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26th European Congress of Arachnology

Arachnology

Israel 2011

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26th European Congress of Arachnology

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Israel 2011

4-8 September 2011

BEN-GURION UNIVERSITY OF THE NEGEV

BLAUSTEIN INSTITUTES FOR DESERT RESEARCH

Sede Boqer Campus, Midreshet Ben-Gurion, Israel

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Preface

The **26th European Congress of Arachnology** (4-8 September 2011) was held for the first time in Israel, and for the first time outside the European continent. The meeting was hosted by the Blaustein Institutes for Desert Research, at the Sede Boqer Campus of Ben-Gurion University of the Negev.

The Congress drew 130 participants and 11 accompanying persons from 27 countries from all continents. The countries with highest number of participants were Israel (30), Czech Republic (13), Germany (11), Taiwan (9), Denmark (8), France (8), and the USA (6). For many of these people it was their first visit to a desert, and their first time in Israel. Overall, 118 participants (more than 90 %) contributed presentations, with 80 oral presentations and 44 posters from 38 participants. Fifteen manuscripts were submitted for evaluation for publication in the current Proceedings volume, of which 11 were accepted for publication after peer review of two or three referees.

The Congress included four invited plenary talks, one in each of the four intense days of oral and poster presentations, six symposia and nine regular sessions covered all aspects of arachnid taxonomy, systematics, ecology, physiology, genetics, and behaviour.

Outstanding plenary talks were given by Lorenzo Prendini of the American Museum of Natural History (New York, USA), who opened with a presentation on the *Assembling the Scorpion Tree of Life*; on the second day, I-Min Tso of Tunghai University (Taiwan) lectured on *The Coloration of Spiders*; Sara Goodacre, University of Nottingham (England) on *Dispersal in Spiders* on day four; and on the last day, Maydianne Andrade of the University of Toronto (Canada) presented a talk titled *Sexual Selection and Ecology Shape Plastic Development & Behavior of Spiders*. The third day of the Congress was devoted to

excursions. Symposia were organized on specific themes: arachnid systematics in the 21st century, prey-specialized spiders: ecological and evolutionary mechanisms, behavioural ecology of foraging and signals, spiders in agro-ecosystems at local and landscape scales, mating behaviour and ecology, and social spiders.

Over half of the participants presenting their work were students. We were able to obtain a large number of contributed prizes for student presentations. Awards were given for 16 outstanding oral and poster presentations in three areas: Arachnology (The European Society of Arachnology (ESA), The Arachnologische Gesellschaft (AG) and Yale University Press (YUP)), Arachnid Ecology (Oxford University Press (OUP)) and Arachnid Behavioural Ecology (Cambridge University Press (CUP)). First prizes for oral presentations went to: Chao-Chia Wu (Taiwan, ESA), Boris Leroy (France, YUP), Miriam Schaider (Austria, AG), Christina Holm (Denmark, OUP) and Ren-Chung Chen (Taiwan, CUP). First prizes for posters were awarded to: Alberto Chiarle (Italy, AG), Chen-Pan Liao (Taiwan, OUP) and Mu-Yun Wang (England, CUP). Second prizes for talks were awarded to: Vera Opatova (Czech Rep., AG), Itai Opatovsky (Israel, OUP), Yong-Chao Su (USA, CUP) and Marija Majer (Denmark, CUP). Second prizes for posters went to: Olena Iaroshynska (Ukraine, AG), Huda Al-Beiruti (Israel, OUP) and Na'ama Berner-Aharon and Reut Berger-Tal (Israel, CUP).

A highly successful social program gave local flavour and excitement to the Congress. This included a reception on the edge of the Zin Canyon followed by the traditional Russian party, an Israeli light dinner followed by a night excursion in the desert, and half-day excursions to the desert springs Ein Aqev and Ein Avdat, to the

archaeological site of Byzantine Avdat, and to the agricultural R&D station at Ashalim. The excursion day ended with relaxation at a local spa and a picnic dinner at a local park. The gala dinner at Farkhan's Bedouin tent was accompanied by a performance of the renowned group, "Jaaman". Finally, a group of about 30 people remained after the Congress to enjoy a tour to the Dead Sea and Jerusalem.

The General Assembly of the ESA members closed the ECA27 meeting. The assembly discussed varied issues such as publication in the proceedings, renewing of the society web site, and the support of the "araneae – Spiders of Europe" Web Project. New elections to council were performed and several new members joined the council: Holger Frick, Efrat Gavish-Regev, Marco Isaia and Maria Chatzaki. Ferenc Samu was confirmed as president and Seppo Koponen and Søren Toft were designated as honorary members.

All of this could not have been arranged and executed without financial help from numerous sources both within and outside BGU and the hard work of all of our students and volunteers. We take the opportunity to thank all of these people, as well as the session chairs, judges of student presentations, the scientific committee, and members of the European Arachnological Society and of course all of the Congress participants.

The papers in this volume of Arachnologische Mitteilungen represent a sample of the topics discussed at the Congress: taxonomy, palaeontology, biogeography, ecology and behaviour. We thank all of the referees for their careful reviews. Last but not least, the proceedings volume would never have been published without the professional attention of Theo Blick, Oliver-D. Finch, Detlev Cordes, and Jason Dunlop.

Yael Lubin &
Efrat Gavish-Regev,
co-organizers

On the spider species described by L. Koch in 1882 from the Balearic Islands (Araneae)

Robert Bosmans & Johan Van Keer

Abstract: Examination of the L. Koch collection of the Zoological Museum in Berlin allows us to propose the following new synonyms and combinations: *Erigone marina* L. Koch, 1882 = *Oedothorax fuscus* (Blackwall, 1834) **n. syn.**; *Theridion elimatum* L. Koch, 1882 = *Enoplognatha diversa* (Blackwall, 1859) **n. syn.**; *Liocranum variabilis* Wunderlich, 2008 = *Zora inornata* L. Koch, 1882 **n. syn.** = *Liocranum inornatum* **n. comb.**; *Lycosa perspicax* L. Koch, 1882 = *Arctosa fulvolineata* (Lucas, 1846) **n. syn.**; *Alopecosella* Roewer, 1960 = *Arctosa* C. L. Koch, 1847 **n. syn.**; *Lycosa subhirsuta* L. Koch, 1882 = *Arctosa lacustris* (Simon, 1876) **n. syn.**; *Philodromus vegetus* L. Koch, 1882 = *Thanatus vulgaris* Simon, 1870 **n. syn.**; *Ozyptila bicuspis* Simon, 1932 = *Ozyptila furcula* L. Koch, 1882 **n. syn.**; *Haplodrassus maroccanus* Denis, 1956 = *Drassus parvulus* L. Koch, 1882 **n. syn.** = *Haplodrassus parvicorpus* (Roewer, 1951) **n. comb.** (replacement name); *Zelotes ruscinensis* Simon, 1914 = *Zelotes semirufa* (L. Koch, 1882) **n. syn.**; *Phlegra simoni* L. Koch, 1882 = *Phlegra bresnieri* Lucas, 1846 **n. syn.**; *Trochosula conspersa* (L. Koch, 1882), *Lycorma fraisnei* (L. Koch, 1882), *Lycorma insulana* (L. Koch, 1882), *Arctosa misella* (L. Koch, 1992) and *Pirata simplex* (L. Koch, 1882) are all retransferred to their original genus *Lycosa* **stat. rev.** *Cheiracanthium occidentale* L. Koch, 1882, *Ozyptila furcula* L. Koch, 1882 and *Zelotes callidus* (Simon, 1878) are redescribed.

Key words: Balearic Islands, L. Koch, redescriptions, spiders, synonymies

In recent years, the number of descriptions of new species has increased considerably, greatly expanding the knowledge of spiders. However, it is also very important to revise or redescribe species from the 19th century. Some of these older descriptions are incomplete and not accompanied by illustrations, but others have adequate descriptions with excellent figures. One of the papers that has been completely forgotten is 'Zoologische Ergebnisse von Excursionen auf den Balearen. II. Arachniden und Myriapoden' by L. KOCH (1882). The author described 28 new species of spiders in it, of which only ten have been fully redescribed, which means that 18 of them are left as poorly known species.

Material and methods

Type material of nine species could be loaned from the Berlin Museum (possible other locations of type material in London or Vienna were not checked). If the material was not present, the descriptions and figures were carefully examined and compared with similar or related species from the Mediterranean.

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The reference material mentioned in the present paper is part of the collection of the first author. Specimens were examined and illustrated using a Wild M5 stereomicroscope. Further details were studied using an Olympus CH-2 stereoscopic microscope with a drawing tube. Left structures are depicted. Male palps were detached and transferred to glycerol for examination under the microscope. Female genitalia were excised using sharpened needles. These were transferred to clove oil for examination under the microscope. Later, palps and epigynes were returned to 70% ethanol.

The following abbreviations are used in the text:
CRB: Collection Robert Bosmans;
MNHNP: Muséum national d'Histoire naturelle, Paris;
ZMB: Zoologisches Museum Berlin

Comments on the species described by L. Koch

Many authors of the 19th or the beginning of the 20th century, for example Thorell and Strand, did not present figures at all, so these species cannot be recognized without examination of the type material. KOCH (1882) reported twenty-eight new spider species from the Balearic Islands. His descriptions are very accurate and were accompanied by excellent figures, which allow the recognition of details in the palpal and epigynal structures. Careful examination of the figures should have allowed identification of several species, especially when compared with

other material from the Mediterranean region. It is therefore surprising that L. Koch's paper has been neglected by previous authors. Of the twenty-eight described species, only ten have subsequently been studied. Out of these ten redescribed species, seven appeared to be synonyms, and only *Iberesia brauni*, *Zelotes semirufus* and *Z. flagellans* remain valid. The ten species concerned are listed in Tab. 1.

Twelve of the eighteen remaining species have received new names by preoccupation, were transferred to other genera or were declared *nomina dubia*. However, none of them were redescribed. The other species have never been subsequently cited, except in catalogues. These species are listed in Table 2.

Taxonomy

Family Dysderidae
Dysdera mordax L. Koch, 1882 (Fig. 17)
  Dysdera mordax L. Koch, 1882: 640, pl. 20, fig. 20.

Type material
Holotype male of *Dysdera mordax* from Spain, Baleares, Mallorca, Palma, beginning of May, Schaufuss leg. (ZMB 7905); examined, but both palps are absent.

Comments
In absence of the palps, a complete new diagnosis of this species cannot be given. In Mallorca, *Dysdera crocata* C. L. Koch, 1838 is the commonest *Dysdera* species (authors' personal observations) and the holotype of *Dysdera mordax* was compared with this species. In *D. mordax*, the rugosity of the prosoma and the sternum is different and the colour is more burgundy red. Spination of the holotype may be incomplete, but no spines are observed on legs I and II (probably lost), leg IV has 2 basal spines on the femora, legs III–IV have 2 pairs of lateral spines and 1 pair of ventral spines on the tibia, and several spines on the metatarsi. In *D. crocata* tibiae III–IV have fewer spines. For the male palp we must rely on the figure of KOCH (1882; see Fig. 1). The bulb is similar to that of *Dysdera crocata*, but more slender, narrowing terminally and more pointed. We consider it a valid species, but topotypic material is needed for a complete redescription.

Distribution
So far, the species is an endemic to Mallorca.

Family Theridiidae
Enoplognatha diversa (Blackwall, 1859) (Figs 2-3)
  Theridion elimatum L. Koch, 1882: 630, pl. 20, fig. 8; **new synonymy.**

Type material
Holotype female of *Theridion elimatum* from Spain, Baleares, Mallorca, Palma Riera, 22 April, Schaufuss leg.; not examined, unavailable in ZMB.

Comments
According to KOCH (1882), the prosoma of this species is yellowish brown, the abdomen grey brown

Tab. 1: List of species described by L. KOCH (1882) which have already been redescribed

Koch's name	Current name	Author(s)
Family Nemesiidae		
Nemesia brauni L. Koch, 1882	*Iberesia brauni* (L. Koch, 1882)	DECAE & CARDOSO (2006)
Family Theridiidae		
Theridion mansuetum L. Koch, 1882	*Enoplognatha mandibularis* (Lucas, 1846)	BOSMANS & VAN KEER (1999)
Meta schaufussi L. Koch, 1882	*Enoplognatha mordax* (Thorell, 1875)	WUNDERLICH in: MERRETT & SNAZELL (1975)
Family Araneidae		
Singa nigrofasciata L. Koch, 1882	*Hypsosinga albovittata* (Westring, 1851)	DENIS (1952)
Epeira mimula L. Koch, 1882	*Neoscona adianta* (Walckenaer, 1802)	ROEWER (1942)
Family Lycosidae		
Lycosa subterranea L. Koch, 1882	*Arctosa fulvolineata* (Lucas, 1846)	LUGETTI & TONGIORGI (1965)
Pardosa venatica L. Koch, 1882	*Pardosa cribrata* Simon, 1876	WUNDERLICH (1984)
Family Corinnidae		
Trachelas flavipes L. Koch, 1882	*Paratrachelas maculatus* (Thorell, 1875)	BOSSELAERS et al. (2009)
Family Gnaphosidae		
Prosthesima flagellans L. Koch, 1882	*Zelotes flagellans* (L. Koch, 1882)	SENGLET (2011)
Prosthesima semirufa L. Koch, 1882	*Zelotes semirufus* (L. Koch, 1882)	SENGLET (2011)

Tab. 2. List of species that have received new names by preoccupation, were transferred to other genera, were declared *nomina dubia* or were never mentioned again in literature

Koch's name	Current name	Action
Family Dysderidae		
Dysdera mordax L. Koch, 1882	*Dysdera mordax* L. Koch, 1882	None
Family Theridiidae		
Theridion elimatum L. Koch, 1882	*Theridion elimatum* L. Koch, 1882	None
Family Linyphiidae		
Erigone marina L. Koch, 1882	*Erigone marina* L. Koch, 1882	None
Family Zoridae		
Zora inornata L. Koch, 1882	*Zora inornata* L. Koch, 1882	Nomen dubium (URONES 2005)
Family Miturgidae		
Cheiracanthium occidentale L. Koch, 1882	*Cheiracanthium occidentale* L. Koch, 1882	None
Family Lycosidae		
Lycosa perspicax L. Koch, 1882	*Alopecosella perspicax* (L. Koch, 1882)	Transfer by ROEWER (1955)
Lycosa subhirsuta L. Koch, 1882	*Lycosa subhirsutella* Roewer, 1955, but transferred back to *Lycosa subhirsuta* in ROEWER (1960)	Replacement name, later transferred back
Lycosa conspersa L. Koch, 1882	*Trochosula conspersa* (L. Koch, 1882)	Transfer by ROEWER (1955)
Lycosa fraissei L. Koch, 1882	*Lycorma fraissei* (L. Koch, 1882)	Transfer by ROEWER (1955)
Lycosa insulana L. Koch, 1882	*Lycorma insulana* (L. Koch, 1882)	Transfer by ROEWER (1955)
Lycosa misella L. Koch, 1882	*Arctosa misella* (L. Koch, 1882)	Transfer by ROEWER (1955)
Lycosa simplex L. Koch, 1882	*Pirata simplex* (L. Koch, 1882)	Transfer by ROEWER (1955)
Pardosa tenuipes L. Koch, 1882	*Pardosa tenuipes* L. Koch, 1882	None
Family Philodromidae		
Philodromus vegetus L. Koch, 1882	*Philodromus vegetus* L. Koch, 1882	Nomen dubium (BRAUN 1965)
Family Thomisidae		
Ozyptila furcula L. Koch, 1882	*Ozyptila furcula* L. Koch, 1882	None
Family Gnaphosidae		
Drassus parvulus L. Koch, 1882	*Drassodes parvicorpus* Roewer, 1955	Replacement name
Prosthesima semirufa L. Koch, 1882	*Zelotes semirufus* (L. Koch, 1882)	Redescription (SENGLET 2011)
Prosthesima plumigera L. Koch, 1882	*Zelotes plumiger* (L. Koch, 1882)	Transfer by ROEWER (1954)
Family Salticidae		
Phlegra simoni L. Koch, 1882	*Phlegra simoni* L. Koch, 1882	None

with a dark folium with white spots and bordered with white, ventrally with two parallel white stripes, legs yellowish brown. The description of such a folium points clearly in the direction of *Enoplognatha* species of the *diversa* or *mandibularis* group. Koch's figure of the epigyne provides further details that point clearly in the direction of *E. diversa* (compare Figs 2-3), the most common *Enoplognatha* species in Spain (BOSMANS & VAN KEER 1999). *Theridion elimatum* L.

Koch, 1882 is therefore considered a junior synonym of *Enoplognatha diversa* (Blackwall, 1859). It should be noted here that another *Theridion* species in Koch's paper (*Theridion mansuetum*) appeared to be a junior synonym of *Enoplognatha mandibularis* (Lucas, 1846), see BOSMANS & VAN KEER (1999).

Distribution

Mediterranean, from the Iberian Peninsula and Morocco in the west, to Crete in the east.
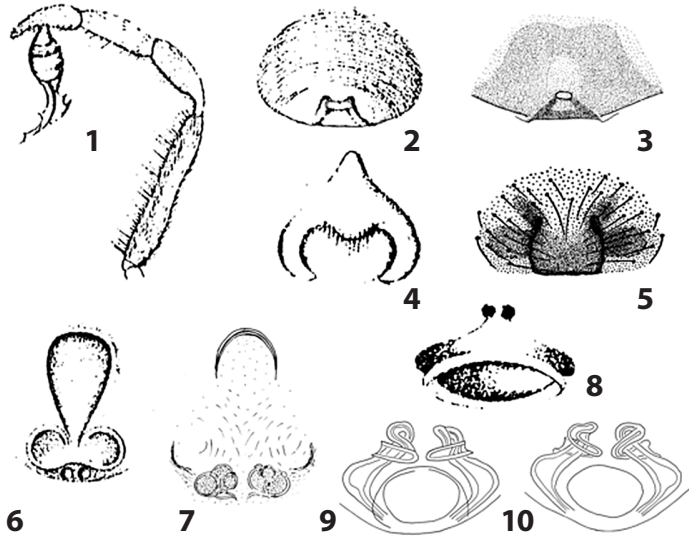
Figs. 1-10: Fig. 1. Male palp of *Dysdera mordax* L. Koch, 1882 in L. KOCH (1882). Figs. 2-3: *Enoplognatha diversa* (Blackwall, 1859) 2. Epigyne of *Theridion elimatum* in KOCH (1882); 3. Epigyne of *Enoplognatha diversa* in BOSMANS & VAN KEER (1999). Figs. 4-5: *Oedothorax fuscus* (Blackwall, 1834). 4. Epigyne of *Erigone marina* in KOCH (1882). 5. Epigyne of *Oedothorax fuscus* in LOCKET & MILLIDGE (1953). Figs. 6-7: *Liocranum inornatum* (L. Koch, 1882). 6. Epigyne of *Zora inornata* in KOCH (1882); 7. Epigyne of *Liocranum variabilis* in WUNDERLICH (2008). Figs. 8-10: *Cheiracanthium occidentale* L. Koch, 1882. 8. Epigyne of *Cheiracanthium occidentale* in KOCH (1882). 9. Vulva, ventral view; 10. Idem, dorsal view.

Family Linyphiidae

Oedothorax fuscus (Blackwall, 1834) (Figs. 4-5)

Erigone marina L. Koch, 1882: 629, pl. 20, fig. 7 (descr. female); **new synonymy.**

Type material

Holotype female of *Erigone marina* from Spain, Baleares, Mallorca, Soller, mid-April, Schaufuss leg. (ZMB 7915); examined.

Comments

Examination of the holotype clearly shows that this species is identical to *Oedothorax fuscus* (Blackwall, 1834) and thus *Erigone marina* becomes a junior synonym of that species. Koch's drawing of the epigyne (Fig. 4) is somewhat confusing but shows clearly the two typical curved lateral folds as in Fig. 5 taken from LOCKET & MILLIDGE (1953).

Distribution

Europe, North Africa, Azores, European part of Russia.

Family Liocranidae

Liocranum inornatum (L. Koch, 1882) new combination (Figs 6-7)

Zora inornata L. Koch, 1882: 639, pl. 20, fig. 19 (descr. female).

Liocranum variabilis Wunderlich, 2008: 506, figs 42-46 (descr. male, female); **new synonymy.**

Type material

Holotype female of *Zora inornata* from Spain, Baleares, Mallorca, Miramare, IV.1866, Schaufuss leg. (ZMB 7920); examined.

Comparative material examined

SPAIN. Caceres: Plasencia, 1 female of *Liocranum majus* Simon, 1878, IV.1990, P. Poot leg. (CRB).

Comments

From Koch's drawing of the epigyne (1882, fig. 19) it is evident that this species does not belong in the genus *Zora*. The figure shows a large, anterior pocket and two smaller lateral pockets (Fig. 6). Examination of the specimen shows it to belong in the Liocranidae and that it is identical to *Liocranum variabilis*, only recently described from Mallorca by WUNDERLICH (2008), see Fig. 7. This latter species thus becomes a junior synonym. *Liocranum inornatum* is closely related to *L. majus* Simon, 1878, recently redescribed by LEDOUX (2008). This author confirmed the synonymy of *L. majus* with *Liocranum apertum* Denis, 1954, *L. pallidulum* Simon, 1878 and *L. segmentatum* Simon, 1878. According to WUNDERLICH (2008), the helmet-like structure is larger in *L. major*.

Distribution

So far, the species is an endemic to Mallorca.

Family Miturgidae

Cheiracanthium occidentale L. Koch, 1882 (Figs. 8-10)

Cheiracanthium occidentale L. Koch, 1882: 637, pl. 20, fig. 16 (descr. female).

Type material

Holotype female of *Cheiracanthium occidentale* from Spain, Baleares, Minorca, Mahon, 18.V.1866, Schaufuss leg. (ZMB 7929); examined.

Comments

KOCH's figure 16 (1882) clearly shows a *Cheiracanthium*-like epigyne (Fig. 8), but does not give enough diagnostic characters for identification. A redescription of the epigyne and vulva is therefore given here. According to the author, the species is related to *Cheiracanthium letochae* L. Koch, 1876 (= *C. elegans* Thorell, 1875). The epigyne has a median depression with an interior margin and is wider than

long. The spermathecae are relatively small, only 1/3 of the width of the depression. The copulatory openings are situated antero-laterally of the depression and the sperm ducts make three coils to the elongated spermathecae (Figs 9-10). In the literature, no species with such a vulva could be found and hence the species is considered valid.

Distribution

Only known from the type locality.

Family Lycosidae

Arctosa fulvolineata (Lucas, 1846) (Figs 11-12)

Lycosa perspicax L. Koch, 1882: 658, pl. 21, fig. 32 (descr. female); **new synonymy.**

Alopecosella perspicax; Roewer, 1955: 225.

Type material

Holotype female of *Lycosa perspicax* from Spain, Baleares, Mallorca, Soller valley, mid-April, Schaufuss leg. (ZMB 7910); examined.

Comparative material examined

FRANCE. Aude: Gruissan, N. les Pujots (N 43°06'30" E 3°3'28"), 3m, 1 female, litter in salt marsh, 1.IV.1980, R. Bosmans leg. (CRB).

Comments

The holotype female has an intact epigyne and on examination it can immediately be recognised as *Arctosa fulvolineata*. *Lycosa perspicax* thus becomes a junior synonym. Koch's figure is sketchy (Fig. 7) but shows the typical antero-median, triangular septum of *A. fulvolineata* (Fig. 8, taken from KNÜLLE 1959). ROEWER (1955) created the new genus *Alopecosella* for this species. Since the type of the genus *Alopecosella* is here transferred to *Arctosa*, the genus *Alopecosella* becomes a junior synonym of *Arctosa*. The only other species of the genus *Alopecosella*, *A. pelusiaca* (Audouin, 1826) has to be returned to *Alopecosa*, where it was placed by CAPORIACCO (1936).

Distribution

Western Europe, Iberian Peninsula, Italy, south of France and the Maghreb.

Arctosa lacustris (Simon, 1876) (Figs 13-16)

Lycosa subhirsuta L. Koch, 1882: 653, pl. 21, figs 28-29 (descr. male, female); **new synonymy.**

Alopecosa subhirsutella Roewer, 1955: 221 (replacement name); **new synonymy.**

Lycosa subhirsuta; Roewer, 1960: 874 (transferred back, without arguments).

Type material

Lectotype male and paralectotype female of *Lycosa subhirsuta* from Spain, Baleares, Soller valley, mid-April and Miramar, May, Schaufuss leg. (ZMB 7911); examined.

Comparative material examined

SPAIN. Caceres: Plasencia (N 40°1'52" E 6°5'18"), 525m, 1 male 1 female, IV.1990, P. Poot leg. (CRB).

Comments

The holotype male has only one palp left with a tegular apophysis as in *Arctosa lacustris*. The female has an intact epigyne with a broad median septum, as clearly shown in Koch's figure 29 (1882), corresponding well with the epigyne of *A. lacustris* (compare Figs 13, 15 with Figs 14, 16 (taken from KNÜLLE 1959). *Lycosa subhirsuta* and its replacement name *Alopecosa subhirsutella* thus become junior synonyms of *Arctosa lacustris*.

Distribution

Mediterranean, Canary Islands.

Lycosa conspersa L. Koch, 1882 stat. rev. (Fig. 17)

Lycosa conspersa L. Koch, 1882: 661 pl. 21, fig. 33 (descr. female).

Trochosula conspersa; Roewer, 1955: 304.

Type material

Type series of two females of *Lycosa conspersa* from Spain, Baleares, Mallorca, Ses Prat de San Jordi, end April, and Soller, mid-May, Schaufuss leg. (ZMB 7912); examined. The two females belong to different species. One of the females is *Arctosa fulvolineata*, the other one has an epigyne corresponding to the original drawing by KOCH (1882) and is selected here as the lectotype.

Comments

This species has not been mentioned since the original description, with the exception of ROEWER'S (1955) transfer to the genus *Trochosula*, without any justification. KOCH's figure 33 (1882) of the epigyne resembles the epigyne of *Hogna radiata* (Latreille, 1817), a widespread species in the Mediterranean. Like many large lycosids in the Mediterranean, this species complex is in need of revision and a conclusion about synonymy has to be postponed. Material from Mallorca is needed to resolve the situation. This is also the case for three other *Lycosa* species described by L. Koch from Mallorca (see below): *Lycosa fraissei*, *L. insulana* and *L. simplex*. They are all large species and Koch's figures 33-36 all show the same type of epigyne (see Figs 17-20). ROEWER (1955) transferred these species (without further justification) to three different genera: *Trochosula*, *Lycorma* and *Pirata*. To facilitate future studies, we consider it better to return them to their original genus. Topotypic material may help solve the identity of these problematic species.

Distribution

The type locality on Mallorca.

Lycosa fraissei L. Koch, 1882 stat. rev. (Fig. 18)

Lycosa fraissei L. Koch, 1882: 666, pl. 21, fig. 36 (descr. male).

Lycorma fraissei; Roewer, 1955: 265 (transfer).

Type material

Holotype male of *Lycosa fraissei* from Spain, Baleares, Mallorca, Fraisse leg.; not examined, unavailable in ZMB.

Comments

A large lycosid of 19 mm total length. The type material is not available. See comments under *Lycosa conspersa*.

Distribution

The type locality on Mallorca.

Lycosa insulana L. Koch, 1882 stat. rev. (Fig. 19)

Lycosa insulana L. Koch, 1882: 664, pl. 21, fig. 35 (descr. female).

Lycorma insulana; Roewer, 1955: 265 (transfer).

Type material

Holotype female of *Lycosa insulana* from Spain, Baleares, Mallorca, Fraisse leg.; not examined, unavailable in ZMB.

Comments

A large lycosid of 16 mm total length. The type material could not be examined. See comments under *Lycosa conspersa*.

Distribution

The type locality on Mallorca.

Lycosa misella L. Koch, 1882 nomen dubium

Lycosa misella L. Koch, 1882: 660 (descr. juvenile).

Arctosa misella; Roewer, 1955: 226 (transfer).

Type material

Juvenile holotype of *Lycosa misella* from Spain, Baleares, Ses Prat de Jordi, end April, Schaufuss leg., not examined, unavailable in ZMB.

Comments

The holotype is a juvenile specimen and its status is unclear. *Lycosa misella* is therefore a *nomen dubium*.

Distribution

The type locality on Mallorca.

Lycosa simplex L. Koch, 1882 stat. rev. (Fig. 20)

Lycosa simplex L. Koch, 1882: 663, pl. 21, fig. 34 (descr. female).
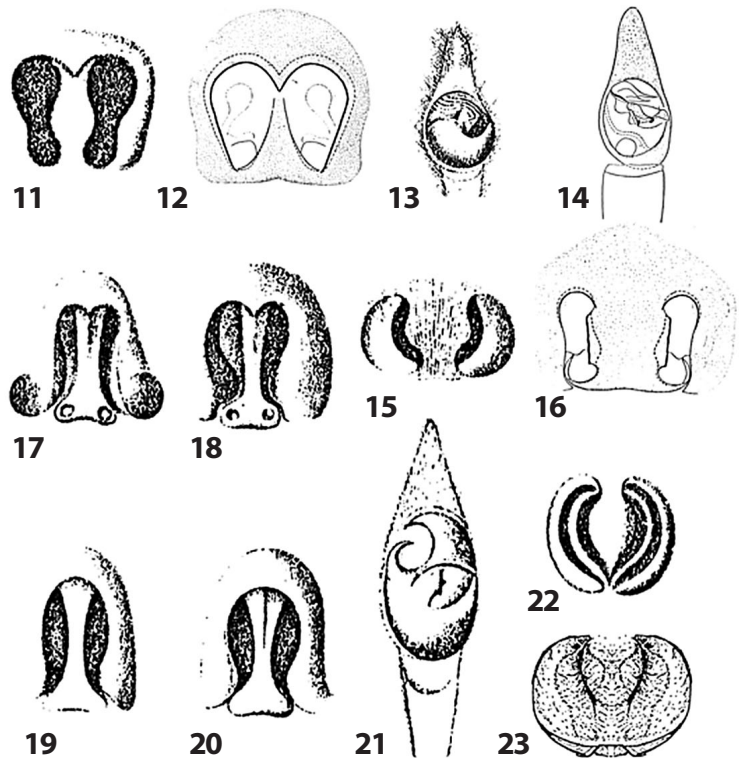
Figs. 11-23. Figs. 11-12: *Arctosa fulvolineata* (Lucas, 1846). 11. Epigyne of *Lycosa perspicax* in Koch (1882); 12. Epigyne of *Arctosa fulvolineata* in Knülle (1959). Figs 13-16. *Arctosa lacustris* (Simon, 1876). 13. Male palp of *Lycosa subhirsuta* in Koch (1882); 14. Male palp of *Arctosa lacustris* in Knülle (1959); 15. Epigyne of *Lycosa subhirsuta* in Koch (1882); 16. Epigyne of *Arctosa lacustris* in Knülle (1959). Fig. 17. Epigyne of *Lycosa conspersa* in Koch (1882). Fig. 18. Epigyne of *Lycosa fraisei* in Koch (1882). Fig. 19. Epigyne of *Lycosa insulana* in Koch (1882). Fig. 20. Epigyne of *Lycosa simplex* in Koch (1882). Fig. 21. Male palp of *Pardosa tenuipes* in Koch (1882). Figs 22-23. *Thanatus vulgaris* Simon, 1870. 22. Epigyne of *Philodromus vegetus* in Koch (1882). 23. Epigyne of *Thanatus vulgaris* in Szita & Samu (2000).

Pirata simplex; Roewer, 1955: 284.

Type material

Holotype male of *Lycosa simplex* Spain, Baleares, Palma city moats, begin May, and Ses Prat de Jordi, beginning of May, Schaufuss leg.; not examined, unavailable in ZMB.

Comments

The holotype could not be examined. According to the original description by Koch (1882), it is a large species (23 mm) suggesting a lycosid genus encompassing larger species, such as *Hogna*, *Lycorma* or *Lycosa*. Koch's (1882) figure of the epigyne does not look like a *Pirata* epigyne at all and the transfer proposed by Roewer (1955) seems a random choice. See also comments under *Lycosa conspersa*.

Distribution

The type locality on Mallorca.

Pardosa tenuipes L. Koch, 1882 (Fig. 21)

Pardosa tenuipes L. Koch, 1882: 649, pl. 21, fig. 24 (descr. male).

Pardosops tenuipes; Roewer, 1955: 197.

Pardosa tenuipes; Tongiorgi, 1966: 351.

Type material

Holotype male of *Pardosa tenuipes* from Spain, Baleares, Ses Prat de Jordi, mid-May, Schaufuss leg.; not examined, unavailable in ZMB.

Comments

ROEWER (1955) created the genus *Pardosops* for this and other species, but TONGIORGI (1966) synonymised it with *Pardosa*. The holotype male could not be examined. KOCH's (1882) figure 24 offers no indication of its affinities (see Fig. 21). Topotypic material is needed to clarify its systematic position.

Distribution

The type locality on Mallorca.

Family Philodromidae

Thanatus vulgaris Simon, 1870 (Figs 22-23)

Philodromus vegetus L. Koch, 1882: 645, pl. 20, fig. 22; **new synonymy.**

Type material

Holotype female of *Philodromus vegetus* from Spain, Baleares, Mallorca, Miramare, begin May, Schaufuss leg.; not examined, unavailable in ZMB.

Comments

Figure 22 in KOCH (1882) shows a rounded epigynal plate with some concentric circles, typical for the epigyne of the common *Thanatus vulgaris* (compare Figs 22 and 23). This species has no less than eight synonyms in the Mediterranean region (LEVY 1977) and there is no doubt that *Philodromus vegetus* is yet another one.

Distribution

Circum-mediterranean.

Family Thomisidae

Ozyptila furcula L. Koch, 1882 (Figs 24-26)

Ozyptila furcula L. Koch, 1882: 648, pl. 21, fig. 23.

Ozyptila bicuspis Simon, 1932: 873, figs 1186-1187, 1208; **new synonymy.**

Type material

Holotype male of *Ozyptila furcula* from Spain, Baleares, Mallorca, Ses Prat de San Jordi, end of April, Schaufuss leg.; not examined, unavailable in ZMB.

Comparative material examined

SPAIN. Jaen: Ribera Baja (N 37°26'58" E 3°50'5"), 870m, 1 male, litter in *Populus* forest, 6.IV.1997, R. Bosmans leg. (CRB).

Comments

The type material of this species is not available, but KOCH's figure 21 (1882) allows a positive identification with respect to the tegular apophysis of specimens collected by us in Spain and North Africa. The tegulum has an oblique banana-shaped tegular apophysis with two postero-median concavities (compare Figs 24 and 25). Such an apophysis exists in three *Ozyptila* species occurring in this region: *O. pauxilla* Simon, 1870, *O. perplexa* Simon, 1875 and *O. bicuspis* Simon, 1932. Koch's species also has two postero-median incisions, and these are absent in *O. pauxilla* and *O. perplexa*. We consider *O. furcula* and *O. biscuspis* the same species and *O. bicuspis* Simon, 1932 becomes a junior synonym of *O. furcula* L. Koch, 1882. *Ozyptila pauxilla* and *O. perplexa* will be redescribed in a separate paper.

Distribution

The species is currently known from the south of France and from Spain.

Family Gnaphosidae

Haplodrassus parvicorpus (Roewer, 1951) new combination (Figs 27-28)

Drassus parvulus L. Koch, 1882: 632, pl. 20, fig. 10-11 (descr. male).

Drassus parvicorpus Roewer, 1951: 443 (replacement name).

Haplodrassus maroccanus Denis, 1956: 196, fig. 4-6; **new synonymy** (here removed from the synonymy of *H. dalmatensis* (L. Koch, 1866)).

Type material

Holotype male of *Drassus parvulus* from Spain, Baleares, Mallorca, Riera near Palma, 22.IV.1882, Schaufuss leg. (ZMB 7913); examined.

Type series of *Haplodrassus maroccanus* from Morocco, Pr. Taroudant, Ouled Teima (= Houara), according to DENIS (1956) composed of 1 male 3 subadult males, 1 female 3 subadult females, 21.II.1954 and 1 subadult female from Amzou; not examined, not found in the MNHNP.

Comparative material examined

SPAIN. Cadiz: Tarifa (N 36°0'50" E 5°36'25"), 2 males 5 females, IV.1992, P. Poot leg. (CRB).

Comments

Drassus parvulus was described by KOCH (1882). Being preoccupied by *Drassus parvulus* Lucas, 1846, ROEWER (1951) offered *Drassus parvicorpus* as a replacement name. The species has never been cited since.

According to KOCH (1882), this species is related to *Drassus minusculus* (= *Haplodrassus dalmatensis*) and differs by the more arched prosoma with a black margin, and the disposition of the eyes, with the PM not touching and the AM separated by nearly their diameter. These characters are too variable in *Haplodrassus*

to distinguish species, but Koch's figure 10 (1882) shows a male palp with a large, subterminal tooth on the tegular apophysis, and his figure 11 shows a palpal tibia with an apophysis as long as wide (Fig. 27). The male palps of the holotype male are both present and in good condition (Fig. 28). Examination shows that they are identical to the palps of *Haplodrassus maroccanus*, described from Morocco by DENIS (1956) and occurring all over the south-western Mediterranean (unpublished data). In *H. dalmatensis*, the tegular apophysis has only a small subterminal tooth, and the tibial apophysis is shorter than wide; thus there are sufficient diagnostic characters to separate the species. *Haplodrassus maroccanus* Denis, 1956 becomes a junior synonym of *H. parvicorpus* (Roewer, 1951 **n. comb.**). The synonymy of *H. maroccanus* with *H. dalmatensis*, proposed by LEVY (2004) is rejected. The species will be fully redescribed in a further paper.

Distribution

Mallorca and Morocco.

Zelotes callidus (Simon, 1878) (Figs 29-35)

Prosthesima callida Simon, 1878: 91 (descr. male, non female = *Z. caucasius*).

Prosthesima semirufa L. Koch, 1882: 636, pl. 20, fig 15 (descr. female); **new synonymy.**

Zelotes callidus; Simon, 1882: 37(descr. male, non female); Simon, 1914: 219 (descr. male, non female).

Zelotes ruscinensis Simon, 1914: 157, 169, fig. 259, 346 (descr. male, female); Senglet, 2004: 104, figs 47-50 (descr. male, female); **new synonymy.**

Zelotes circumspectus; Denis 1935: 117 (descr. female); misidentification.

Zelotes lugens Denis 1941: 162 (correction of the citation of *Z. circumspectus* from 1935); Di Franco 1997: 258 (synonymy by SENGLET 2004).

Zelotes adolescentulus Denis 1952: 118 (synonymy by SENGLET 2004).

Zelotes massiliensis Soyer, 1967: 278 (synonymy by SENGLET 2004).

Zelotes semirufus; Senglet, 2011: 518, figs 2-17, 74 (synonym with *Z. ruscinensis*).

Type material

Holotype male of *Prosthesima* (= *Zelotes*) *callida* from Corsica, Ajaccio (MNHNP, not examined).

Holotype female of *Prosthesima* (= *Zelotes*) *semirufa* from Spain, Baleares, Menorca, Braun leg.; not examined, unavailable in ZMB.

Holotype female of *Zelotes lugens* from France, Var, Vallon de Port Cros (MNHNP, examined).

Holotype male of *Zelotes adolescentulus* from Morocco, Skhirat (MNHNP, examined).

Comparative material examined

SPAIN. Caceres: Torrejon el Rubio (N 39°46'15" W

6°4'12"), 270m, 4 males 2 females, pitfalls, 15.VII-23. VIII.1996, U. Stengele leg. (CRB); Talavan, Finca el Baldio (N 39°43'12" W 6°19'4"), 370m, 10 males 2 females, pitfalls, 10.VII-5.IX.1996, U. Stengele leg. (CRB). Granada: Santa Fé (N 37°11'31" W 3°45'17"), 700m, 1 female, litter in irrigated *Populus* forest, 9.VIII.1991, R. Bosmans leg. (CRB). Malaga: Coin, along Rio Grande N 36°41'29" W 4°48'22"), 110m, 1 female, stones in grassland, 15.VII.1991, R. Bosmans leg. (CRB). Murcia: Puerto Lumbreras (N 37°29'37" W 1°51'9"), 530m, 1 female, under stone, 14.VII.1991, R. Bosmans leg. (CRB). – ALGERIA. Oran: Mers el Hadjad (N 35°47'52" W 0°9'51"), 2 males, litter in garden, IX.1988, R. Bosmans leg. (CRB). – MOROCCO. Essaouira: Ounara E. (N 31° 32'33" W 9°30'47"), 250m, 1 male, stones in garganier steppe, 8.VII.1999, R. Bosmans leg. (CRB).

Comments

The discovery of large series of *Zelotes callidus* in central Spain – including males and females – allows us to resolve a complicated case of synonymy. The males from Central Spain could be identified as *Zelotes callidus*, based on the original figures of SIMON (1878, fig. 23; 1914, figs 297-299); a species originally described from Corsica. Characteristic are the two anterior teeth in the bulb, compare Figs 32-33. The females did not correspond with Simon's figures of *Z. callidus*, which corroborates the observation of SENGLET (2004) that the females described as *Z. callidus* by SIMON (1878, fig. 24; 1914, fig. 354), JÉZÉQUEL (1962, fig. 29) and LEDOUX (1972, fig. 1) all illustrate the epigyne or vulva of *Zelotes caucasius* (L. Koch, 1866).

The females from Central Spain could be identified as *Zelotes semirufus* (L. Koch, 1882) described from Menorca. KOCH's figure of *Zelotes semirufus* (Fig. 29) shows an epigyne with a median plate that is slightly longer than wide, with an open posterior margin, and comparable position of the rounded spermathecae (Fig. 30).

Perhaps the mismatching of the sexes of *Z. callidus* confused Simon in 1878, because in 1914, he described the species again from the south of France as *Z. ruscinensis*. Recently, this latter species was redescribed by SENGLET (2004); who further pointed out that *Zelotes adolescentulus* Denis, 1952, *Z. lugens* Denis, 1941 and *Z massiliensis* Soyer, 1967 are its junior synonyms. All of these taxa now enter into the synonymy of *Zelotes callidus*.

Distribution

Recorded from Morocco, Algeria, Spain, Portugal, France and Italy. DRENSKY (1915) cited the species erroneously from Bulgaria; it was in fact *Zelotes caucasius*.

Zelotes plumiger (L. Koch, 1882)
(Fig. 36)

Prosthesima plumigera L. Koch, 1882: 630, pl. 20, figs 12, 13.

Type material

Holotype male of *Prosthesima* (= *Zelotes*) *plumigera* from Spain, Baleares, Mallorca, Ses Prat de San Jordi, end of April, Schaufuss leg.; not examined, unavailable in ZMB.

Comments

According to KOCH (1882), this species measures 5 mm and the prosoma is brownish black, the abdomen yellowish brown, the legs reddish brown with red femora and the spinnerets yellowish brown. The prosoma is shiny, and covered with long, plumose hairs, hence presumably the specific name '*plumiger*'. Koch's figure (Fig. 36) shows a palp with the bulb tapering to the top, a terminal tooth (the embolus ?) and a retrolateral, curved apophysis (terminal apophysis ?). The affinities of the species are presently unknown, but most probably it does not belong in the genus *Zelotes*. *Gnaphosa artaensis* Wunderlich, 2011 from Mallorca has a very similar palp but there are not enough elements to consider it conspecific with *Zelotes plumiger*. Further investigation on the island could reveal the identity of Koch's species.

Distribution

Only known from the type locality.

Family Salticidae

Phlegra bresnieri (Lucas, 1846) (Figs 37-38)

Phlegra simoni L. Koch, 1882: 667, pl. 21, fig. 37 (descr. female); **new synonymy.**

Type material

Holotype female of *Phlegra simoni* from Spain, Baleares, Minorca, Riera near Palma, 30 May 1872, Schaufuss leg. (ZMB 7932); examined.

Comparative material examined

GREECE. Attiki: Enoee ruins near Marathon (N 38°9'13" E 23°56'33"), 180 m, 3 males, stones in maquis, 19.IV.2000, R. Bosmans leg. (CRB).
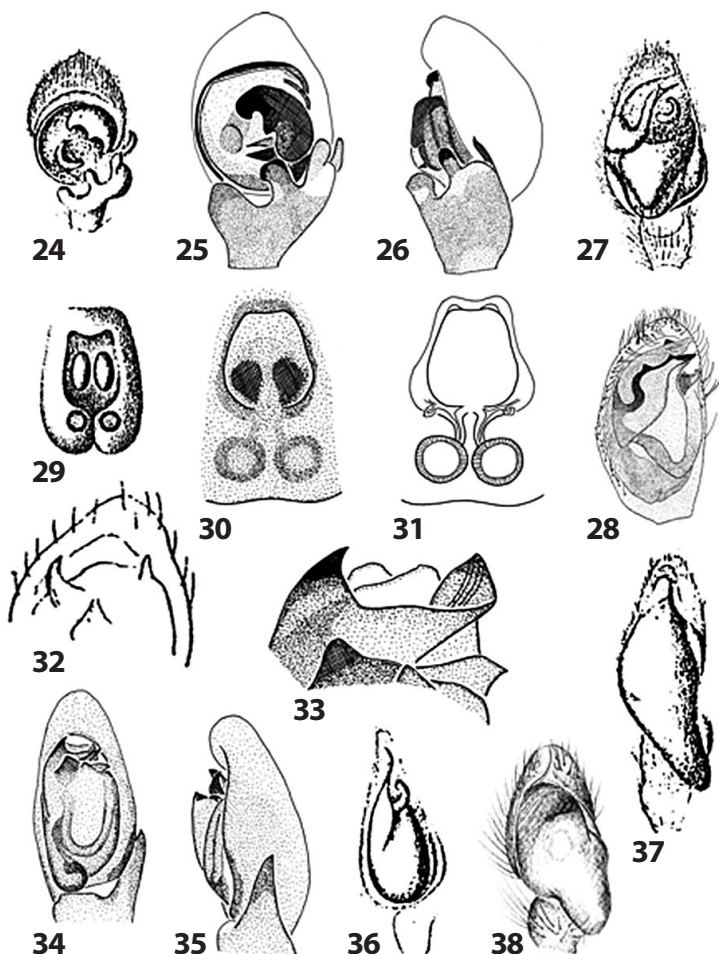
Figs. 24-38. Figs. 24-26: *Ozyptila furcula* L. Koch, 1882. 24. Male palp of *Ozyptila furcula* in KOCH (1882); 25. Male palp, ventral view; 26. Idem, lateral view. Figs. 27-28. *Haplodrassus parvicorpus* (Roewer, 1951). 27. Male palp of *Drassus parvulus* in KOCH (1882). 28. Male palp of *Haplodrassus parvicorpus*, specimen from Tarifa. Figs. 29-35. *Zelotes callidus* (Simon, 1878). 29. Epigyne of *Zelotes semirufus* in KOCH (1882); 30. Epigyne of *Zelotes callidus*, specimen from Talavan; 31. Vulva; 32. Male palp of *Zelotes callidus* in SIMON (1914, fig. 298); 33. Male palp, detail; 34. Male palp, ventral view; 35. Male palp, lateral view; Fig. 36. Male palp of *Zelotes plumiger* L. Koch, 1882 in L. KOCH (1882). Figs. 37-38 *Phlegra bresnieri* (Lucas, 1846). 37. Male palp of *Phlegra simoni* in L. KOCH (1882); 38. Male palp of *Phlegra bresnieri* in METZNER (1999).

Comments

The holotype female could be examined. The dorsal stripes on the prosoma and abdomen have disappeared, but the clypeus is densely covered with white hairs. The long, threadlike embolus is clearly visible and its placement in the genus *Phlegra* is thus confirmed. According to KOCH (1882), *Phlegra simoni* differs from *P. bresnieri* in the male palpal tibia which bears black hairs. Examination of some specimens of *P. bresnieri* from our collection show that the femora

and patellae have white hairs, but only black ones on the tibiae (cfr. SIMON, 1876: 121: "Patte-mâchoire, au moins la patella et le femur, garnie en dessus de poils blancs"). As the palps are otherwise identical (Figs 37, 38), the two species are here synonymised.

Distribution

Southern Europe to Azerbaijan, Ivory Coast, Tanzania.

Conclusions

Taxonomic studies by earlier arachnologists are of variable quality, but until there is proof to the contrary, they all have to be considered valuable. Some authors working on Mediterranean spiders in the past – for instance (but not exclusively) LUCAS (e.g. 1846), O. P.-CAMBRIDGE (e.g. 1872, 1876) and KULCZYŃSKI (e g. 1908, 1911) – presented detailed descriptions accompanied by excellent figures of the general appearance and sexual organs, making identification very easily possible. In most cases, however, examination of the type material is necessary to come to a definitive conclusion. Other authors gave long, very detailed descriptions but presented no figures at all; like for instance PAVESI (e.g. 1880, 1884) and the numerous papers by THORELL (e.g. 1875) and STRAND (e.g. 1906, 1908). Here, recognition of the species is not possible without examining the original type material. However, even if these species are not instantly recognizable, their names remain valid until has been stated in a publication that the types are not available; like for instance many types of Strand destroyed in the last World War.

In the case of the study by L. KOCH (1882) on the spiders of the Balearic Islands, the paper includes good drawings, in many cases making identification possible. Only ten of the 28 described species were redescribed previously, resulting in three valid names and seven synonyms. Type material of ten of the remaining 18 species could be examined by us. Five of these nine species names are valid: *Cheiracanthium occcidentale*, *Dysdera mordax*, *Liocranum inornatum* n. comb. and *Haplodrassus parvicorpis* n. comb. Four out of the nine species appeared to be synonyms of species described earlier. *Erigone marina*, *Lycosa perspicax*, *Lycosa subhirsuta* and *Phlegra simoni* are the junior synonyms of *Oedothorax fuscus*, *Arctosa fulvolineata*, *Arctosa lacustris* and *Phlegra fasciata* respectively. Finally, *Trochosula conspersa* is retransfered to its original genus, *Lycosa*, where it awaits further study.

Of the eight species whose types could not be examined, the drawings of L. Koch were carefully studied and three species could be recognized. *Ozyptila furcula* was recognized and redescribed. *Philodromus vegetus* and *Theridion elimatum* were recognized as junior synonyms of *Thanatus vulgaris* and *Enoplognatha diversa* respectively. *Lycosa fraissei*, *L. insulana*, *L. simplex* and *Pardosa tenuipes* could not be recognized and are left in their original genus. Finally *Lycosa misella* is declared a nomen nudum, since the description was based on a juvenile specimen.

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The scorpion collections (Arachnida, Scorpiones) held in the Museo Regionale di Scienze Naturali of Turin (Italy)

Alberto Chiarle, František Kovařík, Lisa Levi & Elena Gavetti

Abstract: Data and considerations about the history and contents of the scorpion collection housed in the Museo Regionale di Scienze Naturali of Turin (MRSN) are reported. Information on type material and important historical specimens are provided, as well as biographical notes about the major zoologists of the museum.

Key words: Borelli, MZUT, MRSN, scorpiology, Turin collection history

In 1978 the public administration of the Regione Piemonte founded the 'Museo Regionale di Scienze Naturali' (MRSN) in Turin. Since 1980, the zoological treasures kept by the Zoological Museum of the Turin University (MZUT) have been entrusted to the MRSN. The MZUT is one of the oldest and most important Italian university museums. It was founded in 1805, during the French occupation, merging the collections of the former Royal museum of natural history and of the 'Reale Accademia delle Scienze di Torino'. Since the middle of the 19th century the museum began to acquire important and rare material from all over the world. Long and difficult expeditions were organized by the museum as well as by private researchers. During the 20th century the collections were enriched by the activities of the museum's research staff, by exchanges and gifts from other specialists and from travellers. In the first decades of the 20th century the museum's zoological research started to shift its focus towards histology and genetics, and the collections lost their primary role.

In 1936 the MZUT was moved into the 'Ospedale Maggiore di San Giovanni Battista'. Here work began to rearrange the large amount of material; then in a poor state of conservation, due to the partial lack of conserving fluid and the fading (or loss) of several labels. Interesting material and documents were lost or irreparably damaged (TORTONESE 1957). Between 1950 and 1967, notwithstanding their importance, the museum collections were neglected. Specimens in ethanol suffered and exchanges, loans and systematic studies on specimens were interrupted. In 1968, under Professor Umberto Parenti's guidance and thanks to the curators, the MZUT was reorganized.

Since 1980 a large number of transfers have taken place involving all the collections.

The scorpion collection held in the Turin museum is quite large and historically important. The collection dates back to the second half of the 19th century and reflects the global perspective of the institution and the contribution of many eminent zoologists. In this first attempt we review the scorpion collections and illustrate the present situation of this interesting material – neglected for far too long – which is still needed by specialists for describing new species from all over the world.

Material and Methods
We used three different sources to review the scorpion collections, assess their scientific value and the activities within these collections over the years.

Publications
Much of the historical material was published in expedition reports or in scientific journals, mainly in the Museum review, 'Bollettino dei Musei di Zoologia e di Anatomia Comparata della Regia Università di Torino', but also in renowned Italian and international publications.

The historical catalogues
Two kinds of catalogues are present in the museum: the older handwritten catalogues which are, however, partially incomplete, and a recent one, typewritten and then mimeographed. The old loan forms and

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significant correspondence between specialists and curators proved to be very useful in verifying the collection data.

In the period 1975-1978 these catalogues, 'Cataloghi del Museo e Istituto di Zoologia sistematica dell'Università di Torino', were drawn up for most zoological groups and were sent to the most important museums and universities all over the world. In this way the exceptional heritage of the museum became available again to the international community. Thanks to the richness in historical material and type specimens from various countries there was an active international loan correspondence. In the old museum archives we found that more than 350 specialists covering all groups received material on loan for scientific revision and enthusiastically learnt that historically important specimens were not lost, but easily available.

In the 1970s the scorpion collection was reorganized, some material that had dried out was discarded and a new inventory number (Sc. ###), referring to species lots, was used for the catalogue of the extant material. By 'species lots', we mean one or more specimens of the same species stored in the same vial or jar.

Electronic database
Since 1997 all the invertebrate collections have been recorded in an electronic database. Original label information was basically copied, except that country names were added or changed according to current usage and minor emendations were made for homogeneity of style. Unfortunately, old specimens often bear inadequate locality data. The extensive work of comparing the old manuscript catalogue data with electronic database is still in progress; moreover it does not yet contain all the information and systematic notes made by the specialists.

Results
We found numerous discrepancies when comparing the catalogues with the real status of the collections: e.g. number of specimens in each tube, registration numbers, state of conservation and notes about localities. A problem – common to several museum
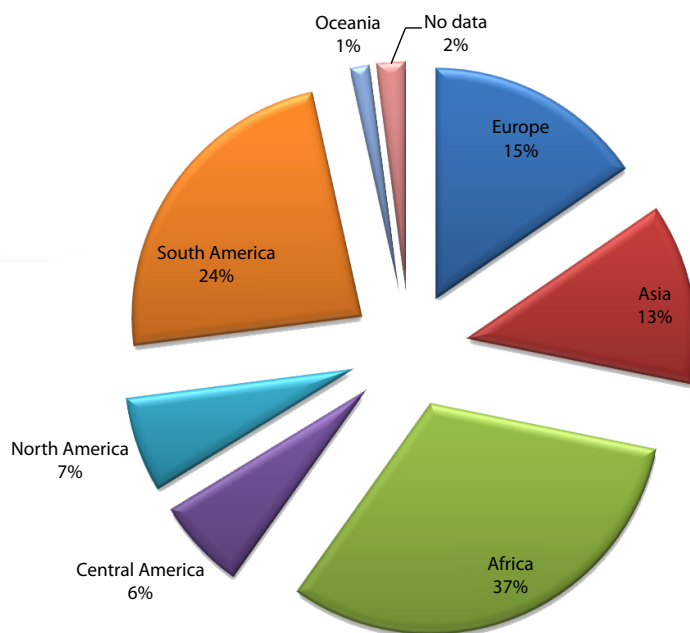
Fig. 1: Number of scorpion lots (MZUT collection) for each continent.

collections – is keeping track of the high number of specimen loans all over the world, some of which were never returned or were seriously damaged during shipment.

The scientific value of the scorpion collection
The historical scorpion collection of the MZUT is quite large with more than 3,300 specimens divided into 777 lots comprising about 300 species, 67 genera, and 11 families from all continents, except Antarctica. The majority of the specimens are preserved in ethanol. We periodically undertake a survey of the collections, checking the conservation of the specimens. In general, the samples are in good condition and the original labels are mostly present, although locality data are often unclear or lacking.

The majority of the lots are from Africa (246) and South America (183); however Europe (120) and Asia (99) are also well represented. Less numerous are the samples from North America (52), Central America (50) and Oceania (11) (Fig. 1). Sixteen samples are without data. With regard to Africa, the states yielding the larger numbers of samples are South Africa (44), Libya (40), Eritrea (38), and Somalia (36). South America is well represented by Ecuador (45), Argentina (36) and Chile (24). Most of the North American samples come from Mexico (39) while with regard to Europe, the state with the

maximum number of samples (91) is Italy.

The work of many specialists over a period of nearly 200 years, describing new species from all over the world, explains the remarkable number of types that makes the Turin Museum collections of great scientific significance. Type material can be attributed to 26 species or subspecies, comprising important samples studied by Borelli at the beginning of the 20th century (Tab. 1).

We also recently relocated the syntypes of *Tityus argentinus* Borelli, 1899 (Fig. 2a) – which was presumed for many years to be lost (cf. FET & LOWE 2000) – the holotype of *Uroplectes silvestrii* Borelli, 1913 = *Butheoloides silvestrii* (Borelli, 1913) and the holotype of *Hemiscorpius tellinii* Borelli, 1904 (KOVAŘÍK & MAZUCH 2011).

Scientists and collectors

The collection gained much significance thanks to the extensive scientific work of Alfredo Borelli (1858-1943). He collected new or important species, examined collections from all over the world for his systematic and taxonomic studies, including samples collected by famous scientists and travellers. His reputation as a scorpiologist was such, that many of the major specialists in 19th century arachnology were corresponding with him to seek advice, to exchange specimens and to send him copies of their own work for comments.

Borelli focused his attention on exotic fauna as well (BORELLI 1900) and explored South America (Argentina, Paraguay and Bolivia) in 1893-94 and in 1895-96 (BORELLI 1899a). He was an entomologist, zoologist and arachnologist: his large entomological collection and his sixty–seven papers on Dermaptera are well known (ZAVATTARI 1943). More than sixty of the scorpion labels bear Borelli's name, either as collector, donor, author or identifier. Borelli published 35 papers describing new species and identifying material from Italian and foreign countries. He was in touch with renowned specialists worldwide and the collection of the Turin museum increased thanks to exchanges and donations. Moreover, he collected vertebrates, especially during his South American expeditions.

An important zoologist who worked with Borelli was Enrico Festa (1868-1939), assistant at the MZUT and a naturalist who travelled extensively and collected in South America and the Mediterranean basin. Among the scorpions collected in Ecuador by Festa there are important type specimens, studied and determined by BORELLI (1899b). Moreover, he visited several localities in Libya: the Benghazi plain, Gheminez, Sidi-Chelan and Coefia. Rich material was collected by Festa in Palestine, Rhodes (BORELLI 1913a) and Italy. BORELLI (1924) studied the material from the expeditions of Enrico Festa and named some new species after him (for example *Tityus festae* Borelli, 1899 (Fig. 2b), *Chactas festae* Borelli, 1899 (Fig. 2c) and *Ananteris festae* Borelli, 1899).

Filippo Silvestri (1873-1949) was an Italian entomologist and professor in Portici (Naples). During his travels in Argentina, Paraguay and Bolivia (1893-1896) he collected several specimens. From the 1912-1913 expedition in Olokemeji and Lagos (Nigeria) he sent more than 30 lots of scorpions to the Turin museum (BORELLI 1913b); one of which is *Uroplectes silvestrii* Borelli, 1913. BORELLI (1901a) described the specimens collected by Silvestri, providing an important contribution to the knowledge of scorpion fauna from South America and, in particular, of the till then poorly-known Argentinean scorpions. Among the scorpions collected there are important type specimens such as *Tityus uruguayensis* Borelli, 1901 (Fig. 2d) and *Tityus mattogrossensis* Borelli, 1901 (Fig. 2e).

The following scientists also contributed to the scorpion collection in Turin and merit being briefly noted. Aleksei Birula (1864-1937), director of St. Petersburg Zoological Museum, was the author of the first book on Russian scorpions (BIRULA 1917). Birula donated and determined Turin specimens from Turkmenistan, Pakistan, Uzbekistan, Armenia, Iran, Azerbaijan and China.

The German naturalist Karl Kraepelin (1848-1915), was a specialist in the study of scorpions, centipedes, spiders and solpugids. He compared several of Borelli's scorpions with specimens in the 'Naturhistorisches Museum Hamburg' (BORELLI 1899b, 1901a). Numerous species were named in his honour e.g. *Iurus kraepelini* von Ubisch, 1922 and *Tityus kraepelini* Borelli, 1899 (a synonym of *Tityus pugilator* Pocock, 1898).

Reginald Innes Pocock (1863-1947) was a British zoologist and assistant at the British Museum of Natural History. POCOCK (1901) compared several specimens, sent by Borelli, with the type specimens in the London museum. Several important species from India and Africa were sent to him for determination. Adolfo Ducke (1876-1959) was an entomological technician (OBRECHT & HUBER 1993) in the Pará Museum (Brazil). Ducke and Francisco Diaz da
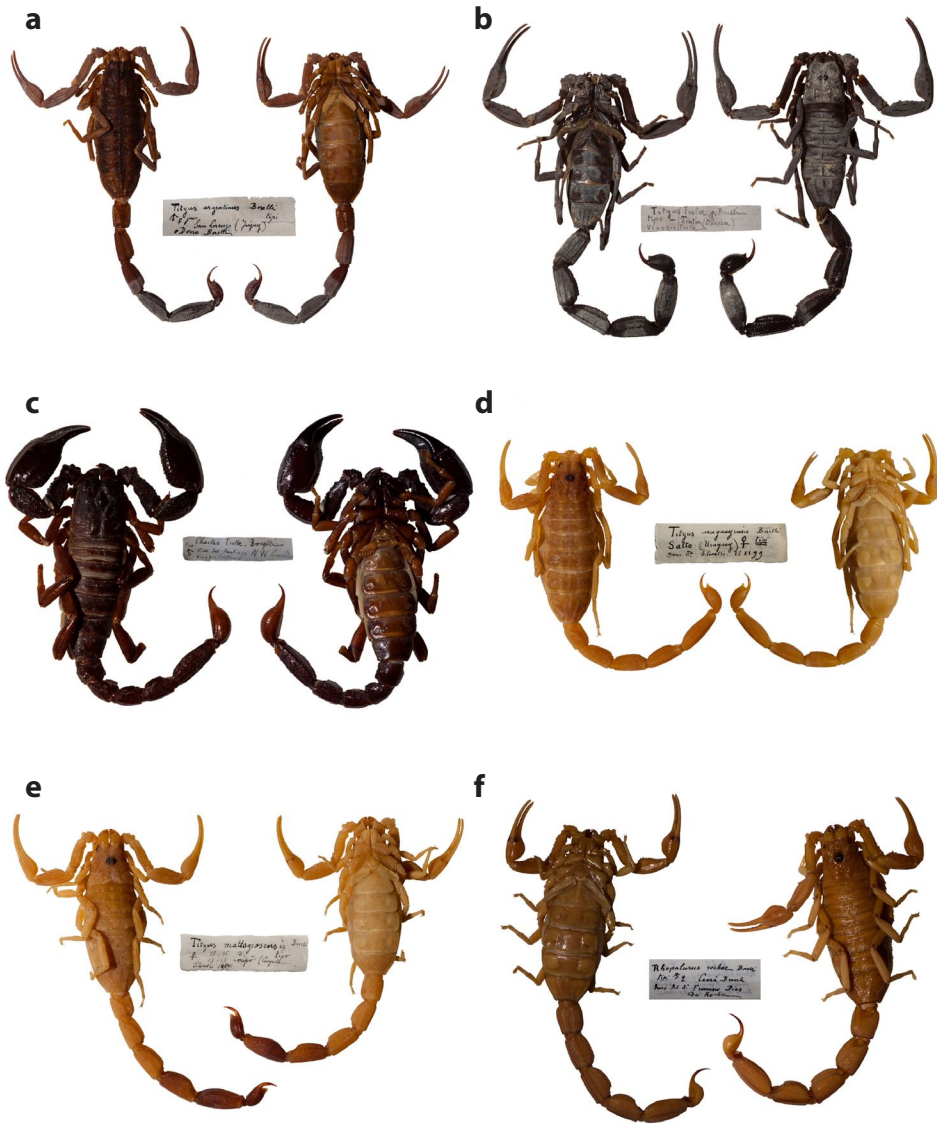
Fig. 2: Type specimens of the MZUT scorpion collection: a. *Tityus argentinus* Borelli, 1899; b. *Chactas festae* Borelli, 1899; c. *Tityus festae* Borelli, 1899; d. *Tityus mattogrossensis* Borelli, 1901; e. *Tityus uruguayensis* Borelli, 1901; f. *Rhopalurus rochae* Borelli, 1910.

Rocha from Rocha Museum sent several Brazilian specimens to Borelli. Among them BORELLI (1910) discovered two new species, *Tityus duckei* Borelli, 1910 (a synonym of *Tityus silvestris* Pocock, 1897) and *Rhopalurus rochae* Borelli, 1910 (Fig. 2f).

Paolo Magretti (1854-1913), a specialist on ants, collected in eastern Sudan and Eritrea (SORDELLI 1914). All of his scorpion samples – described by BORELLI (1901b) – were collected in the surroundings of Keren (Eritrea) in 1883.

Many specimens collected in the surroundings of Cape Town, South Africa, were sent by William Frederick Purcell (1866-1919), a South African arachnologist. He became First Assistant in the South African Museum in 1896. Retiring in 1905, he spent the rest of his life collecting arachnids and insects (IZIKO SOUTH AFRICAN MUSEUM 2011).

About 25 lots came from Costa Rica as a gift of Paul (Paolo) Biolley (1862-1908), naturalist of the 'Museo Nacional in San Jose'. He studied the local invertebrate fauna; increasing the general knowledge

Tab. 1: Scorpion type material in the MZUT/MRSN collection.

Total contents (as of today) of the type material, as listed in the old catalogues; results as in the table. A preliminary revision has been undertaken (Kovařík unpubl., KOVAŘÍK & MAZUCH 2011). A further review of the whole collection, but in particular of the specimens marked with the "*" could impact the effective number of type specimens, their correct nomenclature and any errors. At present, we can not always enter the proper kind of types, due to a lack of information on the original labels and associated documentation.

N.cat. Sc.	Family	Species	*	Locality	Legit/Don	Status
		MZUT				
25	Bothriuridae	*Bothriurus chilensis* (Molina, 1782)	*	Temuco, Chile	Silvestri	Typus
64	Bothriuridae	*Brachistosternus (Leptosternus) intermedius chilensis* Kraepelin, 1911	*	La Ligua, Aconcagua, Chile	Porter	Typus
957	Bothriuridae	*Brachistosternus intermedius borellii* Kraepelin, 1911	*	Cacheuta, Argentina	Silvestri	Typus
4	Buthidae	*Ananteris cussinii* Borelli, 1910		Caguà, Venezuela	Cussini	Lectotypus
5	Buthidae	*Ananteris festae* Borelli, 1899		Rio Peripa Forest, Ecuador	Festa, 1895 – '98	Typus
6	Buthidae	*Ananteroides feae* Borelli, 1911		Caconda Rio Cassine, Guinea Bissau	Silvestri, 1900	Lectotypus, Paralectotypes
7	Buthidae	*Ananteroides feae* Borelli, 1911	*	French Guinea	Silvestri, 1900	Types
18	Buthidae	*Babycurus zambonellii* Borelli, 1902		Chenafena, Eritrea	Zambonelli	Typus
83	Buthidae	*Centruroides chiaravigli* Borelli, 1915		Dinamita, Durango, Mexico	Chiaraviglio	Paralectotypus
313	Buthidae	*Lychas shelfordi* Borelli, 1904		Kuching, Sarawak, Borneo, Malesia	Shelford	Lectotypus, Paralectotypus
421	Buthidae	*Rhopalurus rochae* Borelli, 1910		Cearà, Brazil	da Rocha	Lectotypus
456	Buthidae	*Tityus duckei* Borelli, 1910	*	Parà, Brazil	Ducke	Typus
459	Buthidae	*Tityus festae* Borelli, 1899		Tintin, Darien, Panama	Festa, 1895	Types
461	Buthidae	*Tityus intermedius* Borelli, 1899		Ibarra, Ecuador	Festa, 1895-1898	Lectotypus
460	Buthidae	*Tityus kraepelini* Borelli, 1899	*	Ibarra, Ecuador	Festa, 1895-1898	Lectotypes, Paralectotypes, Paratypes
462	Buthidae	*Tityus mattogrossensis* Borelli, 1901		Coxipò (Cuyabà), Mato Grosso, Brazil	Silvestri, 1890	Typus
470	Buthidae	*Tityus trivittatus confluens* Borelli, 1899		Caija, Boliviano chaco, Bolivia	Borelli, 1983	Types
472	Buthidae	*Tityus trivittatus confluens* Borelli, 1899		S. Francesco, Boliviano chaco, Bolivia	Borelli, 1983	Types
480	Buthidae	*Tityus uruguayensis* Borelli, 1901		Salto, Uruguay	Silvestri, 1899	Lectotypus
480bis	Buthidae	*Tityus uruguayensis* Borelli, 1901		Salto, Uruguay	Silvestri, 1899	Lectotypus

N.cat. Sc.	Family	Species	*	Locality	Legit/Don	Status
989	Buthidae	*Tityus argentinus* Borelli, 1899		San Lorenzo, Jujuy, Argentina	Borelli	Lectotypus
990	Buthidae	*Tityus argentinus* Borelli, 1899		San Lorenzo, Jujuy, Argentina	Borelli	Paralectotypus
991	Buthidae	*Tityus argentinus* Borelli, 1899		San Pablo, Tucuman, Argentina	Borelli	Paralectotypus
958	Buthidae	*Uroplectes silvestrii* Borelli, 1913		Olokemeji, Nigeria	Silvestri, 1912	Holotypus
141	Chactidae	*Chactas dubius* Borelli, 1899		Santiago Valley, Ecuador	Festa, 1895–1898	Typus
142	Chactidae	*Chactas festae* Borelli, 1899		Santiago Valley, Ecuador	Festa, 1895–1898	Typus
256	Chactidae	*Heterochactas wittii* Kraepelin, 1896		Loja, Ecuador	Hamburg Museum	Typus
254	Scorpionidae	*Hemiscorpius tellinii* Borelli, 1904		Halibaret, Eritrea	Tellini	Typus
507	Vaejovidae	*Vaejovis globosus* Borelli, 1915		Dinamita, Durango, Mexico	Chiaraviglio	Typus
508	Vaejovidae	*Vaejovis intermedius* Borelli, 1915		Dinamita, Durango, Mexico	Chiaraviglio	Lectotypus
522	Vaejovidae	*Vaejovis silvestrii* Borelli, 1909		Los Angeles, Sierra Madre, USA	Silvestri	Typus
		MRSN				
13	Bothriuridae	*Orobothriurus* sp.n Ochoa et al., in prep.		Qranganulo, Ancash, Peru	Etonti, 1994	under description
14	Bothriuridae	*Orobothriurus* sp.n Ochoa et al., in prep.		Querococcha, Ancash, Peru	Etonti, 1994	under description
15	Bothriuridae	*Orobothriurus* sp.n Ochoa et al., in prep.		Pastocuri, Ancash, Peru	Etonti, 1994	under description
44	Buthidae	*Tityobuthus lucileae* Lourenco, 1996		Antsirabe, Antananarivo, Vakinankaratra, Madagascar	Duval, 1973	Holotypus, Allotypus

about Costa Rica, and in particular the western coast of Cocos Island (Cognetti de Martiis 1908).

The Museo Regionale di Scienze Naturali (MRSN), Collection
The most recent scorpion acquisitions in the 'Museo Regionale di Scienze Naturali' (MRSN) as of today consist of 122 specimens, 59 tubes and 27 species belonging to 16 genera and 6 families. Except for the Italian and Greek specimens of the genus *Euscorpius*, the other specimens are mainly from South America (collected by C. Bordon, M. Etonti and J. Cei) and Africa, in particular Madagascar (collected by F. Andreone and C. Duval). Two type species are present: *Tityobuthus lucileae* Lourenço, 1996 and *Orobothriurus* sp. n., the latter currently being described by José A. Ochoa and colleagues.

Conclusions

The 'Museo Regionale di Scienze Naturali' of Turin, heir to the prestigious Zoological Museum of Turin University, maintains the important role of ensuring the conservation and availability of these collections. The scorpion collection needs to be revised and the nomenclature must be updated in order to obtain the correct number of species and specimens. Large amounts of the material have already been identified, although there are still some jars to be sorted and examined; among them a rich collection made by the entomologists C. Bordon (Venezuela) and M. Etonti (Greece, Turkey, Peru, Chile). This work will proceed so long as the funding and human resources are available.

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Geography-related sub-generic diversity within the Mediterranean trapdoor spider genus *Nemesia* (Araneae, Mygalomorphae, Nemesiidae)

Arthur E. Decae

Abstract: Three different male and female super-specific types are distinguished according to variations in the morphology of the bulb and spermathecae within the genus *Nemesia* Audouin, 1826. Plotting the distributions of these sexual types on a map of the Mediterranean indicates the existence of geography-related sub-generic diversity in which the *Nemesia* fauna of the eastern Mediterranean differs markedly from that of the western Mediterranean. While the eastern Mediterranean *Nemesia* fauna is highly homogeneous, the fauna of the western Mediterranean is very diverse. The eastern and western *Nemesia* faunae appear to overlap in the central Mediterranean. Efforts to relate the specific bulb types to the particular types of spermathecae described here were only partly successful.

**Key words**: biodiversity, biogeography, distribution, model taxon, taxonomy

The trapdoor spider genus *Nemesia* Audouin, 1826 is currently considered to be a potentially valuable model system for studies in evolutionary biology (DECAE 2010, Arnedo pers. comm.). The fact that *Nemesia* exhibits high species diversity in the geographically confined region of the Mediterranean offers exceptional opportunities for studies on local variation and speciation. Moreover, the common occurrence of *Nemesia* throughout the region, both on islands and continents, in a range of different habitats (from sandy shores to alpine heights and from semi-deserts to humid forests), its supposedly sedentary habits, its poor capacity for dispersal and its probably ancient origin, reveals the genus as a coherent sample of evolving lineages that offer highly prospective opportunities for virtually all lines of biological research. Unfortunately, this potential for biological research into *Nemesia* is hampered by a lack of basic knowledge. The taxonomy of *Nemesia* is poorly resolved and partly confused, the real species diversity cannot even be estimated and there is no good insight into the internal organization of the genus in terms of the possible existence of sub-generic groups. A basic problem is that classical spider taxonomy is exclusively focused on morphological variation in preserved specimens, and that such variation is very difficult to observe in *Nemesia*. Study of the taxonomically most informative morphological structures – male and female sexual organs and the spinnerets – has become common practice only very recently, which means that the whole taxonomical framework of the genus urgently needs revision. A productive first step might be to try recognizing *Nemesia* species groups based on the variation of the bulb and the spermathecae types, and matching the sexes. The recognition of evolutionary older sub-generic groups within *Nemesia* would have particular significance if it could be linked to the geographical dynamics of the Mediterranean; a region with a history of major geographical shifts (AGER 1980) and dramatic geophysical events such as the Messinian salinity crisis (KRIJGSMAN et al. 1999) and the formation of glacial refugia during the Pleistocene (MÉDAIL & DIADEMA 2009). This paper is a first attempt to discover such geography-related sub-generic diversity within *Nemesia*.

Material and Methods

This study is based on variations in the morphology of both male and female sexual organs (i.e. bulbs and spermathecae). Because no objective criteria exist for classifying different types of spider bulbs and spermathecae, the classifications used here are necessarily arbitrary and provisional. The classifications adopted are, however, based on experience resulting from detailed observations of well over one thousand *Nemesia* specimens and as such might function as practical tools for discovering broad scale patterns in *Nemesia* sub-generic diversity. A Ceti-Medo.2 stereomicroscope with camera lucida equipment was

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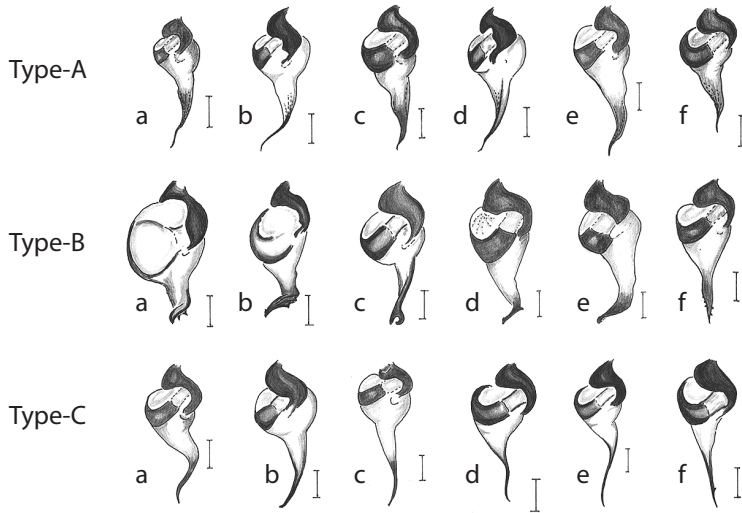
Fig. 1: Classification of three different types of bulbs found within *Nemesia* (18 examples). Top row: Type-A bulbs with distinct longitudinal ribs on the proximal embolus. Middle row: Type-B bulbs, proximally somewhat enlarged bulbs with conspicuous ornamentation or modifications of the embolus tip. Bottom row: Type-C, relatively simple pyriform bulbs, embolus tips pointed, smooth or furnished with tiny denticles, but without ribs or conspicuous modifications. All drawings are taken in ventral view on the right hand bulb. Aa = *N. pannonica*, Ab = *N. spec.* from Sardinia, Ac = *N. spec.* from Puglia, Ad = *N. daedali*, Ae = *N. kahmanni*, Af = *N. spec.* from Molise, Ba = *N. uncinata*, Bb = *N. valenciae*, Bc = *N. carminans*, Bd = *N. spec.* from Murcia, Be = *N. spec.* from Saida, Bf = *N. spec.* from Bejaia, Ca = *N. spec.* from Emilia-Romagna, Cb = *N. manderstjernae*, Cc = *N. spec.* from Andalucía, Cd = *N. bristowei*, Ce = *N. badia*, Cf = *N. bacelarae*. Species indicated as "*N. spec.*" are not yet formally named. Scale lines = 0.25mm.
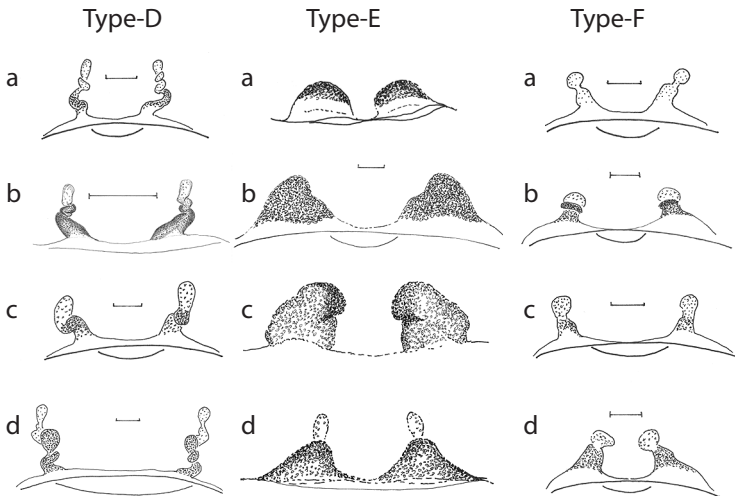
Fig. 2: Classification of three different types of spermathecae found within *Nemesia* (12 examples). Left column: Type-D) spermathecae tube shaped, tripartite, central part twisted and/or folded. Middle column: Type-E spermathecae grossly enlarged, one or two partite spermathecae without twisted parts. Right column: Type F spermathecae, tube shaped two or three partite without twists or folds. All drawings are taken in ventral view. Da = *N. spec.* from Peloponnesus, Db = *N. meridionalis*, Dc = *N. manderstjernae*, De = *N. spec.* from Toscana, Ea = *N. uncinata*, Eb = *N. spec.* SW Portugal, Ec = *N. santeulalia*, Ed = *N. caementaria*, Fa = *N. arboricola*, Fb = *N.athiasi*, Fc = *N. macrocephala*, Fd = *N. ungoliant*. Species indicated as "*N. spec.*" are not yet formally named. Scale lines = 0.25mm.

used for examining and drawing bulbs and spermathecae submerged in 70 % ethanol. Bulbs were drawn from the organ on the right hand side of the spider in ventral view. Spermathecae were prepared for study by dissection and removing the coverage of greasy tissue mechanically with sharpened needles. This method leaves the spermathecae in situ with minimal damage to the spider specimens. Drawings were done in pencil and Artline pens for graphical design. Registration of species identity, geographical origin of each specimen and classification of sexual types were compiled in a Microsoft Excel sheet.

Six different 'sexual types', three male-types (Fig. 1) and three female-types (Fig. 2), could be distinguished. A sample of 107♂♂ and 47♀♀, collected at localities widely spread throughout the Mediterranean Region was classified according to these sexual types. The results were plotted on a map of the Mediterranean using DIVA-GIS (HIJMANS et al. 2005). In an effort to match male and female sexual types, ten established species – for which both sexes were represented in the sample – were compared (Tab. 1) and set in a geographical context.

Results

Plotting 107 male records, classified according to three different bulb-types (Fig. 1), on a map shows a distinct difference between the eastern and western Mediterranean (Fig. 3). Type-A bulbs (i.e. longitudinal ribs on the proximal embolus) are the only bulb-type present in the eastern Mediterranean. In the western Mediterranean

Tab. 1: Match of male and female sexual types in ten established *Nemesia* species present in a sample of 107 ♂ ♂ and 45 ♀ ♀. Ordered alphabetically on male types.

Species	Distribution	Male-type	Female-type
Nemesia caranhaci Decae, 1995	Crete	A	D
Nemesia meridionalis (Costa, 1835)	S Italy	A	D
Nemesia caementaria (Latreille, 1799)	S France	B	E
Nemesia uncinata Bacelar, 1933	S Portugal	B	E
Nemesia athiasi Franganillo, 1920	W Iberian	B	F
Nemesia manderstjernae L. Koch, 1871	SE France	C	D
Nemesia dubia O. P.-Cambridge, 1874	Pyrenees	C	D
Nemesia bacelarae Decae, Cardoso & Selden, 2007	Portugal	C	E
Nemesia ungoliant Decae, Cardoso & Selden, 2007	Portugal	C	F
Nemesia macrocephala Ausserer, 1871	Sicily-Malta	C	F
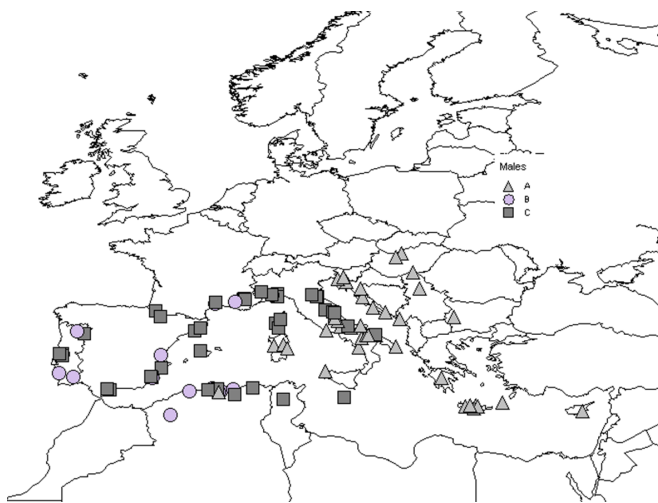
Fig. 3: Geographical distribution of three here distinguished bulb-types found in a sample of 107 male *Nemesia* spiders. Triangle = Type-A, circles = Type-B, squares = Type-C.

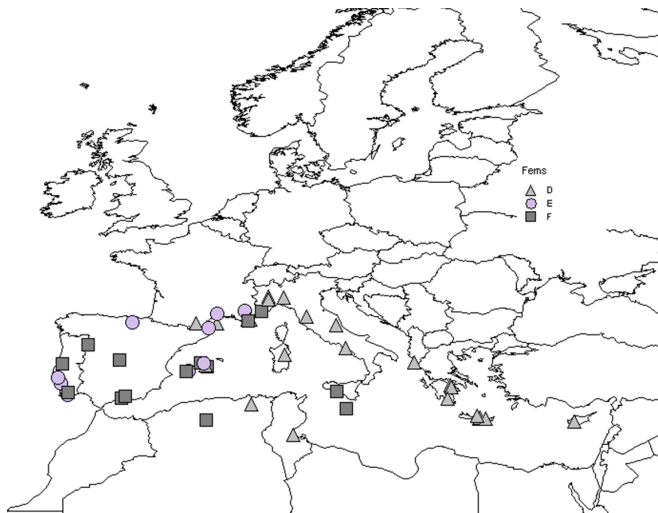**Fig. 4**: Geographical distribution of three here distinguished spermathecae-types found in a sample of 47 female *Nemesia* spiders. Triangle = Type-D, circles = Type-E, squares = Type-F.

bulb-types B and C predominate and only in the central Mediterranean do all bulb-types overlap. Plotting 47 female records, classified according to three different spermathecae-types (Fig. 2), produces a highly similar distribution of sexual types (Fig. 4). D-type spermathecae (tube-shaped with central twists or sharp folds) exclusively populate the eastern Mediterranean, while in the western Mediterranean E and F type spermathecae dominate. As in males, the central Mediterranean is a zone of overlap for all three female sexual-types (Fig. 4).

Relating sexual types of males and females (Tab. 1) indicates that Type-D spermathecae match with either Type-A (*N. caranhaci* & *N. meridionalis*) in the eastern Mediterranean, or with Type-C bulbs (*N. dubia* & *N. manderstjernae*) in the north-western Mediterranean. Type-E spermathecae match with Type-B bulbs (*N. caementaria* & *N. uncinata*) or with Type-C bulbs (*N. bacelarae*). Type-F spermathecae match either with Type-C (*N. ungoliant* & *N. macrocephala*,) or with Type-B (*N. athiasi*).

Discussion

Perhaps the most obvious conclusion to be drawn from this study is that the *Nemesia* fauna in the eastern Mediterranean differs strongly from that in the western Mediterranean. While the eastern fauna appears to be highly homogeneous – all *Nemesia* species occurring east of approximately 14.5 E have Type-A bulbs and Type-D spermathecae – the fauna of the western Mediterranean is highly diverse (Figs. 3 & 4). All designated male and

female sexual types are found in the western Mediterranean, although Type-A males and Type-D females have not yet been found on the Iberian mainland. In the central Mediterranean the eastern and western *Nemesia* faunae overlap. It is not clear from the data if this zone of overlap indicates east-west dispersal of *Nemesia* species or a vicariance pattern related to historical shifts in the local geography (AGER 1980, DECAE 2010). This study does not reveal any locally restricted species groups in the western Mediterranean, although the two different bulb types found in combination with Type-D spermathecae (Tab. 1) might indicate the existence of a local species group in the north-western parts of the region. The combination Type-C/Type-D (*N. dubia* & *N. manderstjernae*) has thus far only been found in an area roughly running from northern Italy to the central Pyrenees. The intuitive expectations that enlarged bulbs (i.e.

Type-B) should match with enlarged spermathecae (Type-E) and that simple bulbs (Type-C) should match with simple spermathecae (Type-F) are only partly corroborated. Two species, both from the western parts of the Iberian Peninsula (*N. bacelarae* & *N. athiasi* see Tab. 1) contradict these expectations. The study sample contains few clearly conspecific males and females. Most specimens included are either representatives of unnamed and undescribed species or single males or females of described species. As such the sample is more or less representative for the current general state of *Nemesia* taxonomy. The *Nemesia* list in the World Spider Catalog (PLATNICK 2012), shows that about half of all species are known by one sex only and about one third of all names listed must be regarded as incertae sedis (personal opinion). This study of sub-generic diversity therefore not only shows the probable existence of geographical patterns
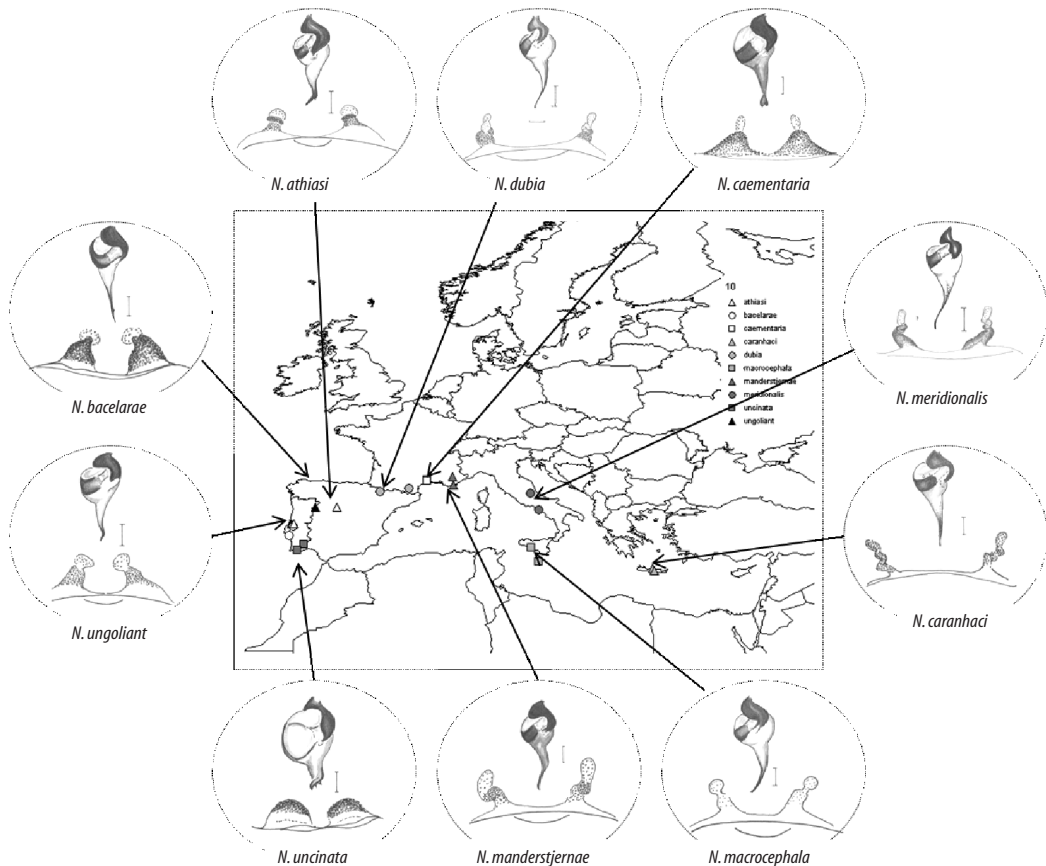
Fig. 5: Geographical distribution of ten established *Nemesia* species. Matching bulb types with types of spermathecae. *N. caranhaci* & *N. meridionalis* (Type-A/Type-D), *N. manderstjernae* & *N. dubia* (Type-C/Type-D), *N. ungoliant* & *N. macrocephala* (Type-C/Type-F), *N. caementaria* & *N. uncinata* (Type-B/Type-E), *N. bacelarae* (Type-C/Type-E), *N. athiasi* (Type-B/Type-F).

in *Nemesia* diversity, it also shows that an improved taxonomy is urgently needed as a prerequisite for exploiting the great potential of *Nemesia* as a biological model taxon as indicated in the Introduction.

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The sejugal furrow in camel spiders and acariform mites

Jason A. Dunlop, Jessica Krüger & Gerd Alberti

Abstract: Camel spiders (Arachnida: Solifugae) are one of the arachnid groups characterised by a prosomal dorsal shield composed of three distinct elements: the pro-, meso- and metapeltidium. These are associated respectively with prosomal appendages one to four, five, and six. What is less well known, although noted in the historical literature, is that the coxae of the 4th and 5th prosomal segments (i.e. walking legs 2 and 3) of camel spiders are also separated ventrally by a distinct membranous region, which is absent between the coxae of the other legs. We suggest that this essentially ventral division of the prosoma specifically between coxae 2 and 3 is homologous with the so-called sejugal furrow (the sejugal interval sensu van der Hammen). This division constitutes a fundamental part of the body plan in acariform mites (Arachnida: Acariformes). If homologous, this sejugal furrow could represent a further potential synapomorphy for (Solifugae + Acariformes); a relationship with increasing morphological and molecular support. Alternatively, outgroup comparison with sea spiders (Pycnogonida) and certain early Palaeozoic fossils could imply that the sejugal furrow defines an older tagma, derived from a more basal grade of organisation. In this scenario the (still) divided prosoma of acariform mites and camel spiders would be plesiomorphic. This interpretation challenges the textbook arachnid character of a peltidium (or 'carapace') covering an undivided prosoma.

Key words: Acariformes, morphology, outgroups, phylogeny, Solifugae, tagmosis

Camel spiders (Arachnida, Solifugae) are a fascinating group of arachnids which, as their name implies, predominantly occur in arid habitats. These fast-moving and voracious predators are also sometimes referred to as wind scorpions or sun spiders. Over a thousand living species are known (HARVEY 2003) and they occur in suitable environments in all subtropical to tropical zones, with the curious exception of Australia. For a summary of their biology see PUNZO (1998). Camel spiders are morphologically and phylogenetically of interest in that they differ in certain key aspects from the typical arachnid groundplan. The best example of this is that the prosoma is not covered by a single dorsal shield. This structure is widely referred to in the arachnid taxonomic literature as the carapace. Strictly speaking – from the perspective of comparative arthropod morphology – the term 'carapace' should be restricted to crustaceans and the arachnid structure is better referred to as a prosomal dorsal shield, or (sensu BÖRNER 1904) a peltidium.

In camel spiders, schizomids (Schizomida) and palpigrades (Palpigradi) the peltidium is not a single plate, but is divided into a series of discrete dorsal sclerites. These are conventionally referred to as the pro-, meso- and metapeltidium. In fact the camel spider propeltidium seems to be even more complex and composed of multiple elements (KÄSTNER 1932, ROEWER 1932).

Authors such as BERNARD (1896, 1897) and KÄSTNER (1932) interpreted this basic tagmosis pattern in camel spiders as plesiomorphic, presumably reflecting a grade of organisation which predates the traditional arachnid prosoma. Other workers explicitly treated a 'divided carapace' as a derived character state (WEYGOLDT & PAULUS 1979, SHULTZ 1990, 2007). Irrespective of polarity, the camel spider condition has interesting parallels with certain mites (Acari), which also express a dorsal sclerite again associated with the chelicerae, pedipalps and the first two pairs of walking legs (COINEAU 1974, EVANS 1992, ALBERTI & COONS 1999, WEIGMANN 2001). This whole body region down to the second pair of legs has been termed the proterosoma and the dorsal sclerite covering it is usually called the prodorsum (e.g. WEIGMANN 2001). The name 'aspidosoma' can also be found in the literature but, as discussed by WEIGMANN, this term should refer to tergites explicitly associated with the gnathosoma, and there is no evidence that these structures have overgrown the rest of the proterosoma as per the evolutionary scenarios proposed by authors

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such as GRANDJEAN (1969), COINEAU (1974) and VAN DER HAMMEN (1989). In general, issues remain among mites with respect to questions of segmental homology and the use of a standard terminology.

These observations also reflect two recurrent problems in arachnid comparative morphology (see e.g. DUNLOP 2000). The first is the use of divergent terminologies for essentially the same structures in mites and non-mite taxa. The second is the use of the same term, e.g. 'carapace', for non-homologous structures across different arthropod groups. Such discrepancies in nomenclature can mask potential synapomorphies. Here, we draw attention to an older – albeit largely overlooked – observation that camel spiders not only have an obvious *dorsal* division of the prosoma, but also express a distinct *ventral* division (Fig. 1), specifically between the coxae of the second and third pair of walking legs (BERNARD 1896, ROEWER 1932, VAN DER HAMMEN 1989). We believe this character to be of some significance and potentially homologous with the so-called sejugal furrow, which also runs between legs two and three in certain lineages of mites (Figs 2–4).

Several studies either proposed that mites should be split into two distinct clades (e.g. VAN DER HAMMEN 1989, ALBERTI 2006) or did not recovered these two lineages as sister taxa in their cladograms (DABERT et al. 2010, PEPATO et al. 2010, REGIER et al. 2010). These groups are here termed Acariformes and Parasitiformes (= Actinotrichida and Anactinotrichida) and these publications imply that Acari, in its traditional sense, may not be monophyletic. The sejugal furrow is widely cited as a fundamental part of the body plan in numerous acariform lineages only (e.g. COINEAU 1974, ALBERTI & COONS 1999, ALBERTI 2006, DUNLOP & ALBERTI 2008). We argue here that it is present in camel spiders too, and should be scored as such in future cladistic analyses. The sejugal furrow may therefore contribute towards a larger set of morphological and molecular data (ALBERTI & PERETTI 2002, DABERT et al. 2010, PEPATO et al. 2010, and references therein) explicitly supporting a novel (Solifugae + Acariformes) clade. However, as noted by Bernard and Kästner above (see also Discussion), an alternative interpretation would be that the body region defined by the propeltidium/sejugal furrow is part of an older arthropod groundplan. If so, this would raise questions about the original pattern of anterior tagmosis among arachnids: namely did the first arachnids have a prosoma or a proterosoma?

Historically, KITTARY (1848) differentiated the camel spider prosoma into a 'head' (the propeltidium) and 'thorax' (meso- and metapeltidium) and observed paired spiracles opening ventrally on a membrane between them. The comprehensive study of BERNARD (1896, p. 308) stated that "The Galeodidae show the primitive metamerism of the body more markedly than any other Arachnid". He added (p. 308) "The Galeodidae can bend the body not only between the 6th and 7th segments (at the waist), but also between the 4th and 5th". While Bernard did not explicitly describe the ventral membrane between segments 4 and 5, its presence can be easily inferred from his illustrations (pl. 27, fig. 15, pl. 29, fig. 6). ROEWER
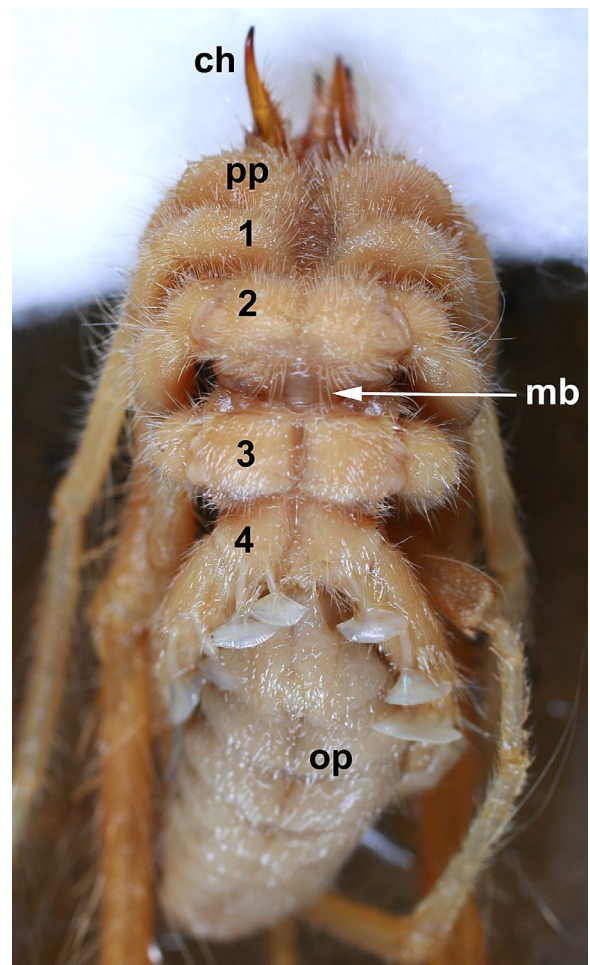
Fig. 1: Camel spider (Solifugae: *Galeodes* sp.) in ventral view. Prosomal region artificially bent slightly backwards to tease out a natural, membranous division (arrowed) between the second and third leg coxae. Abbreviations: ch = chelicerae, mb = membrane (interpreted here as homologous with the sejugal furrow), op = opisthosoma, leg coxae numbered from 1–4.

(1932: 43, fig. 33) explicitly stated for the coxae that "Only these of the 2nd and 3rd walking legs are divided by a wide, soft membrane." [our translation]. KÄSTNER (1932) did not explicitly mention a ventral division, but seems to have been more concerned with the composition of the dorsal prosoma. He did, however, mention structures (also noted by BERNARD 1896) which partly divide the body internally and further help to define and offset this anterior body region. KÄSTNER (1952: fig. 9) seemed to indicate this ventral membrane in a lateral view of a late-stage camel spider embryo. He labelled the region between coxae two and three 'G', but did not define this in the figure legend. It may refer to "Gelenkhaut" [= membrane]. Most recently, VAN DER HAMMEN (1986, 1989: 249), formally stated that for camel spiders "The coxisternal regions of legs II and III (epimera 2 and 3) are transversely separated by the sejugal interval (an intersegmental area of soft skin, which allows of prosomatic articulation)." Here, we confirm these observations and further discuss their potential phylogenetic significance.

Material and Methods

Camel spider gross morphology was examined under a dissecting microscope. Specimens were carefully bent backwards and/or manipulated with tweezers to investigate where the basic division(s) in the ventral body surface lay. To determine whether the resulting observations were typical for the whole order, representatives of nine of the twelve currently recognised families (cf. Harvey 2003) were examined based on alcohol-preserved specimens in the Museum für Naturkunde, Berlin. Specimens of Melanoblossidae, Mummuciidae and Eremobatidae were not available, but all other families revealed a consistent morphology which we thus presume to be the groundplan character for Solifugae. The ventral prosomal anatomy is easier to resolve in larger

specimens, six of which are illustrated here (Figs. 5–10). Specimens were photographed using a Canon Eos digital camera with either a x1 or a x3 macro lens. The resulting images were cleaned and assembled in Adobe Photoshop. Comparative scanning electron micrographs (Figs. 2–4) of representative acariform mites were produced by GA.

Results

In ventral view, the prosoma of camel spiders from a range of different families (Figs 5–10) presents a fairly
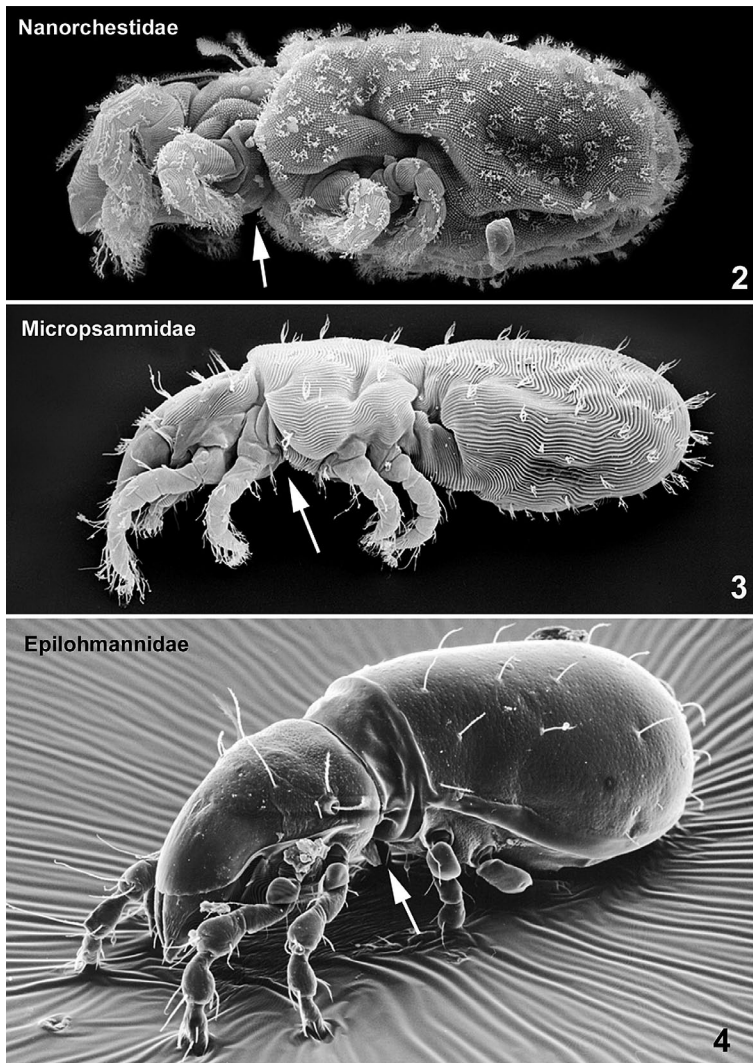
Figs. 2–4: Comparative scanning electron micrographs of selected acariform mites. Note again the principal division between the second and third pair of leg coxae (arrowed); specifically formed here by the so-called sejugal furrow. **2** - *Neonanorchestes ammolitoreus* McDaniel & Bolen, 1981 (Endeostigmata: Nanorchestidae). **3** - *Micropsammus littoralis* Theron & Coineau, 1983 (Endeostigata: Micropsammidae). **4** - *Epilohmannia cylindrica* (Berlese, 1905) (Oribatida: Epilohmannidae). Not to scale.

compact series of pedipalp and limb coxae. There is no plate-like sternum between the leg coxae, as in spiders (Araneae) for example, nor is there a series of ventral sclerites between the coxae as per Palpigradi. Furthermore, there is no superficial evidence of a 'break' between the successive coxal pairs. In fact the dividing line elaborated here is best revealed by simply taking a specimen and gently bending the prosoma backwards or sideways. The ventral surface naturally opens up between the second and third pair of leg coxae (Fig. 1); precisely because they are separated by a pale, flexible membrane; superficially similar to the pedicel (or petiolus) of a spider. In gross morphology this membrane is similar in form to an arthrodial membrane between adjacent limb articles and does not reveal any embedded sclerites. It forms a distinct narrowing, with a maximum width about a third of the width of the adjacent coxal pairs, and can be followed as a dividing line up the lateral sides of the animal – where it merges smoothly into the dorsal membrane dividing the propeltidium from the mesopeltidium. Significantly, physical manipulation of the prosoma reveals that none of the other coxal pairs can be teased apart in this way to the same extent. In other words, the coxae of the pedipalps, plus legs 1 and 2, essentially form an anterior functional unit. The coxae of legs 3 and 4 form a corresponding posterior functional unit. We interpret this as clear ventral evidence of tagmosis; whereby the soft, membranous suture (Fig. 1: mb) defines an anterior body region bearing the chelicerae, pedipalps and first two pairs of walking legs: the same body region that is dorsally associated with the propeltidium.

Discussion

Here we confirm and illustrate previous observations about the flexibility of the camel spider body between the second and third pair of walking legs. The body region defined dorsally by the propeltidium in Solifugae is also delimited ventrally by a membranous region (Fig. 1), which essentially continues laterally and forms a flexible ring around the animal more or less in the middle of its prosoma. This membrane is, incidentally, also the place where a pair of spiracles opens on the lateral sides of the body. In searching for comparable tagmosis features among other arachnids the most obvious candidate is the sejugal furrow of acariform mites; a character which we reiterate does not occur in the parasitiform lineage. Precise definitions of this character in the literature vary slightly, but to quote some recent authors the sejugal (or

dorsosejugal) furrow:
1) is "Pertaining to the furrow or interval separating, in Actinotrichida, propodosoma and metapodosoma." (VAN DER HAMMEN 1980: 140),
2) is "a transverse furrow running between legs II and III and separating them. This furrow […] extends dorsally and thus divides the body into an anterior part, the proterosoma and a posterior part the hysterosoma." (ALBERTI 2006: 327),
3) is a "circumferential zone of body flexibility that passes between the coxae of legs 2 and 3" (SHULTZ 2007: character 7).

We argue here that on all these criteria a sejugal furrow can reasonably be scored as present for Solifugae too. VAN DER HAMMEN (1989: 249) came closest to this by recognising (and naming) a 'sejugal interval' in camel spiders, but idiosyncrasies in his work have limited the impact of his views. First, he frequently referred to the coxae as 'epimera', as part of a novel hypothesis about coxal origins and evolution. The use of the term epimera – and his general habit of describing all arachnids using mite terminology – tended to marginalise his work. Second, van der Hammen rejected cladistics, and his (sometimes detailed and accurate) observations have been largely overlooked by later authors scoring characters for phylogenetic analyses.

Poecilophysidea

The presence of what we interpret as a sejugal furrow in camel spiders further emphasises their morphological similarity to certain mites (Figs. 2–5) (see also DUNLOP 1999, 2000). Specifically, the sejugal furrow is another potential synapomorphy for a relationship of the form (Solifugae + Acariformes). Most authors have recovered camel spiders as the sister group of pseudoscorpiones (WEYGOLDT & PAULUS 1979, VAN DER HAMMEN 1989, SHULTZ 1990, 2007). Basal (i.e. chthoniid) pseudoscorpions do indeed resemble camel spiders quite closely and this traditional Haplocnemata clade (BÖRNER 1904) is supported by a range of characters such as legs with a very short femur and a correspondingly long patella, two-segmented and chelate chelicerae, and tracheal spiracles opening on the 3rd and 4th opisthosomal segments.

Nevertheless, there is also evidence linking mites and camel spiders; a hypothesis with historical precedent (BANKS 1915). Mites, solifuges (and also pseudoscorpions) have a mouth on a projecting 'beak', or rostrum in some terminologies, and also
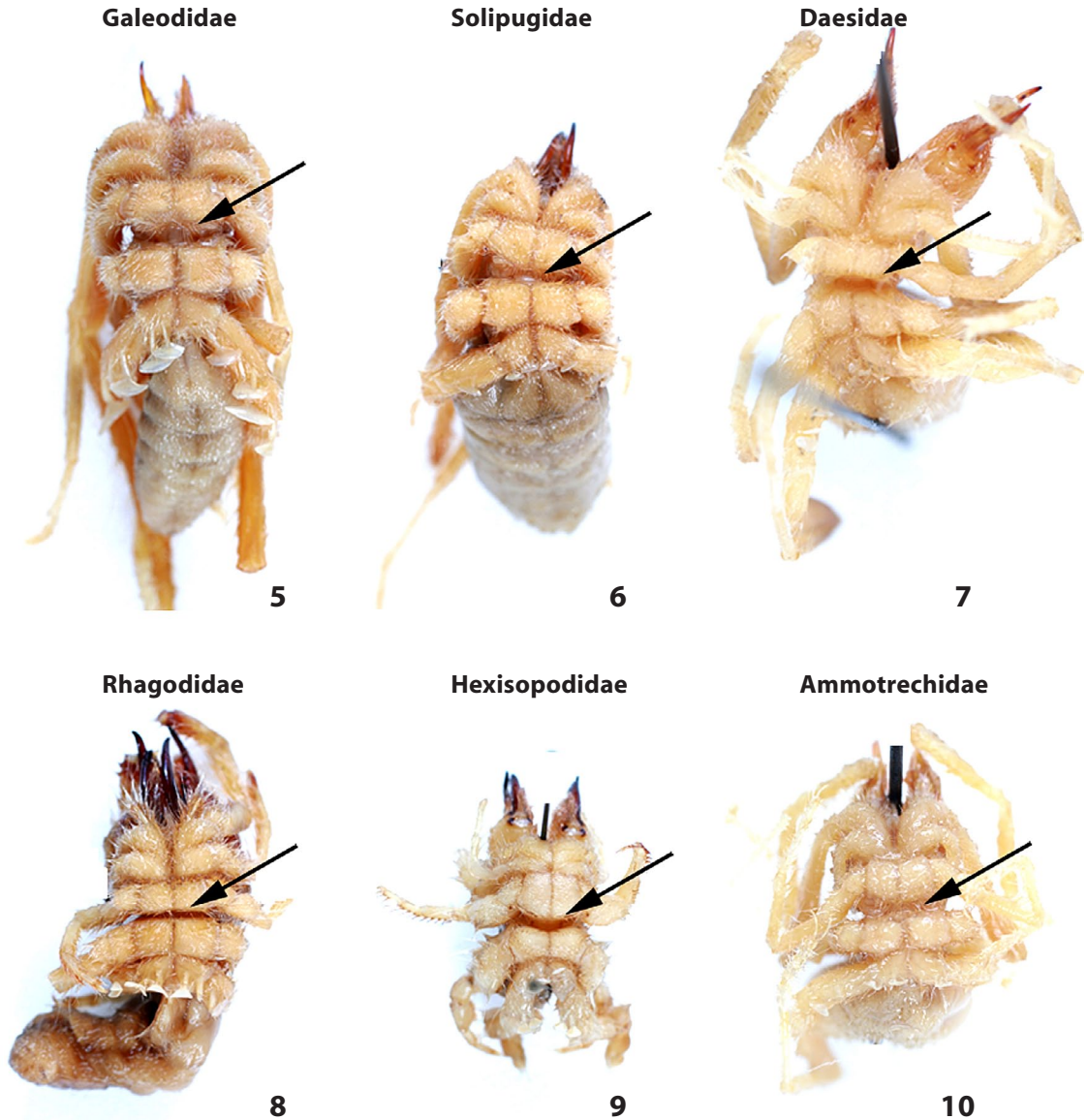
Figs. 5–10: Ventral prosomal region in six of the twelve currently recognised camel spider families. Note again in all cases the principal division between the second and third pair of coxae (arrowed); in larger specimens a pedicel-like membranous region here is clearly evident. **5** - *Galeodes armeniacus* Birula, 1929 (Galeodidae: ZMB 17972). **6** - *Zeria keyserlingi* (Pocock, 1895) (Solpugidae: ZMB 15646). **7** - *Biton* (*Biton*) *kolbei* (Purcell, 1899) (Daesiidae: ZMB 15517). **8** - *Rhagodoca termes* (Karsch, 1885) (Rhagodidae: ZMB 15642). **9** - *Chelypus barberi* Purcell, 1902 (Hexisopodidae: ZMB 48436). **10** - *Pseudocleobis andinus* (Pocock, 1899) (Ammotrechidae: ZMB 15634). Not to scale.

have chelicerae in which the movable digit articulates ventrally relative to the fixed digit (BERNARD 1896, DUNLOP 2000). Two characters of the reproductive system have been elucidated exclusively for Solifugae and Acariformes (cf. ALBERTI 1980a, b, 2000, ALBERTI & PERETTI 2002, KLANN et al. 2009):

namely simple, aflagellate sperm and a large glandular area of the testis producing secretions. The present tagmosis character of a propeltidium/proterosoma/propodosoma/aspidosoma/sejugal furrow can now potentially be added to this list; although we should caution against the risk of character duplication. For

example SHULTZ (2007) scored the 'divided carapace' and the sejugal furrow as two separate characters. However, but it may be better to treat them as parts of a single character complex relating to tagmosis.

In addition to this morphological data, recent molecular (DABERT et al. 2010) and combined (PEPATO et al. 2010) studies have also picked up a strong molecular signal for (Solifugae + Acariformes). It will be interesting to see whether further investigations of this nature continue to support these results. Pepato et al. (2010) even went so far as to recognise a clade Poecilophysidea for camel spiders and acariform mites – and a clade Cephalosomata for poecilophysids plus palpigrades. The latter group potentially share the character of a 'cephalosoma'; a discrete anterior body region (see above) covered by the propeltidium and bearing the first four pairs of appendages.

In this context, we should briefly consider whether a sejugal furrow/interval occurs in the other arachnids with a divided peltidium. VAN DER HAMMEN's (1989) account of palpigrade morphology does not explicitly mention such a furrow between leg coxae 2 and 3, and this character is probably hard to test here since the highly flexible body of these animals is only weakly sclerotised. In palpigrades the coxae of the pedipalps and first walking limbs are associated with a sclerite, and each of the successive pairs of limb coxae are associated with a corresponding separate plate (see e.g. BÖRNER 1904: fig. 4). Or to quote ROWLAND & SISSOM (1980: 76), "Following the deutotritosternum and lying between the second, third, and fourth pair of walking legs are the tetrasternum, pentasternum, and metasternum, respectively." Thus in palpigrades leg coxae 2, 3 and 4 are all to a certain extent 'free'. For schizomids, there is again no mention of a specific furrow between legs 2 and 3 in VAN DER HAMMEN (1989). The classic and detailed study of BÖRNER (1904: fig. 2) is likewise circumspect about a specific zone of flexibility here.

A cephalosoma or a divided carapace?

But is 'Cephalosomata' a clade or a grade? We suggest that both acariform mites and camel spiders share an anterior tagma bearing four pairs of appendages which is essentially separated from the rest of the body by a membranous zone for which the mite term 'sejugal furrow' is available and appropriate. WEYGOLDT & PAULUS (1979) and SHULTZ (2007: characters 6–7) interpreted both a divided carapace (in camel spiders, palpigrades and schizomids) and the presence of a

sejugal furrow (in acariform mites) as derived conditions; justifying polarity by using *Limulus* (Xiphosura) – with its large, unitary prosomal dorsal shield and lack of ventral segmental differentiation – as the outgroup.

Further down the euarthropod tree we encounter alternative outgroups such as sea spiders (Pycnogonida) in which the fundamental tagmosis is between a so-called cephalosoma, bearing four pairs of appendages (VILPOUX & WALOSZEK 2003: Fig. 13), and the successive separate segments of the trunk. This cephalosoma is segmentally homologous to the anterior tagma of camel spiders, acariform mites and palpigrades (DUNLOP & ARANGO 2005: Fig. 5). Adopt sea spiders as the outgroup and the 'divided carapace' / sejugal furrow could be interpreted as a plesiomorphic state; retained from an earlier grade of organisation. This is essentially the argument put forwards by BERNARD (1886) and KÄSTNER (1932, 1952) who thought that the divided camel spider prosoma revealed the original arachnid morphology. Authors such as REMANE (1962: 214) have argued that the arachnid prosoma fundamentally consists of a four-segmented head region – bearing the chelicerae, palps and legs 1 and 2 – plus two additional segments bearing leg pairs 3 and 4 respectively. Further discussion can be found in KRAUS (1976), who again favoured the idea that separate prosomal elements reflect a '4+2' arachnid groundplan, or WEYGOLDT & PAULUS (1979) who preferred instead to interpret these divisions as derived and homoplastic features, possibly adapted for increasing prosomal mobility.

Finally, we should mention a series of early Palaeozoic arthropods expressing raptorial anterior limbs – the 'great appendage' arthropods, or Megacheira in some schemes – which some authors interpret as stem-group Chelicerata (CHEN et al. 2004). These fossils also appear to preserve an anterior body tagma bearing four pairs of appendages which authors such as Waloszek and co-workers have termed the 'euarthropod head' (see also REMANE's 1962 hypothesis) and which they interpret as a fundamental part of the body plan in early arthropods (cf. CHEN 2009: Fig. 11). Using megacheirans as an outgroup would again polarise the tagmosis pattern of mites, camel spiders (and palpigrades?) as a plesiomorphic, groundplan, character state for arachnids. In this scenario, a unitary prosomal dorsal shield (or peltidium) emerges as a derived character state; perhaps even homoplastic across Arachnida.

Acknowledgements

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Spiders (Araneae) of Chernivtsi City (Ukraine)

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Abstract: The spider fauna of buildings and other urban habitats (city parks, green areas of industrial enterprises, and housing estates) of Chernivtsi city was surveyed. In the period 2002-2011, 212 species belonging to 26 families were recorded. Previous studies found a total of 173 species of spiders belonging to 26 families from the territories which are now included in the city limits of Chernivtsi. Currently, the total spider species list for Chernivtsi includes 260 species of 30 families, of which 125 species (21 families) were recorded both by earlier researchers and by ourselves. The most important reasons for changes in urban spider assemblages are as follows: species habitat change, introduction of alien species, and description of new species unknown in the late 19th – early 20th centuries.

Key words: retrospective analysis, species composition, urban ecosystems

Urban habitats are becoming increasingly dominated by human-related factors and processes (GRIMM et al. 2000); yet most ecological studies focus on more natural and less human-altered ecosystems (SHOCHAT et al. 2004). Recent studies of the effect of urbanization on species composition show that urbanization can increase or decrease species richness, depending on the taxonomic group, the spatial scale of analysis, and the intensity of urbanization (MCKINNEY 2008). Certain studies focusing on changes in spider assemblages in urban habitats were undertaken during the last decades (KRZYŻANOWSKA et al. 1981, ANTOV et al. 2004, SHOCHAT et al. 2004, HORVÁTH et al. 2010, VARET et al. 2010). Yet, we do not know enough about the causes of changes in spider assemblages in urban environments. Some of them are due to alien spider species introduced to Europe (KOBELT & NENTWIG 2008). Habitat structure and productivity were shown to influence spider diversity and abundance in urban environments (SHOCHAT et al. 2004), as well as fragmentation of natural habitats due to urbanization (GIBBS & STANTON 2001, GIBB & HOCHULI 2002). However, changes in spider assemblages over time and under increasing urbanization are still poorly understood.

The aim of the present study is to conduct a retrospective analysis of the changes in spider assemblages in Chernivtsi by a comparison of the results of our 10-year research (2002-2011) with the literature-derived data for the period 1874-1986.

Material and methods

The material treated in this paper was collected in 2002-2011 within Chernivtsi city. Chernivtsi is the administrative centre of the Chernivtsi Region in western Ukraine; its population is 240,000 people. The city's area is 153 km^2 (the range of longitude is N 48°14'44.56"-48°23'53.55"; the range of latitude is E 25°49'59.96"-26°2'5.46"; the range of altitude is 151-510 m a.s.l.). The city is situated on the river Prut. According the physiographic subdivision by MARYNYCH et al. (2003), this area belongs to the Ukrainian Carpathians Mountain Region. We collected the material using different methods (hand collecting, pitfall traps, sweeping with a net, and beating) in various urban habitats such as forests and open patches at the city's edge, city parks, green areas of industrial enterprises and housing estates, and buildings. The largest fraction of spider specimens from semi-natural habitats in Chernivtsi was collected by pitfall traps. The traps, with a diameter of 7 cm, were placed in a line, about 6 meters apart from each other and contained ethylene glycol as a preservative; traps were opened during the schedules shown below, and were emptied twice a month.

The study localities were as follows:

Tsetsyno Landscape Conservation Area, located at the city's edge: This is a forest dominated by *Fagus sylvatica* L. partly mixed with *Quercus petraea* Liebl. and *Quercus robur* L. and open patches dominated by Poaceae. The trapping periods were, in both habitats,

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24.04.-04.05.2008 (15 traps) and 02.04.-29.05.2009 (30 traps).

Four city parks: Zhovtnevyi Park, Shevchenko Park, Fedkovych Park and Schiller Park are characterized mostly by artificially planted trees: *Acer*, *Carpinus*, *Tilia*, *Fraxinus*, *Picea*, *Betula*, *Robinia pseudoacacia* L., *Aesculus hippocastanum* L. The trapping periods were 04.-10.07.2006 (15 traps in Schiller Park) and 02.05.-02.12.2007 (15 traps in each of the four aforementioned parks).

Green areas of seven industrial enterprises: Chemical Plant, Mechanical Repair Plant, Brickyard # 1, Industria Factory, Bus-trolley Company, Electronmash Plant, Quartz Plant. The trapping periods were 28.04.-28.05.2008 (15 traps in the area of each enterprise).

Other urban habitats such as public gardens in Cathedral Square, Korduby str., Toliati str., Pidkovy str.; green areas on the grounds of the Biological Faculty of Chernivtsi University and College # 15; the Botanic Garden of Chernivtsi University: The trapping periods were 09.07.-27.07.2007 and 07.05.-05.06.2008 (15 traps in each locality).

Orchards containing fruit trees and beds of strawberries: The trapping periods were 08.04.-10.06.2002 (30 traps).

A description of the city parks was given by FEDORIAK et al. (2010a); the green areas of industrial enterprises and other urban habitats were analyzed by FEDORIAK et al. (2010b). A total of 2496 adults and 499 juveniles (of which 155 were identifiable to species level) were captured by pitfall traps from the 21 localities.

We also collected 499 adults and 1191 juveniles (231 identifiable to species level) inhabiting the trees *Aesculus hippocastanum* L., *Tilia cordata* Mill., *Picea abies* (L.) Karst, *Thuja occidentalis* L., and *Acer negundo* L. during the periods May to October 2006-2008 from the aforementioned city parks and from planted trees on both sides of the streets J. Hlavka, Golovna, Chervonoarmiyska, Kyiivska, Komarova, Korduby, L. Ukrainka, and Y. Fedkovych. Spiders from tree trunks included 197 adults and 576 juveniles (100 identifiable to species level) captured by hand collecting. A total of 302 adults and 615 juveniles (131 identifiable to species level) were collected from lower branches of trees by beating. Other spider specimens from different trees − 171 adults and 534 juveniles (79 identifiable to species level) − were collected in localities such as Tsetsyno Landscape Conservation

Area, the Botanic Garden of Chernivtsi University, and public gardens in Cathedral Square and Chervonoarmiyska str.

A total of 43 adults and 647 juveniles (159 identifiable to species level) were obtained from birds' nests collected from trees in different parts of the city. Additionally we used collecting methods such as hand-sorting litter samples and sweeping from nearly all the mentioned localities at different time periods as well as from the bank sediments of the river Prut; using these methods we caught a total of 476 adult specimens.

In this paper, we also include material collected from different indoor habitats such as the aforementioned industrial enterprises, multi-storey apartment buildings, and greenhouses. The characteristics of buildings and study methods have been already published by FEDORIAK et al. (2010c). A total of 7959 specimens of spiders from buildings were collected: 2995 adults and 4964 juveniles (4464 identifiable to species level).

We also assembled data on urban spiders inhabiting Chernivtsi on the basis of all available literature records for the period of 1874-1986 (NOWICKI 1874, ROŞCA 1930, 1935, 1936a, 1936b, 1937, 1938, LEGOTAI 1964, CHUMAK & PICHKA 1982, CHUMAK 1986). We included the species recorded by earlier researchers both from Chernivtsi and from settlements such as Tsetsyno, Hot Urban, Klokuchka, Rosha, and Zhuchka, which later became parts of Chernivtsi.

NOWICKI (1874) recorded 26 species without mentioning details of collecting methods and habitats. ROŞCA (1930-1938) recorded 159 species from Chernivtsi, as the area of the city is currently defined. A description of habitats and collecting methods was not provided, but the author mentioned such habitats as the beech forest on Mt. Tsetsyno, banks of the river Prut, the Botanical Garden, and buildings. ROŞCA (1936) provided each species with information on the 'ecological group' to which it belonged, depending on its habitat preferences and other peculiarities: terrestrial forms, plant forms, domestic forms, and hydrophilic forms. Recently, we discussed the distribution of spiders in Chernivtsi according to Roşca's publications (FEDORIAK & ZHUKOVETS 2011). LEGOTAI (1964) mentioned two species from Chernivtsi without any details of collecting methods and habitats. CHUMAK & PICHKA (1982) and CHUMAK (1986) recorded three spider species collected in greenhouses of the Botanic Garden of Chernivtsi

from plants, walls, and the soil surface.

The scientific nomenclature follows Platnick (2012). Invalid species names in the literature-derived data are omitted from the analysis (appendix 1). *Lephtyphantes collinus* (L. Koch, 1872) (Roşca 1936) is considered to be *Megaleptyphantes pseudocollinus* Saaristo, 1997 (see Saaristo 1997). According to the division by Klausnitzer (1987), all urban habitats are subdivided into two large groups (buildings and other terrestrial habitats). Thus we analyzed spiders inhabiting buildings (indoor habitats) separately from those inhabiting other (outdoor) habitats.

No publications of earlier researchers contained precise numerical data on abundances of the recorded species. Roşca (1936, 1937) provided almost every species with information on how often it was observed in Bukovyna: 'very often', 'often', 'not often' or 'rarely'. Therefore we applied only a presence/absence comparison. When discussing our own material, in order to separate the most abundant species in each of the treated spider assemblages, we followed Stöcker & Bergmann (1977) with dominance classes such as: 31.7-100 % – eudominant; 10.1-31.6 % – dominant; 3.2-10.0 % – subdominant; 1.1-3.1 % – recedent; less than 1 % – subrecedent. All calculations in this paper relate to adult specimens.

Results

During the period 2002-2011, we collected a total of 14878 specimens representing 212 species belonging to 114 genera and 26 families. The commonest families were: Linyphiidae (25.9 %), Theridiidae (11.3 %), Lycosidae (10.4 %), Thomisidae (6.1 %), Araneidae (6.1 %), Agelenidae (6.1 %), and Salticidae (5.7 %). In Table 1 the most abundant spider species from the soil surface (epigeal fauna), trees, and buildings of Chernivtsi are sorted in descending abundance according to their localities.

In total, 107 **epigeal** species were captured using pitfall traps from different green areas of Chernivtsi. *Pardosa lugubris* sensu stricto is the most abundant species of the epigeal spider fauna (19.6 % of adults) dominating in city parks, public gardens and other green territories; yet, it is the eudominant species in the industrial enterprises areas sampled. Prokopenko (2000) mentioned *P. lugubris* as a dominant species in five parks of Donetsk (Ukraine). However, it was not abundant in other localities we surveyed – only three specimens were trapped from the Tsetsyno Landscape Conservation Area and from the orchards. The cumulative percentage of *Pachygnatha degeeri*

(Tetragnathidae) was nearly the same as for *P. lugubris* (19.5 %). *P. degeeri* is the only species that dominates the epigeal spider faunas of all the sampled localities, apart from the orchards. *Alopecosa pulverulenta* (5.1 %) is the subdominant species of the Tsetsyno Landscape Conservation Area (5.7 %), green areas of industrial enterprises (7.2 %), and the orchards (6.0 %). *Pardosa agrestis* (4.6 %) is distributed very unevenly in the investigated sites: 42.2 % of the adults were trapped from the orchards, 2.8 % – from the Tsetsyno Landscape Conservation Area, and 0.3 % – from the city parks. Some other Lycosidae species were also abundant in the epigeal fauna of Chernivtsi city (in descending cumulative percentage): *Pardosa prativaga* (4.7 %), *P. paludicola* (3.7 %), *Trochosa terricola* (3.5 %), *T. ruricola* (3.3 %). The cumulative percentages of the other species did not reach 3 % of the adult spider specimens captured by pitfall traps in the sampled localities. Of the representatives of other families some linyphiids, such as *Diplostyla concolor* (2.6 %) and *Diplocephalus picinus* (1.8 %), and thomisids, *Xysticus cristatus* (2.2 %), were also abundant in the epigeal spider fauna of Chernivtsi.

Enoplognatha ovata (42.5 %) is the most abundant species inhabiting **trees** of Chernivtsi, followed by *Steatoda bipunctata* (5.8 %), *Lepthyphantes minutus* (4.6 %), *Platnickina tincta* (3.6 %), and *Entelecara acuminata* (3.1 %). We collected these species both from tree crowns and trunks. *Enoplognatha ovata* prefers crowns, while *S. bipunctata, L. minutus, P. tincta,* and *E. acuminata* were found mainly on tree trunks. Some other species were abundant (>3 %) on tree trunks: *Moebelia penicillata, Clubiona lutescens, Erigone dentipalpis, Hylyphantes graminicola,* and *Hypomma cornutum* – in the city parks, while *Micaria subopaca, Clubiona brevipes, Linyphia triangularis, Parasteatoda tepidariorum, Salticus zebraneus, Neottiura bimaculata,* and *Dictyna uncinata* – in the trees planted on the street margins.

During our research we collected a total of 83 species (7959 spiders) from **indoor habitats** of Chernivtsi, of which *Pholcus phalangioides* (50.2 %) was the most abundant species in buildings of different types. Cumulative percentages of *Parasteatoda tepidariorum* (11.7 %), *Steatoda castanea* (5.9 %), *Tegenaria domestica* (2.9 %), *Steatoda triangulosa* (2.8 %), *Pholcus alticeps* (2.8 %), *Ph. ponticus* (2.6 %), *Steatoda grossa* (2.5 %), *Ph. opilionoides* (2.4 %), *Spermophora senoculata* (2.3 %), and *Lepthyphantes leprosus* (2.1 %) were higher than those of the other species in the buildings of Chernivtsi.

Tab. 1: The most abundant spider species from Chernivtsi. Numbers in brackets show relative abundance (% of adults).

Locality	Dominance classes		
	Eudominant	Dominant	Subdominant
Epigeal fauna			
Tsetsyno Landscape Conservation Area		*Pachygnatha degeeri* (25.2)	*Pardosa paludicola* (9.1) *Trochosa terricola* (8.5) *Alopecosa pulverulenta* (5.7) *Pardosa alacris* (5.3) *Pardosa palustris* (5.0) *Trochosa ruricola* (4.9) *Xysticus cristatus* (4.1) *Inermocoelotes inermis* (3.8) *Inermocoelotes falciger* (3.4)
City parks		*Pachygnatha degeeri* (19.2) *Pardosa lugubris* (18.7) *Diplostyla concolor* (16.0)	*Erigone dentipalpis* (6.2) *Ozyptila praticola* (4.9) *Diplocephalus cristatus* (4.3) *Centromerus sylvaticus* (3.5)
Green areas of industrial enterprises	*Pardosa lugubris* (49.1)	*Pachygnatha degeeri* (18.0) *Pardosa prativaga* (13.5)	*Alopecosa pulverulenta* (7.2) *Pardosa amentata* (5.0)
Other urban habitats	*Diplocephalus picinus* (32.0)	*Pachygnatha degeeri* (22.4) *Pardosa lugubris* (16.8)	*Trochosa ruricola* (4.0) *Tenuiphantes flavipes* (3.2)
Orchards	*Pardosa agrestis* (42.2)	*Xerolycosa miniata* (14.6)	*Pardosa palustris* (9.5) *Alopecosa pulverulenta* (6.0) *Trochosa ruricola* (6.5) *Xysticus cristatus* (6.0)
Trees			
City parks	*Enoplognatha ovata* (41.1)		*Platnickina tincta* (4.9) *Steatoda bipunctata* (4.9) *Entelecara acuminata* (4.6)
Sides of streets	*Enoplognatha ovata* (39.9)		*Micaria subopaca* (7.5) *Steatoda bipunctata* (6.4) *Platnickina tincta* (4.6) *Entelecara acuminata* (3.5)
Buildings			
Greenhouses	*Pholcus phalangioides* (34.1) *Parasteatoda tepidariorum* (32.1)	*Pholcus opilionoides* (16.3)	*Parasteatoda tabulata* (5.0)
Buildings of the Industrial enterprises	*Pholcus phalangioides* (46.9)	*Parasteatoda tepidariorum* (12.9)	*Pholcus ponticus* (7.8) *Tegenaria domestica* (7.2) *Steatoda triangulosa* (4.0) *Pholcus alticeps* (3.8) *Megalepthyphantes nebulosus* (3.4) *Steatoda castanea* (3.2)
Apartment buildings	*Pholcus phalangioides* (55.4)		*Steatoda castanea* (8.7) *Parasteatoda tepidariorum* (6.6) *Steatoda grossa* (4.3) *Spermophora senoculata* (4.0)

Spiders recorded from Chernivtsi during 1874-1986 were represented by 173 species, belonging to 96 genera and 26 families (Tab. 2, appendix 2). The commonest families were as follows: Linyphiidae (24.3 %), Lycosidae (13.9 %), Thomisidae (9.8 %), Theridiidae (9.2 %), Araneidae (6.9 %), and Salticidae (6.6 %). Nine species were recorded from buildings and 166 from other urban habitats.

Taking into account the information provided by earlier researchers and that resulting from own work, the total spider fauna of Chernivtsi city consists of 260 species from 131 genera and 30 families (appendix 2). Of these, 125 species were mentioned in the literature and occurred in our data. We found 87 species that were not previously reported from Chernivtsi, whereas 48 species of those reported earlier were not found during our survey. Obviously, there were 'exclusive species' that were mentioned only in the literature or occurred only in our data. The share of 'exclusive species' is higher at present (Tab. 2); the majority of them belong to Linyphiidae, Lycosidae, Theridiidae, Thomisidae, Gnaphosidae, and Agelenidae.

Differences between the historical records and our data were found in species numbers of various families (Tab. 2). In 15 families the number of species increased by 50 %. We noticed the greatest increase in species numbers for Gnaphosidae (4.5-fold), Dictynidae (2-fold), Agelenidae (1.6-fold), and Theridiidae (1.5-fold). Species numbers remained the same in eight families. In comparison with the historical data, we found a smaller number of species of the following three families: Thomisidae, Lycosidae, and Miturgidae. We found no species of Cybaeidae, Sparassidae, Uloboridae, and Zoridae in the area of Chernivtsi, whereas earlier researchers recorded one species from each of these families.

Discussion

ROȘCA (1936) singled out synanthropic species ('domicole') as a separate ecological group of spiders. Overall, he mentioned seven species as synanthropic. Of these, following Roșca's terminology, four species were collected 'very often': viz., *Pholcus opilionoides*, *Ph. phalangioides*, *Steatoda bipunctata*, and *S. castanea*; three were collected 'often': viz., *Tegenaria atrica*, *T. domestica,* and *Steatoda grossa*. We collected all these species in buildings in Chernivtsi. Percentages of all of them, except *S. bipunctata*, are higher indoors than in any of the semi-natural habitats such as city parks, lawns. At the same time, ROȘCA (1936) regarded *Parasteatoda tepidariorum* as a species living in trees

Tab. 2: Total numbers of species of different families collected during 2002-2011 (our data) and recorded during 1874-1986 (historical, literature-derived data) from Chernivtsi.

Family	Our data	Historical data	Exclusive species	
			Our data	Historical data
Agelenidae	13	8	6	1
Amaurobiidae	2	2	0	0
Anyphaenidae	1	1	0	0
Araneidae	13	12	3	2
Clubionidae	7	6	2	1
Corinnidae	1	1	0	0
Cybaeidae	0	1	0	1
Dictynidae	6	3	3	0
Dysderidae	3	1	2	0
Gnaphosidae	9	2	7	0
Hahniidae	1	0	1	0
Linyphiidae	55	42	28	15
Liocranidae	1	1	0	0
Lycosidae	22	24	7	9
Mimetidae	2	2	0	0
Miturgidae	1	2	1	2
Nesticidae	1	0	1	0
Philodromidae	6	6	2	2
Pholcidae	5	2	3	0
Pisauridae	1	1	0	0
Salticidae	12	11	3	2
Scytodidae	1	0	1	0
Segestriidae	1	1	0	0
Sparassidae	0	1	0	1
Tetragnathidae	10	8	3	1
Theridiidae	24	16	10	2
Thomisidae	13	17	3	7
Uloboridae	0	1	0	1
Zodariidae	1	0	1	0
Zoridae	0	1	0	1
Totals	**212**	**173**	**87**	**48**

(his ecological group – 'arboricole') and noted that it was very common in bushes and trees. In our samples, only 0.5 % of the specimens collected from parks and other semi-natural habitats of Chernivtsi belong to *P. tepidariorum*, with the species being much more

abundant in synanthropic habitats (inside buildings; see Tab. 1). Regarding other synanthropic species that are now abundant indoors, Roşca (1936) considered *Lepthyphantes leprosus* to occur under stones ('lapidicole'); *Pholcus alticeps*, *Ph. ponticus,* and *Steatoda triangulosa* were not reported by earlier researchers.

Among 'arboricole' species, seven were collected 'very often' (Roşca 1936): viz., *Metellina segmentata, Parasteatoda simulans, Parasteatoda tepidariorum, Philodromus dispar, Tetragnatha obtusa, Theridion pictum,* and *Theridion pinastri.* We collected all of them except *P. tepidariorum* (see above) and *Metellina segmentata* more often from trees than from other habitats in Chernivtsi. Thirteen 'arboricole' species were collected 'often' (Roşca 1936): viz., *Ero aphana, Ero furcata, Cryptachaea riparia, Neottiura bimaculata, Paidiscura pallens, Parasteatoda lunata, Philodromus poecilus, Platnickina tincta, Salticus scenicus, Sitticus pubescens, Tetragnatha nigrita, Thanatus arenarius, Theridion varians.* Of these, four species (*P. poecilus, T. arenarius, T. nigrita,* and *P. lunata*) were not found during our survey; the others with two exceptions (*S. scenicus* and *P. pallens*) were found mainly in trees.

Blick (2011) recently published a list of the 20 most abundant spider species on tree trunks in German forests; we captured ten of the mentioned species from trees in Chernivtsi: *Anyphaena accentuata, Diplocephalus cristatus*, *Drapetisca socialis*, *Enoplognatha ovata*, *Lathys humilis, Lepthyphantes minutus*, *Meioneta innotabilis*, *Moebelia penicillata, Philodromus collinus*, and *Xysticus audax.*

In general, Roşca (1936, 1937) recorded 152 species from outdoor habitats in the present area of Chernivtsi. Of these, he specified that 22 species were collected 'very often', 112 – 'often', 12 – 'not often', and two – 'rarely'; for four species such information was not provided. According to our data, 183 species inhabit semi-natural habitats in Chernivtsi. However, of the species mentioned by Roşca (1936) from the 'very often' and 'often' categories we failed to locate 15 species: *Coelotes atropos, Clubiona caerulescens, Centromerus ludovici, Hypomma bituberculatum, Erigone atra, Mansuphantes mansuetus, Frontinellina frutetorum, Neriene peltata, Alopecosa trabalis, Pirata piraticus, Thanatus arenarius, Evarcha laetabunda, Zora pardalis, Xysticus luctuosus* and, *Xysticus lanio.*

Thus, it seems fair to conclude that the spider assemblages of these areas have undergone some changes. Several reasons are likely to be responsible for such changes:

1. **Species habitat change.** The spider fauna of urban green areas differs from that of natural and even suburban habitats (Krzyżanowska et al. 1981, Shochat et al. 2004). Regarding our study area, some species were recorded by earlier researchers from the city, whereas we found them only outside the city. For example, we collected *Araeoncus humilis, Erigone atra,* and *Arctosa stigmosa* only on the banks of mountain rivers in the Chernivtsi Region (Evtushenko & Fedoriak 2003) and never from Chernivtsi itself. On the other hand, we collected certain species (e.g., *Inermocoelotes falciger, Histopona torpida, Drassyllus pusillus*) from Chernivtsi, whereas earlier researchers recorded them from a number of localities outside the city (Roşca 1930, 1936).

2. **Introduction of alien species.** Europe received at least 2000 small alien invertebrate species, including spiders, and most of them were introduced within the last 100 years (Kobelt & Nentwig 2008). We collected five adults of *Agelenopsis potteri* in buildings within Chernivtsi and seven more in other habitats of the city. *A. potteri* is a Nearctic species (Chamberlin & Ivie 1941) which was recorded from Kyrgyzstan, Russia, and Ukraine (Marusik & Kopponen 2000, Marusik et al. 2007, Prokopenko & Hoydyk 2006). We also trapped five adults of *Zodarion rubidum* on the grounds of Chernivtsi enterprises and one more in the city park (Fedoriak et al. 2010b, 2010c). *Z. rubidum* is spreading throughout Europe along railroads (Pekár 2002).

3. **Descriptions of new species unknown in the late 19th – early 20th centuries.** Of the 212 species we collected from Chernivtsi, five were described after 1930: *Pholcus alticeps* Spassky, 1932; *Saloca kulczynskii* Miller & Kratochvíl, 1939; *Parasteatoda tabulata* (Levi, 1980); *Enoplognatha latimana* Hippa & Oksala, 1982, and *Megaleptyphantes pseudocollinus* Saaristo, 1997. Obviously, these species could be recognised neither by Nowicki nor by Roşca, the researchers who undertook the most profound earlier inventories of the spider fauna.

Other reasons for the changes in the species assemblages of Chernivtsi spider fauna cannot be excluded: e.g., possible differences in the collection methods used by earlier researchers and by ourselves, or collections that were not taken from comparable sites.

Conclusions

Spiders are shown to be a species-rich group in urban habitats of Chernivtsi city (212 spider species belonging to 114 genera and 26 families were found during 2002-2011). This suggests the necessity of surveying urban habitats while estimating spider biodiversity of different regions.

Pardosa lugubris and *Pachygnatha degeeri* were the most abundant species of the epigeal spider fauna, *Enoplognatha ovata* of trees, and *Pholcus phalangioides* of the synanthropic spider fauna.

Differences in spider species composition between the data recorded in 1874-1986 and our own (2002-2011) may reflect changes in the spider fauna of Chernivtsi city as a result of the combination of several processes, namely: species habitat change, introduction of alien species and description of new species unknown in the late 19th – early 20th centuries.

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Appendix 1: List of invalid species names recorded during 1874-1986 from Chernivtsi.

Species	Citation	Notes
Porrhomma calypso (Bertkau, in Förster & Bertkau, 1883)	(Roşca 1930), (Roşca 1936)	Nomen dubium (PLATNICK 2012), we omitted it from the analysis
Aranea rayi var. *betulae* Sulz., *Aranea Rayi* Scop.	(Roşca 1936) (Roşca 1936)	Both species are considered to be *Araneus marmoreus* Clerck, 1757
Lycosa chelata O. F. Muller. *Lycosa lugubris* Walck.	(Roşca 1930) (Roşca 1930)	Both species are considered to be *Pardosa lugubris* (Walckenaer, 1802)
Tarentula andrenivora Walck. *Tarentula pulverulenta* Cl.	(Roşca 1930) (Roşca 1930)	Both species are considered to be *Alopecosa pulverulenta* (Clerck, 1757)
Xysticus cristatus L. Koch. *Xysticus viaticus* Linne.	(Roşca 1930) (Roşca 1930)	Both species are considered to be *Xysticus cristatus* (Clerck, 1757)

Appendix 2: List of spider species collected during 2002-2011 (our data) and recorded during 1874-1986 (historical, literature-derived data) from Chernivtsi. Names of the earlier researchers: N – Nowicki, R – Roşca, L – Legotai, Ch & P – Chumak & Pichka, Ch – Chumak.

Taxa	Our data, adults (ind.)		Historical data	
	Build-ings	Other habitats	Buildings	Other habitats
Agelenidae				
Agelena labyrinthica (Clerck, 1757)	2	4		R 1936
Agelenopsis potteri (Blackwall, 1846)	5	7		
Allagelena gracilens (C.L. Koch, 1841)	1			R 1936
Coelotes atropos (Walckenaer, 1830)				R 1936
Histopona torpida (C.L. Koch, 1837)		10		
Inermocoelotes falciger (Kulczyński, 1897)		34		
Inermocoelotes inermis (L. Koch, 1855)		43		R 1936
Malthonica ferruginea (Panzer, 1804)	10	3		R 1936
Malthonica pagana (C.L. Koch, 1840)	1			
Malthonica picta (Simon, 1870)	1			
Tegenaria agrestis (Walckenaer, 1802)	4	3		
Tegenaria atrica C.L. Koch, 1843	7		R 1936	
Tegenaria domestica (Clerck, 1757)	88	1	R 1936	
Tegenaria parietina (Fourcroy, 1785)	1	1		R 1936
Amaurobiidae				
Amaurobius ferox (Walckenaer, 1830)	8			R 1936
Callobius claustrarius (Hahn, 1833)		1		R 1936
Anyphaenidae				
Anyphaena accentuata (Walckenaer, 1802)	1	2		R 1936
Araneidae				
Araneus diadematus Clerck, 1757	8	4		R 1936
Araneus marmoreus Clerck, 1757	1	1		N 1874
Araneus quadratus Clerck, 1757	1			N 1874
Araneus saevus (L. Koch, 1872)		1		
Araneus sturmi (Hahn, 1831)				N 1874
Araneus triguttatus (Fabricius, 1793)		1		
Araniella cucurbitina (Clerck, 1757)		7		R 1936, L 1964
Araniella opisthographa (Kulczyński, 1905)	1			R 1936
Argiope bruennichi (Scopoli, 1772)		1		R 1936
Gibbaranea bituberculata (Walckenaer, 1802)				N 1874
Gibbaranea gibbosa (Walckenaer, 1802)		1		R 1937
Larinioides ixobolus (Thorell, 1873)	4	1		
Larinioides sclopetarius (Clerck, 1757)	1			N 1874
Mangora acalypha (Walckenaer, 1802)		4		R 1936
Singa nitidula C.L. Koch, 1844		3		R 1936
Clubionidae				
Clubiona brevipes Blackwall, 1841		6		
Clubiona caerulescens L. Koch, 1867				N 1874, R 1936
Clubiona comta C.L. Koch, 1839		14		
Clubiona germanica Thorell, 1871		1		R 1936
Clubiona lutescens Westring, 1851		14		R 1936
Clubiona marmorata L. Koch, 1866		1		N 1874
Clubiona neglecta O. P.–Cambridge, 1862		1		R 1936
Clubiona pallidula (Clerck, 1757)	1	4		R 1936
Corinnidae				
Phrurolithus festivus (C.L. Koch, 1835)		5		R 1936

Taxa	Our data, adults (ind.)		Historical data	
	Build-ings	Other habitats	Buildings	Other habitats
Cybaeidae				
Cybaeus angustiarum L. Koch, 1868				R 1936
Dictynidae				
Cicurina cicur (Fabricius, 1793)		3		R 1936
Dictyna arundinacea (Linnaeus, 1758)		6		
Dictyna civica (Lucas, 1850)	1			
Dictyna uncinata Thorell, 1856	1	10		R 1936
Lathys humilis (Blackwall, 1855)		4		R 1936
Nigma walckenaeri (Roewer, 1951)	4	1		
Dysderidae				
Dysdera crocata C.L. Koch, 1838		1		R 1936
Harpactea rubicunda (C.L. Koch, 1838)	6	1		
Harpactea saeva (Herman, 1879)		4		
Gnaphosidae				
Drassodes pubescens (Thorell, 1856)		1		
Drassyllus pusillus (C.L. Koch, 1833)		10		
Haplodrassus signifer (C.L. Koch, 1839)		2		
Haplodrassus silvestris (Blackwall, 1833)		1		R 1936
Micaria formicaria (Sundevall, 1831)		1		
Micaria nivosa L. Koch, 1866		1		
Micaria pulicaria (Sundevall, 1831)		4		
Micaria subopaca Westring, 1861		13		
Scotophaeus scutulatus (L. Koch, 1866)	3			R 1936
Hahniidae				
Hahnia nava (Blackwall, 1841)		4		
Linyphiidae				
Agyneta decora (O. P.-Cambridge, 1871)		3		
Araeoncus humilis (Blackwall, 1841)				R 1936
Bathyphantes gracilis (Blackwall, 1841)	3			
Bathyphantes nigrinus (Westring, 1851)	1	4		R 1936
Centromerita bicolor (Blackwall, 1833)		2		
Centromerus ludovici Bösenberg, 1899				R 1936
Centromerus sylvaticus (Blackwall, 1841)		13		R 1936
Ceratinella major Kulzyński, 1894		1		
Dicymbium nigrum (Blackwall, 1834)		10		R 1936
Dicymbium tibiale (Blackwall, 1836)		2		R 1936
Diplocephalus cristatus (Blackwall, 1833)		24		R 1936
Diplocephalus latifrons (O. P.-Cambridge, 1863)		4		
Diplocephalus picinus (Blackwall, 1841)		45		
Diplostyla concolor (Wider, 1834)	2	70		R 1936
Dismodicus bifrons (Blackwall, 1841)		1		
Drapetisca socialis (Sundevall, 1833)		1		N 1874, R 1936
Entelecara acuminata (Wider, 1834)	1	23	Ch & P 1982, Ch 1986	R 1936
Erigone atra Blackwall, 1833				R 1936
Erigone dentipalpis (Wider, 1834)	5	35		R 1930, R 1937
[1]*Erigone remota* L. Koch, 1869				R 1936
[2]*Erigone tirolensis* L. Koch, 1872				R 1936
Frontinellina frutetorum (C.L. Koch, 1834)				N 1874, R 1936
Helophora insignis (Blackwall, 1841)		6		
Hylyphantes graminicola (Sundevall, 1830)		5		R 1937
Hypomma bituberculatum (Wider, 1834)				R 1936

Taxa	Our data, adults (ind.)		Historical data	
	Build-ings	Other habitats	Buildings	Other habitats
Hypomma cornutum (Blackwall, 1833)		5		
Lepthyphantes leprosus (Ohlert, 1865)	64	1		R 1936
Lepthyphantes minutus (Blackwall, 1833)	1	36		
Linyphia hortensis Sundevall, 1830		6		R 1936
Linyphia triangularis (Clerck, 1757)	4	13		R 1936
Macrargus rufus (Wider, 1834)		1		
Mansuphantes mansuetus (Thorell, 1875)				R 1936
Megalepthyphantes nebulosus (Sundevall, 1830)	44	2		
Megalepthyphantes pseudocollinus Saaristo, 1997		2		R 1936
Meioneta fuscipalpa (C.L. Koch, 1836)		1		
Meioneta innotabilis (O. P.-Cambridge, 1863)		1		
Meioneta mollis (O. P.-Cambridge, 1871)		3		
Meioneta rurestris (C.L. Koch, 1836)	5	11		
Micrargus herbigradus (Blackwall, 1854)		1		
Micrargus subaequalis (Westring, 1851)		3		
Microlinyphia pusilla (Sundevall, 1830)		1		R 1936
Microneta viaria (Blackwall, 1841)		3		R 1936
Moebelia penicillata (Westring, 1851)	1	11		
Nematogmus sanguinolentus (Walckenaer, 1841)		2		
Neriene clathrata (Sundevall, 1830)	4	10		
Neriene emphana (Walckenaer, 1841)				R 1936
Neriene montana (Clerck, 1757)	7	9		R 1936
Neriene peltata (Wider, 1834)				R 1936
Neriene radiata (Walckenaer, 1841)				R 1936
Oedothorax apicatus (Blackwall, 1850)	1	1		R 1936
Oedothorax fuscus (Blackwall, 1834)				R 1936
Oedothorax insignis (Bösenberg, 1902)				R 1936
Oedothorax retusus (Westring, 1851)		1		
Pityohyphantes phrygianus (C.L. Koch, 1836)				N 1874
Porrhomma pygmaeum (Blackwall, 1834)		2		
Saloca kulczynskii Miller & Kratochvil, 1939		1		
Stemonyphantes lineatus (Linnaeus, 1758)		2		
Tapinocyba pallens (O. P.-Cambridge, 1872)		2		
Tenuiphantes cristatus (Menge, 1866)		1		R 1936
Tenuiphantes flavipes (Blackwall, 1854)		15		R 1936
Tenuiphantes mengei (Kulczyński, 1887)	1	7		R 1936
Tenuiphantes tenebricola (Wider, 1834)		3		R 1936
Tenuiphantes tenuis (Blackwall, 1852)	1	3		R 1936
Tenuiphantes zimmermanni (Bertkau, 1890)	3	1		R 1936
Thyreostenius parasiticus (Westring, 1851)	1	5		
Trematocephalus cristatus (Wider, 1834)		7		R 1936
Walckenaeria cucullata (C.L. Koch, 1836)		5		R 1936
Walckenaeria fusca Roşca, 1935				R 1936
Walckenaeria mitrata (Menge, 1868)		2		
Walckenaeria obtusa Blackwall, 1836		2		R 1936
Liocranidae				
Agroeca brunnea (Blackwall, 1833)		1		R 1936
Lycosidae				
Alopecosa accentuata (Latreille, 1817)		4		N 1874, R 1930
Alopecosa barbipes (Sundevall, 1833)				R 1936
Alopecosa cuneata (Clerck, 1757)		18		

Taxa	Our data, adults (ind.)		Historical data	
	Build-ings	Other habitats	Buildings	Other habitats
Alopecosa pulverulenta (Clerck, 1757)		132		R 1936
Alopecosa roeweri (Roşca, 1937)				R 1937
Alopecosa trabalis (Clerck, 1757)				N 1874, R 1936
Arctosa cinerea (Fabricius, 1777)		2		N 1874
Arctosa figurata (Simon, 1876)				R 1936
Arctosa lutetiana (Simon, 1876)				R 1936
Arctosa stigmosa (Thorell, 1875)				R 1936
Aulonia albimana (Walckenaer, 1805)		4		
Lycosa singoriensis (Laxmann, 1770)				N 1874, R 1936
Pardosa agrestis (Westring, 1861)	1	115		R 1936
Pardosa agricola (Thorell 1856)		1		
Pardosa alacris (C.L. Koch, 1833)		53		N 1874
Pardosa amentata (Clerck, 1757)	1	78		R 1936
Pardosa fulvipes (Collett, 1876)		8		
Pardosa lugubris (Walckenaer, 1802)		503		R 1936
Pardosa monticola (Clerck, 1757)		1		
Pardosa nigriceps (Thorell, 1856)		1		
Pardosa paludicola (Clerck, 1757)		93		R 1936
Pardosa palustris (Linnaeus, 1758)	1	74		R 1936
Pardosa prativaga (L. Koch, 1870)	1	122		R 1930
Pardosa pullata (Clerck, 1757)		32		R 1936
Pardosa sphagnicola (Dahl, 1908)		1		R 1936
Pirata piraticus (Clerck, 1757)		6		R 1936
Piratula hygrophila (Thorell, 1872)				R 1936
Trochosa robusta (Simon, 1876)				R 1936
Trochosa ruricola (De Geer, 1778)	3	88		R 1936
Trochosa terricola Thorell, 1856		89		R 1936
Xerolycosa miniata (C.L. Koch, 1834)		32		
Mimetidae				
Ero aphana (Walckenaer, 1802)		5		R 1936
Ero furcata (Villers, 1789)		1		R 1936
Miturgidae				
Cheiracanthium erraticum (Walckenaer, 1802)				R 1936
Cheiracanthium mildei L. Koch, 1864	12			
Cheiracanthium oncognathum Thorell, 1871				R 1936
Nesticidae				
Nesticus cellulanus (Clerck, 1757)	13			
Philodromidae				
Philodromus albidus Kulczyński, 1911	1	5		
Philodromus aureolus (Clerck, 1757)	1	1		R 1936
Philodromus cespitum (Walckenaer, 1802)	2	3		R 1936
Philodromus collinus C.L. Koch, 1835		2		
Philodromus dispar Walckenaer, 1826		3		R 1936
Philodromus poecilus (Thorell, 1872)				N 1874, R 1936
Thanatus arenarius L. Koch, 1872				R 1936
Tibellus oblongus (Walckenaer, 1802)		1		R 1936
Pholcidae				
Pholcus alticeps Spassky, 1932	85			
Pholcus opilionoides (Schrank, 1781)	72	3	R 1936	
Pholcus phalangioides (Fuesslin, 1775)	1503	1	R 1936, Ch & P 1982	

Taxa	Our data, adults (ind.)		Historical data	
	Build-ings	Other habitats	Buildings	Other habitats
Pholcus ponticus Thorell, 1875	77			
Spermophora senoculata (Duges, 1836)	69			
Pisauridae				
Pisaura mirabilis (Clerck, 1757)	1	10		R 1936
Salticidae				
Asianellus festivus (C.L. Koch, 1834)		5		N 1874, R 1937
Ballus chalybeius (Walckenaer, 1802)		1		N 1874, R 1936
Evarcha arcuata (Clerck, 1757)		1		R 1936
Evarcha falcata (Clerck, 1757)		1		R 1936
Evarcha laetabunda (C.L. Koch, 1846)				R 1936
Heliophanus auratus C.L. Koch, 1835		2		R 1937
Heliophanus cupreus (Walckenaer, 1802)		2		R 1936
Heliophanus flavipes (Hahn, 1832)		2		
Heliophanus tribulosus Simon, 1868				R 1936
Myrmarachne formicaria (De Geer, 1778)	1			R 1936
Salticus scenicus (Clerck, 1757)	1	2		R 1936
Salticus zebraneus (C.L. Koch, 1837)		7		
Sibianor aurocinctus (Ohlert, 1865)		2		
Sitticus pubescens (Fabricius, 1775)	3	1		R 1936
Scytodidae				
Scytodes thoracica (Latreille, 1802)	18			
Segestriidae				
Segestria senoculata (Linnaeus, 1758)	1	1		R 1936
Sparassidae				
Micrommata virescens ornata (Walckenaer, 1802)				N 1874
Tetragnathidae				
Metellina mengei (Blackwall, 1870)	4	1		R 1936
Metellina segmentata (Clerck, 1757)	5	2		R 1936
Pachygnatha clercki Sundevall, 1823	1	3		R 1936
Pachygnatha degeeri Sundevall, 1830	3	517		R 1936
Pachygnatha listeri Sundevall, 1830		12		
Tetragnatha dearmata Thorell, 1873		2		
Tetragnatha extensa (Linnaeus, 1758)		1		R 1936
Tetragnatha montana Simon, 1874		6		R 1936
Tetragnatha nigrita Lendl, 1886				R 1936
Tetragnatha obtusa C.L. Koch, 1837	1	4		R 1936
Tetragnatha pinicola L. Koch, 1870	1			
Theridiidae				
Asagena phalerata (Panzer, 1801)		5		
Cryptachaea riparia (Blackwall, 1834)		1		R 1936
Dipoena melanogaster (C.L. Koch, 1837)		3		
Enoplognatha latimana Hippa & Oksala, 1982		5		
Enoplognatha ovata (Clerck, 1757)	2	590		R 1936, L 1958
Enoplognatha thoracica (Hahn, 1833)		1		
Episinus angulatus (Blackwall, 1836)	1			
Neottiura bimaculata (Linnaeus, 1767)		9		R 1936
Ohlertidion ohlerti (Thorell, 1870)				R 1936
Paidiscura pallens (Blackwall, 1834)		1		R 1936
Parasteatoda lunata (Clerck, 1757)				R 1936
Parasteatoda simulans (Thorell, 1875)	28	10		R 1936
Parasteatoda tabulata (Levi, 1980)	60	1		

Taxa	Our data, adults (ind.)		Historical data	
	Build-ings	Other habitats	Buildings	Other habitats
Parasteatoda tepidariorum (C.L. Koch, 1841)	349	18	Ch & P 1982	R 1936
Phylloneta impressa (L. Koch, 1881)	3	1		R 1936
Platnickina tincta (Walckenaer, 1802)	3	28		N 1874, R 1936
Robertus arundineti (O. P.- Cambridge, 1871)		2		
Steatoda albomaculata (De Geer, 1778)		1		
Steatoda bipunctata (Linnaeus, 1758)	14	43	R 1936	
Steatoda castanea (Clerck, 1757)	178	1	R 1936	
Steatoda grossa (C.L. Koch, 1838)	76	1	R 1936	
Steatoda triangulosa (Walckenaer, 1802)	85	1		
Theridion mystaceum L. Koch, 1870		2		
Theridion pictum (Walckenaer, 1802)		1		R 1936
Theridion pinastri L. Koch, 1872	1	2		R 1936
Theridion varians Hahn, 1833	2	13		N 1874, R 1936
Thomisidae				
Diaea dorsata (Fabricius, 1777)		1		R 1936
Ebrechtella tricuspidata (Fabricius, 1775)		4		R 1936
Misumena vatia (Clerck, 1757)		2		R 1936
Ozyptila atomaria (Panzer, 1801)		3		
Ozyptila praticola (C.L. Koch, 1837)	1	36		R 1930
Ozyptila pullata (Thorell, 1875)				R 1936
Ozyptila rauda Simon, 1875		3		
Pistius truncatus (Pallas, 1772)				N 1874
Runcinia grammica (C.L. Koch, 1837)				R 1936
Synema globosum (Fabricius, 1775)				N 1874
Tmarus piger (Walckenaer, 1802)				N 1874
Xysticus acerbus Thorell, 1872		24		R 1936
Xysticus audax (Schrank, 1803)		6		R 1936
Xysticus bifasciatus C.L. Koch, 1837		7		R 1936
Xysticus cristatus (Clerck, 1757)		57		R 1936
Xysticus erraticus (Blackwall, 1834)		1		
Xysticus kochi Thorell, 1872		45		R 1936
Xysticus lanio C.L. Koch, 1835				N 1874, R 1936
Xysticus luctuosus (Blackwall, 1836)				R 1936
Xysticus ulmi (Hahn, 1831)		5		R 1936
Uloboridae				
Hyptiotes paradoxus (C.L. Koch, 1834)				N 1874
Zodariidae				
Zodarion rubidum Simon, 1914		6		
Zoridae				
Zora pardalis Simon, 1878				R 1936
Number of species in each category	**83**	**192**	**9**	**166**
Totals (our data and historical data)	**212**		**173**	
Total	**260**			

[1]*Erigone remota* and [2]*Erigone tirolensis* are recorded from Chernivtsi (Roşca 1936) with a note that they were found on the bank of the Prut river in a pile of rubbish and were probably transported from somewhere else.

Maintenance of polymorphism in the orb weaving spider species *Agalenatea redii* (Araneae, Araneidae)

Catherine Geay, Raymond Leborgne, Olivier François & Alain Pasquet

Abstract: The maintenance of polymorphism within populations may be the consequence of several elements of species life history such as use of space, activity rhythms, predation, parasitism and reproduction. The present study focuses on the latter aspect using an orb weaving spider, *Agalenatea redii*, which presents five different morphs of the opisthosoma pattern in the adult stage. Over the course of four years, from 2008 to 2011, adult spiders (males, females and pairs) were observed at different sites. In 2011, we also conducted a six-week survey of a single population, observing the number of spiders of each morph and the morph of paired spiders. We collected field data on the spatial and temporal distribution of spiders based on their sex and morph. Using a distance analysis, we compared the field distribution with a simulated one in which pairs were associated at random. The results showed that although there were changes over time and space in the proportions of females of the different morphs, as well as in the proportion of the pair associations, pairing according to morphs probably occurs at random.

Key words: colour pattern, field data, mating, orb weaver

HUXLEY (1955) defined polymorphism as the existence of at least two different phenotypes in a population whose rarest form is too frequent to be solely a consequence of recurrent mutations (GRAY & MCKINNON 2007). Polymorphism can be found in many species such as the mollusc *Cepaea nemoralis* (COOK 2007), the anuran *Bufo canorus* (HOFFMAN & BLOUIN 2000), the spider *Enoplognatha ovata* (HIPPA & OKSALA 1981) and in females of many damselfly species (ROBERTSON 1985, CORDERO 1992, CORDERO et al. 1998, ANDRÉS et al. 2000). The number of morphs can be limited, such as in melanic moths (MAJERUS 1998) or large, as in the meadow spittlebug, *Philaenus spumarius* (HALKKA & HALKKA 1990); a phenomenon called exuberant polymorphism (OXFORD 2009).

Many theories have been put forward to explain the evolution and maintenance of polymorphism. For instance, spatial and temporal habitat heterogeneity has long been known to promote phenotypic and genetic variations (FULLER et al. 2005). BOND & KAMIL (2006) used digital moths preyed upon by real birds to show that the evolution of polymorphism

depended on an interaction between habitat structure and predator pressure. The importance of predation in favouring the rarer morphs has also repeatedly been shown, for example in *Lutianus griseus* (REIGHARD 1908) or in *Cepaea hortensis* (CLARKE 1962). Another factor is linked to differences in reproductive behaviour and mate choice, which maintain polymorphisms (*Cepaea nemoralis,* CAIN & SHEPPARD 1950, 1954; guppies *Poecilia reticulate*, GRAY & MCKINNON 2006) often consisting of morphological variation, for example in colouration (ANDERSSON 1994).

One of the great, persisting issues in ecology and evolution are the numerous cases of polymorphism linked with colour morphs. Indeed, many natural colour polymorphisms have been shown to be caused by non-selective processes such as migration and dispersal (DEARN 1984, KING & LAWSON 1995, REILLO & WISE 1988), or genetic drift and local population bottlenecks (BRAKEFIELD 1990).

Our study was conducted on the spider species *Agalenatea redii*, which presents five different morphs: α, γ, δ, ε and ζ (Fig. 1) in both sexes. The aim of this study was to evaluate over several years the maintenance and stability of the polymorphism in different spider populations using their temporal and spatial distribution. First, a multi-annual study was carried out on different sites to test if polymorphism was maintained across space and time. Afterwards, the study of a breeding season was carried out to determine whether there was a differential emergence of morphs during a season limiting the possibility of morph pairing. Finally, a detailed study of the spatial

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distribution of individuals at a single site was done to test whether aggregation could contribute to an increase in the probability of meeting and reproduction of the different morphs. We calculated the frequency of paired individuals according to morph and sex in the different experiments. We also looked at pair composition (homomorph or heteromorph) and we tested whether or not the frequency of these pairs fitted a random theoretical distribution of spider pairs.

Material and methods

Biological model

Agalenatea redii is an orb-weaving spider, whose geographical distribution extends across the whole of Europe (JONES 1990). This species has an annual biological cycle with post-embryological development spread over the entire year: eggs are protected in cocoons, they are laid at the end of spring and the young spiders remain in the egg sacs at juvenile stages (often sub-adult) during winter. The adults (5.5 to 7 mm for females and 3.5 to 4.5 mm for males, ROBERTS 1996) have a short appearance time that generally starts at the beginning of spring with reproduction, and ends early in the summer when the eggs are laid. This spider is characterized by a polymorphism of the dorsal pattern on the opisthosoma. Five morphs are present in both males and females (α, γ, δ, ε, ζ) (JONES 1990) (Fig. 1).

Dynamics of the population

Multi-annual study

Data from several populations of *Agalenatea redii* studied from 2008 to 2010 at different sites in the area of Nancy (Meurthe-et-Moselle, France, 48°41'N, 6°17'E, 272 m a.s.l.) were compiled. These data enabled us to characterize dynamics of the population according to the sexes, morphs and pairs (by distinguishing homomorph from heteromorph pairs). For these studies, two spiders (one male and one female) were considered as forming a pair when they were both present at the same time on the same stem and less than 3 cm apart, which is the mean distance between a male and a female (there was no direct link with potential fertilization) (personal observations). In 2008 four sites were surveyed (number of spiders; N1 = 207). In 2010 three sites were surveyed (N2 = 399). In 2011 only one site was examined (N3 = 551). Visual hunting was the method employed to spot and identify spiders, while being careful of all the supports (dry stems of vegetation) used by spider. At the beginning of spring the green vegetation had not yet grown and only the dry stems of the previous year remained, which allowed us to search exhaustively for spiders.

Single breeding season study

For this study, we surveyed one site during the reproductive period (from March 28th to May 6th,
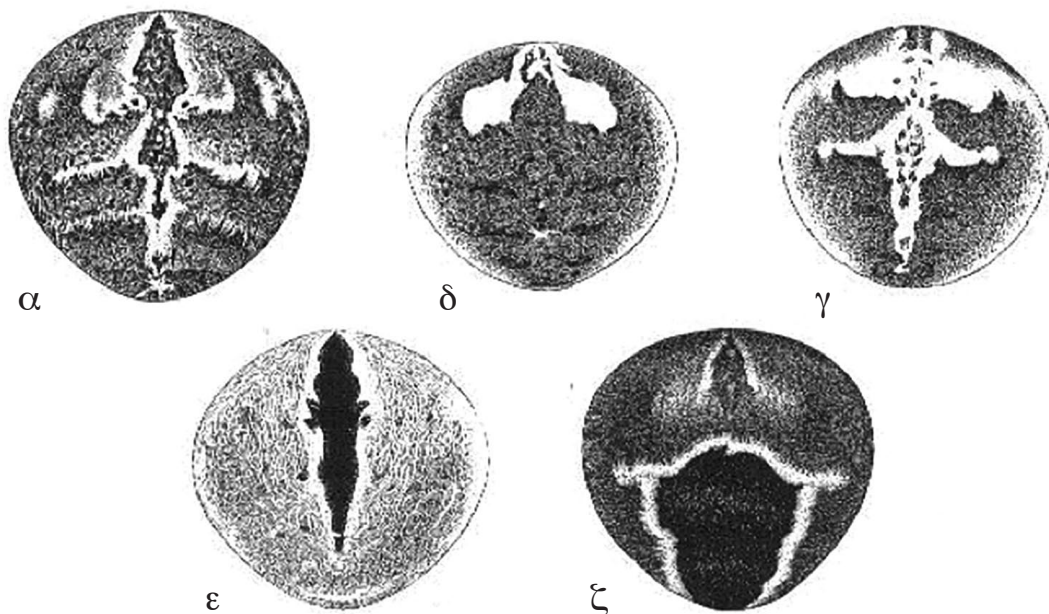

Fig. 1: Schematic representation of morphs observed in the species *Agalenatea redii* (from DÉOM 1996).

2011). Two transects (26 and 28 m, respectively) were performed in the field using a string to mark them. The spiders were located on vegetation in a strip of one meter on either side of the transect lines.

Spatial distribution of the spiders

On the site of the 2011 survey, a positional map of the spiders was constructed on March 22nd for a rectangular area (10 m * 26 m), divided into units of one square meter. Spiders were located and morph and sex were noted. The position of each individual or each pair was entered into the computer to determine the spatial distances between the individuals and the type of distribution. To do this, a dispersion index I (based on the index of FISHER 1922) was calculated based on the map distances:

(1) $I = S^2/X$

(2) $X = S_{(1\ to\ s)}\ x_i/n$,

where x_i is the number of individuals of morph i and s is the number of different morphs in all the n units of the surveyed area,

(3) $S^2 = S_{(1\ to\ s)}\ (x_i - X)^2/n-1$.

A test of threshold significance was performed (at $\alpha=5\%$) and compared to the Chi-square table: X^2 (p=0.05, df=59)=77.93 and X^2 (p=0.95, df=59)=42.34). Two conditions were then checked: $I*$(number of units (n) -1)$>X^2$ if the distribution is aggregative and $I*$(number of units (n) -1)$<X^2$ if the distribution is uniform. The type of distribution can provide a clue to the pairing. If the distribution is uniform it means that pairing is random, but if the distribution is aggregative it suggests that pairing may not be due to chance.

Statistical analysis

The relationship between the various morph proportions for males, females and pairs were analyzed based on the 2008/2010/2011 data. The temporal follow up of a 2011 population was evaluated using a Monte Carlo method (METROPOLIS & ULAM 1949) specifically programmed for this study. The null hypothesis was: at each period and every location, the male morph is independent of his female partner's morph. The statistical test employed looks like the Chi-square test of independence. It differs from the latter in the following points. The theoretical frequency ($f_{th\ x,y,z,t}$) of male morph x and female morph y pairs, at location z and period t was estimated with the product of the entire male frequency (paired or alone)

of morph x among the males at location z and period t and the frequency of all females (paired or alone) of morph y among the females at location z and period t. The theoretical number ($N_{th\ x,y,z,t}$) of morph x and y pairs, at location z and period t, was estimated by the product of their frequency ($f_{th\ x,y,z,t}$) and the total number of pairs at location z and period t.

According to this calculation, the theoretical number is the null hypothesis and $N_{obs\ x,y,z,t}$ is the number of male morph x and female morph y pairs among the males at location z and period t. The test was done using a distance calculation with two methods: the first by calculating the square distance:

(1) $sq = \sum_{x,y,z,t} (N_{obs\ x,y,z} - N_{th\ x,y,z,t})^2$

and the second by calculating the absolute value of distance:

(2) $ad = \sum_{x,y,z,t} |N_{obs\ x,y,z} - N_{th\ x,y,z,t}|$.

One hundred thousands simulations were carried out on each distance. For each simulation in every location z, at every period t, the males and females of location z and period t mated randomly. We calculated the number N of simulations in which the distance
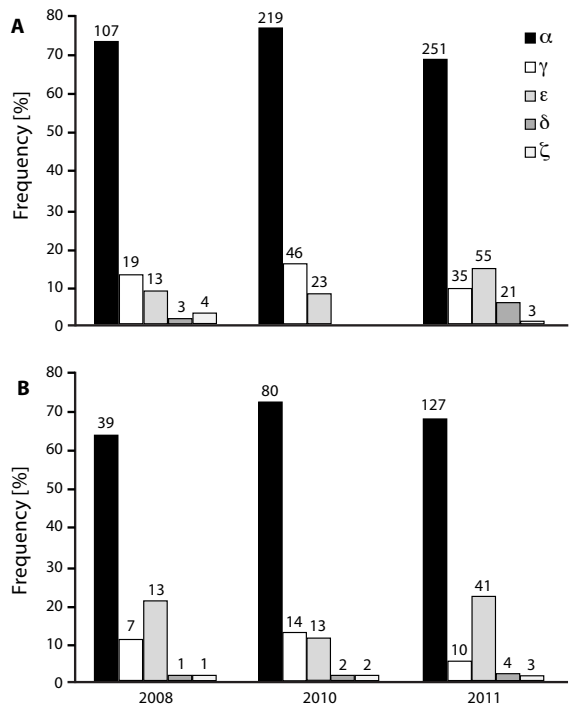
Fig. 2: Changes in the proportion of female (A) and male (B) morphs (from the left to right: morphs (α, γ, δ, ϵ, ζ) according to the year of observation (number of captured spiders on the graph).
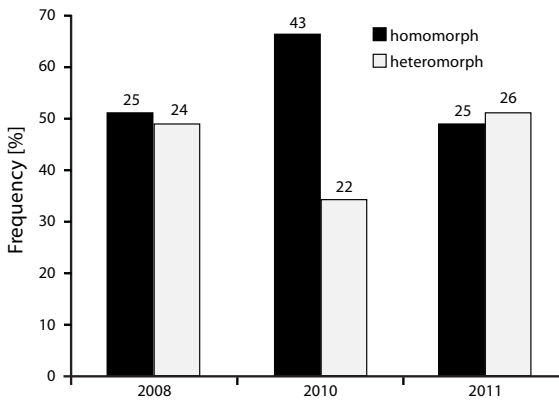
Fig. 3: Frequencies of homomorph and heteromorph pairs (%) observed over the period 2008–2011 (number of spider pairs on the graph).
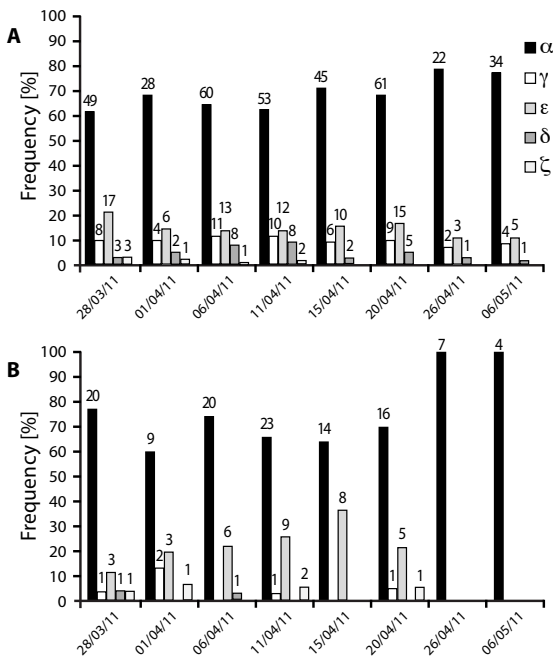

Fig. 4: Changes over time in the proportion of female (A) and male (B) morphs (number of spiders on the graph) during a reproductive season survey in 2011.

between the random distribution of the simulation and the theoretical distribution was greater than the distance between the real distributions observed in the wild and the theoretical distribution. The test's level of significance was then N/100000. The different frequencies were compared with a Chi-square test.

Results
Multi-annual study
Ratio of males and females of different morphs

The distribution of morphs over the years appeared to be the same for the males (Chi-square test, $X^2=9.66$; df=8; p=0.29) but not for the females, which varied every year (Chi-square test, $X^2=41.14$; df=8; p<0.01). Indeed the ratio of morphs amongst females fluctuated between 2008–2010 (Chi-square test, $X^2=14.57$; df=4; p<0.01), 2010–2011 (Chi-square test, $X^2=32.17$; df=4; p<0.01), and 2008–2011 (Chi-square test, $X^2=10.28$; df=4; p<0.05) (Fig. 2).

Proportion of heteromorph and homomorph pairs of spiders

Over the three years (from 2008 to 2010), the division between homomorph and heteromorph pairs did not differ (Chi-square test, $X^2=4.22$; df=2; p=0.12) (Fig. 3). Furthermore, the Monte Carlo simulations showed that there was no significant difference from a random association of the two morphs, based on their frequencies in the population (N=100000 runs, square distance (sq): p=0.61; absolute distance (ad): p=0.72).

Single breeding season study
Proportion of males and females of different morphs

The ratios of morphs among the females did not vary according to the observation dates (Chi-square test, $X^2=19.34$; df=28; p=0.89). The same pattern was witnessed among the males (Chi-square test, $X^2=22.56$; df=28; p=0.75) (Fig. 4).

Proportion of heteromorph and homomorph pairs of spiders

The distribution of the heteromorph and homomorph pairs was independent of the date, and thus of

Tab. 1: Results of the simulations by date for the pairs observed on field transects and according to the proportion of each morph in each pair.

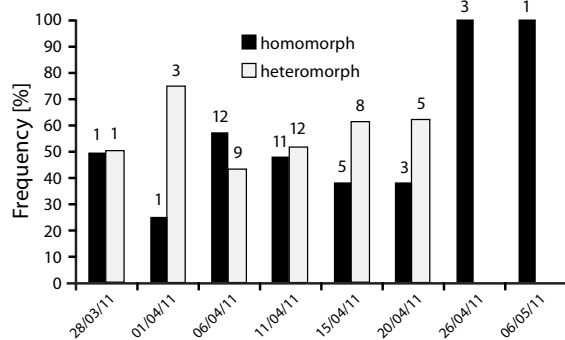| probability	Date of observation in 2011					
	28/03	01/04	06/04	11/04	15/04	20/04
square distance (sq)	0.36	0.48	0.57	0.81	0.094	0.11
absolute distance (ad)	0.36	0.34	0.37	0.72	0.32	0.14

Fig. 5: Proportion of homomorph and heteromorph pairs (%) observed in 2011 with the number of spiders on the graph.

the time within the reproductive period (Chi-square test, X^2=6.65; df=7; p=0.51) (Fig. 5). Moreover, the simulation showed that the observed pair distribution according to the proportion of spiders did not diverge from a random distribution for all dates (N=100000 runs, square distance (sq): p=0.44; absolute distance (ad): p=0.28) or for each observation dates (p>0.05) (Tab. 1).

Spatial distribution of spiders at a site

The spatial distribution of all individuals (males and females all morphs together) in the sample site appeared aggregative (I*(n-1)=85.7). The same was true for the spatial distribution of the males (I*(n-1)=91.7) although that of the females appears to be random (I*(n-1)=71.7).

Discussion

This study carried out a spatio-temporal description of polymorphism in the orb weaving spider, *Agalenatea redii*. The first result was that morphs were not equally probable within a population. Indeed one morph (a) predominated in both males and females. The second result revealed that morph distribution was stable over time for males and females, at least during one reproductive season. The difference of distribution between the female morphs observed during these three years could be due to the absence in 2010 of particular low frequency morphs. This information supported, however, the idea of the maintenance of polymorphism in this species.

The comparisons of field data on morph frequencies with random morph associations showed that pair distributions depending on available morphs did not differ from field distributions either during a reproductive period (2011) or over several years

(from 2008 to 2010). A similar result was found for the damselflies *Ischnura graellsii* (CORDERO 1992), *Ceriagrion tenellum* (ANDRÉS et al. 2002), and for *Ischnura ramburi* (ROBERTSON 1985), where it was observed that males mated with females at random.

In *Agalenatea redii*, males remained with sub-adult or adult females before mating and also some days after (personal observations), as in *Zygiella x-notata* (BEL-VENNER & VENNER 2006). Our study of male distribution (all morphs together) showed an aggregative distribution. This male distribution could reflect the presence of a female signal (pheromones, dragline cues) used to locate them. However, if the encounters were at random, these signals would not be specific to morphs.

Several hypotheses have been proposed in the literature to explain the maintenance of polymorphism in different species. It could be genetic, such as in the spiders *Enoplognatha ovata* (OXFORD 1983, 2009) or *Pityohyphantes phrygianus* (GUNNARSSON 1987). In this case the preservation of morphs that showed a low frequency in the population could be due to an effect of genetic drift (OXFORD 2005). This did not seem to be the case in *Agalenatea redii,* because different morphs were maintained over time and space.

Non-selective processes, such as dispersal and migration (FORD 1975, KIMURA 1983), may cause polymorphism. Our study was conducted on different populations separated by several km from each other. They were not isolated populations. There was a continuum between the different populations, so exchange of individuals between study populations by emigration/immigration processes was possible. However, there is no reason to expect that morphs have different dispersal properties, and so differential emigration is not likely to explain the maintenance of polymorphism in *Agalenatea redii.*

Another hypothesis is the preference for a male morph as in the ladybird *Harmonia axyridis* where females show a male morph preference in relation to the season (UENO et al. 1998). Therefore, polymorphism would be the consequences of directional sexual selection that would change with time. In our case the frequencies of the morphs remained stable over the reproductive season, which makes this hypothesis unlikely.

Polymorphism may be part of an alternative reproductive strategy. For example, one morph may be less attractive – but more competitive – than another (KINGSTON et al. 2003). FINCKE (1994) suggested the hypothesis that polymorphism could be maintained by

a mechanism of negative frequency-dependent selection and this was tested by FITZPATRICK et al. (2007). This hypothesis implies that the rarer morphs have a higher phenotypic aptitude by avoiding, for example, the costs of a long copulation (VAN GOSSUM et al. 1999). In other words, a less prevailing morph can be less appealing, but more reproductively competitive and consequently have higher reproductive success (COOK et al. 1994, KINGSTON et al. 2003), and polymorphism in a population can be stable only if all the present morphs support equal selective advantages (FINCKE 1994, BIZE & ROULIN 2007).

To conclude, our results did not allow us to elucidate mechanisms by which polymorphism is maintained in *Agalenatea redii* populations and hypotheses remain to be tested. Thus, we have to study the behaviour and performance of the males of different morphs based on their pairing with homomorph or heteromorph females.

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Spiders in Fauna Europaea: dual use of the database

Peter J. van Helsdingen

Abstract: The history and current work of the project Fauna Europaea is outlined. The different sources used for building up the database and the efforts to keep it updated are described. Available models of national checklists are discussed and the ideal checklist is described. The double use of the database as a matrix behind the official site of Fauna Europaea – as well as a directly visible document on the website of the European Society of Arachnology – are indicated and the differences in transparency, links to literature sources, and facilities such as distribution maps and calculations of numbers of scores per species or of species per country are discussed. The future of the project is briefly outlined. The need for a European identification tool for spiders is stressed.

Key words: Araneae, checklist, European distribution, European project, European Society of Arachnology, identification tool, PESI

Fauna Europaea is an initiative set up and funded by the European Commission. The actual work started in 1999 with the establishment of a Central Bureau and the organization of the work load. The goal was to set up a database of published distribution records of all valid terrestrial and freshwater animal species, including synonyms. All European countries as politically defined (European parts of Russia, satellite archipelagos of Spain and Portugal) were included: EU and non-EU, and smaller member-states such as Monaco, the Vatican, and Andorra. Registration of species distributions was expected to be carried out at country level (or parts of countries for the larger countries, such as European Russia, or with known distribution barriers or zoogeographical districts within the country, such as Greece, Portugal, and Spain). The site (FAUNA EUROPAEA 2011) thus aims to inform the user about the presence or absence of a given species in the selected country or region. Literature sources should also be provided.

This goal was achieved by bringing together one or more specialists for each taxonomic group to serve as group-coordinators. The Fauna Europaea website mentions more than 500 experts, including the 63 group-coordinators. The website was launched in 2004.

Sources

General sources

I built up the database for the spiders in 2003 and subsequently try to keep it up-to-date with the much appreciated help of many colleagues from all over Europe, and based on different sources.

The available literature forms the ever increasing primary source for the database. I started to work with Platnick's World Catalog (PLATNICK for the years 2002–2003), extracting all the names of spider species in Europe, and next browsed the literature – libraries, the internet, Zoological Record – for distribution data and newly described species. Platnick provides a fresh version of his Catalog twice a year and the changes in his catalogue, nomenclatorial changes as well as new species and distribution data, form one of the sources for the regular update of the Fauna Europaea database. Platnick's Catalog is a reliable source for taxonomic registration but less detailed in its indication of the distributions, which are summarized where appropriate (e.g. Palaearctic, Western Mediterranean). For zoogeographic purposes, therefore, all possible literature sources are browsed, such as papers published in journals, checklists published on paper, or on the internet.

Many people are helpful through supplying recently published information or by pointing out administrative errors which have crept into the database.

Available sources per country

Checklists and catalogues apparently serve different meanings in different countries. The two terms are used indifferently. In my opinion a checklist is just a

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list of names, while a catalogue includes references to the sources.

In its most simple and ideal form a country checklist should list the names of all species with published records for that country in a directly visible overview. Recent synonyms should be added for the sake of convenience and for newly added names a source reference should be given. The following examples demonstrate what I think is the most practical format for a country checklist, supplying all the relevant information needed, and which formats are impractical.

The Danish checklist
The Danish checklist (SCHARFF & GUDIK-SØREN-SEN 2011) complies with all the above criteria. It shows the names of all species occurring in Denmark in a simple, readable way, while recent name changes and relevant historical particulars are made visible. Families, genera within the family, and species within the genus are in alphabetical order. The list carries the date of the last update, so the user can see the status (age) of the list. The new additions to the list are marked in a distinct way making the user aware of recent changes at a glance.

The Portuguese checklist
In the Checklist of Portugal (CARDOSO 2011) maps and literature references can be brought forward for each species, giving such a checklist the character of a catalogue. This looks very attractive and makes use of the most recent software developments, but is restricted with regards to obtaining an overview of the fauna of the country. For instance, it is not possible to extract a complete list of the spider fauna of the country, and even though the date of the last update is mentioned one cannot detect which changes were made because they are not marked. The additional information on literature sources and the distribution maps form excellent extras, but the basic information remains concealed. On the website there is a link to the Catalogue of the spiders of Portugal which has the same construction and therefore the same lack of overview of the complete spider fauna of Portugal.

There are several examples of this type of checklist or catalogues on websites.

The British checklist
In the checklist of the British Isles (BRITISH ARACH-NOLOGICAL SOCIETY 2011) the families are grouped in taxonomic clusters, which make such a list slightly less user-friendly. The alphabetical order is not used, not even within a family, which renders the list extremely user-unfriendly and frustrating. In this particular case one sticks to a traditional sequence followed in identification literature which is not functional even there and lacks a scientific or practical basis. For example, the taxonomic clustering within the Linyphiidae does not have any phylogenetic basis and is not explained. Recent changes are not marked and it is not clear if and when updates were carried out. The consultation of such a checklist thus becomes a tedious job.

The website of Fauna Europaea
The website has not changed its visual format since its launch in 2004, but the possibilities and facilities have greatly improved since. The site allows the user to check the occurrence of all known spider species in all European countries. Using the "Distribution" button one can request an overview of the distribution (presence or absence per country) of each species, or extract a distribution map showing the country distribution. One can find the numbers of species within a family or a genus occurring in Europe and can request a map of the distribution of that taxon. Detailed information is offered on the number of European species within a genus. Through the "Taxon Tree" one can zoom in on every taxonomic unit, from family down to (sub)species and find answers to the above questions.

However, it is impossible to extract a complete list of all spider species for a country. Likewise it is impossible, or is apt to fail, to get an answer to the number of species for a country. The database holding all the data remains hidden behind the screen. There is also no entry to literature references. This should be improved upon in the future.

Hosting by the European Society of Arachnology
The same database in spreadsheet format was offered by the author to the European Society (ESA) for general use; an initiative welcomed by ESA. The database is accessible through links on the ESA website for two Excel spreadsheets, one for nomenclature ("Taxonomic Sheet") and one for distribution ("Faunistic Sheet"). In the last column of the taxonomic sheet the numbers of literature references can be found which relate to the numbered list in the separate document "References". The second part of the latter document contains entries to the main faunistic sources for each country, such as printed catalogues and checklists as well as links to internet sites with such information.

There are no facilities to convert the data into maps. Since the original spreadsheets are available for examination one can immediately see which species occur in each country and from which countries each species has been recorded. One can also count the species for each country, by counting through the columns or automatically via spreadsheet facilities. This is already carried out for each new version which appears on the ESA website where the bottom row and the last column but one provide these additions.

The presence of a species is indicated by a "P". Nomina dubia and imported (non-native or invasive) species are indicated in the database, as "nd" and "Pi", respectively, but are not included in the automatic count, thus excluding them from the "Indigenous fauna" of the country, here called "true species".

Tab. 1: Composition of the spider fauna of Europe.

A. Species (incl. subspecies) (end of 2011)	4892
B. Nomina dubia	302
C. Introduced species	99
D. "True" indigenous species (A – (B + C))	4491
E. Unique records / endemics	2041
World-wide (PLATNICK 2011)	42473

Tab. 2: Numbers and percentages of unique records / endemics in certain families. For explanation of "true" and "unica", see text and Tab. 1.

Number of "true" species		Number and percentage of unica
All European spiders	4491	2041 (**45.4%**)
Agelenidae	200	93 (50.0%)
Araneidae	150	56 (40.0%)
Dysderidae	331	227 (70.5%)
Gnaphosidae	480	178 (41.3%)
Linyphiidae	1366	534 (42.4%)
Lycosidae	303	124 (44.1%)
Nemesiidae	62	36 (61.0%)
Philodromidae	106	38 (41.8%)
Salticidae	400	136 (39.4%)
Theridiidae	258	72 (30.2%)
Thomisidae	193	64 (36.2%)
Zodariidae	111	60 (55.0%)

The taxonomic table allows nomenclatorial changes to be followed and the tracking of changes in taxonomic status (synonymies, changes in taxonomic level).

Possibilities for statistical analysis
Analysis of this last but one column reveals – excluding nomina dubia and non-native (imported) species – a strikingly large number of records from only one country or region (Tab. 1). Such unique records form 45.4% of all species; a surprisingly high score (Tab. 2). Among these are, of course, all the endemic species found in a single country. Among these "unica" we may also expect potential synonyms awaiting recognition by revisers. If we carry out the analysis for families we find for some families even higher scores than the 45.4% for the overall European spider fauna (Tab. 2). Families with much higher percentages of such unica or one-country species are the Dysderidae (70%), Nemesiidae (58%), and Zodariidae (57%). This agrees with the recognized speciation patterns in these families as indicated in the literature. In these three families the rates of dispersal are low and isolated populations develop relatively easy into separate taxonomic units. Of course one should consider the possibility of a relatively high percentage of one-country species in families which have been neglected taxonomically and are waiting for revision. This may be true for the Nemesiidae (DECAE 2005, 2012, DECAE et al. 2007) which still need a lot of taxonomic attention, but hardly can be the case in the Dysderidae, which were revised by Deeleman and others (DEELEMAN & DEELEMAN 1988, AR-NEDO et al. 2007, ŘEZÁČ et al. 2008) and the Zodariidae, which were studied thoroughly by PÉKAR et al. (2003, 2005, 2011) and BOSMANS (1994, 1997, 2009).

In contrast with these families, some other families (Theridiidae, Thomisidae) show a much lower percentage than the mean value of 45.4%. Apparently more species of these two families have, on average, a wider range.

Future of Fauna Europaea
Presently, validation of the database is carried out through national Focal Points, while group-coordinators continue to supply the updates. The project

is now embedded in PESI (2011, A Pan-European Species-directories Infrastructure) under which the geographical coverage will probably expand to include the Caucasus and Turkey (first step), the Northern African countries bordering the Mediterranean Sea (step two) and possibly the Arabian Peninsula (step three) – but this is the present proposal and decisions still have to be taken in relation to the availability of funding.

Other initiatives such as the Catalogue of Life, Encyclopedia of Life, and Species 2000 all link through to the Fauna Europaea website and follow its nomenclature and faunal composition.

Discussion

The differences between the two facilities – the official Fauna Europaea site and the one on the ESA website – are obvious. The spreadsheets on the ESA website are transparent and can be more easily checked for relevant information but lack facilities for mapping, while the official Fauna Europaea website only shows the derived information and keeps the basic information hidden away but offers the mapping facilities.

Keeping Fauna Europaea up-to-date is a never ending task because taxonomy is a dynamic process with new species being described all the time and distribution data being published continuously. Therefore regular updates are necessary; otherwise the database becomes obsolete and useless. This should have absolute priority over extending its geographical range.

The project being successful as it is, I personally had expected that other sets of countries would have started such projects, but so far I am not aware of any comparable initiative. It is unlikely that more detailed distributions for countries will be aimed at, for instance by subdividing larger countries (Germany, France, Italy) into smaller regions. Here we have to depend on the efforts of the individual countries, some of which have made available such overviews on the internet or in print already.

What is really urgently needed is a pan-European identification facility which would make identification easier and better and thus improve on the quality of published data and consequently on the quality of the Fauna Europaea database. Collections and published records contain too many misidentifications which are, at least partly, caused by insufficiently available identification tools. In these modern times with its advanced internet possibilities it should be possible to have a European identification key with supporting illustrations and diagnoses for all European species, linked to distribution maps as supplied by Fauna Europaea. There exists an attempt to develop such an identification tool (NENTWIG et al. 2011) but its rate of progress is very low, new species are only added by name without illustrations and are not (yet) inserted into the identification key. Inclusion of the original illustrations would be a first step. This is not the place to discuss merits and flaws of that site, but it is evident that there is still a lot of work to be done.

A possible attractive alternative is the new series of books on European spiders which just started with a first volume (LE PERU 2011) and three more to follow. It presents diagnoses and illustrations for all European species, mostly of the genitalia, and distribution maps on a more detailed scale than Fauna Europaea in that it indicates – for some countries – the region where it occurs in a country and not the whole country (e.g. a coastal zone in southern France for truly Mediterranean species). However, there is no identification key, but only a non-dichotomous, synoptic characterization of genera in the introduction to a family (in contrast to the key for at least the larger part of the species in NENTWIG et al. 2011), while Europe is defined in a different way (e.g. the European part of Russia is not included and smaller stamp-sized countries or nonrelevant regions, such as the Vatican, are fused with a neighbouring country). The book certainly might be a handy tool for quick recognition of species. Alas, it is not on the internet but printed which makes it outdated very soon.

Acknowledgements

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Observations on web-invasion by the jumping spider *Thyene imperialis* in Israel (Araneae: Salticidae)

Peter Jäger

Abstract: Observations on *Thyene imperialis* (Rossi, 1846) in Israel, Negev desert, invading a web of *Cyclosa deserticola* Levy, 1998 are reported. The female leapt into the orb-web to catch *Cyclosa* spiders. Photographs are provided, and a link to additional film material is given.

Key words: araneophagy, behaviour, Plexippinae

In jumping spiders, Salticidae Blackwall, 1841, diverse predatory strategies have evolved, including "araneophagy, aggressive mimicry, myrmicophagy and prey-specific prey catching behavior" (review: JACKSON & POLLARD 1996: 287). Probably one of the best reviewed cases is the genus *Portia* Karsch, 1878 (JACKSON 1986, JACKSON 1995, JACKSON & HALLAS 1990, JACKSON & WILCOX 1993, WILEY & JACKSON 1993). It not only enters webs, but also performs "specialised vibratory signals to trick the owner of the alien web" – as do other Spartaeinae (JACKSON 1990). In the same paper, Jackson states that all web-invading members of the subfamily Spartaeinae he studied "have the property of not adhering to either cribellate or ecribellate glue of sticky threads". In the Mediterranean, the Spartaeinae *Cyrba algerina* Lucas, 1846 has been known to perform web-invasion based on aggressive mimicry (CERVEIRA et al. 2003: Israel, Portugal). These more complex types of behaviour have to be differentiated from simple leaping into alien webs, e.g. by *Plexippus paykulli* (Audouin, 1826) or others (discussed in JACKSON & MACNAB 1989).

During the 26th European Congress of Arachnology in Israel the author was able to observe an adult female of *Thyene imperialis* (Rossi, 1846) invading an orb-web of an Araneidae species. This short note provides information adding to our knowledge of the predatory behaviour of Salticidae and to raise questions about *Thyene* in particular.

In the afternoon of 4.9.2011 several orb-webs of *Cyclosa deserticola* Levy, 1998 (preserved specimens identified using LEVY [1998] and deposited in Sen-

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ckenberg, SMF 62339) were found beside road 40 from Be'er Sheva to Mizpe Ramon in the Negev desert. The site was ca. 5 km SW of Midreshet Ben-Gurion at 30°50'50.73"N and 34°45'4.91"E at ca. 500 m altitude. The webs were constructed in the wind shadow of a single group of shrubs which were between 50 and 150 cm high (Fig. 1). Characteristically the webs were decorated with one or two bunches of prey items below and/or above the hub (Fig. 2). In one female's web a male was waiting at the edge of the web (Fig. 2). In an area of 1–2 m^2 about 10 webs were found.

In one of these webs a jumping spider was present instead of the expected *Cyclosa* spider. It was later identified as adult female of *Thyene imperialis* (deposited in Senckenberg, SMF 62300). It walked across the web, first approaching a bunch of prey remnants. Then it walked to the centre and pulled on radial threads above the hub using its front legs, as is also known to occur in orbweb spiders (Araneidae) during prey localization behaviour. Afterwards it continued to walk on the web's sticky spiral without any problems (the stickiness of the threads was confirmed later). Since no camera was at hand, the *Thyene* was caught alive and kept for the next day.

Next morning at ca. 9 o'clock the captured *T. imperialis* female was placed on a twig close to a thread of a *Cyclosa* web. When the *Cyclosa* female moved into the centre, *Thyene* oriented towards *Cyclosa* (as it also oriented towards cars on the nearby road) and maintained its orientation towards it [in the following text the term "detected" is used for this behaviour]. When touching the frame threads of the orb-web, *Thyene* did not enter the web. Afterwards, it was caught again and placed in an open vial near the *Cyclosa* (now at the top end of the orb-web). Here, it immediately detected *Cyclosa*, although the latter showed no movement. Steady wind, however, moved
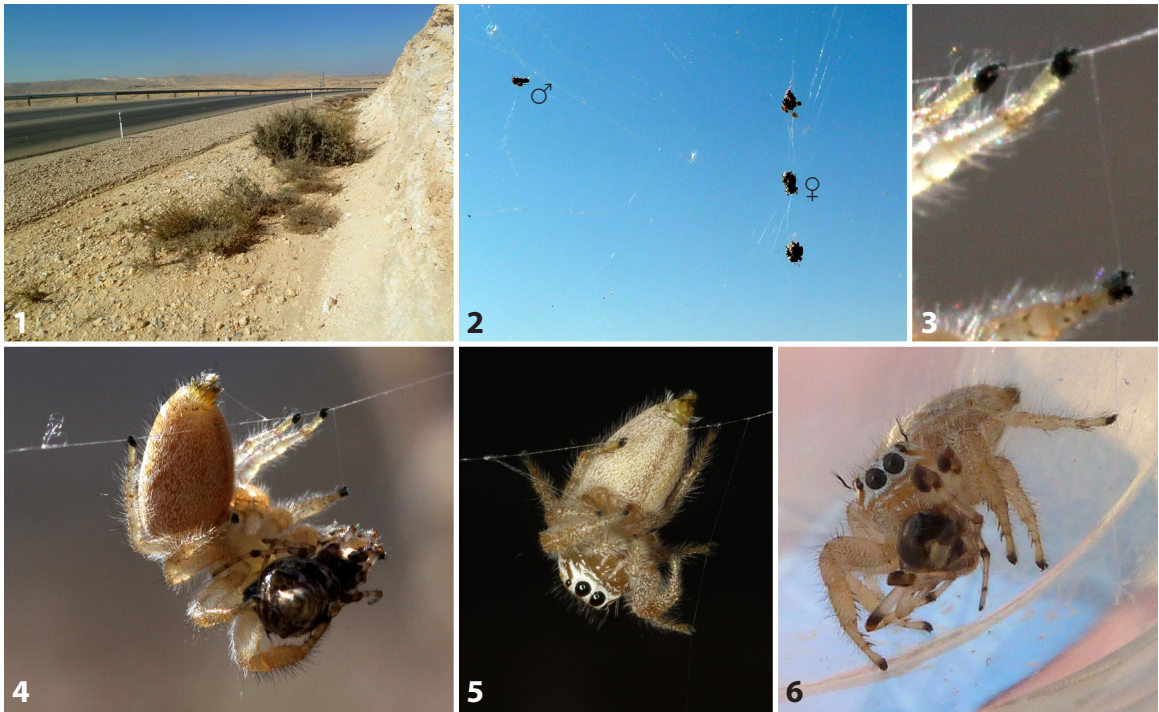
Figs. 1-6: 1. Israel, Negev desert, SW Midreshet Ben-Gurion, habitat with shrubs with *Cyclosa deserticola* webs. **2.** Web of *C. deserticola*, female in centre with two bunches of prey remnants above and below the hub, male top left. **3.** Tip of legs of *Thyene imperialis*, touching thread with paired tarsal claws. **4.** Female *T. imperialis*, feeding on female *C. deserticola* on top frame thread of the *Cyclosa* orb-web. **5.** Ditto directly after dropping *Cyclosa*. **6.** Same female of *T. imperialis* feeding on male *C. deserticola* in plastic vial.

the web including *Cyclosa* and prey items. After a few seconds *Thyene* jumped from the vial onto the web and caught *Cyclosa* (Fig. 4). During the feeding process it changed its position from time to time and attached its dragline to the frame thread of *Cyclosa*. Fifteen minutes later it dropped *Cyclosa* (Fig. 5) and walked along the top frame thread of the orb-web to a twig (short films can be viewed at: http://www.senckenberg.de/thyene). Before it could escape it was again captured in a vial and retained for ten minutes. It was placed for a second time in front of a *Cyclosa*, this time a male in the centre of its web. Again, after few seconds *Thyene* detected the spider, although no active movement was performed by *Cyclosa*. This time *Thyene* pulled *Cyclosa* out of its web from its position on the vial (Fig. 6). Both spiders were kept within the vial and one hour later the dead *Cyclosa* male was dropped.

The behaviour of *Thyene imperialis* observed may be compared with that of *Plexippus paykulli* in terms of leaping into alien webs and attacking their residents (JACKSON & MCNAB 1989). *Thyene* is considered a member of the Plexippinae Blackwall, 1841 by PROSZYNSKI (1976), METZNER (1999) and MAD-

DISON et al. (2008). It cannot be stated from the single observation whether *Thyene* performs web-invasion occasionally or routinely. It remains also unclear whether web-invading behaviour of *Thyene* lacks components typical for Spartaeinae (e.g., producing signals that modify the behaviour of the resident spider; Jackson pers. comm.).

However, *Thyene* enters alien webs and walks within them, including on the web's sticky threads without a problem. It was clear from photos taken in the field that *Thyene* holds onto the threads with its paired claws (Fig. 3) and that it also touches parts of the sticky threads (which were confirmed to still be sticky). One possible explanation for *Thyene* not adhering to the silk could be that it uses a similar protective coating against sticky threads as proposed for orb-weavers by FABRE (1905: 114) and KROPF et al. (2012). Moreover, it would be interesting to know whether all *T. imperialis* individuals are web-invaders and whether other web types are involved. From some photos, *Thyene* appears to use the basal part of its paired and toothed claws, which are close to the claw tuft hairs (Fig. 3). Could there be a similar interaction between these two elements as present in

the unpaired claw with serrated bristles (carabiner effect) in web-building spiders? All these questions can be answered only after more observations and elaborate experiments.

Acknowledgements

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Assemblages of herb-dwelling spiders (Araneae) of various steppe types in Ukraine and the Central Chernozem region of Russia

Nina Y. Polchaninova

Abstract: A total of 107 spider species from 15 families were recorded in the herbaceous vegetation of the steppe ecosystems of Ukraine and the Central Chernozem region of Russia. Araneidae, Thomisidae, Salticidae and Theridiidae were the most species-rich. The species composition depended on the steppe type; adjacent forest habitats influenced steppe fauna in the forest-steppe and northern part of the steppe natural zone. The number of generalist, forest and wetland dwelling species in the steppe vegetation showed a tendency to decrease towards the south. Dominance of herb-dwelling spiders was specific to each steppe type; no single species was found to predominate in all the steppe habitats.

Key words: dominance structure, species distribution, spider communities, steppe ecosystems

Steppes are the most transformed ecosystem in Ukraine. The steppe natural zone comprises 40% of the country and about 80% of this territory was once covered with steppe vegetation. Presently, only 3% of relatively undisturbed virgin steppes have survived intact. They are preserved mainly in nature reserves or on gully slopes and saline lands not suitable for agriculture (KOTENKO 1996).

All steppe reserves are isolated to various degrees, such that they can be considered as ecological islands, surrounded by agricultural landscapes (MALYSHEV 1980). Different components of the steppe biota respond to isolation in different ways (KOTENKO 1996, HANSER & HUNTLY 2006, LAIOLO & TELLA 2006). Spiders move quite easily from natural habitats to agricultural fields, however many of them do not penetrate beyond the field margins. Crops are populated mainly by eurytopic species typical of meadows or disturbed habitats (SEYFULINA & TCHERNYSHEV 2001, SEYFULINA 2010).

Adjacent habitats have an undeniable impact on steppe communities (CHERNOV & PENEV 1993), especially in the forest-steppe zone where forest and steppe are both zonal plant formations, and an active species interchange can be supposed to take place. To the north and to the south the difference in microclimatic conditions between zonal and intrazonal habitats increases, which results in higher species specificity of their animal and plant assemblages (CHERNOV 1975). Habitat preference of species depends on the natural zone (KÜHNELT 1943, WALTER 1960, BEI-BIENKO 1966). According to the so-called 'principle of zonal change of habitats' (BEI-BIENKO 1966), or the principle of 'relative stenotopy' (SCHAEFER 1992), widespread species moving northwards can change their habitats to dryer warmer open sites with sparse vegetation, while going southwards, the same species inhabit moister and shadier habitats with dense vegetation cover. These two phenomena were illustrated by the example of spider communities of the Urals transect (ESYUNIN 2009), oak forests of the East European Plain (ESYUNIN et al. 1994), and Ukrainian steppes (POLCHANINOVA 1990a, 1996). Investigation of the spider fauna and ecology in the area in question began in the 1980s in the Central Chernozem Reserve of Russia (PICHKA 1984 , 1984b) and in the steppe reserves of Ukraine (POLCHANINOVA 1988, 1990b). Based on the data obtained, a first attempt was made to analyze the fauna and spider communities of the steppe ecosystems of Ukraine (POLCHANINOVA 1990b). Further research focused on all steppe reserves in Ukraine (GURIANOVA & KHOMENKO 1991, POLCHANINOVA 1998, POLCHANINOVA & PROKOPENKPO 2007a, PROKOPENKO 2001, PROKOPENKO et al. 2008) and the adjacent territory of Russia (POLCHANINOVA 2003, 2009, PONOMAREV 2005, 2010). Thus, it became possible to analyse the species composition and dominance structure of spider assemblages to see whether they depend on the steppe type. The present paper is part of a comprehensive study of spider communities of steppe ecosystems of Ukraine and European Russia and concerns herb-dwelling spiders only.

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Materials and methods

The material was collected from three localities in the Central Chernozem region of Russia, and eight localities in the Left-bank Ukraine (Fig. 1). Central Chernozem is a segment of the Eurasian chernozem (black soil containing a high percentage of humus) belt that lies within the East European Plain (also known as the Russian Plain). It is a well-delimited geographical and administrative region. The Left-bank Ukraine in the present context is a territory that stretches from the left bank of the Dnieper River eastward to the border of the state.

We investigated five types of fragments of virgin steppes in the East European Plain (classification according to GRIBOVA et al. 1980). Meadow, forb-bunchgrass and bunchgrass steppes belong to the category of zonal steppes, while sandy and chalky steppes belong to the azonal steppes. In Russian geobotany, meadow steppes situated in the forest steppe natural zone are called 'northern steppes' in contrast to genuine steppes, which form two subzones of the steppe natural zone (Fig. 1, Tab. 1). We regard sandy steppes situated in different steppe subzones separately as northern and southern variants. The studied localities, investigation period and abbreviations used further in the tables and graphs are given in Tab. 1. Here and additionally in the graphs and tables, the localities are arranged from north to south. Names of settlements and nature reserves are translated from Russian and Ukrainian respectively.

Fig. 1: Map of localities (I – forest-steppe zone, II – steppe zone: IIa – subzone of forb-bunchgrass steppes, IIb – subzone of bunchgrass steppes. For number of locality, see Tab. 1).

Tab. 1: List and characteristics of study sites including type of steppe habitat.

Nature zone/ subzone	Name of locality	Steppe type	Years of study	site area (ha)	abbrev.	Region
Forest-steppe zone	1. Streltsovskaya steppe	meadow steppe	1998 1999 2007	730	mead1	Kursk Area, Central Chernozem Res. 51°36´N 36°12´E 248 m a.s.l.
	2. Kazatskaya steppe	meadow steppe	1999 2000 2007	1010	mead2	Kursk Area, Central Chernozem Res. 51°32´N 36°20´E 230 m a.s.l.
	3. Yamskaya steppe	meadow steppe	2001 2002	500	mead3	Belgorod Area, Belogorye Res. 51°11´N 37°45´E 193 m a.s.l.
	4. Mikhailivska Tsilyna	meadow steppe	1985 1986 1988	160	mead4	Symska Area Ukrainian steppe Res. 50°34´N 44°12´E 172 m a.s.l.

Nature zone/ subzone	Name of locality	Steppe type	Years of study	site area (ha)	abbrev.	Region
Steppe zone: Northern subzone of forb-bunchgrass steppe	5. Striltsivskyi step	forb-bunchgrass steppe	1986 1988 2009	1000	forb1	Luhansk Area, Luhanskyi Natural Res. 49°17´N 40°00´E 147 m a.s.l.
	6. Khomutivskyi step	forb-bunchgrass steppe	1982 1983 2004	1000	forb2	Donetsk Area, Ukrainian steppe Res. 47°17´N 38°10´E 57 m a.s.l.
	7. Striltsivskyi zakaznyk	chalky steppe	2009 2011	80	chalk	Luhansk Area 49°18´N 39°50´E 100 m a.s.l.
	8. Dnieprovsko-Orilskyi Res.	Northern sandy steppe	1999 2000 2003	300	sandN	Dnipropetrovsk Area 48°30´N 34°45´E 53 m a.s.l.
Steppe zone: Southern subzone of bunchgrass steppe	9. Askania-Nova Res.	bunchgrass steppe	1984 1985 1988	11000	bunch	Kherson Area, 46°28´N 33°58´E 29 m a.s.l.
	10. Ivano-Rybalchanskyi	Southern sandy steppe	1989 1990 1991	2074	sandS1	Kherson Area, Chernomorskyi Res. 46°27´N 32°07´E 6 m a.s.l.
	11. Solenoozernyi	Southern sandy steppe	1995 1996 1998	1325	sandS2	Kherson Area, Chernomorskyi Res. 46°27´N 31°58´E 1 m a.s.l.

In each locality, investigations were carried out for two consecutive years. The material was collected by sweeping with an entomological net (d=30 cm), as well as by hand collecting. Quantitative samples were taken every month from May to September, five samples of 50 sweeps each. The material obtained from two vegetation seasons was considered as a general sample. For comparative analysis, we chose plots in nature reserves with strictly protected steppe, because traditional regime management such as hay mowing dramatically impacts upon species composition and structure of spider communities (POLCHANINOVA 2004). In order to obtain more information on the spider species composition of local faunas and various steppe types, we conducted additional research in different years, and also used the data from available publications (PICHKA 1984a, 1984b, GURYANOVA & KHOMENKO 1991, PROKOPENKO 2001). In total, more than 12,000 spider specimens were collected. A list of species is given in the Appendix. Species are arranged by families according to PLATNICK (2012).

With the method of net sweeping, a large number of juvenile spiders were collected. In many cases, they could be identified to species level as they belonged to a single species of the genus in a given locality, or differed in period of maturity. For the genera whose immature specimens could not be distinguished, we considered the genus as a whole in general quantitative analysis, and then species relationships within the genus were estimated separately based on mature individuals.

In order to determine relative abundance, we used the Tischler rating scale, where eudominant n≥10%, dominant 5≤n<10%, subdominant 2.5≤n<5%, recedent 1≤n<2.5%, and subrecedent n<1% (TISCHLER 1949). We considered eudominants and dominants together as a dominant complex. The ecological groups of species were determined based on the data on their habitat preference within the forest-steppe and steppe zones of the East European Plain (Tab. 2). We define grassland species as species occurring in all habitats with predominance of herbaceous vegetation, in our case meadows, steppes, and open slopes of gullies. We consider permanent residents of one or more steppe types to be typical species. Sometimes they may occur in other habitats as rare finds.

Similarity of spider assemblages of the studied habitats was determined by cluster analysis performed in Statistica 7 (STATSOFT INC. 2004). Two year quantitative samples (see above) were pooled together and a percentage of each species of the total sample at each site was calculated. We used the Ward's algorithm as a

cluster method and Euclidian distance as a similarity measure.

Results

Species composition and species richness

A total of 107 spider species from 15 families were recorded in herbaceous vegetation at 11 study sites. Four families were the most species-rich: Araneidae (20 species, 18.7% of total species in study sites), Salticidae (19 species, 17.8%), Thomisidae (18 species, 16.8%), and Theridiidae (13 species, 12.1%). Only Araneidae were distributed quite evenly, ranging from 22% of the species in forb steppes to 27% in the sandy ones. Linyphiidae and Clubionidae occurred mainly in meadow steppes (Appendix). Thomisidae reached their maximum of species richness in bunchgrass steppes (23%) and fell to a minimum in meadow steppes (13%). Salticidae are known to increase in terms of the number of species towards the south (NENILIN 1984, MIKHAILOV 1997). In our collection, we found unexpectedly few salticid species in the bunchgrass steppe (4 species, 10%); in the other steppe types this increase could be seen not in absolute but only in relative numbers because of impoverishment of the species composition in the southern steppes (9 species, 15% in meadow steppes, 11 species, 17% in forb steppes, 9 species, 20% in northen sandy steppes, 7 species, 21% in the southern ones).

A third of the species found in meadow steppe have not been recorded southwards in genuine steppe. The spider fauna of meadow steppe situated in forest-steppe zone differs significantly from that of steppe habitats in steppe zone. Within the steppe zone, spiders are more evenly spread, and the fauna of each steppe type has only 7-12% of species not found in other steppe types.

Species richness of herb-dwelling spiders was maximal in both fragments of the forb steppe and minimal in both fragments of the southern sandy steppe (Appendix). In the largest steppe fragment (bunchgrass steppe in Askania-Nova) the species richness was slightly lower than that in the smallest one (chalky steppe in Milove District).
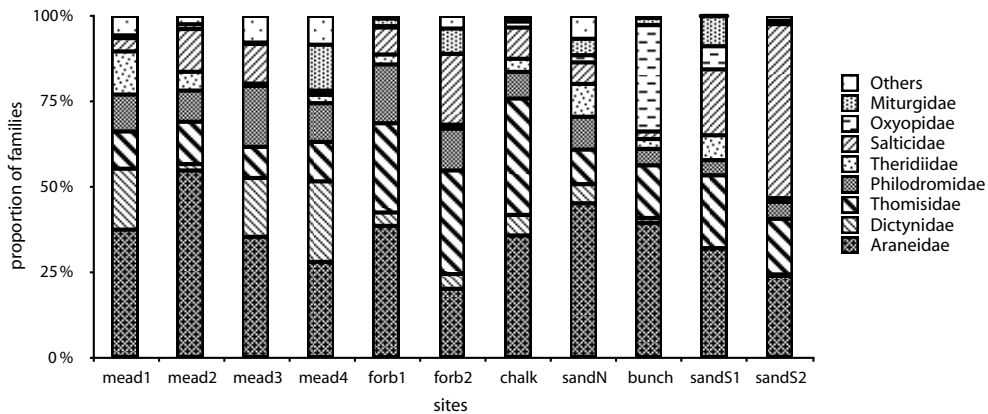
Ecological groups of species

Meadow steppes are characterized by a large number of forest and wetland species (Tab. 2). Some of them appear in the steppe in wet years, and nine species are permanent residents. The number of wetland and forest species gradually decrease towards the south. In different steppe types, generalist species comprised 15-20%. The number of steppe species at all sites was significantly lower than that of species widely distributed in grasslands. In meadow steppes, we found no steppe species.

There were no specialist species in the herb layer of steppe vegetation. Eight species which were considered to be typical were also found in other habitats; however, they reached their maximal abundance only in a certain steppe type. These species are *Run-*

Tab. 2: Ecological groups of spiders of various steppe types.

Ecological groups	Number of species in steppe type					
	meadow steppe	forb-bunch-grass	chalky	sandy N	bunch-grass	sandy S
generalist	10	11	9	8	6	5
wetland + forest	17	7	2	4	3	1
forest	7	3		1		
wetland	7	2		2		
grassland + forest edges	5	10	9	9	5	6
grassland	9	12	10	11	9	8
steppe		8	6	2	6	2
unspecified	6	9	2	4	7	5
typical				1		
			1			
			2			1
				1	1	
						3

Fig. 2: Family abundance (proportion of total numbers of families at each site) in spider assemblages of herbaceous vegetation of steppe habitats. Sites are arranged from north to south.
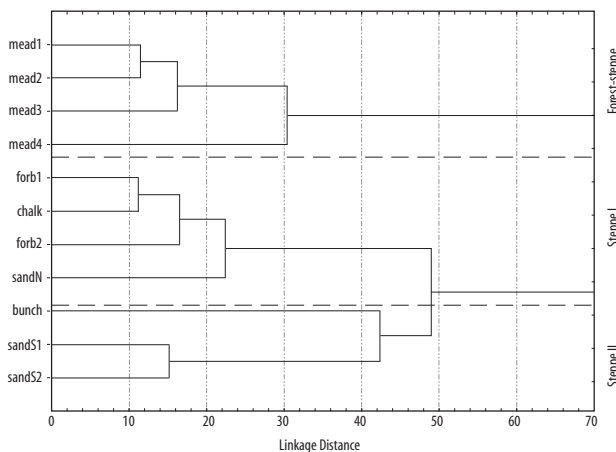
Fig. 3: Dendrogram of biocoenotic similarity of herb dwelling spider assemblages of various sites based on the % of each species in the two year samples in each site using Ward's method as cluster algorithm and Euclidian distance as similarity measure.

cinia grammica, *Pellenus seriatus* and *Yllenus vittatus* in southern sandy steppe, *Heliophanus lineiventris* in southern sandy and bunchgrass steppe, and *Uloborus walckenarius* in sandy and chalky steppes.

Thirteen generalist and grassland dwelling species occurred in almost all investigated steppe fragments (Appendix). Four species found in steppes of the forest-steppe and northern steppe subzone changed their habitat preference to forests or wetlands in the southern subzone. Ten wetland species spread to the south through steppe fragments no further than sites 'forb1' and 'sandyN'; southwards they also moved into intrazonal habitats. Five steppe species were widely spread in the steppe zone, but absent in meadow steppes; three species occurred in meadow steppes only in the site 'mead3'. It is the driest eastern site with a character of vegetation closer to genuine steppes.

Among five steppe species of the southern steppe subzone, three species occurred in sandy and chalky steppes of the northern subzone while two species did not extend beyond zonal boundaries. We did not find tendencies in distribution of the other species; 22 species were found as singletons, therefore we cannot judge their habitat preference.

Family abundance

The herbaceous vegetation of steppe habitats was dominated by Araneidae at all sites (Fig. 2). The second largest family Thomisidae preferred forb and chalky steppes. The relative number of Dictynidae went down from meadow steppes to bunchgrass and southern sandy ones. Philodromidae, likewise, were least abundant in the three southern sites while they reached a maximum in forb steppes and in the 'mead4' site. The distribution of Salticidae did not show a latitudinal trend. An unusually large individual number of this family was found in one of the sandy steppe sites. A characteristic feature of the spider assemblage of the bunchgrass steppe was the high abundance of Oxyopidae.

Biocenotic similarities

A dendrogram of biocoenotic similarity of spider assemblages of various sites brings them together based on a zonal-subzonal principle (Fig. 3). First, two clusters of the sites of the forest-steppe and steppe zone are separated, and then the sites of northern and southern subzones are divided into two groups. As expected, assemblages of two neighbouring fragments of southern steppes were similar, however, their similarity was less manifest than that of the two

adjacent meadow steppe plots and even of the forb and chalky ones.

Dominance structure

In the study areas, 13 species occurred in all steppe habitats. In addition, two species were found sporadically in both northern and genuine steppes. However none of them dominated in all steppe types.

Neoscona adianta was distinguished by the widest habitat spectrum (Tab. 3). It is common in various grasslands, but in the south it is particularly abundant. *Phylloneta impressa*, another dry grassland species, preferred sandy and chalky steppes. *Dictyna arundinacea*, by contrast, was eudominant in meadow steppes and occurred in high numbers in the forb ones. This species is characteristic of grasslands and forest edges in the forest-steppe and northern part of the steppe zone. The group of species with a narrower dominance spectrum was represented by *Neottiura bimaculata* and *Araneus quadratus* in meadow steppes, and by *Thomisus*

Tab. 3: Dominant spider species in different steppe habitats.

⬤ – eudominant n≥10%, ● – dominant, 5≤n<10%, ◉ – subdominant 2,5≤n<5%,
• – recedent ≤n<2,5%, · – subrecedent n<1% of spiders collected in each locality

Species	Localities										
	1	2	3	4	5	6	7	8	9	10	11
Neottiura bimaculata	⬤	●	·		·						
Araneus quadratus	⬤	⬤	⬤		·	·					
Cheiracanthium punctorium		·	·	⬤	·	·					
Evarcha spp.	·	·	●	●	·			●			
Dictyna arundinacea	⬤	⬤	⬤	⬤	·	·	●	●	·		·
Tibellus spp.	⬤	·	⬤	·	⬤	⬤	·	·	●		·
Xysticus spp.	⬤	●	●	●	⬤	⬤	⬤	⬤	●	●	•
Agalenatea redi	·	●	·		●	●	⬤	·	·	·	·
Mangora acalypha	●	·	·	●	⬤	·	⬤	⬤	·	·	·
Neoscona adianta	·	●	⬤	·	●	●	●	⬤	⬤	⬤	⬤
Heliophanus spp.	●	●	●	·	·	●	·	·	·	⬤	⬤
Phylloneta impressa	·	·	·	·	·	·	●	●	·	⬤	⬤
Cheiracanthium pennyi		·			·	·	·	●	·	⬤	·
Philaeus chrysops					●	●	●		·		●
Thomisus onustus					·	●	●	·	⬤	●	●
Uloborus walckenaerius							·	●		·	·
Oxyopes heterophthalmus							·	·	⬤	●	·
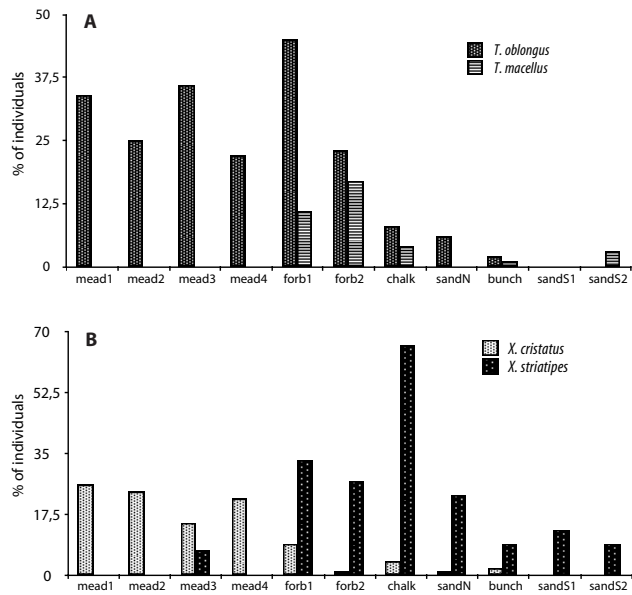
Fig. 4: Relative abundance (% of individuals out of the total number of spiders collected at each site) of (A) *Tibellus oblongus* and *T. macellus* and (B) *Xysticus cristatus* and *X. striatipes* in herbaceous vegetation of different steppe habitats. Sites are arranged from north to south.

onustus and *Philaeus chrysops* in genuine steppes. Six species were dominants at only one site (*Uloborus walckenaerius*, *Cheiracanthium pennyi*, *C. punctorium*, *Philodromus histrio*, *Pellenes seriatus*, and *Yllenus vittatus*).

Of further interest are the latitudinal changes of abundance of common species of the same genus. In the pairs *Tibellus oblongus–macellus* and *Xysticus cristatus–striatipes,* the first species of each pair was abundant in the forest-steppe and in the north of the steppe zone (Fig. 3). The second species of each pair appeared in genuine steppes, and in case of *Xysticus,* replaced the first one. Further to the south they all decreased in number or disappeared in steppe plots, although they remained quite common in adjacent forest stands (POLCHANINOVA 1990a). *Heliophanus flavipes* occurred in all steppe types. In the three southern sites, *H. lineiventris* co-occurred with *H. flavipes* and together they made up a significant proportion of the individuals found in these sites (Tab. 3). *Evarcha arcuata* was common in meadow steppes and in the northern sandy steppe. *E. michailovi* occurred in forb steppes and penetrated into one site of meadow steppes. Southward in the subzone of bunchgrass steppes, neither of these species was found.

Despite the local differences in species composition and dominance structure of spider assemblages, a number of characteristic features can be distinguished for every steppe type. All the spider complexes of steppe herbage had a polydominant structure.

In the four sites of meadow steppes, the group of dominants consisted of *Dictyna arundinacea* (16.0-24.3%), *Tibellus oblongus* (8.7-14.2%) and *Xysticus cristatus* (6.0-9.3%). *Araneus quadratus* was a member of this complex in three sites, *Neottiura bimaculata*, *Larinioides patagiatus*, *Cheiracanthium punctorium*, *Evarcha arcuata*, and *Neoscona adianta* were local dominants in not more than one site each. *Marpissa pomatia*, *Hypsosinga sanguinea,* and *Singa hamata* were subdominants in the meadow steppes. Southwards in genuine steppes they did not occur, or were found only as a few specimens. However we can not consider them to be typical species of meadow steppes because they were also numerous in wetlands (personal observation). The specificity of the spider assemblage of the driest eastern site 'mead4' is worth mentioning. The abundance of *Neoscona adianta* and the appearance of *Evarcha michailovi* and *Xysticus striatipes* make it similar to the assemblages of forb steppes.

Xysticus striatipes (9.3-15.7%), *Tibellus* spp. (10.7-12.6%), and *Neoscona adianta* (8.0-9.7%) were common dominants of forb steppes, with *Agalenatea redii* and *Mangora acalypha* co-occurring with them in the northern site, and *Philaeus chrysops*, *Evarcha michailovi*, *Heliophanus flavipes* and *Thomisus onustus* in the southern one. A range of species typical of dry grasslands appear in these steppes (*Heterotheridion nigrovariegatum*, *Theridion innoccuum*, *Heriaeus oblongus*, *Tibellus macellus, Xysticus marmoratus, Synageles hilarulus*, and *Philaeus chrysops*). However, we found no species specific for the forb steppes only.

The dominance complex of chalky steppe included *Xysticus striatipes* (25.5%), *Agalenatea redii* (11.6%), *Neoscona adianta* (10.0%), *Tibellus* spp. (6.4%), *Philaeus chrysops* (6.7%), and *Dictyna arundinacea* (5.8%). In the northern sandy steppe it consisted of *Neoscona adianta* (14.9%), *Xysticus striatipes* (11.0%), *Mangora acalypha* (8.9%), *Dictyna arundinacea* (5.8%), *Philodromus histrio* (7.7%), and *Uloborus walckenaerius* (5.3%). In the area investigated, the latter two species are associated with vegetation of sandy soil. They were also common in calcareous lands (POLCHANINOVA

2010). *Simitidion simile* and *Cyclosa oculata* preferred the same habitats but they had larger ecological flexibility, inhabiting meadows, shrubby steppes and even open deciduous forests (POLCHANINOVA & PROKOPENKO 2007b). *Gibbaranea bituberculata* and *G. ullrichi* came to the steppe plots from neighbouring pine forests.

The spider assemblage of the bunchgrass steppe was characterized by large numbers of three eudominants *Neoscona adianta* (29.8%), *Oxyopes heterophthalmus* (26.2%), and *Thomisus onustus* (14.0%), the occurrence of one subdominant *Xysticus striatipes*, and single finds of other species. Southern sandy steppes were dominated at both sites by *Heliophanus flavipes*, *H. lineiventris* (15.6-20.0%), *Neoscona adianta* (11.0-12.2%), and *Phylloneta impressa* (5.6-6.3%). In one of them (Ivano-Rybalchansky site) the dominance complex was supplemented with *Oxyopes heterophthalmus*, *Cheiracanthium pennyi*, *Thomisus onustus*, and *Runcinia grammica*, and in the other one (Solenoozerny) with *Pellenes seriatus* and *Yllenus vittatus*. The presence of the latter three species and the abundance of *H. lineiventris* is characteristic of the southern sandy steppes.

Discussion

Spider species richness of the investigated steppe fragments depended on the steppe type. The low number of species on the largest site of bunchgrass steppes can be explained by the monotonous plain relief and absence of neighbouring intrazonal habitats. Presumably, invertebrate communities within small sites increase in species richness due to species exchange with adjacent habitats (MAGURA & KODOBOCZ 2007). This statement is true for the forest-steppe and northern part of the steppe zone where an active interchange takes place (CHERNOV 1975). In our investigations, we recorded the presence of forest and wetland species in meadow steppes. However in the south of the steppe zone, despite a rich local fauna in general and the existence of neighbouring forest stands and lakes, the species composition of spiders of steppe fragments remained the poorest. Only one wetland species was found there.

About 12% of the species of the investigated area occurred in all steppe types. Another 12% changed their habitat preference spreading from north to south and moved from steppe sites to shaded and moist ones. These data illustrate well the 'principle of zonal change of habitats' by BEI-BIENKO (1966). Some of them, such as *Neottiura bimaculata*, changed

both habitat and vegetation layer moving from herbs to the ground (POLCHANINOVA 1990a). A group of southern species which spread to the north through the dry open sites made up only 4% of the species found in the steppe habitats. Our data confirm a decrease of generalist, forest and wetland dwelling species to the south and predominance of grassland species in genuine steppes. The same tendencies in distribution of ecological groups of spiders were shown by ESYUNIN (2009) in a transect through the Urals.

The relative abundance of spider families in steppe vegetation changes depending on the steppe type. This is confirmed by data on steppe localities in other regions. Thus, in mountain steppes of Bashkiria (Southern Urals), Tetragnathidae, Thomisidae, and Araneidae were dominants in numbers, while Thomisidae comprised the main part of the biomass (EFIMIK 1989). According to our data, Araneidae was the most abundant family while Tetragnathidae occasionally occurred in steppe as rare finds. In the east of the Russian Plain, in stony and forb steppes of Samarskaya Luka, Thomisidae reached the highest abundance followed by Araneidae and Salticidae (KRASNOBAEV 2003). In eastern Hungary (Great Hungarian Plain), dry sandy grassland communities that are close to sandy steppes were also dominated by Araneidae and Thomisidae while Salticidae and Dictynidae comprised a second-ranked group (HORVATH et al. 2009).

No single species dominated in all the steppe types and even within one type, a dominance complex was composed of different species. Meadow steppes were dominated by wetland species and genuine steppes by wide-spread grassland species. In azonal steppes, the complex included species inhabiting sparse vegetation of sandy and chalky soils. Dominant spider species of steppe and steppe-like habitats of the Urals also vary depending on zonal and local conditions (ESYUNIN 2009).

In conclusion the spider assemblages of the northernmost meadow steppes and the southernmost sandy steppes differed dramatically, as expected, because of zonal-climatic differences. From a zonal standpoint, the first have much in common with meadows (PONOMAREV & POLCHANINOVA 2006), and the latter with brackish meadows and salt-marshes with dense vegetation (POLCHANINOVA 1998). In our study, the most specific were herb dwelling spider assemblages of the bunchgrass steppe represented in Ukraine by a single site in the middle of plowed Dnieper lowland.

The second specific groups were assemblages of sandy steppes in the northern steppe subzone because these fragments are isolated and differ in microclimatic conditions and vegetation structure from other grasslands. Steppes of a certain type are formed under both climate and soil conditions of the zone and local topography (GRIBOVA et al. 1980). Accordingly, the structure of the animal communities of the steppes is a reflection of these conditions (MORDKOVITCH 1982). Assemblages of herb-dwelling spiders are characteristic of each steppe type and differ in species composition and dominance structure.

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Appendix: Occurrence of herbaceous vegetation spiders in investigated steppe habitats of Ukraine and Central Chernozem Russia. For a description of the localities, see Tab. 1.

Ecological groups: gn – generalist species, wf – wetland and forest, for – forest, wt – wetland, grf – grassland and forest edges, gr – grassland, st – steppe, un – unspecified, typ – typical.

Species	ecological group	Type of steppe habitats										
		meadow steppe				forb – bunchgrass		chalky	sandy Northern	bunchgrass	sandy Southern	
		1	2	3	4	5	6	7	8	9	10	11
Mimetidae												
Ero furcata (Villers, 1789)	for	+		+								
Uloboridae												
Uloborus walckenaerius Latreille, 1806	typ							+	+		+	+
Theridiidae												
Dipoena coracina (C.L. Koch, 1837)	un									+		
Enoplognatha latimana Hippa & Oksala, 1982	un				+					+		
E. ovata (Clerck, 1757)	wf	+			+	+	+					
Euryopis saukea Levi, 1951	st					+		+				
Heterotheridion nigrovariegatum (Simon, 1873)	st					+		+				
Neottiura bimaculata (Linnaeus, 1767)	wf	+	+	+	+	+						
Parasteatoda simulans (Thorell, 1875)	for			+								
Phylloneta impressa (L. Koch, 1881)	grf	+	+	+	+	+	+	+	+	+	+	+
Simitidion simile (C.L. Koch, 1836)	grf					+		+	+		+	+
Theridion innocuum Thorell, 1875	typ					+	+	+	+	+		
T. melanurum Hahn, 1831	un								+			
T. mystaceum L. Koch, 1870	yn			+								
T. pinastri L. Koch, 1872	for			+								
Linyphiidae												
Dactylopisthes mirificus (Georgescu, 1976)	un					+	+					
Erigone dentipalpis (Wider, 1834)	wtf	+	+		+					+		
Floronia bucculenta (Clerck, 1757)	wtf	+	+									
Gonatium paradoxum (L. Koch, 1869)	wtf			+								
Hylyphantes nigritus (Simon, 1881)	wtf		+									
Linyphia hortensis Sundevall, 1830	wtf	+										
L. tenuipalpis Simon, 1884	gn			+			+	+				
L. triangularis (Clerck, 1757)	gn	+	+	+		+	+	+				
Russocampus polchaninovae Tanasevitch, 2004	un			+								
Tetragnathidae												
Metellina segmentata (Clerck, 1757)	wtf			+								
Araneidae												
Aculepeira ceropegia (Walckenaer, 1802)	un					+				+		
Agalenatea redii (Scopoli, 1763)	gr	+	+	+		+	+	+	+	+	+	+
Araneus diadematus Clerck, 1757	for		+	+			+					
Araneus quadratus Clerck, 1757	wt	+	+	+	+		+					
Araniella cucurbitina (Clerck, 1757)	wtf					+		+	+			
Argiope bruennichi (Scopoli, 1772)	gr	+	+	+		+	+	+	+	+	+	+
A. lobata (Pallas, 1772)	st							+	+	+	+	
Cercidia prominens (Westring, 1851)	gn	+	+	+	+	+	+	+		+	+	+
Cyclosa conica (Pallas, 1772)	for	+		+								
C. oculata (Walckenaer, 1802)	grf			+		+		+	+			
Gibbaranea bituberculata (Walckenaer, 1802)	grf								+	+		

Species	ecological group	Type of steppe habitats										
		meadow steppe				forb – bunchgrass		chalky	sandy Northern	bunchgrass	sandy Southern	
		1	2	3	4	5	6	7	8	9	10	11
G. ullrichi (Hahn, 1835)	typ								+			
Hypsosinga albovittata (Westring, 1851)	un					+		+			+	+
H. pygmaea (Sundevall, 1831)	gr	+	+	+			+		+	+	+	
H. sanguinea (C.L. Koch, 1844)	grf	+		+		+	+	+	+			
Larinioides patagiatus (Clerck, 1757)	wt		+	+	+				+			
L. suspicax (O. Pickard-Cambridge, 1876)	wt				+							
Mangora acalypha (Walckenaer, 1802)	gn	+	+	+	+	+	+	+	+	+	+	+
Neoscona adianta (Walckenaer, 1802)	gr	+	+	+	+	+	+	+	+	+	+	+
Singa hamata (Clerck, 1757)	wt	+	+			+			+			
Pisauridae												
Pisaura mirabilis (Clerck, 1757)	wtf	+	+	+			+		+			
Oxyopidae												
Oxyopes heterophthalmus (Latreille, 1804)	typ					+		+	+	+	+	+
O. lineatus Latreille, 1806	un											+
Dictynidae												
Archaeodictyna consecuta (O. Pickard-Cambridge, 1872)	un								+			
A. minutissima (Miller, 1958)	un									+		
Dictyna arundinacea (Linnaeus, 1758)	grf	+	+	+	+	+	+	+	+	+	+	+
D. latens (Fabricus, 1775)	grf					+	+	+		+	+	
D. uncinata Thorell, 1856	wtf			+	+							
Miturgidae												
Cheiracanthium elegans Thorell, 1875	un						+					
C. erraticum (Walckenaer, 1802)	grf	+	+	+			+					
C. pennyi O. Pickard-Cambridge, 1873	gr					+	+	+	+	+	+	+
C. punctorium (Villers, 1789)	wt	+	+	+	+	+	+					
Clubionidae												
Clubiona caerulescens L. Koch, 1867	for	+										
Clubiona diversa O. Pickard-Cambridge, 1862	wt		+	+								
C. lutescens Westring, 1851	wtf				+							
C. neglecta O. Pickard-Cambridge, 1862	wtf	+	+	+	+							
C. pseudoneglecta Wunderlich, 1994	gn					+	+					
Sparassidae												
Micrommata virescens (Clerck, 1757)	wtf	+	+	+	+	+			+	+	+	
Philodromidae												
Philodromus cespitum (Walckenaer, 1802)	gn	+	+	+	+	+	+	+	+	+		
P. histrio (Latreille, 1819)	gn					+	+	+	+	+	+	
Thanatus atratus Simon, 1885	un									+	+	
T. pictus L. Koch, 1881	un						+			+		
T. vulgaris Simon, 1870	un						+					
Tibellus macellus Simon, 1875	st					+	+	+		+		
T. oblongus (Walckenaer, 1802)	gn	+	+	+	+	+	+	+	+	+		+
Thomisidae												
Embrechtella tricuspidata (Fabricius, 1775)	gn	+	+	+	+	+	+	+	+			
Heriaeus oblongus Simon, 1918	grf					+	+	+	+	+	+	
Misumena vatia (Clerck, 1757)	gn	+	+	+	+		+		+			
Runcinia grammica (C.L. Koch, 1837)	typ										+	+
Synema globosum (Fabricius, 1775)	un									+		

Species	ecological group	Type of steppe habitats										
		meadow steppe				forb – bunchgrass		chalky	sandy Northern	bunchgrass	sandy Southern	
		1	2	3	4	5	6	7	8	9	10	11
Thomisus onustus Walckenaer, 1805	gr				+	+	+	+	+	+	+	+
Tmarus piger (Walckenaer, 1802)	for						+		+			
Xysticus acerbus Thorell, 1872	gr					+	+		+			
X. cristatus (Clerck, 1757)	gn	+	+	+	+	+	+	+	+	+	+	+
X. kochi Thorell, 1872	gn			+	+	+	+	+	+	+		+
X. laetus Thorell, 1875	gr					+		+		+		
X. lanio C.L. Koch, 1835	for					+						
X. luctuosus (Blackwall, 1836)	for	+										
X. marmoratus Thorell, 1875	st						+			+		
X. mongolicus Schenkel, 1863	un								+			
X. ninnii Thorell, 1872	st					+		+		+		
X. striatipes L. Koch, 1870	gr			+		+	+	+	+	+	+	+
X. ulmi (Hahn, 1831)	wtf	+	+	+	+							
Salticidae												
Carrhotus xanthogramma (Latreille, 1819)	grf					+	+	+			+	
Evarcha arcuata (Clerck, 1757)	gn	+	+	+	+	+	+	+	+			
E. falcata (Clerck, 1757)	wtf		+			+			+			
E. laetabunda (C.L. Koch, 1846)	un			+		+						
E. michailovi Logunov, 1992	un			+		+	+					
Heliophanus auratus C.L. Koch, 1835	gn		+	+	+	+	+	+	+			
H. cupreus (Walckenaer, 1802)	wtf		+			+	+	+	+	+		
H. flavipes (Hahn, 1832)	gr	+	+	+		+	+	+	+	+	+	+
H. lineiventris Simon, 1868	typ									+	+	+
Marpissa pomatia (Walckenaer, 1802)	wtl	+	+	+								
Myrmarachne formicaria (De Geer, 1778)	un						+					
Pellenes seriatus (Thorell, 1875)	typ										+	+
Philaeus chrysops (Poda, 1761)	st					+	+	+	+	+		
Salticus scenicus (Clerck, 1757)	un							+	+			
Sibianor aurocinctus (Ohlert, 1865)	un	+		+								
Synageles hilarulus (C.L. Koch, 1846)	un					+						
S. subcingulatus (Simon, 1878)	grf						+		+			
Yllenus horvathi Chyzer, 1891	un											+
Y. vittatus Thorell, 1875	typ								+		+	+
Total number of species in locality		36	35	46	33	50	50	41	45	39	29	24
Total number of species in steppe type		61				64		41	45	39	33	

Behavioural analysis of web building anomalies in the orb-weaving spider *Zygiella x-notata* (Araneae, Araneidae)

Camille Toscani, Raymond Leborgne & Alain Pasquet

Abstract: Among animal constructions, spider's orb webs represent regular geometrical architecture models. Their construction is the result of successive, simple and reproducible behavioural patterns, often considered as stereotyped. It has recently been shown that spider's building behaviours vary, which can alter web regularity. The final capture spiral results from the laying of successive threads between two radii, here termed 'spiral units'. We defined a theoretical normal web, as a web in which each turn of the final spiral should be parallel to the preceding one. Weaving of the spiral units sometimes leads to anomalies in the orb web. Anomalies were identified and analysed in the orb-weaving spider *Zygiella x-notata* (Clerck, 1757). From video recordings of web construction, we noted the displacements of the legs and of the abdomen of the spider. We compared the frequency of displacements, and their duration, between the construction of spiral units that produce a normal turn and ones that produce an anomalous turn. The position of the legs on the web's threads was also analysed. Results showed that anomalies were not the consequences of a modification in activity but more likely the result of the position on the radii of the fourth leg. These results suggest that spiders use local information to build the final capture spiral.

Key words: behavioural variability, building behaviour

Many animal species belonging to different taxa (mammals, birds, reptiles, arthropods) can build more or less complex constructions. The success of these building behaviours is linked to morphological capacities and to coordination of movements (HANSELL 2005, 2007). These constructions are the result of a succession of repeated behaviours, which involve cognitive complexity (HANSELL & RUXTON 2008). A wide diversity of constructions can be observed at the inter-specific level, but at the intra-specific level, variations in building behaviours can lead to differences in construction. By comparison with a normal structure defined by the observer, some variations can appear as anomalies of construction. For example, some wasp nests do not possess a pedicel, which results from confusion in the program of construction (KARSAI & THERAULAZ 1995).

In spiders, the orb-web is the result of successive, simple and reproducible behavioural patterns organised in time (VOLLRATH 1992). The architecture of the web contains radii and a final – also called the capture or sticky – spiral. This spiral consists of a succession of segments of silk line attached to two

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successive radii. We name these linear segments 'spiral units'. They are the elementary parts of the final capture spiral. We defined a regular final spiral by the continuity of the spiral unit arrangement around the hub and by the parallelism of each turn of the spiral with the preceding one; i.e. the spiral unit is expected to be parallel with the preceding unit in the same sector, as defined by two successive radii. Despite the apparent regularity of the orb-web, capture spirals vary in form, size and density (estimated by the distance between two spiral turns). Different factors can affect this regularity, such as gravity (VOLLRATH & MOHREN 1985), loss of legs (VOLLRATH 1987) and experimental application of neurotoxins or other substances (WITT & REED 1965, HESSELBERG & VOLLRATH 2004).

Given that the orb-web is a direct reflection of successive behaviours (ZSCHOKKE & VOLLRATH 1995), it is a good model for studying variability in the sequence of building behaviour. Previous studies have shown that the spider uses the first pair of legs (L1) to determine spacing relative to the turn of the auxiliary spiral (VOLLRATH 1987) and that leg position is decisive in the control of interspiral distance (KRINK & VOLLRATH 1999). Construction of the final spiral is accomplished by producing a silk line, step by step between two successive radii. At each step, the spider executes the same behaviour in order to deposit the thread line between the site on the

Abbreviations	Explanation
NSU	Normal spiral unit
NP	Non-parallel spiral unit. In a sector between two radii, two adjacent spiral units meet at a point on a radius.
T2	Two adjacent spiral units stuck together.
R2	Second radius of the spiral unit.
SU	Spiral unit
L1	The first pair of legs.
L4P	The fourth leg oriented to the web's periphery, i.e., the direction opposite to the hub.

radius where the thread was just attached and a new site on the next radius. We hypothesize that leg displacement during final spiral building is dictated by local configuration (THERAULAZ et al. 1998) – i.e. immediate stimuli at the time of building, such as the position of an already laid preceding spiral unit – rather than knowledge of the global web structure. Anomalies, defined as alterations or discontinuities within a regular final spiral, have recently been identified in *Zygiella x-notata* (Clerck, 1757) (Araneae, Araneidae) (Pasquet unpubl.). We used this species to understand the mechanisms of building anomalies through the behaviours of spiral unit construction. The understanding of anomalous building behaviour will help to provide a better comprehension of orb-web building behaviour and of how simple organisms can build large, complex structures.

Material and methods

Zygiella x-notata is an orb-weaving spider abundant in the west Palearctic region. Adult females were collected is the north-east of France (Nancy, 48°41'N, 6°17'E, 272 m a.s.l.) in 2008 and 2010. Spiders were maintained in the laboratory in plastic boxes (10×7×2 cm), where they were fed with flies (*Lucilia caesar*) and supplemented with water once per week.

To allow observations of web-building behaviour, spiders were placed into wooden frames (50×50×10 cm) closed by two panes of glass that were suitable for *Zygiella* to build webs with the same characteristics as webs built in their natural habitat. After a maximum of 96h, or after construction was complete, spiders were returned to their boxes. Video recordings of capture spiral building (n=17) (Fig. 1) were made (camera Sony HDR-CX550) and analysed using the software "The Observer XT-10.0".

Three types of construction were observed and compared. The first type (NSU) was the pattern found in all webs (control). Here, the spider built a spiral unit parallel to the previous one in the same sector (Fig. 2). The second pattern (NP) was when the unit built was not parallel to the previous one in the same sector and the two units met at the same point on the next radius of the sector. The third pattern (T2) was when the unit stuck to the previous one in the same sector. In the 17 webs recorded, we took at random 15 T2 anomalies and 15 NP anomalies. For each anomaly, we associated a normal spiral unit (NSU, n=30) constructed just before an NP or T2 anomaly. We never sampled the same type of anomaly twice in the same web.

By analysing video recordings (24 images/s) we noted the building time of the spiral units, and we counted all the displacements of each of the eight legs for the construction of a spiral unit (i.e. the number of leg displacements). We noted the number and the duration of displacements of L4P – the fourth leg oriented to the web's periphery, i.e. the direction opposite to the hub – between the moment when it stopped extending the thread from the spinneret and the moment when it was placed on R2 (the second radius, where the current spiral unit was fixed) (Fig. 2). These legs were observed because they are known to play an important role in the final capture spiral construction (EBERHARD 1988). Finally we noted the individual positioning of the abdomen and of L4P on R2 (position R2/0, R2/1 or R2/2), where the current spiral unit was fixed (see Fig. 2). If the current spiral unit was attached at R2/2, a normal spiral unit was formed. If it was fixed at R2/0 or R2/1, an anomalous spiral unit appeared. The position in R2/0 or R2/1 was not linked to a particular anomaly.

We compared the construction of an anomalous spiral unit and the associated control one by conducting paired t-tests or Wilcoxon nonparametric tests (in case of non-normality of the data). Four parameters were taken into account: building time of the spiral unit, number of all leg displacements, number and mean duration of L4P displacements (n=15 for each type of anomaly). Normality of the data was tested by Shapiro-Wilk tests. Position of the abdomen and L4P during spiral unit building was compared between normal and anomalous spiral units using a McNemar test (abdomen: n=30, (the two anomalies were combined) L4P, n=15 for each anomaly). The means were given with standard deviation (mean ±

standard deviation), and the medians with lower and upper quartiles, and p<0.05 was considered as significant. The statistical software R 2.15.0 and StatXact3 were used (R 2012, STATXACT3 1995).

Results

Analysis of leg displacement

When normal and anomalous final spiral unit construction were compared, no difference in mean building time between a normal spiral unit (NSU) and an anomalous one (NP or T2) was found (paired t-test, mean NP=5.93 ± 0.37s, mean NSU=6.01 ± 0.43s, n=15, t=0.28, p=0.78; Wilcoxon test, median T2=6.24s (5.38s, 7.28s), median NSU=6.08s (5.36s, 7.82s), n=15, W=-5, p=0.88).

The mean number of leg displacements did not differ when the spider constructed a normal spiral unit or an anomalous spiral unit (Wilcoxon test: median NP=75 (60, 95), median NSU=75 (59, 89), n=15, W=-14, p=0.71; median T2=72 (68, 87), median NSU=80 (71, 88), n=15, W=11, p=0.78).

The mean duration of L4P displacements when the spider built a normal spiral unit was not significantly different than when an anomalous one was built (Wilcoxon test: median NP=0.36s (0.28s, 0.42s), median NSU=0.24s (0.16s, 0.30s), n=15, W=-37, p=0.16, median T2=0.20s (0.12s, 0.36s), median NSU=0.28s (0.22s, 0.44s), n=15, W=24, p=0.47).

The mean number of L4P displacements also did not differ significantly when the spider built a normal or an anomalous spiral unit (Wilcoxon test: median NP=3 (2, 3), median NSU=2 (2, 3), n=15, W=-16, p=0.49, median T2=2 (2, 4), median NSU=4 (2, 5), n=15, W=10, p=0.75).

Position of the abdomen

During the attachment of the spiral unit, the position of the abdomen on R2 was not significantly different between an anomalous spiral unit and a normal one (McNemar test, n=30, p=1). In both cases, the abdomen was predominantly positioned in the same location as the L4P (84.4% of cases). In 15.6% of cases, it was located above the L4P on R2.
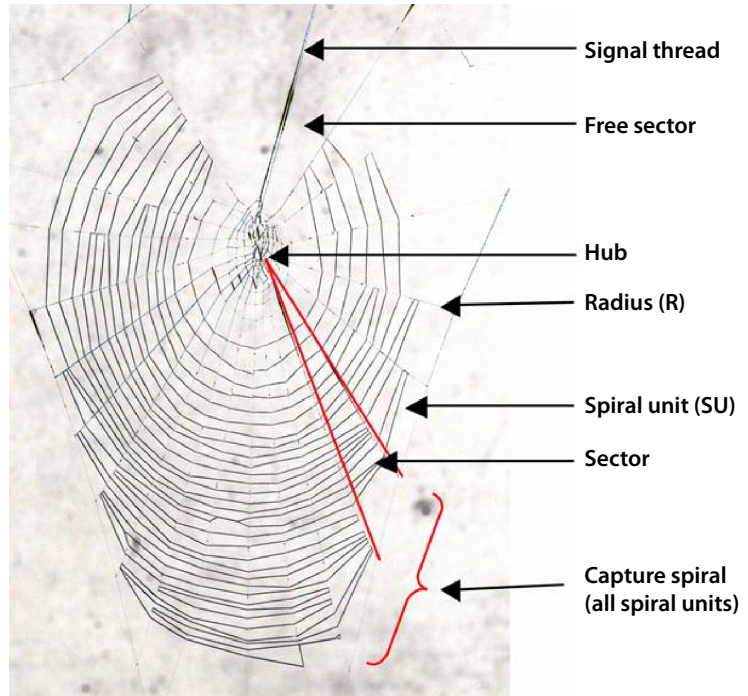
Fig. 1: Web of *Zygiella x-notata*. The hub, the radii and the capture spiral of the web are represented; a part of the frame is not visible. The spiral unit is represented by the thread between two radii and as a segment of the final capture spiral.
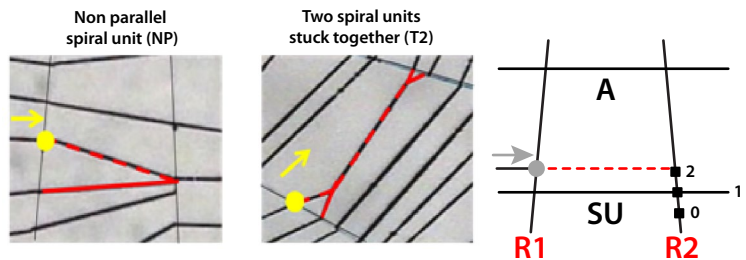
Fig. 2: The two pictures on the left represented the two anomalies that were analysed (NP and T2). The scheme on the right represents the normal situation, with the red dotted line, which symbolizes the spiral unit (SU) recorded and analysed from radius 1 to radius 2. 0, 1 and 2 were the possible positions of the attachment of the line on R2; if the attachment was made at position 2, we obtained a normal spiral unit, if it was in 0 or 1 we obtained an anomalous spiral unit. The grey or yellow arrow represents the direction of spider movement and the grey or yellow point represents the starting point of spiral thread unit construction on radius R1.

Position of the L4P

The position of the L4P was significantly different when the spider deposited a NP spiral unit than when it built a normal one (McNemar test, n=15, Qobs=10.1, p=0.001). The L4P positions were in R2/2 in 80% of cases when the spider built a normal spiral unit, whereas this position was never selected when building a NP spiral unit. In this case, the L4P positions were on R2/1 or R2/0 in 100% of the cases. Positioning of the L4P was also different between T2 spiral unit and a normal one (McNemar test, n=15, Qobs=11.1, p<0.001). Indeed, in 93.3% of normal spiral unit construction, the L4P was positioned on R2/2, whereas this position was selected in only 6.7% of cases for T2 spiral units. Therefore, in a normal spiral unit construction the position of the L4P was different than during the construction of an anomalous one (Fig. 3).
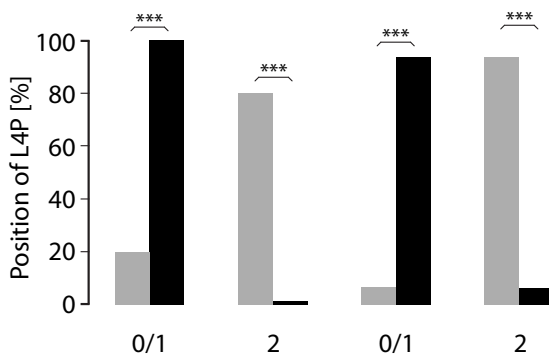
Fig. 3: Comparisons of the positions of L4P (0/1 or 2, see text) between an anomalous spiral unit (black bars) and a normal parallel one (grey bars). On the left, the case of NP anomalies and on the right the case of T2. ***: McNemar test p<0.001.

Discussion

Parallelism between turns of the final capture spiral in orb webs can fail to occur in some sectors of the webs. We studied here the effects of weaving behaviour on these anomalies. To do this, we observed the behaviour of the spider *Zygiella x-notata* during building spiral units (segments of thread attached to two successive radii). We defined normal spiral units as a sector with two consecutive parallel spiral units and anomalous spiral units – i.e. a sector with two consecutive non-parallel spiral units – and we compared different parameters measured during spiral unit construction. No difference in activity (leg displacements and abdomen positioning) was found between the construction of a normal spiral unit and an anomalous one for the four parameters measured: building time, number of leg displacements, mean duration and number of L4P displacements. Therefore, activity does not seem to result in anomalous construction of spiral units.

We analysed the position of L4P on the second radius (R2) at the end of the construction of the spiral units, and we observed a difference in its position between anomalous and normal spiral units. The position of L4P was almost always in R2/0 or R2/1 for the two anomalies investigated in this study (NP and T2), whereas the L4P positions in R2/2 produce normal units. The position of the abdomen, however, did not differ between an anomalous and a normal spiral unit. In conclusion, it is a modification in the position of L4P on the radius, which leads to the building of an anomalous spiral unit. Nevertheless, placement of L4P on the radius remains one of the last steps of the building sequence, and any modification of its position is most likely caused by a change in the position of L1 (first pair of leg) because L4 took the place of L1 on the next radius. Thus we concur with previous studies which hypothesized that L1 is largely implicated in the establishment of the final capture spiral (VOLLRATH 1987). This shows that spiders use information to decide where to attach the spiral of the previous unit on the radius.

It is known that the local configuration of the environment may influence the building behaviour of an animal (HANSELL 2000, THERAULAZ et al. 1998). During the completion of complex structures, animals may use the initial parts of the construction as markers for subsequent stages of construction, as in the building of nests by termites or bees (GRASSÉ 1959, DOWNING & JEANNE 1990). Thus, a construction that is the result of a repeated response to local stimulus is subject to variation at each building step (HANSELL 2005). This is the case in orb-web building; the spider takes into account previous elements of the construction for the building of further elements, and errors can occur in this process. Such errors via architecture modification could lead to modifications in the performance of the web, as studied by CRANFORD et al. (2012).

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Tests for attraction to prey and predator avoidance by chemical cues in spiders of the beech forest floor

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Abstract: Spiders leave draglines, faeces and other secretions behind when traveling through their microhabitat. The presence of these secretions may unintentionally inform other animals, prey as well as predators, about a recent and possible current predation risk or food availability. For a wolf spider, other spiders including smaller conspecifics, form a substantial part of their prey, and larger wolf spiders, again including conspecifics, are potential predators. We tested two hypotheses: that large wolf spiders may locate patches of potential spider prey through the presence of silk threads and/or other secretions; and that prey spiders may use secretions from large wolf spiders to avoid patches with high predation risk. We used large (subadult or adult) *Pardosa saltans* to provide predator cues and mixed dwarf spiders or small (juvenile) *P. saltans* to provide prey cues. Subadult wolf spiders were significantly attracted to litter contaminated by dwarf spiders or small conspecifics after 6 hours but no longer after 24 hours. In contrast, neither dwarf spiders nor small *P. saltans* showed significant avoidance of substrate contaminated by adult *P. saltans*. However, small *P. saltans* showed different activity patterns on the two substrates. The results indicate that wolf spiders are able to increase the efficiency of foraging by searching preferentially in patches with the presence of intraguild prey. The lack of a clear patch selection response of the prey in spite of a modified activity pattern may possibly be associated with the vertical stratification of the beech litter habitat: the reduced volume of spaces in the deeper layers could make downward rather than horizontal movement a fast and safe tactic against a large predator that cannot enter these spaces.

Key words: Anti-predatory response, Araneae, cannibalism, IGP, Lycosidae, prey detection

A kairomone is "a chemical that is produced by one organism conveying information to another organism of a different species; it is advantageous to the recipient but detrimental to the producer of the chemical" (RESH & CARDÉ 2003). Many animals do not leave a single chemical but instead a complex of secretions, and recipients may benefit by using several senses to detect the multitude of simultaneous visual, mechanical or chemical cues (DICKE & GROSTAL 2001) to get more detailed information about the previous occupant of the patch than can be obtained from a single chemical cue. Spiders leave draglines as witnesses of their locomotory activity, but faeces and other secretions may be released as well. Other animals that are able to decode this information, whether potential prey or predators, may benefit either through avoiding a predator by leaving the patch, or by concentrating their search in patches where prey have recently been active. Silk lines and other secretions thus have "kairomonal function" in the sense of unintentionally informing other individuals about the level of activity in the patch and the identity of previous occupants. In many predator-prey contexts, especially in the case of spiders, restriction of the kairomone concept to interspecific information transfer is unfortunate. Conspecifics may be as important as prey or predators as any heterospecific animal, and unintentional information may benefit these to the same extent. Finally, many experimental setups (including the one used in this paper) are not designed to identify the exact cue(s) to which the animals respond. Therefore, in this study we analyse to what extent secretions left by spiders are used by other spiders – whether of the same or different species – as sources of information about potential prey and predators.

There is substantial evidence to support the use of silk and/or other secretions as information sources allowing anti-predatory responses in spiders, especially among wolf spiders (DICKE & GROSTAL 2001, PERSONS et al. 2001, BARNES et al. 2002, PERSONS et al. 2002, PERSONS & LYNAM 2004). Much less is known about whether spiders can use cues from their prey and thus increase foraging efficiency. A few studies have established that some spiders can detect cues from other spider prey species when foraging (KESSLER & LAAN 1990, PERSONS & RYPSTRA 2000), but none

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of these have included a test of whether cannibalistic spiders may similarly utilize cues from individuals of their own species.

Non-web building spiders spend a considerable amount of time in search of prey, and estimates of average capture rates are usually quite low (e.g. NYFFELER & BENZ 1988). As a result, these spiders are often limited by food in nature (WISE 1993). Their success will be increased if they can search non-randomly by recognizing patches of the habitat that are rich in potential prey while poor in the spider's own predators. The present experiments were intended to gain evidence about the use of silk and/or other secretions for prey detection and predator avoidance among spiders of the beech forest floor. A dominant predator in the habitat is the wolf spider *Pardosa saltans* Töpfer-Hofmann, 2000, while an assemblage of dwarf spiders as well as small juveniles of *P. saltans* are the most abundant potential intraguild prey. We expected that large *P. saltans* would be attracted to litter contaminated by secretions from the potential intraguild prey, while these should tend to avoid litter contaminated by secretions from large wolf spiders.

Materials and methods
Spiders
The wolf spider *Pardosa saltans* is a common species of deciduous forests in Denmark. Like other *Pardosa* species, it has a mixed searching and sit-and-wait foraging behaviour, named the "sit-and-move" tactic by SAMU et al. (2003); i.e. they spend most of the time waiting for prey to come to them, but frequently change position. Presumably they end up in patches of high prey availability. Apart from insects, wolf spiders prey on other spiders including individuals of their own genus and species which may form a large proportion of their prey (EDGAR 1969). Cannibalism among wolf spiders is typically committed by a larger spider preying on a smaller, where the latter usually is only half or less of the mass of the former (SAMU et al. 1998). For the design of the experiments we took advantage of the fact that *P. saltans* in Denmark has a biennial life cycle (TOFT 1976, as *P. lugubris*) with reproduction in late spring. Animals of the second year cohort (i.e. subadults and adults after two overwinterings as juveniles) could therefore be used as predators/cannibals, and small juveniles of the first year cohort (i.e. after one overwintering) as their conspecific prey. Other litter dwelling dwarf spiders (linyphiids and theridiids) found in the same habitat were used as intraguild prey.

Individuals of *P. saltans* were collected by hand from a beech stand in the mixed forest Lillering Skov west of Århus, Denmark (N 56° 8' 32", E 9° 56' 38", 45 m a.s.l.) during spring months. The cohorts were easily distinguished by their body size even when the large cohort was still not mature (small juveniles: 3-4 mm, subadults: 5-7 mm). Litter from the same area was subsequently sifted for dwarf spiders. We used the mixture of different species obtained by sifting. After the experiments they were identified as being from the family Linyphiidae (including – in order of decreasing abundance – *Microneta viaria*, *Diplocephalus picinus*, *Tenuiphantes tenebricola*, *Porhomma pallidum*, *Bathyphantes gracilis*, *Macrargus rufus*, *Saloca diceros*, *Walckenaeria obtusa*, *W. cucullata*, and some unidentified juveniles) and Theridiidae (*Robertus lividus*). All spiders were kept in individual tubes and stored under cool and moist conditions until the experiments were set up. The spiders used for the predator avoidance experiments were fed intermittently during this period, and they were observed to produce webs both in the tubes and, subsequently, in the experimental petri dishes.

Procedure
We used the same experimental design, taken from KESSLER & LAAN (1990), in both the attraction and avoidance experiments. The collected beech litter was washed in boiling water to remove any silk and other secretions it may have contained and laid out for two days to dry thoroughly. The clean and dry beech litter, selected to be of approximately the same size and the same amount, was placed in 9 cm diameter petri dishes with a small piece of damp cotton in the centre for moisture. The spiders intended to provide the cues were then placed individually in the beech litter dishes and allowed to stay there for 48 hours. Control litter was treated the same way except there was no spider in the petri dishes. In the attraction-to-prey series of experiments dwarf spiders or small *P. saltans* were used for pre-treatment of the litter, and large (subadult) *P. saltans* acted as test predators. In the predator-avoidance series of experiments, adult *P. saltans* of both sexes were used for the pre-treatment against which dwarf spiders or small *P. saltans* were tested.

Immediately after the cue-providing spiders were removed from the petri dishes, one dish-full of contaminated litter was transferred to one side of a larger petri dish (14 cm diameter). This was done with a pair of forceps to prevent human contamination. The

pile of litter from the small petri dish was transferred as a whole in order to prevent breakage of the silk lines. A similar amount of control litter was placed in the other side of the large petri dish, transferred with forceps and as a whole pile as well. There was a piece of damp cotton in the centre for moisture. We controlled for side biases by facing the contaminated side of half the petri dishes towards one side of the room and the other half towards the other side. In the attraction experiments a series of control dishes with clean litter in both sides were included in order to further rule out any side bias due to unrecognised external factors. The test spider was then placed in an inverted glass tube in the centre of the petri dish between the two groups of litter. It was given one minute to settle there before removing the tube and allowing the spider to move about freely. The position of the large wolf spiders was recorded as being either in the clean litter or in the contaminated litter after 6 hours and again after 24 hours.

The predator-avoidance experiments did not have separate double-control replicates. They were run both with litter as described above and repeated with filter paper instead of litter in the dishes. In the latter series we added an inspection after 2 hours to account for the possibility that predator avoidance might be a faster, but less enduring, response than attraction to prey. All experimental series were replicated 20-30 times. Each spider specimen was used only once. A further supplementary experiment was also performed using filter paper as the substrate and with one half contaminated by an adult female, an adult male or a small juvenile *P. saltans* and using small juvenile *P. saltans* as test animals (n = 12 in each group). For 45 minutes the duration of the activities "sit" and "run" were measured with stop-watches for both the contaminated and the clean filter paper. We expected

different responses to adult and juvenile contamination, since small juveniles of the same size as the test spiders would not pose a similar threat as the larger conspecifics. In all experiments observations of spiders that could not unequivocally be assigned to one response, e.g. if the spider was in the spaces between litter types or filter papers, were ignored. The results on patch choice were analysed with the binomial one-tailed tests (SIEGEL & CASTELLAN 1988) and the duration of behaviours by paired *t*-tests (JMP 8.0).

Results

Attraction to prey cues

Spiders of the control group showed no preference for a particular side of the petri dish at any of the two check times (6 or 24 hours) (Tab. 1). Thus there was no side bias inherent in the experimental set-up. After 6 hours, subadult *P. saltans* were significantly positioned in the litter contaminated by dwarf spiders as well as in litter contaminated by small *P. saltans* (Tab. 1). This pattern persisted at the 24 hours inspection but it was no longer statistically significant, indicating a weakening effect of the cue that earlier attracted the test spiders.

Avoidance of predator cues

There was no indication that linyphiids or small *P. saltans* juveniles avoided settling in litter contaminated by a potential spider predator (adult *P. saltans*), whether the predator was a female or a male (Tab. 2). Repeating the same experiment using filter paper instead of litter did not change this result. However, the activity of small juvenile *P. saltans* differed between contaminated and clean filter paper (Fig. 1). Overall, the spiders spent much more time sitting than running (paired *t*-test, t_{35} = 19.3, P < 0.0001). The time spent running was significantly lower on contaminated than on clean substrate (t_{35} = 3.49, P = 0.0013). The same was true for sitting, though this was not statistically significant (t_{35} = 1.84, P = 0.075). It made no difference whether contamination was by a female, a male or a juvenile (all P > 0.05).

Tab. 1: Positions of subadult *Pardosa saltans* at prescribed inspection times in petri dishes in which one side had clean beech litter and the other had litter contaminated by exposure to potential intraguild (dwarf spiders) or conspecific prey (in the control experiment both sides had clean litter).

Prey contaminant	Time of inspection	No. in contaminated litter	No. in clean litter	P*
Control (clean litter)	6 h	9	11	0.748
	24 h	10	10	0.588
Dwarf spiders	6 h	16	4	**0.006**
	24 h	13	7	0.132
Small *P. saltans* juveniles	6 h	15	5	**0.021**
	24 h	13	7	0.132

*One-tailed binomial test

Tab. 2: Positions of test spiders at prescribed inspection times in petri dishes in which one side had clean beech litter and the other had litter contaminated by exposure to potential intraguild (dwarf spiders) or conspecific predator.

Predator contaminant	Test spider (substrate)	Time of inspection	# in contam. litter	# in control litter	P*
P. saltans ad. ♀	Dwarf spiders (litter)	6 h	13	16	0.36
		24 h	16	12	0.29
P. saltans ad. ♂		6 h	16	13	0.36
		24 h	15	13	0.43
P. saltans ad. ♀	*P. saltans* juvs (litter)	6 h	10	11	0.50
		24 h	9	12	0.20
P. saltans ad. ♂		6 h	11	12	0.66
		24 h	11	11	0.58
P. saltans ad. ♀	Dwarf spiders (filter paper)	2 h	16	13	0.36
		6 h	15	15	0.57
		24 h	13	16	0.36
P. saltans ad. ♂		2 h	12	16	0.29
		6 h	13	15	0.42
		24 h	12	15	0.29

*One-tailed binomial test

Discussion

Using the same experimental design (though with pine needles instead of beech litter), KESSLER & LAAN (1990) obtained significant responses indicating attraction of adult females to other conspecific females, and of adult males to adult conspecific females. They also found one linyphiid species that avoided litter contaminated by a potential predator (*P. lugubris/saltans* in their case too). However, they did not see a significant attraction by wolf spiders to linyphiid-contaminated litter. The present study shows that wolf spiders may choose to settle in a patch which has recently been visited by potential spider prey, irrespective of whether this prey is of a different family or a conspecific. In contrast, we failed to document direct avoidance of a habitat patch infested with predator cues. However, measurements of the activity of small juvenile *P. saltans* when released in the petri dishes indicated a differential response to clean vs. contaminated filter paper. The fact that they spent more time sitting on the clean paper and less time running on the contaminated paper is consistent with an avoidance response, i.e. getting away quickly from a contaminated area and staying in a clean area. Our expectation of a weaker response to contamination from juveniles of the same size as the test spiders compared with contamination from adults was not fulfilled. This may be because cannibalism between

same-sized conspecifics can be frequent if the opponents differ in hunger level (PETERSEN et al. 2010). The contaminating spiders left silk lines in the litter and possibly other substances. BARNES et al. (2002) showed that spiders can detect the difference between old and new chemical cues. This was the case in a predator avoidance situation where the cues were of the same type as in our study, i.e. silk and/or other secretions from another spider. Both mechanical and chemical cues may be involved in their detection. In our experiments great care was taken to keep the silk lines intact during manipulations. The weakening of the response after 24 hours may therefore suggest that it is more volatile or easily degradable kairomones associated with the silk or left on the substrate, and not the silk lines as such, that informed the spider about the presence of potential prey. In nature there may be both mechanical and chemical degradation of the silk, though also here chemical degradation of associated chemicals is likely to be faster than physical destruction of silk lines. An alternative explanation for the fading response is the accumulation of the test spider's own silk and secretions during the test period. These would have made it increasingly more difficult to recognize the prey spider's cues as the test progressed. Although this experiment produced evidence that *P. saltans* are able to distinguish between patches which are, or are not, inhabited by intraguild or conspecific

prey, it is still unknown if they can distinguish between patches with different densities of these prey, and to what extent they can detect patches in the habitat with high densities of their various insect prey. It is also unknown to what extent these abilities help the spiders improve their foraging efficiency compared with random unguided searches.

In summary, *Pardosa saltans* may use prey cues (silk and/or other secretions) to locate areas with intraguild and/or conspecific prey, but they seem not to directly avoid areas with predator cues. This result is surprising because, a priori, it would be expected that selection for avoiding predators is stronger than selection to obtain a meal. A possible biological explanation may be found in the vertical stratification of deciduous forest litter habitats. Top litter has large spaces, but these become smaller in deeper layers where the old litter is gradually transformed into amorphous humus or mull, and the size of spiders inhabiting these layers decreases accordingly. WAGNER et al. (2003) found the deepest stratum of deciduous forest litter dominated by tiny dictynids and linyphiids and all other families were rare. Thus, small spiders may seek refuge in deeper layers where they are inaccessible to larger spiders. It is even possible that vertical movement may be the safer option, because a horizontal response would only bring the spider to another possibly dangerous patch. The possibility of escaping by vertical movement was not available in the experiments, but has been documented by FOLZ et al. (2006) in a wolf spider from agricultural fields. Due to the structure of this habitat, the escape response here consisted of climbing the vegetation.

Acknowledgements
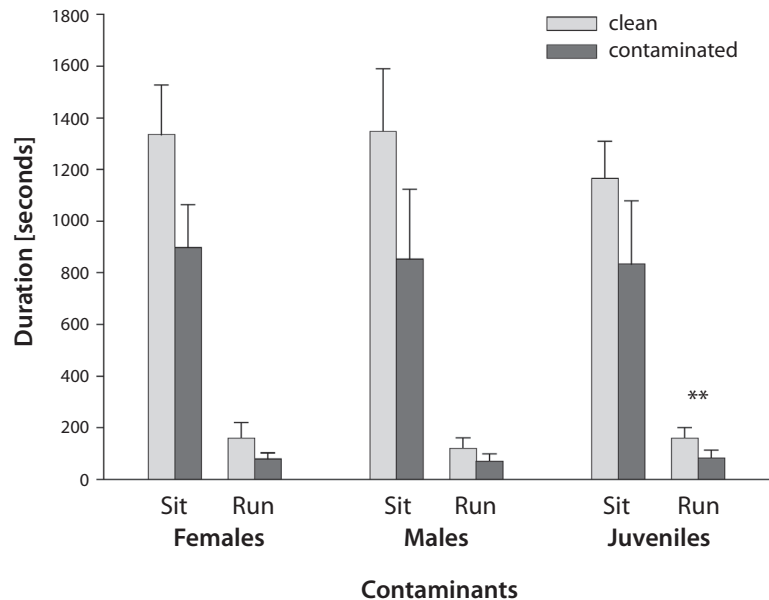
Fig. 1: Duration (mean ± SE) of the activities "sit" and "run" by small juvenile *P. saltans* during the first 45 minutes after release into a petri dish with filter paper, one half of which was clean (control) the other half contaminated with silk and/or other secretions from either adult females, adult males, or small juveniles of *P. saltans*. Pairwise comparisons showed significant difference between clean and contaminated for "run" in the juvenile contaminant group ($P = 0.0040$; indicated by **) and for "run" in the adult female and male contaminant groups combined ($P = 0.029$).

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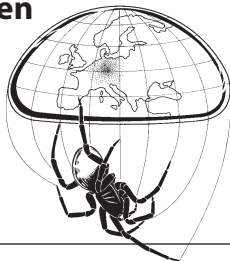
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SCHULZE E., G. WERNER & H. MEYER (1969): Title of the article. In: MÜLLER F. (Ed.): Title of the book. Ulmer, Stuttgart. pp. 136-144

SCHULZE E. & W. SCHMIDT (1973): Title of the book. Vol. 2/1. 2. Aufl., Parey, Hamburg u. Berlin. 236 pp.

PLATNICK N.I. (2005): The world spider catalog. Version 5.5. – American Museum of Natural History, Internet: http://research.amnh.org/entomology/spiders/catalog/index.html (accessed at [date])

WÖLFEL C.H. (1990a): Title of the Thesis. Diss. Univ. XY, Zool. Inst. I. 136 pp.

WÖLFEL C.H. (1990b): Title of the report. Gutachten i.A. Bundesamt für Naturschutz. (unpubl. ms.)

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