0.03$ ), but not with direction of incline (likelihood ratio = 0.3, Pearson = 0.5) and amount of vegetation (two-tailed T test,  $p = 0.6$ ) (Table 5).

### **Discussion**

In this study we aimed at exploring the identity and diversity of the large lycosids of Israel and Palestine. We used genital and somatic morphology as well as burrow building behavior to hypothesize how many species of *Lycosa* are found in our material. Our initial hypothesis using morphology suggested three to five species, while using burrow building behavior our hypothesis suggested only two species: a door- and a turret-building species. Testing these hypotheses with molecular analyses recovered three species of *Lycosa*, of which two are new to science. We found one additional specimen that may be a fourth species also new to science; however, we could not test this species hypothesis with either burrow building behavior or molecular analysis as we had only one female specimen collected more than 30 years ago with no information on its burrow construction. This specimen differs in its genital structures from all the other material we had; however, because we had no male and only one specimen, we decided to document it but not formally describe it. In addition, we report here one species of *Geolycosa*, a genus new to the region.

We also aimed to differentiate between a number of possible hypotheses as to the origins of southern Levantine *Lycosa*: the local species could be nested in the western north African clade and therefore would have originated from the aforementioned region either relatively recently or before the radiation into the current lineages; conversely, they could belong to a sister clade to the African *Lycosa*. Our results point to a relatively recent radiation within the western north African clades and at least two waves of eastward migration. Furthermore, we aimed to understand the ecological relationships between the southern Levantine species and to map their distribution to the different available habitats. We found that the seeming sympatry of two species at low resolution is resolved into apparent niche partitioning at high resolution, with *Lycosa hyraculus* sp. nov. using the loess plains as a preferable habitat, and



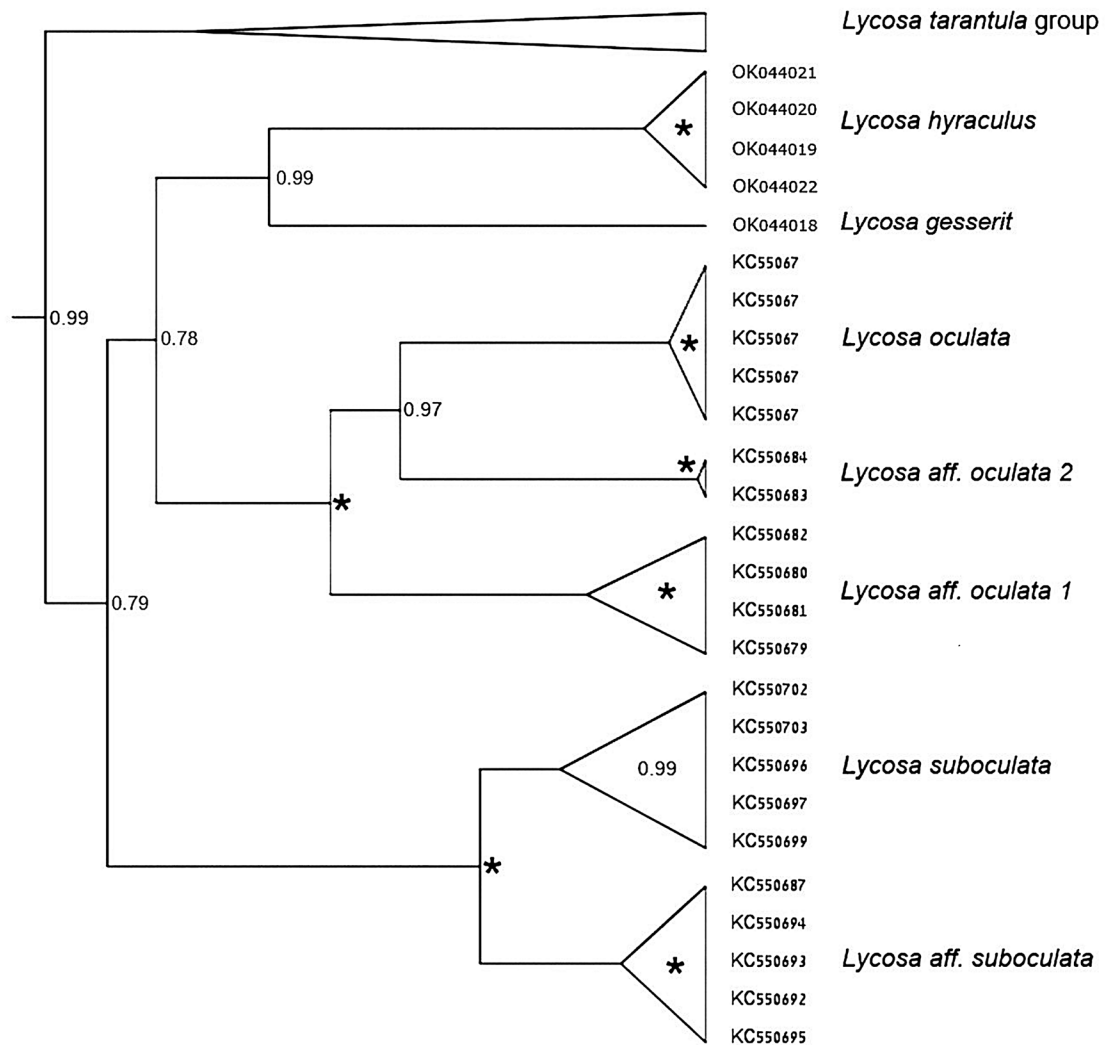
**Fig. 23.** Bayesian phylogeny cladogram, showing the topology of *Lycosa* Latreille, 1804. Posterior probabilities of 1 marked by asterisk. Specimens used for this phylogeny detailed in Table 2. Photos by I. Armiach Steinpress.

*L. piochardi* occupying the hill habitat when in sympatry with *L. hyraculus*, and both habitats when *L. hyraculus* is absent.

**Morphology**

**Intraspecific variation**

*Lycosa piochardi* is a species with a high variation in genital and somatic morphology. Size (Fig. 14), dorsal coloration (Fig. 17), ventral pattern (Fig. 15) and epigyne shape (Fig. 9) are all found in several variants. While the shade of the dorsal coloration could be tied to the color of the surface (lighter on desert soils, darker on Mediterranean soils), the other characters do not seem to be closely tied to environmental factors and tend to vary within local populations. Because of this variation, *L. piochardi* was historically identified as several taxa, such as *L. tarantula*, *Allocosa olivieri* (Simon, 1876) and even



**Fig. 24.** Bayesian phylogeny cladogram, showing the topology of the *oculata* group. Posterior probabilities of 1 marked by asterisk. Specimens used for this phylogeny detailed in Table 2.

**Table 5.** Results of ecological survey of *Lycosa* spp. in the 13–14 Sep. 2020.

habitat parameters		<i>L. hyraculus</i> sp. nov.	<i>L. piochardi</i>	significance of difference
Individuals per habitat type	Plain	26	9	Pearson’s test: 0.03
	hill	5	7	
Individuals per surface incline: angle	<10°	23	5	Pearson’s test: 0.005
	>10°	6	9	
	n.a.	2	2	
Individuals per surface incline: direction	east	8	3	Pearson’s test: 0.0013
	west	2	0	
	north	11	2	
	south	4	9	
	n.a.	1	2	
mean distance from a shrub (cm)		285.8 (SD = 269.169)	68 (SD = 68.159)	two-tailed T-test: p < 0.0001
mean % of stones on surface		22.54 (SD = 23.1)	65.39 (SD = 31.99)	two-tailed T-test: p = 0.003
Individuals per vegetation cover	negligible	3	0	two-tailed T-test p = 0.022
	sparse	23	9	
	abundant	5	7	

as *Hogna radiata* (Latreille, 1817) (Shulov 1943). To explore the possible existence of several species we chose the specimens in the phylogeny as to represent a wide range of habitats (stony desert, sandy desert, Mediterranean scrub, Mediterranean grassland, maquis and alpine tragacanth steppe), retreat types (turreted burrow, silk-lined burrow and specimens hiding under stones), epigyne shapes (types D, F, H, I, K as seen in Fig. 9) and ventral patterns (types A, B, C, E as seen in Fig. 15). All specimens of *L. piochardi* were recovered in the COI phylogeny as both monophyletic and closely related, likely belonging to a single species.

Size ranges of males and females are generally overlapping, but a few females (n = 27, ~15% of measured females) in our dataset are ‘gigantic’, with a carapace longer than 11.71 mm (the longest male carapace

in the dataset), up to 14.29 mm. It is unknown what factors influence the size of the spiders in this study and whether ‘gigantism’ in females is of any significance.

#### Abnormal variation in lab grown female specimens

Describing new species from individuals raised in captivity, without seeing wild adult might be problematic. Many of the specimens in this dataset were collected in the wild and raised to maturity in captivity. We have noticed that in both *L. piochardi* and *L. hyraculus* sp. nov., females that took more than one molt to mature in captivity sometimes developed epigyne shapes different from those of specimens that were collected mature or molted to maturity shortly after collection (Fig. 27). Some of these epigynes were pedomorphic or weakly sclerotized, but others did not appear unusual, except (apparently) not being found in nature. Compared to the symmetrical, almost triangular epigynes of specimens from the field, the epigynes of captive-raised specimens of *Lycosa* tended to be asymmetrical and almost rectangular, with wide atria (wild specimens usually have narrow atria). We assume all of these to be abnormal, resulting from some discrepancy between the natural and laboratory conditions.

Male genitalia were seemingly unaffected and were identical in shape to the genitalia of specimens collected from the wild. We have decided to describe the laboratory raised specimen, HUI INV-AR20631, as a new species (*Lycosa gesserit* sp. nov.) only after both seeing that the male pedipalp differs from other species (Figs 2, 20), and receiving supporting data in the molecular phylogeny (Figs 23–24).



**Fig. 25.** *Lycosa piochardi* Simon, 1876, habitat extremes. **A.** Alpine tragacanth steppe, Mt. Hermon. **B.** Natural woodland, Odem Forest. **C.** Sandy desert, western Negev. **D.** Dead Sea oasis, En Gedi. Photos by I. Armiach Steinpress.

## Biogeography

This study concentrated on Israel and Palestine, whereas only a few specimens from other countries were available to us. Therefore, the species list presented in this paper should not be seen as exhaustive for the southern Levant, as additional species may be found in Jordan and Egypt (Sinai Peninsula). *Lycosa piochardi* can be assumed to be distributed throughout the region, but the other species of *Lycosa* appear to have more restricted local distributions. *Lycosa hyraculus* sp. nov. is confined in Israel to the central Negev Desert and is also found in the central Sinai Peninsula, which is a continuation of the aforementioned geographical region. *Lycosa gesserit* sp. nov. and *Lycosa* sp. were recorded from Israel and are likely found in hyperarid habitats in Jordan and the Sinai Peninsula.

Planas *et al.* (2013) constructed a phylogeny of western Mediterranean *Lycosa* and suggested that all western European species originated in a few expansion events from western north Africa. Our additions to this phylogeny do not alter the topology presented by Planas *et al.* and indeed support their conclusions. In our phylogeny *L. piochardi* is a sister species of *L. baulnyi* from the southern Atlas Mountains. The phylogeny supports *L. piochardi* as monophyletic, but lacks the resolution to show any topology within the clade. *Lycosa hyraculus* sp. nov. and *L. gesserit* sp. nov. appear as sister species in the *L. oculata* clade. These findings support the hypothesis that the southern Levantine species originated in separate expansion events, possibly from Africa. Despite the similarity to *Lycosa praegrandis*, the hypothesis that *L. piochardi* represents a northern lineage related to *L. praegrandis* was not supported, as the two species are not closely related in our phylogeny. A north African origin of the genus could be suggested, as all the non-African species (*L. hyraculus*, *L. gesserit*, *L. piochardi*, *L. praegrandis*, *L. tarantula* + *L. hispanica*) in our phylogeny have African sister clades. Adding genetic material from other west Asian and north African countries (e.g., Iran, Egypt, respectively) should further clear up the delimitation and historical biogeography of this genus.

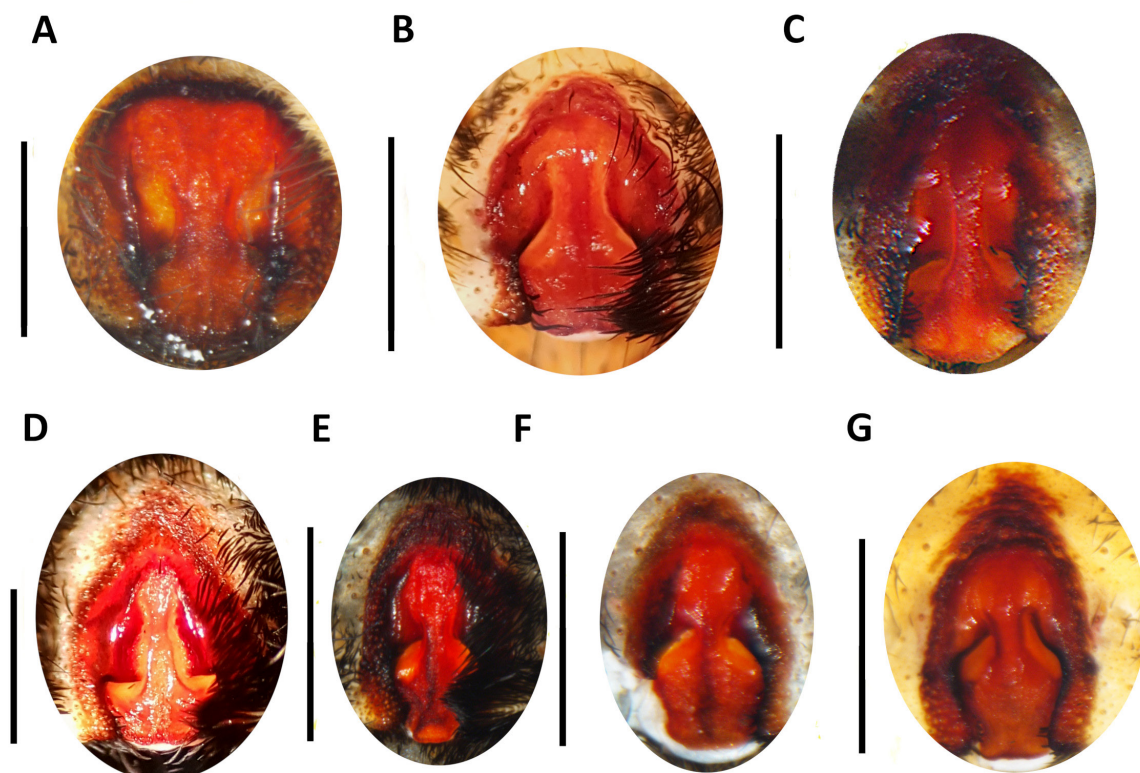
It is interesting to note that according to Planas *et al.* (2013), species of *Lycosa* are sympatric only when they belong to different lineages (of the four main lineages outlined by those authors). This is also the case in our study area. Additionally, it is consistent with the apparent lack of sympatry between *L. praegrandis* and *L. piochardi*, despite the geographical proximity (as both belong to the same main lineage – the ‘*baulnyi* group’). If we take this to be a general rule, it would be more reasonable to assume that *L. piochardi* is indeed a species with high variation in genital and somatic morphology, rather than a



**Fig. 26.** *Lycosa piochardi* Simon, 1876, ten carapace molts shed between 9 Mar. 2018–1 Jun. 2020, by a single specimen (HUI INV-AR20813) in laboratory conditions. Scale bar = 10 mm. Photo by I. Armiach Steinpress.

number of closely related sympatric species. Identifying the region where there is a replacement between *L. praegrans* and *L. piochardi* may contribute to understanding their ecology and biogeographic history.

Another interesting observation, in apparent contradiction with the lack of sympatry between related lineages mentioned above, is the phylogenetic and geographical proximity of *L. hyraculus* sp. nov. and *L. gesserit* sp. nov. (Figs 1, 24). They appear to maintain separate populations in proximity to one another, suggesting a reduced mobility. These species belong to the *L. oculata* group, which in Planas *et al.* (2013) is the most speciose clade, most species of which occupy small, closely located distributions. The species of the *oculata* group are also very similar in morphology, a fact that is accentuated by the discovery of three of them during the study of Planas *et al.* (2013), based on molecular phylogeny. All this is suggestive of the tendency to become isolated and to form species with restricted distributions. While isolation due to low dispersibility may be the reason for the existence of the two species in geographical proximity, another possible reason for the proximity of *L. hyraculus* and *L. gesserit* may be the ecological vicariance. *Lycosa hyraculus* inhabits arid desert habitats, where the annual precipitation is between 200 and 75 mm, and at an elevation lower than 500 m a.s.l., while the only specimen of *L. gesserit* was found in the hyperarid (precipitation under 75 mm) Har Karkom, at an elevation over 600 m a.s.l. Each species could be adapted to very specific climatic conditions, such as levels of humidity (DeVito *et al.* 2004). Yet, there seems to be a gap between the distributions of the two species, where despite apparently suitable conditions and repeated searches, only *L. piochardi* was found. Due to this restricted distribution and apparent low mobility, *L. hyraculus* might come under danger of extinction,



**Fig. 27.** *Lycosa* ♀♀ raised in laboratory for more than one molt, possibly aberrant epigynes, ventral view. **A.** *L. hyraculus* sp. nov. HUI INV-AR20665. **B–G.** *Lycosa piochardi* Simon, 1876. **B.** HUI INV-AR20576. **C.** HUI INV-AR20552. **D.** HUI INV-AR20668. **E.** HUI INV-AR20563. **F.** HUI INV-AR20783. **G.** HUI INV-AR20549. Scale bars = 0.5 mm. Photos by I. Armiach Steinpress.

as loess plains in Israel are being developed for housing and agriculture and as the current climate change may further aridify this habitat.

### Ecological survey

The coexistence of two similarly-sized, congeneric species always raises the question of resource partitioning. In our preliminary survey in the central Negev Desert, the distribution of the two species of *Lycosa* across the two main habitat types (plain and hill) was found to be significantly differential. The different association of the species with magnitude of incline, percentage of stones on surface and distance to shrubs may be explained by the attributes of the different habitats, but even though most specimens of *L. piochardi* were found in the plain habitat, they inhabited steeper surfaces compared to *L. hyraculus* sp. nov. The differential occupation of incline directions may be due to microhabitat preference. South and north slopes differ greatly in evaporation, due to different exposure to the sun (Pavlíček *et al.* 2003) and are known to have differences in biomass and species composition. The difference in amount of vegetation in the vicinity of the two species of *Lycosa* may suggest that *L. piochardi* in the survey area has a tendency to be found in patches of ground more densely vegetated than those typical of *L. hyraculus*. Based on these preliminary findings, we would like to suggest that in the survey area some specialization of *L. hyraculus* and *L. piochardi* occurs both at the habitat and microhabitat level. *Lycosa piochardi* is dominant in steep hill habitats, while *L. hyraculus* is dominant in flat plain habitats. Yet, in some habitats these species coexist, and there may exist a finer niche partitioning, in which *L. piochardi* is found in the steeper, more densely vegetated patches, while *L. hyraculus* is found in the flatter, more sparsely vegetated patches. At localities where only *L. piochardi* is found, it was observed occupying all habitats. Further collection of data will be needed to explore the behavioral/ecological interactions of *L. hyraculus* and *L. piochardi*.

### Acknowledgments

We would like to thank Irene Steves, who was the first to work on the yet unnamed *Lycosa hyraculus* sp. nov. We would also like to express our gratitude to all the people that provided us with specimens. Among others, Shlomi Aharon, Pinchas Amitai, Jesús Ballesteros Chaves, Jan Beccaloni, Dar Ben-Natan, Iris Bernstein, David David, Zeana Ganem, Yael Lubin, Ivan Magalhaes, Anastasia Novikova, Ittai Renan, Yakov Salaviz, Avi Shmida, Boaz Shacham, Benny Shalmon, Dany Simon, Itay Tesler, Akiva Topper, Assaf Uzan, Daniel Waysman, Amir Weinstein, Aylon Zvik, and Yoram Zvik. Special thanks to Luis Piacentini, for the advice on sequencing; and to Prof. Dany Cohen for endowing IAS with a student-stipend, thus allowing for writing of this paper.

### References

- Arganda-Carreras I., Kaynig V., Rueden C., Eliceiri K.W., Schindelin J., Cardona A. & Sebastian Seung H. 2017. Trainable Weka Segmentation: a machine learning tool for microscopy pixel classification. *Bioinformatics* 33 (15): 2424–2426. <https://doi.org/10.1093/bioinformatics/btx180>
- Armiach I., Bernstein I., Tang Y. & Gavish-Regev E. 2016. Activity-density data reveal community structure of Lycosidae at a Mediterranean shrubland. *Arachnologische Mitteilungen* 52: 16–24. <https://doi.org/10.5431/aramit5204>
- Bagliivi G. 1695. *De anatome, morsu & effectibus tarantulae*. Typis Dom. Ant. Herculis, Romae [Roma].
- Bowden J.J. & Buddle C.M. 2012. Life history of tundra-dwelling wolf spiders (Araneae: Lycosidae) from the Yukon Territory, Canada. *Canadian Journal of Zoology* 90 (6): 714–721. <https://doi.org/10.1139/z2012-038>
- Breitling R. 2019. Barcode taxonomy at the genus level. *Ecologica Montenegrina* 21: 17–37. <https://doi.org/10.37828/em.2019.21.2>

- Costa A. 1875. Relazione di un viaggio per l'Egitto, la Palestina e le coste della Turchia asiatica per ricerche zoologique. *Atti della Reale Accademia delle Scienze Fisiche e Matematiche di Napoli* 7: 1–40.
- DeVito J., Meik J.M., Gerson M.M. & Formanowicz D.R. Jr. 2004. Physiological tolerances of three sympatric riparian wolf spiders (Araneae: Lycosidae) correspond with microhabitat distributions. *Canadian Journal of Zoology* 82 (7): 1119–1125. <https://doi.org/10.1139/Z04-090>
- Dippenaar-Schoeman A.S. & Jocqué R. 1997. *African Spiders: An Identification Manual, Vol. 9*. ARC-Plant Protection Research Institute, Pretoria.
- Drummond A.J. & Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7: 214. <https://doi.org/10.1186/1471-2148-7-214>
- Folmer O., Hoeh W.R., Black M.B. & Vrijenhoek R.C. 1994. Conserved primers for PCR amplification of mitochondrial DNA from different invertebrate phyla. *Molecular Marine Biology and Biotechnology* 3 (5): 294–299.
- Framenau V.W. & Vink C. 2001. Revision of the wolf spider genus *Venatrix* Roewer (Araneae: Lycosidae). *Invertebrate Taxonomy* 15 (6): 927–970. <https://doi.org/10.1071/IT01008>
- Fuhn I.E. & Niculescu-Burlacu F. 1971. Fam. Lycosidae. In: *Fauna Republicii Socialiste România 260 Arachnida Volumul V, Fascicula 3*. Academiei Republicii Socialiste România, Bucharest.
- Gernhard T. 2008. The conditioned reconstructed process. *Journal of Theoretical Biology* 253 (4): 769–778. <https://doi.org/10.1016/j.jtbi.2008.04.005>
- Hebert P.D., Ratnasingham S., Zakharov E.V., Telfer A.C., Levesque-Beaudin V., Milton M.A., Pedersen S., Jannetta P. & DeWaard J.R. 2016. Counting animal species with DNA barcodes: Canadian insects. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371 (1702): 20150333. <https://doi.org/10.1098/rstb.2015.0333>
- Hedin M.C. & Maddison W.P. 2001. A combined molecular approach to phylogeny of the jumping spider subfamily Dendryphantinae (Araneae: Salticidae). *Molecular Phylogenetics and Evolution* 18 (3): 386–403. <https://doi.org/10.1006/mpev.2000.0883>
- Just P., Opatova V. & Dolejš P. 2019. Does reproductive behaviour reflect phylogenetic relationships? An example from Central European *Alopecosa* wolf spiders (Araneae: Lycosidae). *Zoological Journal of the Linnean Society* 185 (4): 1039–1056. <https://doi.org/10.1093/zoolinlean/zly060>
- Koch C.L. 1836. *Die Arachniden*. Dritter Band. C.H. Zeh'sche Buchhandlung, Nürnberg. <https://doi.org/10.5962/bhl.title.43744>
- Koch C.L. 1838. *Die Arachniden*. C.H. Zeh'sche Buchhandlung, Nürnberg. <https://doi.org/10.5962/bhl.title.43744>
- Kovblyuk M.M., Otto S., Marusik Y.M. & Ponomarev A.V. 2012. Redescription of the Caucasian species *Geolycosa charitonovi* (Mcheidze, 1997) (Araneae: Lycosidae), with the first description of the male. *Bulletin of the British Arachnological Society* 15 (8): 245–252. <https://doi.org/10.13156/arac.2012.15.1.245>
- Kulczyński W. 1911. Fragmenta Arachnologica. XVI, XVII. *Bulletin international de l'Académie des Sciences de Cracovie* 1911: 12–75.
- Kumar S., Stecher G., Li M., Knyaz C. & Tamura K. 2018. MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution* 35 (6): 1547–1549. <https://doi.org/10.1093/molbev/msy096>
- Lendl A. 1887. A *Trochosa infernalis* (Motsch.) párzásáról és párzási szerveiről. Über die Begattung und die Copulationsorgane von *Trochosa infernalis* Motsch. *Természetráji Füzetek* 11 (1): 30–40, 51–57.

- Linnaeus C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus differentiis, synonymis, locis. Editio decima, reformata*. Holmiae.  
<https://doi.org/10.5962/bhl.title.542>
- Logunov D.V. 2020. On three species of *Hogna* Simon, 1885 (Aranei: Lycosidae) from the Near East and Central Asia. *Arthropoda Selecta* 29 (3): 349–360. <https://doi.org/10.15298/arthsel.29.3.08>
- Loksa I. 1972. Araneae II. *Fauna Hungariae* 109: 1–112.
- Magalhaes I.L.F. 2019. Spreadsheets to expedite taxonomic publications by automatic generation of morphological descriptions and specimen lists. *Zootaxa* 4624 (1): 147–150.  
<https://doi.org/10.11646/zootaxa.4624.1.12>
- Magalhaes I.L.F. 2019. Spreadsheets to expedite taxonomic publications by automatic generation of morphological descriptions and specimen lists. *Zootaxa* 4624 (1): 147–150.  
<https://doi.org/10.11646/zootaxa.4624.1.12>
- Mcheidze T.S. 1997. *Spiders of Georgia: Systematics, Ecology, Zoogeographic Review*. Tbilisi Univ.
- Miller F. 1971. Pavouci-Araneida. *Klíč zvěřeny ČSSR* 4: 51–306.
- Montgomery T.H. 1904. Descriptions of North American Araneae of the families Lycosidae and Pisauridae. *Proceedings of the Academy of Natural Sciences of Philadelphia* 56: 261–325.
- Motschulsky V. 1849. Note on two venomous spiders from southern Russia. *Bulletin of the Imperial Society of Naturalists in Moscow* 1: 289–290.
- Nadolny A.A. & Zamani A. 2020. A new species of wolf spiders of the genus *Lycosa* (Aranei: Lycosidae) from Iran. *Zoosystematica Rossica* 29 (2): 205–212. <https://doi.org/10.31610/zsr/2020.29.2.205>
- Nentwig W., Blick T., Gloor D., Jäger P. & Kropf C. 2019. Tackling taxonomic redundancy in spiders: the infraspecific spider taxa described by Embrik Strand (Arachnida: Araneae). *Arachnologische Mitteilungen* 58: 29–51. <https://doi.org/10.30963/aramit5809>
- Pavlíček T., Sharon D., Kravchenko V., Saaroni H. & Nevo E. 2003. Microclimatic interslope differences underlying biodiversity contrasts in “Evolution Canyon”, Mt. Karmel, Israel. *Israel Journal of Earth Sciences* 52 (1): 1–9.
- Piacentini L.N. & Ramírez M.J. 2019. Hunting the wolf: a molecular phylogeny of the wolf spiders (Araneae, Lycosidae). *Molecular Phylogenetics and Evolution* 136: 227–240.  
<https://doi.org/10.1016/j.ympev.2019.04.004>
- Planas E., Fernández-Montraveta C. & Ribera C. 2013. Molecular systematics of the wolf spider genus *Lycosa* (Araneae: Lycosidae) in the Western Mediterranean Basin. *Molecular Phylogenetics and Evolution* 67 (2): 414–428. <https://doi.org/10.1016/j.ympev.2013.02.006>
- Rambaut A. 2018. FigTree 1.4.4. Available from <http://tree.bio.ed.ac.uk/software/figtree/> [accessed 17 Jun. 2022].
- Roewer C.F. 1955. *Katalog der Araneae von 1758 bis 1940, bzw. 1954. 2. Band, Abt. a (Lycosaeformia, Dionycha [excl. Salticiformia]). 2. Band, Abt. b (Salticiformia, Cribellata) (Synonyma-Verzeichnis, Gesamtindex)*. Royal Belgian Institute of Natural Sciences, Brussels.
- Roewer C.F. 1959. Araneae Lycosaeformia II (Lycosidae). *Exploration du Parc National de l’Upemba, Mission G.F. de Witte* 55: 1–518.
- Schindelin J., Arganda-Carreras I., Frise E., Kaynig V., Longair M., Pietzsch T., Preibisch S., Rueden C., Saalfeld S., Schmid B., Tinevez J., White D.J., Hartenstein V., Eliceiri K., Tomancak P. & Cardona A. 2012. Fiji: an open-source platform for biological-image analysis. *Nature Methods* 9 (7): 676–682.  
<https://doi.org/10.1038/nmeth.2019>

- Shulov A. 1943. *On Spiders in Palestine*. Hebrew Teachers Association, Tel-Aviv. [Mimeo, in Hebrew.]
- Silva D. 1996. Species composition and community structure of Peruvian rainforest spiders: a case study from a seasonally inundated forest along the Samiria river. Proceedings of the XIII<sup>th</sup> Congress of Arachnology: Geneva, 3–8 September 1995. *Revue suisse de Zoologie* vol. hors série 2: 597–610. Available from <https://www.biodiversitylibrary.org/page/43628730> [accessed 17 Jun. 2022].
- Simon C., Frati F., Beckenbach A., Crespi B., Liu H. & Flook P. 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the entomological Society of America* 87 (6): 651–701
- Simon E. 1864. *Histoire Naturelle des Araignées (Aranéides)*. Librairie encyclopédique de Roret, Paris. <https://doi.org/10.5962/bhl.title.47654>
- Simon E. 1876. Études arachnologiques. 4<sup>e</sup> mémoire. VII. Révision des espèces européennes du groupe de la *Lycosa tarentula* Rossi. *Annales de la Société entomologique de France* (5) 6: 57–91.
- Steves I., Pinshow B., Berliner P. & Krasnov B.R. 2017. *The Possible Role of Trapdoors in Maintaining Favorable Thermal and Hydric Conditions in Spider Burrows*. PhD thesis, Ben-Gurion University of the Negev. Available from <https://primo.bgu.ac.il/> [accessed 17 Jun. 2022].
- Strand E. 1915. Dritte Mitteilung über Spinnen aus Palästina, gesammelt von Herrn Dr J. Aharoni. *Archiv für Naturgeschichte* 81 (A2): 134–171.
- Suchard M.A., Lemey P., Baele G., Ayres D.L., Drummond A.J. & Rambaut A. 2018. Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus Evolution* 4 (1): vey016. <https://doi.org/10.1093/ve/vey016>
- Thorell T. 1875. Descriptions of several European and North African spiders. *Kongliga Svenska Vetenskaps-Akademiens Handlingar* 13 (5): 1–204.
- Wallace H.K. 1942. A revision of the burrowing spiders of the genus *Geolycosa*. *The American Midland Naturalist* 27 (1): 1–62. <https://doi.org/10.2307/2421024>
- World Spider Catalog. 2022. *World Spider Catalog. Version 22.5*. Natural History Museum Bern. Available from <http://wsc.nmbe.ch> [accessed 9 Dec. 2021]. <https://doi.org/10.24436/2>
- Yom-Tov Y. & Tchernov E. 1988. *Zoogeography of Israel*. W. Junk.
- Yule G.U. 1925. II.—A mathematical theory of evolution, based on the conclusions of Dr. J.C. Willis, F.R.S. *Philosophical transactions of the Royal Society of London. Series B* 213 (402–410): 21–87. <https://doi.org/10.1098/rstb.1925.0002>
- Zamani A., Nadolny A.A., Esyunin S.L. & Marusik Y.M. 2021. New data on the spider fauna of Iran (Arachnida: Araneae), part VIII. *Zoosystematica Rossica* 30 (2): 279–297. <https://doi.org/10.31610/zsr/2021.30.2.279>
- Zonstein S. & Marusik Y.M. 2013. Checklist of the spiders (Araneae) of Israel. *Zootaxa* 3671 (1): 1–127. <https://doi.org/10.11646/zootaxa.3671.1.1>
- Zonstein S.L., Marusik Y.M. & Omelko M.M. 2015. A survey of spider taxa new to Israel (Arachnida: Araneae). *Zoology in the Middle East* 61 (4): 372–385. <https://doi.org/10.1080/09397140.2015.1095525>
- Zyuzin A.A. 1990. Studies on burrowing spiders of the family Lycosidae (Araneae). I. Preliminary data on structural and functional features. *Acta Zoologica Fennica* 190: 419–422.
- Zyuzin A.A. & Logunov D.V. 2000. New and little-known species of the Lycosidae from Azerbaijan, the Caucasus (Araneae, Lycosidae). *Bulletin of the British Arachnological Society* 11: 305–319.

*Manuscript received: 13 December 2021*

*Manuscript accepted: 1 June 2022*

*Published on: 26 July 2022*

*Topic editor: Tony Robillard*

*Section editor: Rudy Jocqué*

*Desk editor: Pepe Fernández*

Printed versions of all papers are also deposited in the libraries of the institutes that are members of the *EJT* consortium: Muséum national d'histoire naturelle, Paris, France; Meise Botanic Garden, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Real Jardín Botánico de Madrid CSIC, Spain; Leibniz Institute for the Analysis of Biodiversity Change, Bonn – Hamburg, Germany; National Museum, Prague, Czech Republic.