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EVALUATION OF PREY FOR THE SPIDER *DICYMBIUM BREVISETOSUM* LOCKET (ARANEAE: LINYPHIIDAE) IN SINGLE-SPECIES AND MIXED-SPECIES DIETS

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Abstract

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The objective of this study was to asses effects of dietary mixing of prey of different quality for a generalist predator. Prey of three qualities were tested in single-species and mixed-species diets: the cereal aphid *Rhopalosiphum padi* as a low quality prey, and two qualities of fruit flies *Drosophila melanogaster* representing intermediate quality (Normal flies) and high quality (Enriched flies) prey. The two types of fruit flies were obtained by rearing the flies on different media. It was expected that aphids might contribute positively to the diet of intermediate quality flies, but contribute nothing or negatively to that of high quality flies. The value of prey was assessed by fitness parameters in an egg production experiment. Females of the linyphiid spider *Dicymbium brevisetosum* were assigned to one of 6 diet treatments: 1) Normal *D. melanogaster*, 2) Normal *D. melanogaster* + *R. padi*, 3) Enriched *D. melanogaster*, 4) Enriched *D. melanogaster* + *R. padi*, 5) *R. padi*, and 6) *R. padi* added to Normal *D. melanogaster* until the first eggsac appeared, then only *R. padi*. The following parameters were recorded: no. of egg sacs per female, no. of eggs/sac, and hatching success. Females on single-species diets of aphids produced fewer eggsacs containing fewer eggs than spiders on fruit fly diets. Normal flies supported a high egg laying rate but low hatching success compared to Enriched fruit flies. Mixing aphids with Normal fruit flies had no effect on the measured fitness parameters, whereas mixing aphids with Enriched flies resulted in a lower total production of spiderlings suggesting a toxic effect of aphids on spiders.

A survivorship experiment with hatchlings was conducted in order to investigate the effect of maternal diet on the offsprings´ ability to utilise a low quality prey (*R. padi*). Two hatchlings from each of the first eggsacs produced by females in the egg production experiment on diet treatments 1) Normal *D. melanogaster*, 2) Normal *D. melanogaster* + *R. padi*, 3) Enriched *D. melanogaster*, and 4) Enriched *D. melanogaster* + *R. padi,* were kept individually on a diet of *R. padi* and survival time was recorded. Maternal diet affected survival of those offspring feeding exclusively on *R. padi*. A lower survival was found on offspring from females reared on Normal fruit flies

compared to Enriched fruit flies, thus quality of offspring may vary with that of maternal diet. The results emphasise that effects of dietary mixing depend on the characteristics of the prey types composing the diet. Negative effects of adding aphids to Enriched flies was found by a lowered hatching success, while positive effects of adding aphids to Normal flies was found in the survival of offspring.

Introduction

Many spiders are polyphagous predators feeding on a varied range of prey types. It is often assumed that more than one prey type is needed to obtain a complete nutrient composition of the diet and polyphagy may be a feeding strategy for predators to optimise nutrient intake for successful growth, development and reproduction. Mixed diets frequently result in better growth rates and survival or in a higher fecundity than single-species diets, with several instances found in spiders (MIYASHITA, 1968; SUZUKI, KIRITANI 1974; GREENSTONE, 1979; HOLMBERG, TURNBULL, 1982; THANG et al., 1990; UETZ et al., 1992; TOFT, 1995; TOFT, WISE, 1999). In some cases, however, mixed diets had no or even a negative effect on the measured fitness parameters compared to a pure diet of the best constituent (SUNDERLAND et al., 1996; MARCUSSEN et al., 1999; TOFT, WISE, 1999; BILDE, TOFT, submit.). Optimising nutrient composition of diet may not only be a question of prey mixing but of mixing the right types of prey or avoiding toxic prey (prey with defensive substances). The characteristics of prey which influence its quality as food was summarised by TOFT (1996) as 1) energy gained per unit handling time (the traditional measure of prey quality (STEPHEN, KREBS, 1986)), 2) nutrient constituents, and 3) defensive substances. A prey with a high energy content may be deficient with respect to nutrients while defensive substances may reduce the quality of otherwise valuable prey.

In assessing the value of prey species TOFT (1995) compared the cereal aphid *Rhopalosiphum padi* L. to fruit flies *Drosophila melanogaster* (MEIG.) as food for the linyphiid spider *Erigone atra* (BLACKWALL) in single-species and mixed-species diets. In pure diets aphids were of extremely low quality and fruit flies of intermediate quality, measured by egg production rate and hatching success. The mixed diet of aphids and fruit flies improved the hatching success of eggs significantly, resulting in an overall much higher production of spiderlings than in the pure fruit fly groups (TOFT, 1995). In a similar study three cereal aphid species (*R. padi*, *Sitobion avenae* (F.), *Metopolophium dirhodum* (WLK.)) were assessed for *E. atra* in comparison with *D. melanogaster* (BILDE, TOFT, submit.), but in contrast to the study of TOFT (1995) the fruit flies were nutritionally improved by rearing them on an enriched medium. Mixing *R. padi* and *M. dirhodum* with fruit flies did not improve any of the measured fitness parameters relative to a pure diet of fruit flies, while *S. avenae* in combination with fruit flies reduced egg production of the spiders (BILDE, TOFT, submit.). Apparently both positive, neutral and negative effects are possible outcomes of mixing aphids and fruit flies. The two studies suggest that the nutritional state of the fruit flies determined whether aphids contributed positively or

negatively to spider fitness in a mixed diet. If the right prey type containing all necessary nutrients and a minimum of defensive substances is provided, no beneficial effects of mixing with other prey may be expected.

In the experiments reported here, three types of prey for a spider were evaluated: a low quality prey (the aphid *Rhopalosiphum padi*); an intermediate quality prey (Normal fruit flies *Drosophila melanogaster*, reared on plain medium); and a high quality prey (Enriched fruit flies, reared on nutritionally improved medium). Spiders were fed single-species diets and combinations of aphids and fruit flies in mixed diets to test the effect of mixing prey of different qualities. Diet quality was assessed by egg production and hatching success. The value of *R. padi* in mixed diets was expected to depend on the nutritional value of the fruit flies, i.e. positive effects of mixing aphids with Normal fruit flies, and no or negative effects of mixing with Enriched fruit flies. A survivorship experiment with hatchlings was performed to test the effect of maternal diet on offsprings´ ability to utilise a low quality prey (*R. padi*). It was hypothesised that offspring of females fed a nutritionally superior diet (Enriched fruit flies) would survive longer on a diet of aphids than offspring of females fed a deficient diet (Normal fruit flies).

Material and methods

The spider *Dicymbium brevisetosum* Locket, a small (c. 2-3 mm) sheet-web spider of the family Linyphiidae, was used in the experiments. Adult females and males were collected as aeronauts in the field on 1 April 1999. It is doubtful whether *D. brevisetosum* and *D. nigrum* (Blackwall) are separate species, and only males can be distinguished. All males collected (>100) had the *D. brevisetosum* characteristics. Spiders were kept at 5^0C until 17 April when the experiment was initiated. Throughout the experiment females and males were kept in pairs in cylindrical plastic tubes (h 6 cm, d 2 cm) with a base of plaster-of-Paris mixed with charcoal to maintain high humidity. The experiment was carried out at 20^0C and a photoperiod of 16L:8D.

The two qualities of fruit flies used in the experiments were reared on instant *Drosophila* medium (Formula 4-24 Plain, Carolina Biological Supply; Burlington, NC, USA): Normal flies were reared on plain medium and Enriched flies on medium mixed with crushed dog food (Techni-Cal maintenance®) to improve nutritional quality of the flies (Kristensen, Toft, unpubl.). The aphid species *R. padi* is one of the most abundant cereal aphids in Europe (Vickerman, Wratten, 1979). They were reared on wheat seedlings in laboratory cultures.

Eggsac production and number of offspring

Females were randomly assigned to one of 6 prey treatments: 1) Enriched *D. melanogaster*, 2) Enriched *D. melanogaster* + *R. padi*, 3) Normal *D. melanogaster*, 4) Normal *D. melanogaster* + *R. padi*, 5) *R. padi*, and 6) *R. padi* added to Normal *D. melanogaster* until the first eggsac appeared, then only *R. padi* (in the following termed "aphid + starter fly group"). Diets 1, 3, 5 and 6 are single-species diets, while diets 2 and 4 are mixed diets; diets 1-4 are termed the fruit fly diet groups and diets 5-6 the aphid-only diet groups. Replication was initially 20 females in each diet group, but due to some accidental deaths during the experiments and because females that never started egg laying were excluded from the analyses, sample sizes varied between 13-20 in the final analyses. The experiment was terminated when seven eggsacs had been laid by a female or after two months at most.

Spiders were watered and fed live prey in excess 2-3 times per week, so prey were always available. The tubes were checked daily for new eggsacs. When an eggsac appeared the female and male were transferred to a new plastic tube.

Eggsacs were kept under experimental conditions until hatching. Emergence date and number of hatchlings were recorded. Eggsacs were always dissected in order to record undeveloped eggs, embryos and larvae so that total egg number could be determined. Only eggs producing emerging spiderlings were considered as hatched.

Maternal effects on survival of offspring

Maternal diet effects were investigated in offspring which were all kept on a low quality diet of *R. padi*. Offspring from females of the egg production experiment under the diet treatments 1) Enriched *D. melanogaster*, 2) Enriched *D. melanogaster* + *R. padi*, 3) Normal *D. melanogaster*, and 4) Normal *D. melanogaster* + *R. padi* were used in the experiment. These treatments were selected to focus on differences between the two qualities of fruit flies. Two spiderlings from each of the 1st eggsacs laid were transferred individually to plastic tubes and fed nymphs of *R. padi*; aphids and water was supplied 2-3 times per week. Deaths were recorded by daily inspections. Replication was 18-25 hatchlings in each group.

Statistical analyses

The rate of eggsac production (log-transformed), number of eggs per eggsac, hatching success (arcsine transformed) and number of offspring produced per eggsac was analysed with Repeated Measures ANOVA. Sphericity was tested with Mauchley´s test and if necessary appropriate transformations applied; as the assumption of sphericity was fulfilled only univariate tests were performed. Too few eggsacs were produced in the aphid-only diet groups for these to be included in the Repeated Measures ANOVA. Survival data were analysed with Log-rank test (cf. Pyke, Thompson, 1986).

Results

Egg production experiment

Females in the aphid-only diet groups produced eggsacs at a lower rate and in much lower numbers than females of the fruit-fly diet groups (Fig. 1). The rate of eggsac production was higher in females provided Enriched flies and Enriched flies + aphids compared to the two Normal fly diet groups (Repeated Measures ANOVA of dates of laying eggsacs 1-5; time × treatment, $P<0.001$).

Females of the aphid-only diet groups produced much fewer eggs per eggsac than those of the fruit fly diet groups (Fig. 2). Egg numbers in the aphid + starter fly group were similar to the egg numbers found in the first eggsac of the fruit fly diet groups, but then declined steeply as soon as the spiders were provided with only aphids. There was a significant difference in egg numbers between the fruit fly diet treatments (Overall Repeated Measures ANOVA; $P<0.05$) with the highest egg number found for the single-species diet of Enriched flies and the lowest egg number found for the Normal flies + aphid diet. Egg numbers increased with eggsac number for the first c. three eggsacs and then decreased slightly again (Repeated Measures ANOVA, effect of eggsac number; $P<0.0001$).

Comparing the number of viable eggs with total eggs a different pattern emerged (Fig. 3). Hatching success in the Enriched fruit fly treatments remained high (from 80% decreasing to 60% with time) while steeply decreasing towards zero in the Normal fruit fly diet groups

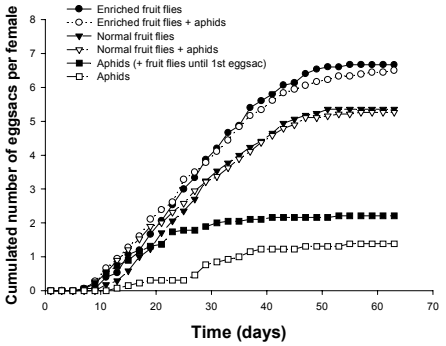

Fig. 1. Course of eggsac production by the average female *Dicymbium brevisetosum* on six diet treatments.

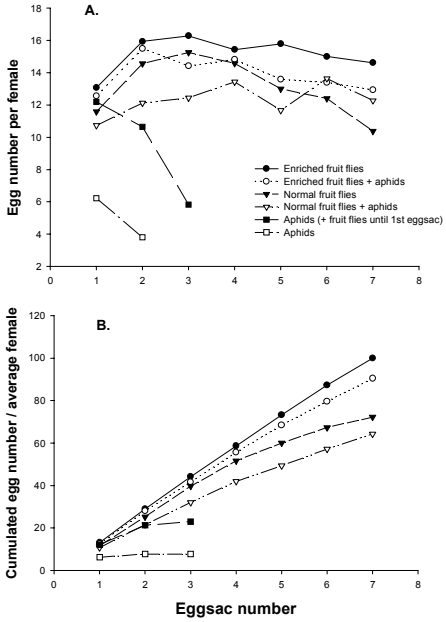

Fig. 2. A. Average number of eggs laid in successive eggsacs by *Dicymbium brevisetosum* on six diet treatments. B. Cumulative number of eggs laid by an average *Dicymbium brevisetosum* female on six diet treatments.

(Repeated Measures ANOVA of hatching success of eggsacs 1-5; $P<0.0001$). In the pure aphid diet treatment hatching success was high for the first eggsac but dropped to zero in the second eggsac; in the aphid + starter fly group hatching success resembled that of the Normal fruit fly diet groups (cf. Fig. 3). No significant effect of mixing aphid and fruit flies on viability of eggs was detected. As a result of higher hatching percentage total reproductive success of the Enriched fruit fly diets was far better than of any of the other diets tested (Fig. 4, Repeated Measures ANOVA of spiderlings hatched from eggsac 1-5; $P<0.0001$). The combined effect of slightly lower egg production and hatching success of the mixed Enriched fly + aphid diet group compared to the pure diet of Enriched flies (cf. Fig. 2 and 3) meant that significantly fewer spiderlings hatched in total from the mixed group (Fig. 4B, contrast analysis, Enriched flies + aphids vs. Enriched flies, $P<0.05$). No difference in number of offspring was found between the Normal fruit fly diet and the mixed diet of Normal flies + aphids.

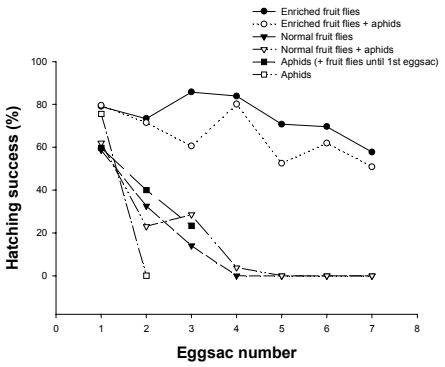

Fig. 3. Average hatching success (%) of successive eggsacs laid by *Dicymbium brevisetosum* on six diet treatments.

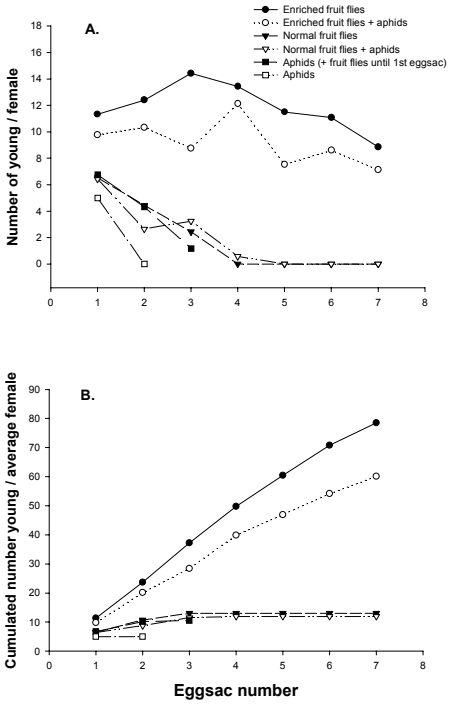

Fig. 4. A. Average number of spiderlings hatched from successive eggsacs laid by *Dicymbium brevisetosum* on six diet treatments. B. Cumulative number of spiderlings hatched per average *Dicymbium brevisetosum* female on six diet treatments.

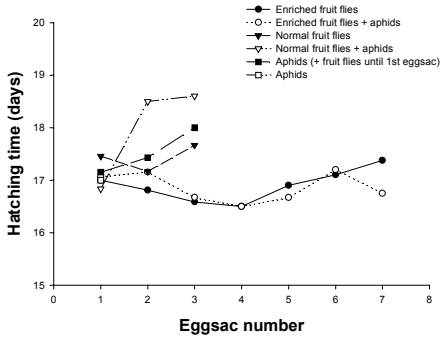

Fig. 5. Average hatching time (days) of successive eggsacs laid by *Dicymbium brevisetosum* on six diet treatments.

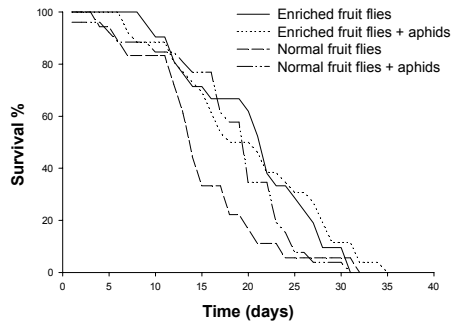

Fig. 6. Survivorship curves for hatchlings of *Dicymbium brevisetosum* from females on four diet treatments. All spiderlings were fed *R. padi*.

Hatching time of eggsacs (Fig. 5) was c. 17 days for the first eggsac of all diet treatments. This was persistent for all eggsacs produced on the Enriched fruit fly diets, while hatching time increased marginally to c. 18 days from first to third eggsac in the Normal fly diet treatment (Repeated Measures ANOVA of hatching time, $P=0.075$).

Survival of offspring

Survivorship curves for first instar spiderlings from females reared on four different diets are shown in Fig. 6. An overall effect of maternal diet on survival of offspring was revealed (Log-rank test, $P<0.05$). A lower survival (median 14 days) was found in hatchlings

from females reared on Normal flies compared to spiderlings from females reared on the three other diets, (Normal flies + aphids: median 20 days, Enriched flies + aphids: median 19.5 days, Enriched flies: median 22 days).

Discussion

Egg production experiment

In single-species diets distinct differences in quality between the three tested prey types were found. Enriched fruit flies supported a continuously high egg production rate and a high hatching percentage of eggsacs whereas hatching success rapidly decreased when Normal fruit flies were offered, although a relatively high rate of egg production was upheld. This result indicates that Enriched flies contain energy as well as a sufficient nutrient composition for production of viable eggs, while Normal flies, although containing energy for egg production, do not contribute sufficient nutrients for the eggs to hatch properly. If spiders fed Normal flies use nutrients from their own body reserves to increase the quality of eggs in the first one or two eggsacs, the low hatching success of the following eggsacs may result from depletion of body reserves. Enriched flies also supported a substantially higher egg production and hatching success than Normal flies in similar experiments with *E. atra* (Toft, 1995; Bilde, Toft, submit.). The aphid *R. padi* is clearly of very low value to *D. brevisetosum* resulting in low egg numbers and a declining hatching success from first to second eggsac. Only approximately half the number of spiders tested initiated egg production on the pure aphid diet, suggesting that alternative prey in combination with aphid prey is needed to obtain sufficient energy or nutrients for egg laying. Indeed, in the treatment where Normal flies were added until the first eggsac was produced, almost all spiders initiated egg production, while egg numbers immediately declined after the first eggsac when only aphids were provided. As females not initiating egg laying were excluded from the analyses the real difference between these two groups is larger than appears from the figures.

Slightly lower egg-laying rates and hatching success resulting in a lower total production of offspring were found in the mixed diet of Enriched fruit flies + aphids compared to the pure diet of Enriched flies. The lower reproductive outcome as a consequence of dietary mixing indicates toxic effects of the aphids on the spider. Prey is defined as toxic if inclusion of the prey in the diet lowers the measured fitness parameter significantly. A similar toxic effect of adding the cereal aphid *S. avenae* to Enriched fruit flies was found in an experiment with *E. atra* (Bilde, Toft, submit.). Negative effects on spider fitness parameters have also been demonstrated when low quality Collembola were added to fruit flies in mixed diets (Marcussen et al., 1999; Toft, Wise, 1999). No indication of improvement of diet was found when aphids were added to Normal flies compared to the single-species diet of Normal flies. This was an unexpected result, as Toft (1995) found a significant improvement of spider fitness (*E. atra*) when adding *R. padi* to a diet of Normal flies. It would seem as if the Normal flies are of lower quality to *D. brevisetosum* than to *E. atra*, as *E. atra*

produced more viable eggsacs on a diet of Normal flies contrary to *D. brevisetosum* (Toft 1995). Adding aphids to Normal flies, both of which are low quality prey species to *D. brevisetosum* (cf. Fig. 4) is apparently not enough to improve overall dietary composition. When providing a mixed diet of cereal aphid species (*R. padi*, *S. avenae* and *M. dirhodum*) to other species of generalist predators no beneficial effect on predator fitness was found and in those studies all three aphid species were low quality prey in pure diets (Bilde, Toft, 1999, submit.; Toft, 2000). It might thus be hypothesised that cereal aphids can contribute positively to predator fitness in a mixed diet together with an intermediate quality prey, for example by adding nutrients to an energy-rich but nutrient deficient prey (Wallin et al., 1992; Bilde, Toft, 1994; Toft, 1995). If only low quality prey is available, e.g. due to defensive substances in the prey (aphids), energy sources may be lacking to utilise the nutrients of the prey. In conclusion, dietary mixing cannot unequivocally be regarded as beneficial to predators. If a high quality prey is available either no or even negative effects of mixing may be the result. Improvement of nutritional quality of diet by prey mixing depends on the characteristics of the individual prey types composing the diet.

Effects of maternal age were found in an experiment with *E. atra* where hatching time of eggsacs increased with eggsac number independent of diet treatment (Bilde, Toft, submit.). Such effects were not found in *D. brevisetosum* where hatching time of eggsacs was relatively constant on the two diets of Enriched fruit flies throughout the seven eggsacs recorded. The increasing developmental time of eggs seen on the Normal fruit fly diets could be an effect of lower quality eggs produced on nutritionally inferior diets, resulting from increasing nutrient depletion. Nutrient depletion could explain both a lowered hatching success and increasing developmental time of eggs seen of the Normal fly diet treatments.

Maternal effects on survival of offspring

Maternal diet had an effect on the survival of offspring with the lowest survival found in spiderlings from females reared on Normal fruit flies. This was the predicted result as a single-species diet of Normal fruit flies was expected to be of relatively low nutritional quality and subsequently producing the lowest quality eggs of the four diets tested. The mixed Normal fly + aphid diet did not improve any fitness parameters in the egg production experiment compared to the pure diet of Normal flies, nevertheless an improvement of survival of spiderlings was found comparing the two diet treatments. This result suggests that effects of diet cannot be completely evaluated from the fitness of the affected animals alone, but that subsequent generations may be affected through maternal effects. As a consequence, survival of spiderlings in an unfavourable environment (in this case with abundance of low quality prey) may be dependent on the quality of the maternal diet. This might have some importance in cereal fields, where spring breeding spiders reproduce on various prey types, i.e. Collembola, prior to the arrival of cereal aphids in the fields. With availability of high quality prey in the reproductive period, the juvenile spiders may be better able to cope with cereal aphids and thus be more effective in the limitation of these pests. Maternal diet effect

on offspring size was not measured in the study presented here, but such phenotypic effects which may influence survival (Wallin et al., 1992; Tanaka, 1995) have been demonstrated in spiders; i.e. Toft (1995) found offspring size to depend on the quality of maternal diet. This result seems consistent with the effects of maternal diet on offspring quality (survival) found here.

Summarising over both experiments, the prediction that the value of *R. padi* in mixed diets depend on the nutritional value of the fruit flies was confirmed: negative effects of adding aphids to Enriched flies was found by a lowered hatching success, while positive effects of adding aphids to Normal flies was found in the survival of offspring.

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PORTUGUESE SPIDERS (ARANEAE): A PRELIMINARY CHECKLIST

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Abstract

Cardoso P.: Portuguese spiders (Araneae): a preliminary checklist. In Gajdoš P., Pekár S. (eds): Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava), Vol. 19, Supplement 3/2000, p. 19-29.

With 642 described species and 8 subspecies, continental Portuguese spiders are still poorly known. A preliminary species checklist is presented and the country is evaluated in terms of its known spider species distribution. What has been done and what has to be done are two of the main topics to be addressed.

Introduction

Arachnology is a neglected science in Portugal. Only two Portuguese researchers have dedicated part of their life to arachnology – Amélia Bacelar and António de Barros Machado. Both of them worked in the area during the second quarter of this century and only occasional work has been done in the last 50 years, mainly by foreign researchers who saw in continental Portugal a good area to develop their studies.

The first published reference to a Portuguese spider was made by Sundevall on the occurrence of *Achaearanea lunata* (Olivier) in this country in 1831 (in Bacelar, 1928). Since then, many researchers have made considerable species lists, e.g. Karsch (1893 in Bacelar, 1928), Bertkau (1893a, 1893b in Bacelar, 1928), Simon (1881, 1898b in Bacelar, 1928), Franganillo (1920 in Bacelar, 1928), Bacelar (1927a, 1927b, 1928, 1932, 1933a, 1933b, 1933c, 1935, 1936, 1940), Machado (1937, 1941, 1944, 1945, 1949, 1986), Schenkel (1938), Ferrández (1986, 1990a, 1990b, 1996) and Bosmans (1994). Some other smaller papers, in terms of numbers of species, have referred to the presence of spiders in Portugal: Frade, Bacelar (1931a, 1931b), Blauwe (1980), Blasco (1986), Ribera (1988, 1993), Ferrández, Céspedes (1990), Machado, Ferrández (1991), Barrientos, Ribera (1992), Roberts (1995), Urones et al. (1995), Snazell, Murphy (1997).

Besides published papers, several important collections (e.g. Barros Machado, John Murphy, Tânia Nobre and the author) include many individuals captured in Portugal.

All these papers, together with the collections referred to, have made possible the compilation of a preliminary checklist, which includes 642 species and 8 subspecies, some of them endemic to Portugal. A map of records shows which areas are relatively well worked and which are unknown.

Material and methods

The following species checklist has been compiled. It follows the taxonomical approach of PLATNICK's catalogue (1997). For those species not represented in published collections, the location is indicated as: BMC – Barros Machado collection, JMC – John Murphy collection, PCC – Pedro Cardoso collection, TNC – Tânia Nobre collection. Doubtful records are indicated with a question mark after the species name.

List of species

ATYPIDAE
Atypus affinis EICHWALD, 1830
CTENIZIDAE
Ummidia aedificatoria (WESTWOOD, 1841)
NEMESIIDAE
Nemesia athiasi FRANGANILLO, 1920
Nemesia berlandi FRADE ET BACELAR, 1931
Nemesia caementaria (LATREILLE, 1798) ?
Nemesia dubia O. P.-CAMBRIDGE, 1874
Nemesia fagei FRADE ET BACELAR, 1931
Nemesia gravieri FRADE ET BACELAR, 1931
Nemesia hispanica L. KOCH in AUSSERER, 1871
Nemesia meridionalis (COSTA, 1835)
Nemesia simoni O. P.-CAMBRIDGE, 1874
Nemesia uncinata BACELAR, 1933
Spiroctenus lusitanus FRANGANILLO, 1920
FILISTATIDAE
Filistata insidiatrix FORSKÄL, 1775
Pritha nana (SIMON, 1868) – JMC
Pritha pallida (CHYZER ET KULCZYŃSKI, 1897)
SICARIIDAE
Loxosceles rufescens (DUFOUR, 1820)
SCYTODIDAE
Scytodes fusca WALCKENAER, 1837 – JMC
Scytodes thoracica LATREILLE, 1802
Scytodes velutina HEIN. ET LOWE, 1836
LEPTONETIDAE
Leptoneta berlandi MACHADO ET RIBERA, 1986
Leptoneta conimbricensis MACHADO ET RIBERA, 1986
Paraleptoneta synthetica MACHADO, 1951
PHOLCIDAE
Holocnemus caudatus DUFOUR, 1820
Holocnemus hispanicus WIEHLE, 1933
Holocnemus pluchei (SCOPOLI, 1763)
Pholcus opilionoides (SCHRANK, 1781)
Pholcus phalangioides (FUESSLIN, 1775)
Spermophora senoculata (DUGÈS, 1836)
SEGESTRIIDAE
Ariadna insidiatrix AUDOUIN, 1826
Segestria bavarica C. L. KOCH, 1843
Segestria florentina (ROSSI, 1790)
Segestria fusca SIMON, 1882 ? - JMC
Segestria pusiola SIMON, 1882
Segestria senoculata (LINNAEUS, 1758)
DYSDERIDAE
Dysdera alentejana FERRÁNDEZ, 1996
Dysdera cribata SIMON, 1882 ? - JMC
Dysdera crocota C. L. KOCH, 1838
Dysdera erythrina (WALCKENAER, 1802)
Dysdera falciformis BARRIENTOS ET FERRÁNDEZ, 1982
Dysdera flavitarsis SIMON, 1882 ? - JMC
Dysdera fuscipes SIMON, 1882

Dysdera gamarrae Ferrández, 1984
Dysdera lusitanica Kulczyński, 1915
Dysdera machadoi Ferrández, 1996
Dysdera nubila Simon, 1882 ? - JMC
Harpactea algarvensis Ferrández, 1990
Harpactea fageli Brignoli, 1980
Harpactea hombergi (Scopoli, 1763)
Harpactea magnibulbi Machado et Ferrández, 1991
Harpactea parvula (Dufour, 1820)
Harpactea proxima Ferrández, 1990
Harpactea stalitoides Ribera, 1993
Harpactea subiasi Ferrández, 1990
Rhode scutiventris Simon, 1882

OONOPIDAE

Dysderina loricata (Simon, 1873) – JMC
Oonops sp. (Machado, unpubl.) – BMC
Oonops domesticus Dalmas, 1916
Oonops pulcher hispanicus Dalmas, 1916 – BMC, JMC
Oonops tubulatus Dalmas, 1916
Orchestina algerica Dalmas, 1916 – JMC

PALPIMANIDAE

Palpimanus gibbulus Dufour, 1820

MIMETIDAE

Ero aphana (Walckenaer, 1802)
Ero flammeola Simon, 1881
Ero furcata (Villers, 1789)
Ero quadrituberculata Kulczyński, 1905 – BMC
Ero tuberculata (De Geer, 1778)

ERESIDAE

Eresus cinnaberinus (Olivier, 1789)
Eresus cinnaberinus frontalis (Latreille, 1817)
Eresus sedilloti Simon, 1881
Eresus solitarius Simon, 1873 ? - JMC
Stegodyphus lineatus Latreille, 1817

OECOBIIDAE

Oecobius cellariorum (Dugès, 1836)
Oecobius maculatus (Simon, 1870)
Oecobius navus Blackwall, 1859
Uroctea durandi (Latreille, 1809)

ULOBORIDAE

Hyptiotes flavidus (Blackwall, 1862)
Hyptiotes paradoxus (C. L. Koch, 1834)
Polenecia producta (Simon, 1873)
Uloborus plumipes Lucas, 1846
Uloborus walckenaerius Latreille, 1806

NESTICIDAE

Nesticus lusitanicus Fage, 1931

THERIDIIDAE

Achaearanea açoreensis (Berland, 1932)
Achaearanea lunata (Clerck, 1757)
Achaearanea tepidariorum (C. L. Koch, 1841)
Anelosimus aulicus (C. L. Koch, 1838)
Anelosimus pulchellus (Walckenaer, 1802)
Argyrodes argyrodes (Walckenaer, 1841)
Argyrodes nasicus (Simon, 1873)
Argyrodes rostratus Blackwall, 1877
Crustulina guttata (Wider, 1834)
Crustulina scabripes Simon, 1881
Dipoena coracina (C. L. Koch, 1837) – JMC
Dipoena melanogaster (C. L. Koch, 1837)
Dipoena testaceomarginata (Simon, 1881)
Dipoena umbratilis (Simon, 1873)
Enoplognatha diversa (Blackwall, 1859) – JMC
Enoplognatha franzi Wünderlich, 1995 – JMC
Enoplognatha mandibularis (Lucas, 1846)
Enoplognatha nigromarginata (Lucas, 1846)
Enoplognatha ovata (Clerck, 1757)
Enoplognatha testacea Simon, 1884
Enoplognatha thoracica (Hahn, 1833)
Episinus algericus Lucas, 1846
Episinus angulatus (Blackwall, 1836)
Episinus maculipes Cavanna, 1876
Episinus truncatus Latreille, 1809
Euryopis acuminata (Lucas, 1846)
Latrodectus tredecimguttatus (Rossi, 1790)
Neottiura bimaculatum (Linnaeus, 1767)
Neottiura bimaculatum pellucidum (Simon, 1873)
Nesticodes rufipes (Lucas, 1846) – JMC
Paidiscura dromedaria (Simon, 1880) – JMC
Paidiscura pallens (Blackwall, 1834)
Pholcomma gibbum (Westring, 1851)
Phoroncidia hankiewiczi (Kulczyński, 1911)
Phoroncidia paradoxa (Lucas, 1846)
Robertus arundineti (O. P.-Cambridge, 1871)
Robertus monticola Simon, 1914
Simitidion simile (C. L. Koch, 1836)
Steatoda albomaculata (De Geer, 1778)
Steatoda bipunctata (Linnaeus, 1758) – BMC
Steatoda grossa (C. L. Koch, 1838)
Steatoda nobilis (Thorell, 1875) – JMC
Steatoda paykulliana (Walckenaer, 1806)
Steatoda phalerata (Panzer, 1801)
Steatoda triangulosa (Walckenaer, 1802)
Theridion blackwalli O. P.-Cambridge, 1871 – JMC
Theridion curvimanum Simon, 1914 – JMC
Theridion impressum L. Koch, 1881
Theridion melanostictum O. P.-Cambridge, 1876 – JMC
Theridion melanurum Hahn, 1831
Theridion musivum Simon, 1873
Theridion mystaceum L. Koch, 1870 – JMC, PCC
Theridion nigropunctatum Lucas, 1846
Theridion petraeum L. Koch, 1872 – JMC
Theridion pinastri L. Koch, 1872
Theridion pyrenaeum Denis, 1944 – JMC
Theridion sisyphium (Clerck, 1757)
Theridion tinctum (Walckenaer, 1802)

Theridion uncinatum Lucas, 1846
Theridion varians Hahn, 1833
Theridion varians rusticum (Simon, 1873)
Theridula gonygaster Simon, 1873 – JMC
Theridula opulenta (Walckenaer, 1841)
MYSMENIDAE
Cepheia longiseta (Simon, 1881) – JMC
LINYPHIIDAE
Acartauchenius depressifrons (Simon, 1884)
Acartauchenius nasutus (O. P.-Cambridge, 1879)
Alioranus pauper (Simon, 1881) – JMC
Araeoncus humilis (Blackwall, 1841)
Bathyphantes gracilis (Blackwall, 1841)
Bolyphantes nigropictus Simon, 1884
Centromerita concinna (Thorell, 1875)
Centromerus dilutus (O. P.-Cambridge, 1875)
Centromerus pabulator (O. P.-Cambridge, 1875)
Centromerus paradoxus (Simon, 1884)
Centromerus prudens (O. P.-Cambridge, 1873)
Ceratinella brevipes (Westring, 1851) – JMC
Ceratinopsis romana (O. P.-Cambridge, 1872)
Cnephalocotes obscurus (Blackwall, 1834)
Diplocephalus graecus (O. P.-Cambridge, 1872) – JMC
Diplocephalus permixtus (O. P.-Cambridge, 1871)
Erigone atra Blackwall, 1833
Erigone dentipalpis (Wider, 1834)
Erigone promiscua (O. P.-Cambridge, 1872)
Erigonoplus globipes (L. Koch, 1872) ? - JMC
Frontinellina frutetorum (C. L. Koch, 1834)
Gnathonarium dentatum (Wider, 1834)
Gonatium ensipotens (Simon, 1881)
Gongylidiellum vivum (O. P.-Cambridge, 1875)
Helophora insignis (Blackwall, 1841)
Hybocoptus corrugis (O. P-Cambridge, 1872) – JMC
Hybocoptus decollatus (Simon, 1881)
Hypomma cornutum (Blackwall, 1833)
Lepthyphantes bacelari Schenkel, 1938
Lepthyphantes berlandi Fage, 1931 – BMC
Lepthyphantes bolivari Fage, 1931
Lepthyphantes cernuus Simon, 1884 – JMC
Lepthyphantes flavipes (Blackwall, 1854)
Lepthyphantes homonymus Denis, 1934
Lepthyphantes keyserlingi (Ausserer, 1867)
Lepthyphantes leprosus (Ohlert, 1865)
Lepthyphantes mansuetus (Thorell, 1875) – JMC
Lepthyphantes stygius Simon, 1884
Lepthyphantes tenebricola (Wider, 1834)
Lepthyphantes tenuis (Blackwall, 1852)
Lepthyphantes zimmermanni (Bertkau, 1890) – BMC
Lepthyphantes zonatus Simon, 1884
Lessertia dentichelis (Simon, 1884)
Linyphia triangularis (Clerck, 1757)
Linyphia ulicicolens Franganillo, 1920
Mecopisthes crassirostris (Simon, 1884)
Megalepthyphantes collinus (L. Koch, 1872)
Megalepthyphantes collinus occidentalis Machado, 1949
Meioneta fuscipalpus (C. L. Koch, 1836)
Meioneta rurestris (C. L. Koch, 1836)
Microctenonyx subitaneus (O. P.-Cambridge, 1875)
Microlinyphia pusilla (Sundevall, 1830)
Nematogmus sanguinolentus (Walckenaer, 1841)
Neriene clathrata (Sundevall, 1830)
Neriene furtiva (O. P.-Cambridge, 1870)
Neriene radiata (Walckenaer, 1841)
Oedothorax fuscus (Blackwall, 1834)
Oedothorax retusus (Westring, 1851)
Ostearius melanopygius (O. P.-Cambridge, 1879)
Parapelecopsis mediocris (Kulczyński, 1899)
Parapelecopsis nemoralis (Blackwall, 1841) – JMC
Pelecopsis inedita (O. P.-Cambridge, 1875)
Pelecopsis suzannae (Simon, 1915)
Prinerigone vagans (Audouin, 1826)
Saaristoa abnormis (Blackwall, 1841)
Stemonyphantes lineatus (Linnaeus, 1758)
Tiso vagans (Blackwall, 1834) – JMC
Trichoncus scrofa Simon, 1884
Trichoncus trifidus Denis, 1965 – JMC
Trichopterna cucurbitina (Simon, 1881)
Troxochrus scabriculus (Westring, 1851)
Turinyphia clairi (Simon, 1884)
Walckenaeria acuminata Blackwall, 1833
Walckenaeria atrotibialis O. P.-Cambridge, 1878 – JMC
Walckenaeria corniculans (O. P.-Cambridge, 1875)
Walckenaeria erythrina (Simon, 1884)
TETRAGNATHIDAE
Meta bourneti Simon, 1922
Meta menardi (Latreille, 1804)
Meta nigra Franganillo, 1920
Metellina mengei (Blackwall, 1869)
Metellina merianae (Scopoli, 1763)
Metellina segmentata (Clerck, 1757)
Pachygnatha clercki Sundevall, 1823
Pachygnatha degeeri Sundevall, 1830
Tetragnatha extensa (Linnaeus, 1758)
Tetragnatha montana Simon, 1874
Tetragnatha nigrita Lendl, 1886 – JMC
Tetragnatha nitens (Audouin, 1826)
Tetragnatha obtusa C. L. Koch, 1837
Tetragnatha trichodes Thorell, 1878
ARANEIDAE
Aculepeira armida (Audouin, 1825)
Aculepeira carbonaria (L. Koch, 1869)
Aculepeira ceropegia (Walckenaer, 1802)
Agalenatea redii (Scopoli, 1763)
Araneus angulatus Clerck, 1757
Araneus diadematus Clerck, 1757

Araneus grossus (C. L. Koch, 1844)
Araneus marmoreus Clerck, 1757
Araneus pallidus (Olivier, 1789)
Araneus pyreneus (Simon, 1874)
Araneus quadratus Clerck, 1757
Araneus sericeus (Franganillo, 1918)
Araneus spinivulvus (Dufour, 1835)
Araneus sturmi (Hahn, 1831)
Araneus triangulosus (Franganillo, 1913)
Araneus triguttatus (Fabricius, 1775)
Araniella cucurbitina (Clerck, 1757)
Araniella opisthographa (Kulczyński, 1905)
Argiope acuminata Franganillo, 1920
Argiope bruennichi (Scopoli, 1772)
Argiope lobata (Pallas, 1772)
Argiope trifasciata (Forskäl, 1775) – JMC, PCC
Cercidia prominens (Westring, 1851)
Cyclosa algerica Simon, 1885
Cyclosa conica (Pallas, 1772)
Cyclosa insulana (Costa, 1834)
Cyclosa sierrae Simon, 1870
Cyrtophora citricola (Forskäl, 1775)
Gibbaranea bituberculata (Walckenaer, 1802)
Gibbaranea gibbosa (Walckenaer, 1802)
Gibbaranea ulrichi (Hahn, 1835)
Hypsosinga albovittata (Westring, 1851)
Hypsosinga heri (Hahn, 1831)
Hypsosinga pygmaea (Sundevall, 1831)
Hypsosinga sanguinea (C. L. Koch, 1844)
Larinia lineata (Lucas, 1846)
Larinioides cornutus (Clerck, 1757)
Larinioides patagiatus (Clerck, 1757)
Larinioides sclopetarius (Clerck, 1757)
Mangora acalypha (Walckenaer, 1802)
Nemosculus laurae (Simon, 1868)
Neoscona adianta (Walckenaer, 1802)
Neoscona subfusca (C. L. Koch, 1837)
Nuctenea umbratica (Clerck, 1757)
Singa lucina (Audouin, 1826)
Singa nitidula (C. L. Koch, 1844)
Singa sanguinea (C. L. Koch, 1844) – BMC
Zilla diodia (Walckenaer, 1802)
Zygiella atrica (C. L. Koch, 1845)
Zygiella keyserlingi (Ausserer, 1871)
Zygiella kochi (Thorell, 1870)
Zygiella montana (C. L. Koch, 1834)
Zygiella stroemi (Thorell, 1870)
Zygiella x-notata (Clerck, 1757)

LYCOSIDAE

Allocosa dufouri (Simon, 1876)
Alopecosa albofasciata (Brullé, 1832)
Alopecosa alpicola (Simon, 1876) – PCC
Alopecosa barbipes (Sundevall, 1833)
Alopecosa cuneata (Clerck, 1757)
Alopecosa pulverulenta (Clerck, 1757)
Alopecosa simoni (Thorell, 1872)
Alopecosa trabalis (Clerck, 1757)
Arctosa cinerea (Fabricius, 1777)
Arctosa excellens (Simon, 1876)
Arctosa fulvolineata (Lucas, 1846)
Arctosa lacustris (Simon, 1876)
Arctosa letourneuxi (Simon, 1885) ? - JMC
Arctosa perita (Latreille, 1799)
Arctosa variana C. L. Koch, 1847 – BMC, JMC
Arctosa villica (Lucas, 1846)
Hogna hispanica (Walckenaer, 1837)
Hogna radiata (Latreille, 1817)
Lycosa alba Franganillo, 1913
Lycosa virgulata Franganillo, 1920
Pardosa hortensis (Thorell, 1872)
Pardosa lugubris (Walckenaer, 1802)
Pardosa monticola (Clerck, 1757)
Pardosa morosa (L. Koch, 1870) ? - JMC
Pardosa nigriceps (Thorell, 1856)
Pardosa occidentalis Simon, 1881
Pardosa proxima (C. L. Koch, 1847)
Pardosa proxima poetica Simon, 1876
Pardosa pseudostrigillata Tongiorgi, 1966 – JMC
Pardosa pullata (Clerck, 1757)
Pardosa strigillata Simon, 1876
Pardosa venatrix (Lucas, 1846)
Pirata latitans (Blackwall, 1841)
Pirata piraticus (Clerck, 1757)
Trochosa ruricola (De Geer, 1778)
Trochosa terricola Thorell, 1856
Xerolycosa miniata (C. L. Koch, 1834)
Xerolycosa nemoralis (Westring, 1861)

PISAURIDAE

Pisaura mirabilis (Clerck, 1757)

OXYOPIDAE

Oxyopes globifer Simon, 1876 (n. sp., Machado, unpubl.)
Oxyopes heterophthalmus Latreille, 1804
Oxyopes lineatus Latreille, 1806
Oxyopes nigripalpis Kulczyński, 1891

ZOROPSIDAE

Zoropsis media Simon, 1878
Zoropsis spinimana (Dufour, 1820)

AGELENIDAE

Agelena agelenoides (Walckenaer, 1844)
Agelena labyrinthica (Clerck, 1757)
Histopona torpida (C. L. Koch, 1834)
Lycosoides coarctatus (Dufour, 1831)
Malthonica lusitanica Simon, 1898
Tegenaria agrestis (Walckenaer, 1802)
Tegenaria atrica C. L. Koch, 1843
Tegenaria bucculenta (Koch, 1868)

Tegenaria campestris C. L. Koch, 1834
Tegenaria domestica (Clerck, 1757)
Tegenaria duellica Simon, 1875
Tegenaria feminea Simon, 1870
Tegenaria ferruginea (Panzer, 1804)
Tegenaria fuesslini Pavesi, 1873
Tegenaria inermis Simon, 1870
Tegenaria montigena Simon, 1937
Tegenaria nigra Franganillo, 1920
Tegenaria pagana C. L. Koch, 1840
Tegenaria parietina (Fourcroy, 1785)
Tegenaria picta Simon, 1870
Tegenaria ramblae Barrientos, 1978
Tegenaria saeva Blackwall, 1844
Textrix caudata L. Koch, 1872
Textrix denticulata (Olivier, 1789)
Textrix pinicola Simon, 1875
HAHNIIDAE
Antistea elegans (Blackwall, 1841)
Hahnia candida Simon, 1875
Hahnia nava (Blackwall, 1841)
DICTYNIDAE
Ajmonia gratiosa (Simon, 1881)
Archaeodictyna consecuta (O. P.-Cambridge, 1872)
Chorizomma subterraneum Simon, 1872
Dictyna arundinacea (Linnaeus, 1758)
Dictyna civica (Lucas, 1850)
Dictyna latens (Fabricius, 1775)
Dictyna uncinata Thorell, 1856
Lathys affinis (Blackwall, 1862) – JMC
Lathys humilis (Blackwall, 1855) – BMC, PCC
Lathys jubata (Denis, 1947) – JMC
Lathys narbonensis (Simon, 1876) – JMC
Marilynia bicolor (Simon, 1871)
Mastigusa arietina (Thorell, 1871)
Mastigusa macrophthalma (Kulczyński, 1897) ?
Nigma flavescens (Walckenaer, 1830)
Nigma hortensis (Simon, 1870)
Nigma puella (Simon, 1870)
Nigma walckenaeri (Roewer, 1951)
AMAUROBIIDAE
Amaurobius erberi (Keyserling, 1863)
Amaurobius ferox (Walckenaer, 1830)
Amaurobius obustus L. Koch, 1868
Amaurobius occidentalis Simon, 1892
Amaurobius scopolii Thorell, 1871
TITANOECIDAE
Nurscia albomaculata (Lucas, 1846) – TNC
Nurscia sequeirai (Simon, 1892)
Titanoeca praefica (Simon, 1870) – JMC, PCC
Titanoeca tristis L. Koch, 1872 – JMC
ANYPHAENIDAE
Anyphaena accentuata (Walckenaer, 1802)
Anyphaena alboirrorata Simon, 1878
Anyphaena numida Simon, 1896
Anyphaena sabina L. Koch, 1866
LIOCRANIDAE
Agraecina lineata (Simon, 1878) – PCC
Agroeca inopina O. P.-Cambridge, 1886
Apostenus fuscus Westring, 1851
Apostenus humilis Simon, 1932 – BMC
Liocranum majus Simon, 1878
Liocranum rupicola (Walkenaer, 1830)
Liocranum segmentatum Simon, 1878 – JMC
Liophrurillus flavitarsis (Lucas, 1846)
Mesiotelus mauritanicus Simon, 1909
Mesiotelus tenuissimus (L. Koch, 1866)
Phrurolinillus tibialis (Simon, 1878)
Phrurolithus festivus (C. L. Koch, 1835)
Phrurolithus nigrinus (Simon, 1878)
Scotina celans (Blackwall, 1841)
Scotina palliardi (L. Koch, 1881)
CLUBIONIDAE
Cheiracanthium erraticum (Walckenaer, 1802)
Cheiracanthium mildei L. Koch, 1864
Cheiracanthium pelasgicum (C. L. Koch, 1837)
Cheiracanthium punctorium (Villers, 1789)
Cheiracanthium seldlitzi (L. Koch, 1864)
Cheiracanthium striolatum Simon, 1878
Cheiracanthium virescens (Sundevall, 1833)
Clubiona aducta Simon, 1932
Clubiona brevipes Blackwall, 1841
Clubiona comta C. L. Koch, 1839
Clubiona corticalis (Walckenaer, 1802)
Clubiona decora Blackwall, 1859
Clubiona diniensis Simon, 1878
Clubiona frutetorum L. Koch, 1867
Clubiona genevensis L. Koch, 1866 – JMC
Clubiona leucaspis Simon, 1932
Clubiona neglecta O. P.-Cambridge, 1862
Clubiona terrestris Westring, 1851
Clubiona vegeta Simon, 1918
CORINNIDAE
Trachelas amabilis Simon, 1878 ? - JMC
Trachelas validus Simon, 1881
ZODARIIDAE
Storena reticulata (Simon, 1870)
Zodarion alacre (Simon, 1870)
Zodarion algarvense Bosmans, 1994
Zodarion elegans (Simon, 1873)
Zodarion fuscum (Simon, 1870)
Zodarion jozefienae Bosmans, 1994
Zodarion machadoi Denis, 1939
Zodarion maculatum (Simon, 1870)
Zodarion rudyi Bosmans, 1994 – JMC
Zodarion styliferum (Simon, 1870)

Zodarion viduum Denis, 1937
PRODIDOMIDAE
Prodidomus amaranthinus (Lucas, 1846) – JMC
GNAPHOSIDAE
Aphantaulax cincta (L. Koch, 1866)
Aphantaulax seminigra Simon, 1878
Berlandina plumalis (O. P.-Cambridge, 1872)
Callilepis concolor Simon, 1914
Callilepis nocturna (Linnaeus, 1758)
Drassodes fugax (Simon, 1878)
Drassodes lapidosus (Walckenaer, 1802)
Drassodes luteomicans (Simon, 1878)
Drassodes villosus (Thorell, 1856)
Drassyllus villicus (Thorell, 1875)
Haplodrassus dalmatensis (L. Koch, 1866)
Haplodrassus dalmatensis pictus (Thorell, 1875) – JMC
Haplodrassus macellinus hebes (O. P.-Cambridge, 1874)
Haplodrassus severus (C. L. Koch, 1839)
Haplodrassus signifer (C. L. Koch, 1839)
Haplodrassus umbratilis (L. Koch, 1866)
Leptodrassus femineus (Simon, 1873)
Leptodrassus hylaestomachi Berland, 1934 – JMC
Leptodrassus tenerrimus O. P.-Cambridge, 1872
Micaria canestrinii Roewer, 1951
Micaria dives (Lucas, 1846)
Micaria formicaria (Sundevall, 1832)
Micaria fulgens (Walckenaer, 1802)
Micaria guttigera Simon, 1878
Micaria pulicaria (Sundevall, 1832)
Micaria romana L. Koch, 1866
Nomisia aussereri (L. Koch, 1872)
Nomisia exornata (C. L. Koch, 1839)
Nomisia fagei Dalmas, 1921
Phaeocedus braccatus (L. Koch, 1866)
Poecilochroa albomaculata (Lucas, 1846)
Poecilochroa dimidiata auspex (Simon, 1878)
Poecilochroa variana (C. L. Koch, 1839)
Pterotricha simoni Dalmas, 1921 – JMC
Scotophaeus blackwalli isabellinus Simon, 1873 – JMC
Scotophaeus musculus (Simon, 1878)
Scotophaeus retusus (Simon, 1878)
Scotophaeus scutulatus (L. Koch, 1866)
Trachyzelotes barbatus (L. Koch, 1866)
Trachyzelotes costatus (Denis, 1952) – JMC
Trachyzelotes fuscipes (L. Koch, 1866) – BMC, JMC
Trachyzelotes holosericeus (Simon, 1878)
Trachyzelotes mutabilis (Simon, 1878)
Trachyzelotes pedestris (C. L. Koch, 1839) – TNC
Zelominor algarvensis Snazell et Murphy, 1997
Zelotes callidus (Simon, 1878) – BMC
Zelotes caucasius (L. Koch, 1866)
Zelotes civicus (Simon, 1878)
Zelotes dentatidens Simon, 1914
Zelotes erebeus (Thorell, 1871) – BMC
Zelotes fulvopilosus (Simon, 1878)
Zelotes fuscipes (Simon, 1878)
Zelotes latreillei (Simon, 1878)
Zelotes longipes (L. Koch, 1867) – PCC
Zelotes manius (Simon, 1878)
Zelotes ruscinensis Simon, 1914
Zelotes spadix (L. Koch, 1866) – JMC
Zelotes subterraneus (C. L. Koch, 1833)
Zelotes tenuis (L. Koch, 1866)
Zelotes thorelli Simon, 1914
ZORIDAE
Zora nemoralis (Blackwall, 1861)
Zora spinimana (Sundevall, 1833)
HETEROPODIDAE
Eusparassus dufouri Simon, 1932 – JMC
Micrommata ligurina (C. L. Koch, 1845)
Micrommata virescens (Clerck, 1757)
Micrommata virescens ornata (Walckenaer, 1802)
Olios argelasius (Walckenaer, 1805)
PHILODROMIDAE
Philodromus albidus Kulczyński, 1911
Philodromus albopictus Simon, 1875
Philodromus aureolus (Clerck, 1757)
Philodromus buxi Simon, 1884 – JMC
Philodromus dispar Walckenaer, 1826
Philodromus emarginatus (Schrank, 1803)
Philodromus emarginatus lusitanicus Kulczyński, 1911
Philodromus fallax Sundevall, 1833
Philodromus glaucinus Simon, 1870
Philodromus histrio (Latreille, 1819)
Philodromus lividus (Simon, 1875)
Philodromus margaritatus (Clerck, 1757)
Philodromus poecilus (Thorell, 1872)
Philodromus pulchellus Lucas, 1846
Philodromus ruficapillus Simon, 1885
Philodromus rufus Walckenaer, 1826
Thanatus formicinus (Clerck, 1757)
Thanatus lineatipes Simon, 1870
Thanatus sabulosus (Menge, 1875) – TNC
Thanatus vulgaris Simon, 1870
Tibellus macellus Simon, 1875
Tibellus maritimus (Menge, 1875) – JMC
Tibellus oblongus (Walckenaer, 1802)
THOMISIDAE
Coriarachne depressa (C. L. Koch, 1837) – JMC
Diaea dorsata (Fabricius, 1777)
Heriaeus hirtus (Latreille, 1819)
Heriaeus melloteei Simon, 1886
Misumena occidentalis (Kulczyński, 1911)
Misumena vatia (Clerck, 1757)
Misumenops tricuspidatus (Fabricius, 1775)
Monaeses paradoxus (Lucas, 1846)

Ozyptila atomaria (Panzer, 1801)
Ozyptila baudueri Simon, 1877
Ozyptila bicuspis Simon, 1932
Ozyptila blitea Simon, 1875
Ozyptila pauxilla (Simon, 1870)
Ozyptila rauda Simon, 1875
Ozyptila simplex (O. P.-Cambridge, 1862)
Ozyptila umbraculorum Simon, 1932
Pistius truncatus (Pallas, 1772)
Runcinia grammica (C. L. Koch, 1837)
Synema globosum (Fabricius, 1775)
Thomisus onustus Walckenaer, 1806
Tmarus piger (Walckenaer, 1802)
Tmarus piochardi (Simon, 1866)
Xysticus acerbus Thorell, 1872
Xysticus audax (Schrank, 1803)
Xysticus bifasciatus C. L. Koch, 1837
Xysticus bufo (Dufour, 1820)
Xysticus cor Canestrini, 1873
Xysticus cristatus (Clerck, 1757)
Xysticus desidiosus Simon, 1875
Xysticus erraticus (Blackwall, 1834)
Xysticus ferrugineus Menge, 1876
Xysticus kempelini Thorell, 1872
Xysticus kochi Thorell, 1872
Xysticus lanio C. L. Koch, 1835
Xysticus lineatus (Westring, 1851)
Xysticus nigrotrivittatus Simon, 1870
Xysticus ninnii Thorell, 1872
Xysticus nubilus (Simon, 1875)
Xysticus pulcher Franganillo, 1920
Xysticus robustus (Hahn, 1832)
Xysticus sabulosus *(Hahn, 1832)*
Xysticus semicarinatus Simon, 1932
Xysticus tortuosus Simon, 1932
Xysticus ulmi (Hahn, 1832)

SALTICIDAE

Aelurillus affinis (Lucas, 1846)
Aelurillus monardi (Lucas, 1846)
Aelurillus v-insignitus (Clerck, 1757)
Ballus chalybeius (Wackenaer, 1802)
Ballus rufipes (Simon, 1868)
Ballus variegatus Simon, 1876
Bianor albobimaculatus (Lucas, 1846)
Bianor aurocinctus (Ohlert, 1865) – JMC
Carrhotus xanthogramma (Latreille, 1819)
Chalcoscirtus infimus (Simon, 1868)
Cyrba algerina (Lucas, 1846)
Euophrys alticola Denis, 1955 – JMC
Euophrys difficilis (Simon, 1868)
Euophrys erratica (Walckenaer, 1826)
Euophrys frontalis (Walckenaer, 1802) – JMC
Euophrys gambosa (Simon, 1868) – JMC
Euophrys herbigrada (Simon, 1871) – PCC
Euophrys innotata (Simon, 1868)
Euophrys lanigera (Simon, 1871)
Euophrys rufibarbis (Simon, 1868)
Euophrys semiglabrata (Simon, 1868)
Euophrys sulfurea (L. Koch, 1867)
Euophrys terrestris (Simon, 1871)
Evarcha jucunda (Lucas, 1846)
Evarcha laetabunda (C. L. Koch, 1846)
Heliophanus agricola Wesolowska, 1986 – JMC
Heliophanus auratus C. L. Koch, 1835
Heliophanus cupreus (Walckenaer, 1802)
Heliophanus flavipes (C. L. Koch, 1832)
Heliophanus kochi Simon, 1868
Heliophanus lineiventris Simon, 1868
Heliophanus recurvus Simon, 1868
Heliophanus rufithorax Simon, 1868
Icius congener Simon, 1871 – JMC
Icius hamatus (C. L. Koch, 1846)
Icius mimianus Franganillo, 1910
Icius notabilis (Simon, 1871)
Leptorchestes berolinensis C. L. Koch, 1846
Leptorchestes mutilloides (Lucas, 1846)
Macaroeris cata (Blackwall, 1867) – JMC
Macaroeris nidicolens (Walckenaer, 1802)
Menemerus bivittatus (Dufour, 1831)
Menemerus illigeri (Audouin, 1826)
Menemerus semilimbatus (Hahn, 1829)
Menemerus taeniatus (L. Koch, 1867) – JMC
Myrmarachne formicaria (De Geer, 1778)
Neaetha membrosa (Simon, 1868)
Neon levis (Simon, 1871)
Neon rayi (Simon, 1875) – JMC
Pellenes geniculatus (Simon, 1868)
Pellenes nigrociliatus (Simon, 1875) – JMC, TNC
Pellenes tripunctatus (Walckenaer, 1802)
Philaeus chrysops (Poda, 1761)
Phlegra bresnieri (Lucas, 1846)
Phlegra fasciata (Hahn, 1826)
Phlegra loripes Simon, 1876
Pseudicius tamaricis Simon, 1885 ? - JMC
Saitis barbipes (Simon, 1868)
Saitis lusitanicus Simon, 1901
Salticus cingulatus (Panzer, 1797)
Salticus major (Simon, 1868)
Salticus mutabilis Lucas, 1846
Salticus olivaceus (L. Koch, 1867) – JMC
Salticus propinquus Lucas, 1846
Salticus scenicus (Clerck, 1757)
Salticus zebraneus (C. L. Koch, 1837)
Sitticus floricola (C. L. Koch, 1837)
Sitticus pubescens (Fabricius, 1775)
Sitticus saltator (O. P.-Cambridge, 1868)

Synageles venator (Lucas, 1836)
Talavera petrensis (C. L. Koch, 1837)
Thyene imperialis (Rossi, 1846) – JMC, TNC
Yllenus salsicola (Simon, 1937)
Yllenus squamifer (Simon, 1881)

Notes

This list includes unpublished references from the following collections; Barros Machado 13, John Murphy 75, the author 8, and Tânia Nobre 5.

The recorded distribution of species depends not only on their real distribution but largely on the areas where most researchers have done their collecting. This is reflected in the total number of species recorded in each UTM (Universal Transverse Mercator) square (10x10 km.), there being very few of squares with a large number of species (Fig. 1).

The squares with most species correspond to areas where individual researchers have worked. Examples of this are the following areas (and respective researchers): Porto (Machado), Douro River (Simon), Algarve (Bacelar, Murphy), Lisboa (Franganillo, Schenkel, Cardoso), Coimbra (Bertkau, Karsch, Bacelar), Guarda (Bertkau).

Most of these are littoral or near littoral areas, mainly around important urban centres. Therefore, future investigation should be conducted in inland, more remote areas, which are very poorly known at present.

Acknowledgements

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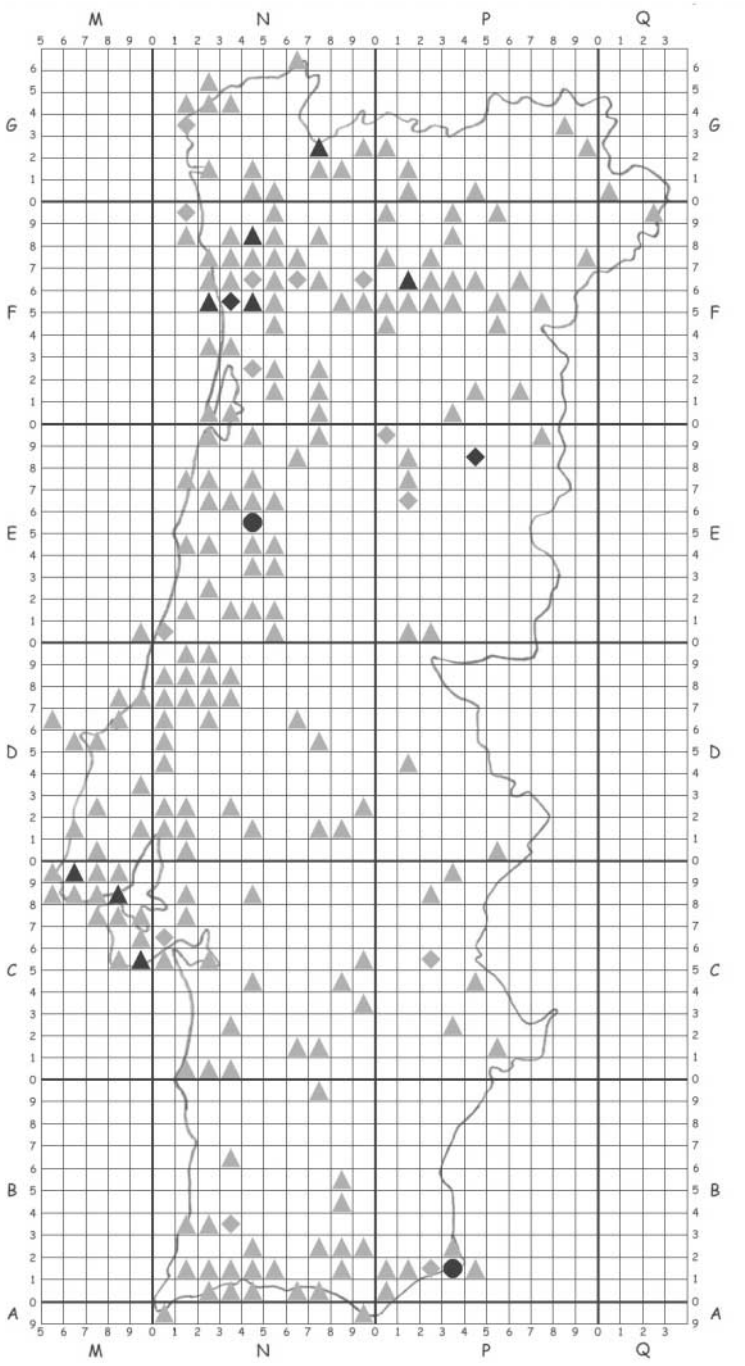

Fig. 1. Continental Portugal divided into UTM squares, showing the number of species known to occur in each square. Number of species: 1-30 (▲), 31-60 (◆), 61-90 (▲), 91-120 (◆), >120 (●).

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DESCRIPTION OF THE SUPPOSED MALE *NEMESIA HISPANICA* L. KOCH IN AUSSERER, 1871 (ARANEAE: NEMESIIDAE)

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Abstract

CARDOSO P.: Description of the supposed male *Nemesia hispanica* L. Koch *in* Ausserer, 1871 (Araneae: Nemesiidae). In GAJDOŠ P., PEKÁR S. (eds): Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava), Vol. 19, Supplement 3/2000, p. 31-36.

The first description of *Nemesia hispanica* was by L. KOCH and appeared in AUSSERER, 1871. However, until now it has only been known from the female. During a study carried out in the Arrábida region of Portugal the author has collected what is thought to be the male of this species. It is described here for the first time. Some considerations of morphology, distribution and taxonomic relationships are briefly presented.

Introduction

Nemesia hispanica was described by L. KOCH in a paper by AUSSERER in 1871 (BONNET, 1958). This description was based solely on the female characters. The species has been found many times in the southern Iberian Peninsula and is the most common mygalomorph in Portugal. Despite this the male had never been collected. A particular characteristic of the species, first noted by MACHADO (1944), is the existence of only two spinnerets, this in a genus where all other members have four. Although there is the possibility that they belong to a new, unknown species, this unique character together with some others, suggests that the two males collected belong to *N. hispanica*.

Material and methods

Some of the characters often used, such as spination, have not been considered here due to their high variability and poor reliability. However, considerable importance has been attributed to the bulb structure and biometric characters which have been shown to be the most stable within species (BLASCO, 1986). All measurements are

made on the specimen of October 19 and are to an accuracy of 0.1 mm. The leg segment measurements refer to the retrolateral view with the legs detached from the body.

Nemesia hispanica *L. Koch* in *Ausserer, 1871 (Figs 1-3)*

Nemesia hispanica Ausserer, 1871: 170; Simon, 1892: 113; Reimoser, 1919: 7; Bacelar, 1928: 172; Frade, Bacelar, 1931: 233.

Material: 1♂, Terras do Risco, October 19, 1997, leg. P. Cardoso, PMC0018a Coll. Cardoso. 1 ♂, Terras do Risco, October 26, 1997, leg. P. Cardoso, PMC0018b Coll. Cardoso. Both specimens here described were taken in pitfall traps during October 1997, in a small area of grassland named Terras do Risco near to the Serra da Arrábida (Setubal, Portugal – UTM29SMC95).

Description: Male. Carapace. Length 7.0 mm, width 5.7 mm. Caput densely covered with silver white pubescence, with a middle line of long black setae, tegument brown, darker along the edges. Thorax slightly convex sloping down from the fovea towards the posterior edge, central parts brown, peripheral parts orange, brushes of black setae on both posterior corners and along the edges. Fovea deep, recurved, as usual for the genus. Eyes: Ocular area wider than high (width/length=2.2). Grouped on an ocular tubercle typical for the genus. Labium: Slightly wider than high, light brown, darker near the sternum, covered with black setae. Maxillae: A single row of denticles near the labium, slightly darker brown than sternum and similarly covered with black setae, anterior edges with scopulae of reddish hair. Chelicerae: Basal segment dark reddish brown, with the inferior margin slightly lighter. Seven teeth along the prolateral margin of the cheliceral furrow, a scopula of long reddish hair along its retrolateral margin. Keeled fang with serration formed by about 10 small black denticles. Sternum: Length 3.4 mm, width 3.0 mm. Widest between the coxae of the second and third legs. Yellowish brown and covered with black setae, denser at the edges. Palps: Femur, prolaterally glabrous with one single distal spine, row of three spines dorso-distally. Patella, prolaterally with one single distal spine. Tibia with prolateral and dorso-distal spines. Tarsus with retrolateral and dorsal spines, enlarging to the front. Bulb: Reddish, with an embolus as long as the basal part. The tip is curved and presents two small denticles on the outer curve preceded by a keel (Fig. 1). This unique embolus is one of the characters that distinguishes the male of this species from other *Nemesia*. The bulb itself is divided into two parts. A basal part, dark reddish brown with a prolateral triangular projection (Fig. 2). A distal part, typically pear-shaped, reddish brown, with an almost red, transverse stripe on the middle, with two thinner dark brown stripes surrounding it (Fig. 3). Legs: Leg I. Femur, prolaterally glabrous. Tibial spur with the usual shape, round and curved. Metatarsus with scopula on the distal part. Tarsus with scopula and no spines. Both tarsus and metatarsus curved downwards. Leg II. Femur, prolaterally glabrous. Metatarsus with scopula on the distal part of the segment. Tarsus with scopula and no spines. Leg III. Tarsus with 1 prolateral spine on the apical half. Leg IV. Femur retrolaterally glabrous, with field of short spines dorso-distally. Tarsus with no scopula or spines. All prosomal appendages, with the exception of the chelicerae are brown. Leg formula: 4231. Leg segments length: Table 1. Abdomen: Grey, with dark patches and evenly covered with black hair and setae.

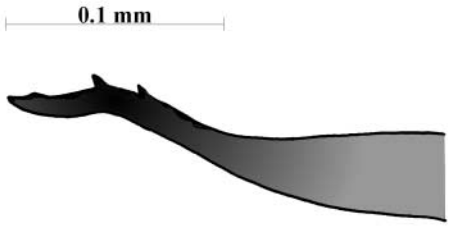

Fig. 1. Embolus tip with two denticles and a small keel in ventral view.

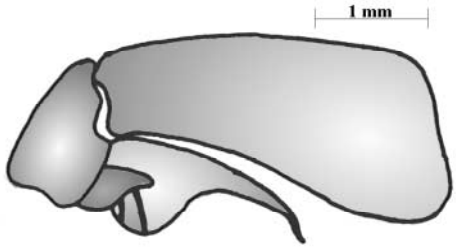

Fig. 2. Apical segment of right palp in prolateral view.

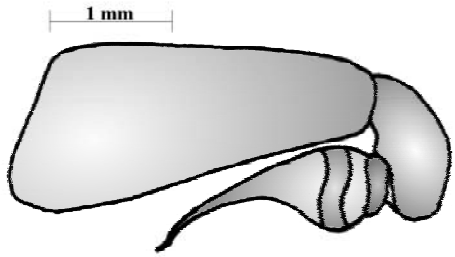

Fig. 3. Apical segment of right palp in retrolateral view.

T a b l e 1. Leg segments (mm).

	Femur	**Patella**	**Tibia**	**Metatarsus**	**Tarsus**
Palp	3.4	2.1	2.7	–	1.6
Leg I	5.5	2.9	4.0	3.9	3.4
Leg II	5.8	2.9	4.5	4.4	3.4
Leg III	5.3	2.5	4.0	5.3	3.3
Leg IV	6.7	3.4	6.4	6.5	3.3

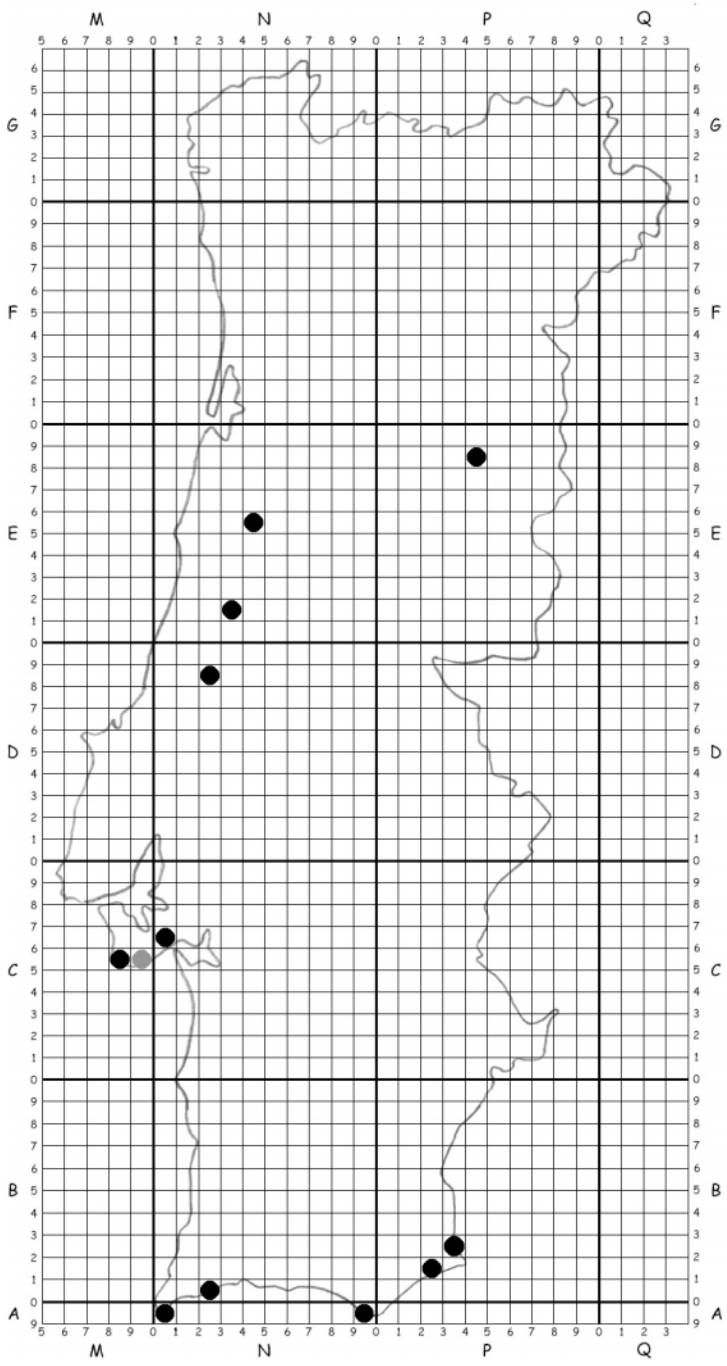

Fig. 4. Distribution map of *Nemesia hispanica* in Portugal, based on UTM (Universal Transverse Mercator) squares and with the capture site of males shown in light grey.

Spinnerets: Only the posterior spinnerets are present, as in *Nemesia hispanica* females and unlike all other *Nemesia* species, which have four (posterior and median, the latest reduced).

Diagnosis: As first noted by MACHADO (1944), the main character which separates this species from all other *Nemesia* species is the presence of only two spinnerets. This character, present in both the males taken, along with the known distribution of *Nemesia* species in Portugal and the large size of the individuals – the females are the largest of all *Nemesia* species found in Portugal (BACELAR, 1932) – strongly suggest that these specimens represent the hitherto unknown male of *N. hispanica*. Unfortunately, in November 1997 severe flooding occurred in the study area, possibly destroying the existing colony. Thus it has not been possible to confirm the species present by the capture of assignable females. Another character that easily permits the identification of males of this species is the unique denticulate and keeled embolus tip.

Distribution: This is the most common Mygalomorphae in Portugal but, even so, only a few records are known (Fig. 4). Previous records: Coimbra (BACELAR, 1928; BACELAR, 1932); Guarda, Setúbal, Cabo Espichel, Sagres, Lagos, Faro, Tavira, Castro Marim (FRADE, BACELAR, 1931; BACELAR, 1932); Ramalhais, Fátima (MACHADO, 1944).

Remarks: The taxonomy of the Genus *Nemesia* is at present confused, since, of the 47 described species, 13 are known only from the male and 19 only from the female (BLASCO, 1986; DECAE, 1995). Males and females have been collected on different occasions, using different methods and several species regularly occur syntopically, making assignment of males and females difficult. The males described here are considered to belong to *N. hispanica* but there is a possibility that they belong to an undescribed species or another known only from the female. In the original description of *N. hispanica*, L. KOCH (in AUSSERER, 1871) makes reference to a double row of denticles on the maxillae near the labium and the specimens here described have one single row. MACHADO (1944) also noted this and other smaller differences but, even so, considered his female specimens to belong to *N. hispanica*. The type specimens of *N. hispanica* are lost, which makes it very difficult to confirm the identity of the males. Another possible species is *Nemesia berlandi* FRADE, BACELAR, 1931 which presents several similarities with the described males, but MACHADO (1944) clearly stated that this species has four spinnerets. This would invalidate the possibility of it being *N. berlandi* but only if MACHADO checked the type specimens (now lost) or others labelled by the describers.

In the general area where they were captured three other *Nemesia* species have been taken. One is *N. meridionalis* (COSTA) and the others have not yet been identified. However, despite being close, the habitat of the other three species (Mediterranean woods) is different to the grassland site of *N. hispanica*. This species, a typical *Nemesia* as defined by RAVEN (1985), seems to be closely related to *N. uncinata* BACELAR, *N. raripila* SIMON and *N. gravieri* FRADE, BACELAR due to the presence of a denticle or denticulate keel on the tip of the embolus in all these species (SIMON, 1914; FRADE, BACELAR, 1931; BACELAR, 1933; BLASCO, 1986). In the original description of *N. uncinata* (BACELAR, 1933) it was suggested that it might be the male of *N. hispanica* but it was apparent that the author was unaware of the existence of only two spinnerets in the latter.

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NEW DATA ON THE SPIDERS OF THE FAMILY DICTYNIDAE (ARANEAE) FROM SIBERIA

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Abstract

DANILOV S.N.: New data on the spiders of the family Dictynidae (Araneae) from Siberia. In GAJDOŠ P., PEKÁR S. (eds): Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava), Vol. 19, Supplement 3/2000, p. 37-44.

Four species of dictynid spiders are described from South Siberia: *Dictyna paramajor* sp.nov. (Krasnoyarsk Prov.), *Dictyna dunini* sp.nov. (Buryatia), *Dictyna dahurica* sp.nov. (Chita Area), *Dictyna shilenkovi* sp.nov. (Irkutsk Area, Buryatia). The female of *Emblyna mongolica* MARUSIK ET KOPONEN, 1998 is described for the first time. New records are presented for *Argenna prominula* TULLGREN, 1948, *Dictyna alaskae* CHAMBERLIN ET IVIE, 1947, *Dictyna schmidti* sensu LETHINEN, 1967 and *Dictyna ubsunurica* MARUSIK ET KOPONEN, 1998. *Emblyna logunovi* MARUSIK ET KOPONEN, 1998 is synonymised with *Emblyna wangi* (SONG ET ZHOU, 1986) comb.nov. (ex. *Dictyna*).

Introduction

The spider family Dictynidae is still insufficiently studied in Siberia. Just a few papers are devoted to this family in the region (MARUSIK, 1988; DANILOV, 1994; MARUSIK, KOPONEN, 1998). Up to now 28 species of Dictynidae are known in Siberia (MIKHAILOV, 1997; MARUSIK, KOPONEN, 1998), 12 of them are described from this region.

In this paper, four new species are described and new records and synonym of other species of Dictynidae from South Siberia are presented. Material was collected by the author and several other researchers. It is deposited in the Institute of General and Experimental Biology, Ulan-Ude, Russia (IGEB) and Zoological Museum of Moscow State University, Russia (ZMMU). All measurements are in millimetres.

Argenna prominula Tullgren, 1948 (Figs 1, 2)

Material: 3 ♂♂ (IGEB): Buryatia, Kurumkansky Distr., Balan-Tamur Lake, larch forest, 1200 m, 16 July 1995, S. Danilov; 18 ♂♂ (IGEB): Chita Area, Kyrinsky Distr., Sokhoninsky Reserve, Verkhny Bukukun locality, larch forest, 1600 m, 21 July 1990, S. Danilov.

Distribution: Holarctic range.

Dictyna alaskae Chamberlin et Ivie, 1947 (Figs 3, 4)

Material: 1 ♂ (IGEB): Irkutsk Area, Slyudyansky Distr., Baikalsk, birch forest, 14 July 1983, S. Didorenko.

Distribution: Holarctic range. In South Siberia, the species has been known in Tuva only (Logunov et al., 1998).

Dictyna dahurica sp.nov. (Figs 5, 6)

Type locality: Russia, Chita Area, Duldurginsky Distr., Toktchin Vill., steppe.

Type material: Holotype. 1 ♀ (ZMMU): Chita Area, Duldurginsky Distr., Toktchin Vill., steppe, 16 July 1997, Ts. Damdinova.

Description: Female. Carapace 1.1 long, 0.8 wide, light brown. Abdomen 2.2 long, 1.5 wide, with typical pattern for 'major' group. Legs light brown. Epigyne as in Figs 5 and 6. Male unknown.

Distribution: Chita Area (Russia).

Etymology: The species is named after the traditional name of the southern part of the Chita Area «Dahuria».

Diagnosis: *D. dahurica* sp. nov. differs from the all known Palearctic *Dictyna* species by the internal structure of its epigyne (Fig. 6), it has narrow receptacula without any widening.

Dictyna dunini sp.nov. (Figs 7, 8)

Type locality: Russia, Buryatia, environs of Ulan-Ude, grassland.

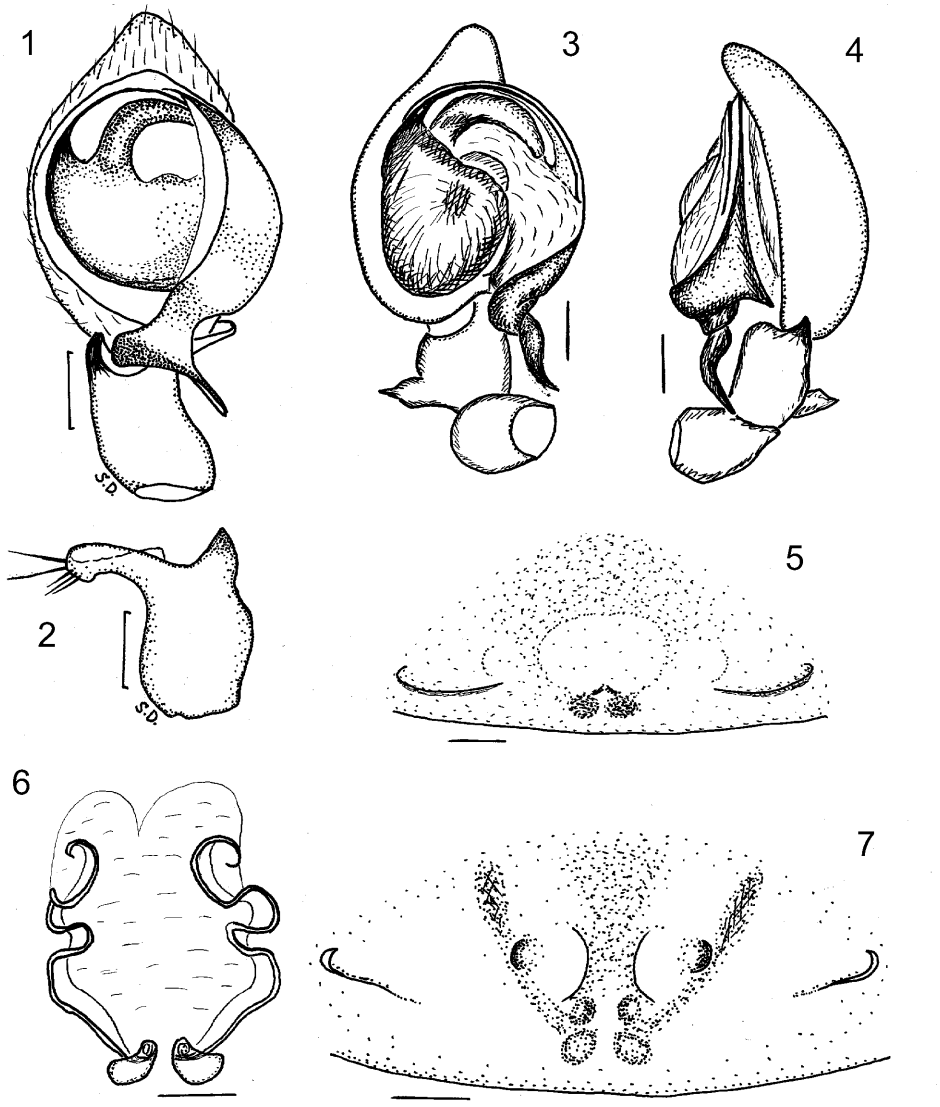
Type material: Holotype. 1 ♀ (ZMMU): Buryatia, environs of Ulan-Ude, grassland, 12 June 1996, S. Rudykh. Paratypes. 1 ♀ (IGEB), Irkutsk Area, Slyudyansky Distr., Baikalsk, birch forest, 14 June 1983, S. Didorenko; 1 ♀+ (ZMMU), Buryatia, environs of Ulan-Ude, mixed forest, 11 October 1995, S. Rudykh; 1 ♀ (IGEB), Buryatia, Kurumkansky Distr., Dzherginsky Reserve, Dzhirga locality, mixed forest, 17 June 1995, S. Danilov.

Description: Female. Carapace 0.85-1.05 long, 0.7-0.8 wide. Abdomen 1.4-1.75 long, 0.9-1.2 wide. Abdomen light grey, anterior part of half of abdomen with an oblong dark stripe. Epigyne as in Figs 7-8.

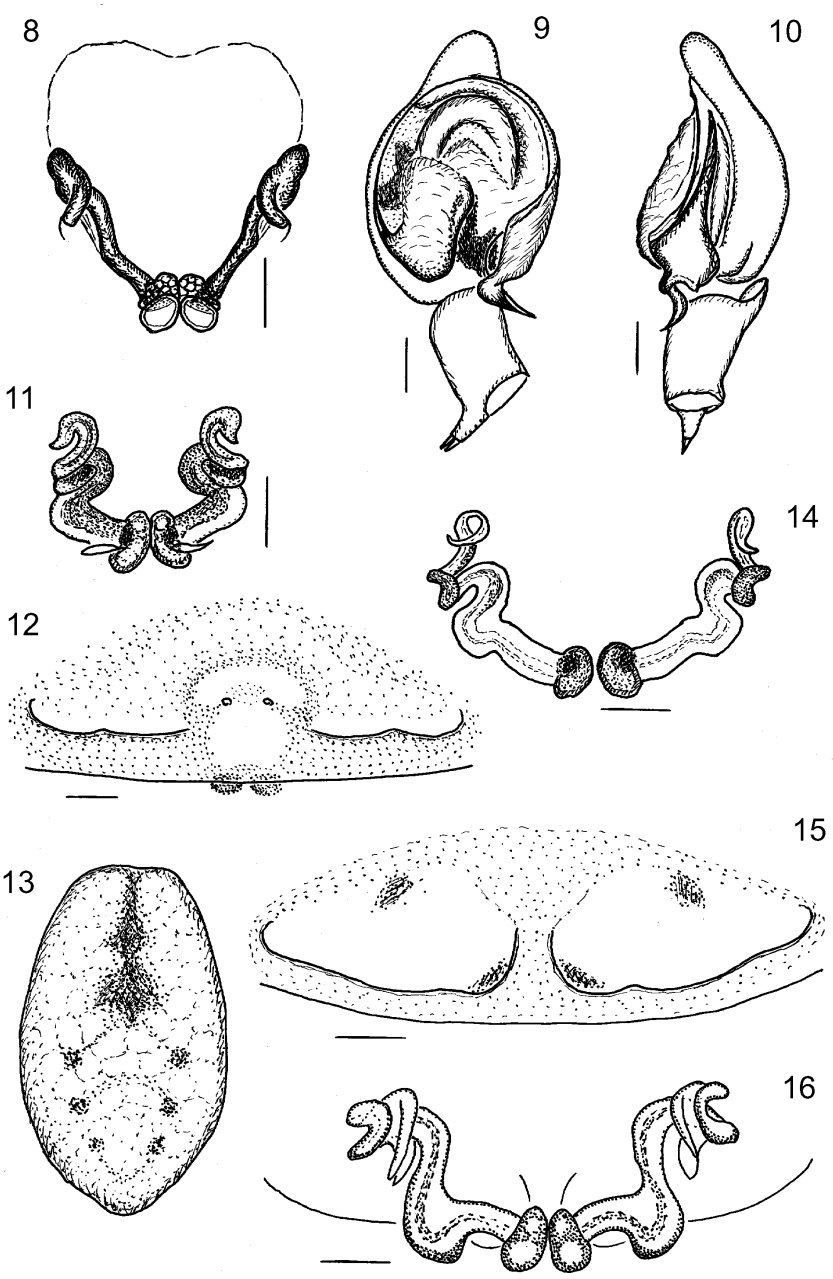
Distribution: Irkutsk Area, Buryatia (Russia).

Etymology: The new species is named after the Russian arachnologist Pyotr Dunin.

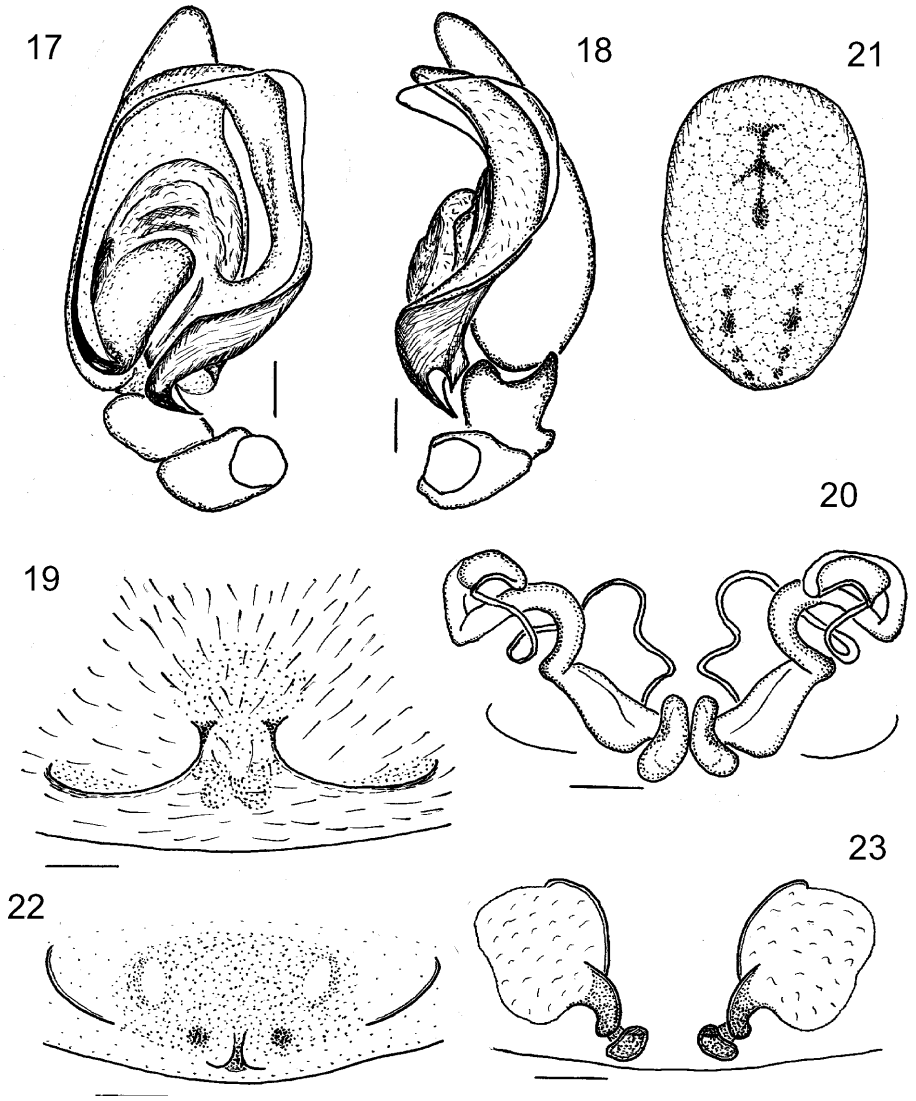
Diagnosis: The species is close, judging by the internal structure of its epigyne, to *D. uvs* Marusik et Koponen, 1998, but differs by the shape and sclerotisation of its epigyne openings.



Figs 1-7. 1-2 *Argenna prominula* Tullgren: (1) male palp, ventral view, (2) tibia of male palp, dorsal view; 3-4 *Dictyna alaskae* Chamberlin et Ivie: male palp, ventral (3) and lateral (4) view; 5-6 *Dictyna dahurica* sp.nov.: epigyne, ventral (5) and dorsal (6) view; 7 *Dictyna dunini* sp.nov.: epigyne, ventral view. Scale lines=0.1 mm.



Figs 8-16. 8 *Dictyna dunini* sp.nov.: epigyne, dorsal view; 9-13 *Dictyna paramajor* sp.nov.: male palp, ventral (9) and lateral (10) view, epigyne, dorsal (11) and ventral (11) view, (13) male abdomen, dorsal view; 14 *Dictyna major* MENGE: epigyne, dorsal view; 15-16 *Dictyna schmidti* sensu LETHINEN: epigyne, ventral (15) and dorsal (16) view. Scale lines=0.1 mm.



Figs 17-23. 17-20 *Dictyna shilenkovi* sp.nov: male palp, ventral (17) and lateral (18) view, epigyne, ventral (19) and dorsal (20) view; 21-23 *Emblyna mongolica* Marusik et Koponen: (21) female abdomen, dorsal view, epigyne, ventral (22) and dorsal (23) view. Scale lines=0.1 mm.

Dictyna paramajor sp.nov. (Figs 9-13)

Type locality: Russia, Krasnoyarsk Prov., Ermakovsky Distr., Kulumys Ridge, larch forest.

Type material: Holotype. 1 ♀ (ZMMU): Krasnoyarsk Prov., Ermakovsky Distr., Kulumys Ridge, larch forest, 18 July 1985, coll. ?. Paratypes. 1 ♂, 1 ♀ (ZMMU): same data as holotype.

Comparative material: *Dictyna major* Menge, 1869, 1 ♀ (IGEB): Buryatia, Ulan-Ude, 12 July 1984, S. Danilov.

Description: Female. Carapace 1.4 long, 1.0 wide, dark brown. Abdomen 2.75 long, 2.25 wide, grey with pattern as in Fig. 13. Legs uniformly yellow. Epigyne as in Figs 11-12. Male. Carapace 1.3 long, 0.85 wide. Abdomen 1.55 long, 1.05 wide. Male coloured as female. Palp as in Figs 9-10.

Distribution: Krasnoyarsk Prov. (Russia).

Etymology: The species name means very close similarity to *D. major* Menge.

Diagnosis: The new species, judging by the general appearance and structure of the palp and epigyne is quite similar to *D. major* (Fig. 14). *D. paramajor* sp. nov. can be separated by its smaller size, the internal structure of epigyne (Fig. 11) and more proximal direction of the apex of the conductor (Figs 9-10).

Dictyna schmidti sensu Lehtinen, 1967 (Figs 15-16)

Material examined: 1 ♀ (IGEB) Krasnoyarsk Prov., Ermakovsky Distr., Kulumys Ridge, larch forest, coll. ?; 1 ♀ (IGEB), Buryatia, Kurumkansky Distr., Kovyli River, dwarf birch overgrowth, 6 July 1996, V. Buyantuev.

Distribution: Transpalaearctic boreal range.

Dictyna shilenkovi sp.nov. (Figs 17-20)

Type locality: Russia, Irkutsk Area, Baikalsk, mixed forest.

Type material: Holotype. 1 ♂ (ZMMU): Irkutsk Area, Baikalsk, mixed forest, 22 June 1977, V. Shilenkov. Paratypes. 2 ♀♀ (ZMMU): same data as holotype; 2 ♀♀ (IGEB): same locality , 25 June 1980, S. Danilov; 1 ♀ (IGEB): Buryatia, 30 km W of Ulan-Ude, mixed forest, 18 July 1992, S. Danilov; 1 ♀ (IGEB): Buryatia, Kabansky Distr., Boyarsk, grassland, 25 July 1993, S. Danilov; 1 ♀ (IGEB): Buryatia, environs of Ulan-Ude, Utochkina Pad', birch and willow overgrowth, 2 June 1994, S. Danilov; 1 ♀ (IGEB): Buryatia, Kurumkansky Distr., Umkhei, mixed forest, 31 May 1997, S. Danilov.

Description: Male. Carapace 1.25 long, 1.0 wide, dark brown. Abdomen 1.35, 1.1 wide, light yellow with pattern: grey median band in frontal part and 4 separated bands. Legs yellow. Palp as in Figs 17-18. Female. Carapace 1.4-1.8 long, 1.3-1.4 wide. Abdomen 2.25-3.05 long, 1.55-2.3 wide. Coloration and abdomen pattern as in male. Epigyne as in Figs 19-20.

Distribution: Irkutsk Area, Buryatia (Russia).

Etymology: The new species is named after Viktor G. Shilenkov, an entomologist at Irkutsk University and collector of the type material.

Diagnosis: The structure of the male palp and epigyne demonstrate that this new species belongs to the '*major*' group, but from it can be distinguished the very similar *D. schmidti*

sensu LEHTINEN by the shape of the conductor (Figs 17-18), as well as by the structure of the epigyne (Fig. 20).

Dictyna ubsunurica MARUSIK ET KOPONEN, 1998

Material examined: 2 ♀♀ (IGEB): Buryatia, Zaigrayevsky Distr., Bryanka River, willow overgrowth, 21 June 1993, S. Danilov; 1 ♂ (IGEB): same locality, 9 July 1995, S. Danilov.

Distribution: Tuva, Buryatia (Russia).

Emblyna mongolica MARUSIK ET KOPONEN, 1998 (Figs 21-23)

Emblyna mongolica MARUSIK ET KOPONEN, 1998: 80, figs 6-9.

Material examined: 1 ♀ (IGEB): Buryatia, Ivolginsky Distr., Topkhar locality, steppe, 19 May 1998, S. Rudykh; 1 ♀ (IGEB): Chita Area, Ononsky Distr., Kubukhay Vill., pine forest, 26 June 1984, S. Danilov; 2 ♂♂, 4 ♀♀ (IGEB): Chita Area, Ononsky Distr., Dahurian Reserve, Zun-Torei Lake, Ostoshi locality, steppe, 29 May –5 June 1999, S. Danilov.

Description: Female. Carapace 0.8 long, 0.75 wide, dark brown. Abdomen 2.0 long, 1.45 wide, light grey with pattern as in Fig. 21. Epigyne as in Figs 22-23. Legs yellow with dark rings on apical parts of the segments, femora and tibia with rings on the middle parts. Male. See MARUSIK, KOPONEN (1998).

Distribution: Tuva, Buryatia and Chita Area (Russia) and Mongolia.

Diagnosis: *E. mongolica* most close to *E. wangi* (SONG ET ZHOU, 1986). Epigynes of these species differ considerably in the form of the receptaculum; *E. mongolica* has a semicircular but *E. wangi* an oblong and curved receptaculum.

Remark: Only the male of *E. mongolica* has been known from the Tuva and Chita Area (Russia) and from Mongolia (MARUSIK, KOPONEN, 1998).

Emblyna wangi (SONG ET ZHOU, 1986) comb.nov.

Dictyna wangi SONG ET ZHOU, 1986: 261, figs 1-4.

Emblyna logunovi MARUSIK ET KOPONEN, 1998: 83, figs 12-17, syn.nov.

Distribution: Russia (Tuva), Mongolia, China (Xinjiang Uygur Autonomous Region).

Remark: MARUSIK, KOPONEN (1998) have described *E. logunovi* from Tuva (Russia), but comparison of its figures with those of *D. wangi* described by SONG, ZHOU (1986) from China undoubtedly shows their conspecifity. Thus, *E. logunovi* is a junior synonym of *D. wangi*, but the latter name must be transferred to genus *Emblyna.*

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A FIRST ANALYSIS ON THE RELATIONSHIP BETWEEN FOREST SOIL QUALITY AND SPIDER (ARANEAE) COMMUNITIES OF FLEMISH FOREST STANDS

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Abstract

De Bakker D., Maelfait J.-P., Hendrickx F., Van Waesberghe D., De Vos B., Thys S., De Bruyn L.: A first analysis on the relationship between forest soil quality and spider (Araneae) communities of Flemish forest stands. In Gajdoš P., Pekár S. (eds): Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava), Vol. 19, Supplement 3/ 2000, p. 45-58.

A project aiming at the development of a practical bio-indication system for evaluating forest soil quality was recently started up. The project is funded by the Flemish Forestry Administration responsible for the protected Flemish forests and is managed by the Institute for Forestry and Game Management (IBW). In the project the arthropod fauna of fifty forest stands distributed all over the Flemish Region was sampled by traps operative from spring 1997 till spring 1998. All these plots were also investigated in relation to the physical and chemical properties of their soil and litter layers. The variation of the composition of the spider communities of these stands is unclear when we compare it with the most important litter and soil parameters, but future investigations with more (structural) parameters will hopefully give a good explanation. On a subregional scale, in forests on the same soil type (loam), spider community composition seems to be determined by humidity and density of tree coverage. Spider species forwhich abundance correlates with these major environmental factors are candidate bio-indicators to monitor forest soil quality.

Introduction

Flemish forests have been fragmented and degraded during several centuries. It is a safe assumption that, at the beginning of the Holocene, there was more woodland in Flanders than there is now. However, the history of woodlands in Flanders cannot be described by a simple model of linear decline, but is characterised by periods of regression and expansion (Tack et al., 1993; Tack, Hermy, 1998). Woodlands in Flanders can be described by three basic factors: deforestation events, changes in dimensions resulting in actual size, and exploitation history (Desender et al., 1999). Forest covers nowadays only about 8% of the total area in Flanders (Hermy, 1989). Communities of organisms bound to the forest are exposed to population dynamic and population genetic effects (e.g. Desender et al., 1999) due to fragmentation and a higher level of pollution derived from industry and agriculture (Maelfait, Hendrickx, 1998). Therefore a project was started up in 1997 to evaluate forest soil quality by means of soil-living arthropods.

A selection of 50 forests was chosen from 400 sampling points of the forest-inventory grid of Flanders. These forests were chosen to represent the full range of forest types found in Flanders.

Different arthropod groups were included in this study: spiders (Araneae), pseudoscorpiones, harvestmen (Opiliones), ground beetles (Coleoptera: Carabidae), other beetle-families (Coleoptera: Chrysomelidae, Staphylinidae, Curculionidae,…), millipedes (Diplopoda), centipedes (Chilopoda), woodlice (Isopoda), certain families of flies (Diptera: Syrphidae, Empididae, Sphaeroceridae, Dolichopodidae, Phoridae,…), plant-parasitic nematodes (Nematoda) and springtails (Collembola).

Material and methods

Pitfall traps were used in this project. These were glass vessels (9.5 cm diameter) placed into the ground so that the top of the trap was level with the soil surface. The traps were filled with a 4% formaldehyde solution in which we added a little detergent to reduce the surface tension. Also salt was added in the winter to prevent the solution from freezing. The advantages of this method can be summarised as follows (Maelfait, Baert, 1975; Maelfait, 1996): (1) the method is standardised, inexpensive and labour-effective, (2) large numbers of animals are caught which allows statistical analysis, (3) the method is commonly used, which allows comparison with earlier sampling campaigns, (4) nocturnal and diurnal animals are caught, (5) the distribution of catches of males and females during short, continuous periods (every fortnight during a complete year cycle is reasonable) allows a good reconstruction of the life cycle of the most abundant species and (6) the catches of a certain species in different types of habitats shows clearly the preference of a certain species for the sampled habitats (see also Obrtel, 1971; Uetz, Unzicker, 1976). The disadvantage of the method is that catches of different species which occur in the same habitat cannot be used to calculate the relative density of these species. This is because species vary in level of activity, which affects their probability of capture (see also Greenslade, 1964; Luff, 1975; Curtis, 1980; Desender, 1984; Desender, Maelfait, 1986).

We placed 3 pitfall traps in one row (approximately 3 meters apart). This gave a total of 150 pitfall traps emptied every fortnight (and every three weeks in the winter). Animals were sorted in the laboratory and preserved in 70% alcohol, to be identified later.

The location of the 50 forest stands is shown in Fig. 1. The list of names of the forests used in this figure is explained in Table 1. Spiders which were caught in May 1997 were identified for all 50 stations, (Table 2). For

8 stands in the region of the Flemish Ardens, the spider fauna was determined (for a graduate thesis) for the whole year cycle (Van Waesberghe, 1998). Due to the large sorting effort, we can only present these preliminary results. In a future contribution, the results of the analysis of the complete data will be displayed. For determination of species we used Locket, Millidge (1951, 1953), Locket et al. (1974) and Roberts (1987, 1998).

Furthermore, some parameters of the soil and litter layer were measured: acidity (pH), electrical conductivity, weight (DS) and the concentration of several mineral elements (Ca, N, S, P, Mg and K). Values for these parameters are shown in Table 3.

Ordinations and classifications were done with the programmes PC-ORD (McCune, Mefford, 1995) and CANOCO for Windows. Statistical tests were performed with the program STATISTICA.

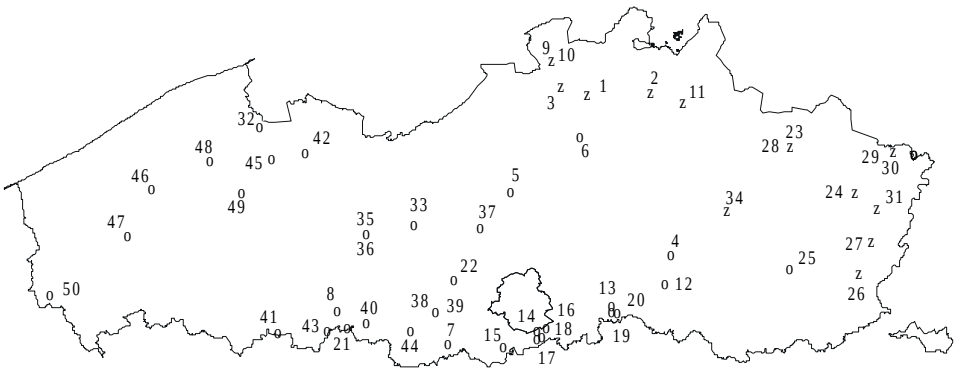

Fig. 1. Position of the sampled forest stands in Flanders (o- forests on sandy loam /loam soil, z- forests on sandy soils). Numbers of forest stands are explained in Table 1.

Results and discussion

The spiders captured during May 1997 were determined for all 50 forest stands (see Table 2). This revealed 9677 adult individuals belonging to 161 species. The complete year cycle of the 8 forest stands in the Flemish Ardens revealed 8 217 adult individuals belonging to 118 species (Van Waesberghe, 1998). 45 species, which have been determined for the 50 forest stands and the 8 stands of the Flemish Ardens, belong to the Red List of spiders of Flanders (Maelfait et al., 1998).

The species used in the analysis were the most abundant ones. In the case of the 50 forest stands we took 50 individuals for analyses. This is equivalent to one capture in every plot during the month of May 1997. We have 30 species that fulfil this condition. The quantitative data of these most abundant species were transformed to percentage distributions per species over the 50 forest stands as a measure of habitat preference (within the available data). Such a transformation ensures that each species (used in the analysis) receives an equal weight. This explains why less abundant species (with strong random variation in numbers, and often also possible accidental immigrants from other environments) are not used in the analysis. The results are used in an indirect gradient-analysis (DCA= Detrended

T a b l e 1. List of sampled forest stands with number, abbreviation, soil type on which the forest is situated, name and dominant tree species occurring in the stand. Forests in bold are the 8 forests with a complete dataset.

No.	Abbr.	Soil type	Forest stand	Main tree species
1	KAMP	Sand	Het Kamp	*Pinus silvestris*
2	BEER	Sand	Beerse Heide	*Pinus silvestris*
3	BRAS	Sand	Inslag	*Pinus silvestris*
4	WALE	Sandy loam	Walenbos	*Quercus robur, Q. petraea*
5	KOOL	Sandy loam	Koolhembos	*Alnus glutinosa*
6	MUIZ	Sandy loam	Muizenbos	*Fraxinus excelsior*
7	**EDIL**	**Loam**	**Bos Ter Rijst Edingen**	*Fraxinus excelsior, Quercus robur*
8	**BURR**	**Loam**	**Burreken**	*Quercus robur*
9	KAL9	Sand	Withoefse Heide	*Pinus silvestris*
10	KA10	Sand	Withoefse Heide	*Pinus silvestris*
11	SEVE	Sand	Sevendonck	*Fagus sylvatica*
12	BINK	Sandy loam	Kapellebos	*Quercus robur*
13	MELE	Sandy loam	Meerdaalwoud level-plot	*Quercus robur*
14	ZO14	Loam	Zoniën 14	*Fagus sylvatica*
15	HALL	Loam	Hallerbos	*Fagus sylvatica*
16	ZO16	Loam	Zoniën bestand 23	*Quercus robur, Carpinus betulus*
17	ZO17	Loam	Zoniën bestand 24	*Quercus robur, Carpinus betulus*
18	ZO18	Loam	Zoniën bestand 25	*Fagus sylvatica*
19	MEDR	Sandy loam	Meerdaalwoud drie eiken	*Betula* sp.
20	MEKO	Sandy loam	Meerdaalwoud grote konijnenpijp	*Fagus sylvatica*
21	**BRDR**	**Loam**	**Brakelbos**	*Fagus sylvatica*
22	RTTD	Sandy loam	RTT-domein	*Quercus robur, Betula* sp.
23	HE23	Sand	Pijnven	*Pinus silvestris*
24	HEID	Sand	Heiderbos	*Pinus silvestris*
25	WIMM	Sandy loam	Oude Mombeek	*Populus x canadensis*
26	GELL	Sand	Gellikerheide	*Pinus silvestris*
27	HECH	Sand	Heiwijk	*Pinus silvestris*
28	HE28	Sand	Pijnven	*Pinus silvestris*
29	BR29	Sand	Grootbroek-Bree I	*Quercus robur, Betula* sp.
30	BR30	Sand	Grootbroek Bree II	*Betula* sp., *Alnus glutinosa*
31	LANK	Sand	Lanklaarderbos	*Betula* sp.
32	PADD	Sandy loam	Paddepoelebos	*Quercus robur, Fraxinus excelsior*
33	SERS	Sandy loam	Zandputten	*Quercus robur*
34	KENI	Sand	Kenisberg-Kruisberg	*Pinus silvestris*
35	GONA	Sandy loam	Aelmoeseneie I	*Quercus robur, Fagus sylvatica*
36	GONB	Sandy loam	Aelmoeseneie II	*Fraxinus excelsior*
37	BUGG	Loam	Buggenhoutbos	*Fagus sylvatica*
38	**NEI7**	**Loam**	**Neigembos - bestand 7**	*Fagus sylvatica*
39	**NE7B**	**Loam**	**Neigembos - bestand 7bis**	*Betula* sp.
40	**PARI**	**Loam**	**Parikebos (Parike)**	*Populus x canadensis*
41	KLUI	Loam	Kluisbos	*Fagus sylvatica*
42	LEEN	Sandy loam	Het Leen	*Quercus robur*
43	**SCNA**	**Loam**	**Bos Terrijst Schorisse**	*Fraxinus excelsior, Alnus glutinosa*
44	**RASP**	**Loam**	**Raspaillebos**	*Quercus rubra, Castanea sativa*
45	DRON	Sandy loam	Drongengoed	*Fagus sylvatica*
46	WIJL	Sandy loam	Wijnendalebos	*Fagus sylvatica*
47	HOUT	Sandy loam	Houthulstbos	*Quercus robur*
48	NIEU	Sandy loam	Nieuwenhoven	*Quercur robur, Fagus sylvatica*
49	RUIG	Sandy loam	Vorte bossen	*Quercus rubra, Fraxinus excelsior*
50	HELL	Sandy loam	Helleketelbos	*Quercus robur, Acer pseudoplatanus*

T a b l e 2. Number of species caught in May 1997 for all 50 forest stands.

Species	No.
AMAUROBIIDAE	
Amaurobius fenestralis (STRO.)	1
DICTYNIDAE	
Cicurina cicur (FABR.)	3
Lathys humilis (BL.)	2
DYSDERIDAE	
Dysdera erythrina (WALC.)	3
GNAPHOSIDAE	
Haplodrassus silvestris (BL.)	74
Haplodrassus umbratilis (L. K.)	1
Micaria fulgens (WALC.)	6
Micaria pulicaria (SUND.)	5
Phaeocedus braccatus (L. K.)	1
Zelotes latreillei (SIMON)	1
Zelotes subterraneus (C. L. K.)	31
CLUBIONIDAE	
Clubiona brevipes BL.	1
Clubiona compta C. L. K.	11
Clubiona corticalis (WALC.)	1
Clubiona lutescens WEST.	9
Clubiona pallidula (CL.)	2
Clubiona reclusa O. P.-C.	4
Clubiona terrestris WEST.	40
LIOCRANIDAE	
Agroeca brunnea (BL.)	126
Apostenus fuscus WEST.	43
Phrurolithus festivus (C. L. K.)	7
Scotina celans (BL.)	1
ZORIDAE	
Zora spinimana (SUND.)	43
ANYPHAENIDAE	
Anyphaena accentuata (WALC.)	20
THOMISIDAE	
Coriarachne depressa (C. L. K.)	2
Ozyptila praticola (C. L. K.)	23
Ozyptila trux (BL.)	149
Xysticus audax (SCH.)	1
Xysticus erraticus (BL.)	1
Xysticus lanio C. L. K.	40
Xysticus ulmi (HAHN)	1
PHILODROMIDAE	
Philodromus aureolus (CL.)	1
Philodromus dispar WALC.	3
SALTICIDAE	
Ballus chalybeius (WALC.)	1
Euophrys frontalis (WALC.)	22

Species	No.
Euophrys petrensis C. L. K.	2
Evarcha falcata (CL.)	1
Marpissa muscosa (CL.)	2
Neon reticulatus (BL.)	11
LYCOSIDAE	
Alopecosa cuneata (CL.)	1
Alopecosa pulverulenta (CL.)	10
Hygrolycosa rubrofasciata (OHLE.)	3
Pardosa amentata (CL.)	50
Pardosa lugubris (WALC.)	306
Pardosa prativaga (L. K.)	2
Pardosa pullata (CL.)	2
Pardosa saltans TÖP.-HOF.	402
Pirata hygrophilus TH.	3106
Pirata latitans (BL.)	11
Pirata piraticus (CL.)	1
Pirata uliginosus (TH.)	98
Trochosa spinipalpis (O. P.-C.)	1
Trochosa terricola TH.	146
Xerolycosa nemoralis (WEST.)	4
PISAURIDAE	
Pisaura mirabilis (CL.)	2
AGELENIDAE	
Coelotes inermis (L. K.)	50
Coelotes terrestris (WIDER)	20
Histopona torpida (C. L. K.)	136
Tegenaria picta SIMON	258
Tegenaria silvestris L. K.	2
HAHNIIDAE	
Antistea elegans (BL.)	1
Hahnia helveola SIMON	8
Hahnia montana (BL.)	36
Hahnia nava (BL.)	1
Hahnia pusilla C. L. K.	109
MIMETIDAE	
Ero furcata (VILL.)	2
THERIDIIDAE	
Anelosimus vittatus (C. L. K.)	1
Crustulina guttata (WIDER)	2
Enoplognatha thoracica (HAHN)	23
Episinus angulatus (BL.)	2
Euryopis flavomaculata (C. L. K.)	81
Robertus lividus (BL.)	120
Theridion bimaculatum (L.)	3
Theridion pallens BL.	4
Theridion varians HAHN	1

T a b l e 2. (cont.)

Species	No.
THERIDIOSOMATIDAE	
Theridiosoma gemmosum (L. K.)	4
METIDAE	
Metellina mengei (BL.)	17
TETRAGNATHIDAE	
Pachygnatha clercki SUND.	23
Pachygnatha degeeri SUND.	2
Pachygnatha listeri SUND.	180
ARANEIDAE	
Cercidia prominens (WEST.)	5
Cyclosa conica (PALL.)	1
LINYPHIIDAE (ERIGONINAE**)**	
Ceratinella brevis (WIDER)	7
Ceratinella scabrosa (O. P.-C.)	57
Dismodicus bifrons (BL.)	10
Dicymbium nigrum (BL.)	1
Dicymbium tibiale (BL.)	33
Diplocephalus latifrons (O. P.-C.)	7
Diplocephalus picinus (BL.)	1329
Erigone atra (BL.)	3
Erigone dentipalpis (WIDER)	5
Erigonella hiemalis (BL.)	2
Glyphesis servulus (SIMON)	14
Gnathonarium dentatum (WIDER)	1
Gonatium rubellum (BL.)	20
Gongylidiellum latebricola (O. P.-C.)	8
Gongylidiellum vivum (O. P.-C.)	3
Gongylidium rufipes (SUND.)	87
Hypomma cornutum (BL.)	1
Leptorhoptrum robustum (WEST.)	1
Maso sundevalli (WEST.)	7
Micrargus herbigradus (BL.)	84
Minyriolus pusillus (WIDER)	36
Monocephalus fuscipes (BL.)	31
Oedothorax fuscus (BL.)	1
Oedothorax gibbosus (BL.)	4
Oedothorax retusus (WEST.)	2
Pocadicnemis pumila (BL.)	182
Saloca diceros (O. P.-C.)	8
Tapinocyba insecta (L. K.)	23
Tapinocyba praecox (O. P.-C.)	1
Tiso vagans (BL.)	2
Walckenaeria acuminata BL.	76
Walckenaeria alticeps (DENIS)	3
Walckenaeria atrotibialis (O. P.-C.)	13
Walckenaeria corniculans (O. P.-C.)	58

Species	No.
Walckenaeria cucullata (C. L. K.)	37
Walckenaeria cuspidata (BL.)	2
Walckenaeria dysderoïdes (WIDER)	32
Walckenaeria furcillata (MENGE)	19
Walckenaeria mitrata (MENGE)	2
Walckenaeria monoceros (WIDER)	1
Walckenaeria nudipalpis (WEST.)	6
Walckenaeria obtusa BL.	9
Walckenaeria unicornis O. P.-C. (LINYPHIINAE)	1
Agyneta ramosa JACK.	170
Agyneta subtilis (O. P.-C.)	18
Bathyphantes nigrinus (WEST.)	31
Bathyphantes parvulus (WEST.)	8
Centromerita concinna (TH.)	1
Centromerus aequalis (WEST.)	44
Centromerus dilutus (O. P.-C.)	6
Centromerus leruthi FAGE 1933	2
Centromerus pabulator (O. P.-C.)	1
Centromerus prudens (O. P.-C.)	5
Centromerus serratus (O. P.-C.)	5
Centromerus sylvaticus (BL.)	18
Diplostyla concolor (WIDER)	127
Lepthyphantes cristatus (MENGE)	36
Lepthyphantes ericaeus (BL.)	4
Lepthyphantes flavipes (BL.)	226
Lepthyphantes mengei KULC.	37
Lepthyphantes pallidus (O. P.-C.)	42
Lepthyphantes tenebricola (WIDER)	21
Lepthyphantes tenuis (BL.)	4
Lepthyphantes zimmermanni BERT.	70
Linyphia hortensis SUND.	37
Macrargus rufus (WIDER)	155
Meioneta saxatilis (BL.)	13
Microneta viaria (BL.)	268
Nereine clathrata (SUND.)	119
Nereine montana (CL.)	4
Nereine peltata (WIDER)	3
Poeciloneta globosa (WIDER)	4
Porrhomma convexum (WEST.)	1
Porrhomma egeria SIMON	10
Porrhomma pallidum JACK.	1
Porrhomma pygmaeum (BL.)	3
Saaristoa abnormis (BL.)	20
Sintula cornigera (BL.)	1
Total	9677

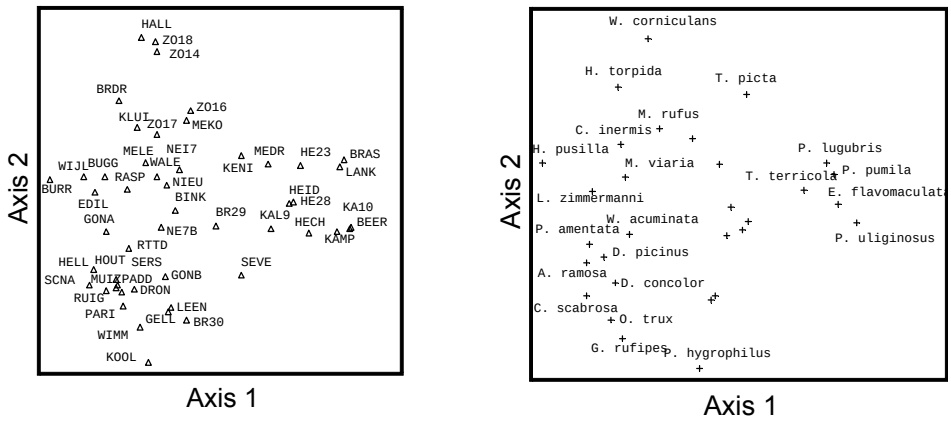

Fig. 2. DCA-ordination of the 50 forest stands on the basis of the most abundant spider species caught in may 1997 (left) and distribution of corresponding indicator spider species (right).

Correspondence Analysis; TER BRAAK, 1988, JONGMAN et al., 1995) and a TWINSPAN (Two Way Indicator Species Analysis; HILL, 1979) which performs a two way-divisive and hierarchical classification where, at every level, the original group of samples and species are divided on the basis of indicator species. For the 8 forest stands of the Flemish Ardens, the number of individuals, to be incorporated into the analysis, was taken at 33. 44 species fulfilled this condition.

Indirect gradient analysis of the stands (DCA) on the basis of the most abundant spider species

The results of the DCA-analysis for the 50 forest stands are shown in Fig. 2 (axis 1 and 2). The eigenvalues of these axes are respectively 0.655 and 0.578 and the total variance explained by the first two axes is 26.7%. The following axes (axes 3 and 4) have eigenvalues which are lower than 0.3 and further increase in variance is minimal. The forests with a more sandy soil (with pine (*Pinus sylvestris*) as the main tree species) are found at the right. We also draw attention to a concentration of deciduous forests in the lower left corner. It consists mainly of more humid forests on loam /sandy loam soils (e.g. Koolhembos, Bos ter Rijst Schorisse, Wimmertingen, Parikebos, Vorte Bossen and Muizenbos). If we look at the corresponding species then we note the following indicator species for the forests on sandy soils: *Pardosa lugubris* (WALCKENAER), *Trochosa terricola* THORELL, *Pocadicnemis pumila* (BLACKWALL), *Euryopis flavomaculata* (C. L. KOCH) and *Pirata uliginosus* (THORELL). These are all species which prefer open, dry habitats. For deciduous forests we note the following indicator species: *Ozyptila trux* (BLACKWALL), *Pirata*

T a b l e 3. Values of the physico-chemical parameters of litter and soil for the 50 forest stands (DS- percent of total weight of soil sample that remains after drying at 105 degrees Celsius, concentrations are expressed in parts per million).

Forest Stand	Litter - parameters								Soil - parameters							
	DS (%)	pH	N (%)	P (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)	S (ppm)	DS (%)	pH	N (%)	P (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)	S (ppm)
KAMP	44.6	3.6	1.29	372	152	1702	268	2565	89.0	3.8	0.07	77	241	571	109	68
BEER	58.7	3.6	1.16	324	196	2101	391	1188	90.1	3.6	0.14	146	314	562	162	280
BRAS	54.2	3.5	1.40	399	174	2606	348	2279	90.8	4.0	0.08	46	208	426	105	107
WALE	36.9	4.6	1.74	596	1158	8383	1009	2454	51.8	3.7	0.89	495	2898	1599	1815	1094
KOOL	33.6	5.8	1.78	588	1265	6714	1543	1575	45.9	4.1	0.97	759	2102	3682	2480	1493
MUIZ	56.3	5.0	1.06	386	1789	14884	1068	916	83.5	6.1	0.24	285	2025	6686	2034	483
EDIL	40.5	5.5	1.18	656	2334	7472	1841	867	310	4.1	0.21	536	2433	1546	2192	368
BURR	40.3	4.1	1.33	529	2640	13048	2605	1317	67.5	4.2	0.37	358	5626	2775	4862	437
KAL9	48.3	3.7	1.47	424	147	3035	410	1667	87.5	4.0	0.11	29	153	250	84	99
KA10	39.9	3.7	1.43	434	202	2936	480	1440	85.4	3.9	0.06	42	156	405	87	141
SEVE	31.0	3.9	1.91	559	529	2954	571	1860	64.3	3.8	0.27	193	634	695	680	787
BINK	45.1	4.1	1.62	652	864	6041	961	1511	76.0	3.8	0.19	195	1826	1068	1439	308
MELE	46.4	4.7	1.57	704	1373	8094	1181	1316	71.9	3.9	0.52	626	2166	1816	2003	728
ZO14	36.5	4.2	1.66	615	481	6567	805	1965	67.0	3.8	0.36	717	1695	1712	1376	664
HALL	34.5	4.4	1.79	655	790	7302	972	1526	72.0	3.8	0.21	617	2248	1633	1686	515
ZO16	44.1	3.9	1.54	608	552	6015	803	1519	63.7	3.6	0.38	645	1692	1698	1244	542
ZO17	44.5	4.2	1.59	632	1049	6174	1113	1295	65.4	3.5	0.51	730	1952	1698	1499	737
ZO18	45.2	4.3	1.59	618	657	6576	897	1385	75.1	3.8	0.28	445	1824	1553	1343	384
MEDR	55.7	3.9	0.96	300	637	2599	724	792	84.3	3.6	0.20	201	959	775	771	360
MEKO	57.5	4.3	1.50	502	704	5244	909	1076	78.2	3.7	0.67	345	1486	1376	1173	511
BRDR	28.3	3.9	1.69	427	637	4853	681	2016	67.9	3.7	0.36	249	4862	1038	3666	527
RTTD	41.4	3.6	1.35	456	598	2698	725	1909	65.8	3.6	0.43	482	1647	1314	1250	693
HE23	43.9	3.6	1.29	417	165	2927	401	1426	89.2	3.7	0.09	182	249	329	160	197
HEID	53.5	3.8	1.36	398	275	3091	394	1476	86.5	3.7	0.08	116	306	353	58	240
WIMM	28.8	2.7	1.33	1216	3985	19228	2255	1177	62.0	5.9	0.50	930	5135	6943	4681	908
GELL	46.7	3.9	1.28	367	288	5135	465	1449	85.2	3.9	0.09	91	286	521	150	222
HECH	34.6	3.7	1.62	386	362	3121	335	1471	78.1	3.6	0.49	221	342	550	214	469
HE28	47.4	3.5	1.35	436	188	3150	393	1587	92.0	3.7	0.08	112	248	332	133	197
BR29	35.9	4.1	2.12	658	411	8876	682	3383	58.0	4.1	0.79	489	779	3256	822	2110
BR30	29.3	4.1	2.06	613	584	9361	711	1940	53.2	4.4	0.78	533	1593	4233	1522	2909
LANK	52.5	4.5	1.35	436	684	4464	811	1323	88.3	4.1	0.15	114	360	407	202	250
PADD	40.0	3.8	1.95	545	517	5327	645	2887	79.0	3.7	0.61	316	568	1242	629	573
SERS	37.3	3.8	1.59	396	626	4636	834	1381	71.1	3.6	0.35	276	1218	1244	958	589
KENI	65.2	4.2	1.17	572	1600	4376	801	1105	93.7	3.8	0.06	452	5915	358	2800	501
GONA	37.5	3.8	1.49	421	1017	3877	977	1869	68.5	3.5	0.29	318	2672	1089	2112	449
GONB	40.1	3.0	1.39	695	5575	10519	1443	1026	79.0	4.2	0.20	372	2760	1971	2843	327
BUGG	40.4	3.6	1.28	355	477	2648	550	1465	79.8	3.5	0.31	343	1294	1025	1011	397
NEI7	46.0	3.9	1.01	361	1518	3507	1204	1301	74.3	3.7	0.25	347	3934	636	2967	430
NE7B	51.1	4.1	1.06	341	1212	2974	1194	1381	73.9	3.7	0.28	324	3020	961	2299	396
PARI	40.9	6.3	1.37	787	3040	18183	1792	1045	74.1	6.5	0.55	716	3226	7803	3178	841
KLUI	42.3	3.8	1.31	491	798	3053	751	1981	64.2	3.6	0.39	518	2359	1295	1845	489
LEEN	28.8	3.5	1.73	353	306	3609	602	2713	70.2	3.4	0.30	358	1549	1183	1149	530
SCNA	47.0	5.3	1.36	655	1650	13427	1632	1261	70.2	3.9	0.37	403	3131	1931	2658	477
RASP	38.6	3.8	1.06	423	1184	3140	1291	878	69.6	3.8	0.21	430	2617	1481	2230	383
DRON	33.3	3.7	1.62	344	1060	5751	1286	1423	75.2	3.7	0.22	200	4364	649	3855	380
WIJL	36.1	3.4	1.81	301	134	1923	447	2599	78.8	3.5	0.18	299	1275	761	1006	330
HOUT	29.1	3.4	1.54	332	736	3763	812	1393	64.7	3.4	0.62	376	1486	1198	1111	580
NIEU	33.9	3.8	1.70	432	386	4772	637	1314	85.0	3.8	0.07	145	918	720	704	156
RUIG	57.3	4.4	1.14	386	1240	4260	1584	1028	69.1	4.0	0.43	410	2226	3412	3002	623
HELL	35.1	3.8	1.61	430	639	3799	922	1623	66.6	3.5	0.35	265	2284	1214	1616	734

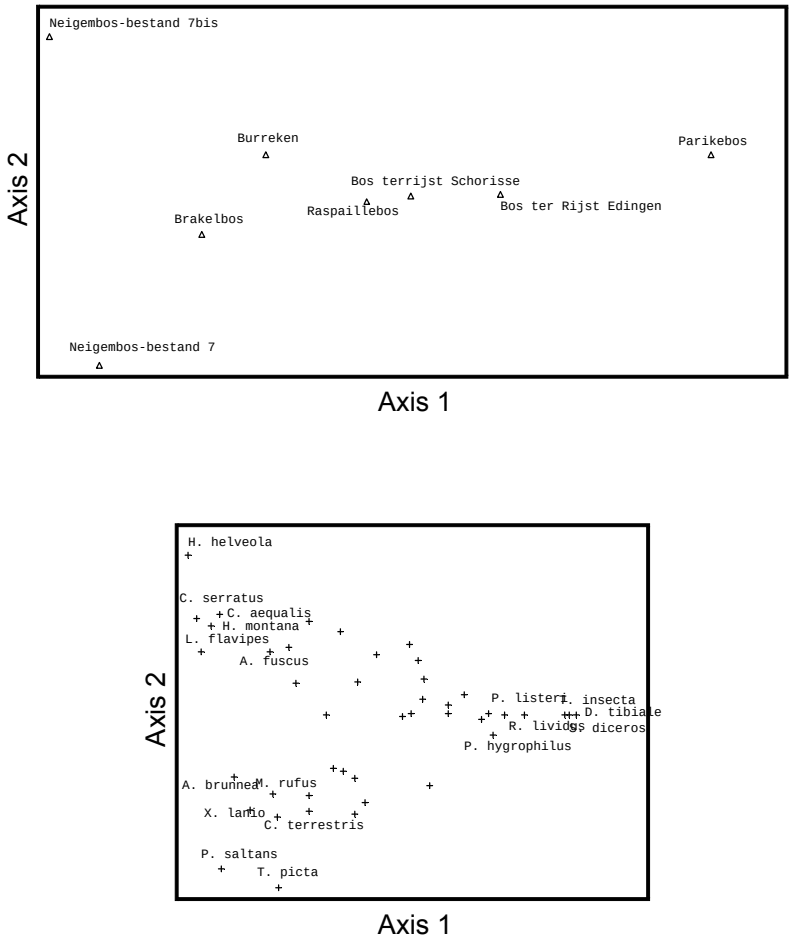

Fig. 3. DCA-ordination of the 8 forest stands of the Flemish Ardens based on the most abundantly caught spider species during a complete year cycle (1997-1998): distribution of the forest stands (above) and distribution of the specific indicator species (below).

hygrophilus THORELL, *Ceratinella scabrosa* (O. P.-CAMBRIDGE), *Gongylidium rufipes* (SUNDEVALL) and *Diplostyla concolor* (WIDER). These are all species which prefer more humid environments. At the top we see large and/or old forests (Zoniënwoud, Hallerbos and Meerdaalwoud) with beech (*Fagus sylvatica*) as the dominant tree species. The indicator species for these forests are *Walckenaeria corniculans* (O. P.-CAMBRIDGE), *Tegenaria picta* SIMON, *Macrargus rufus* (WIDER) and *Histopona torpida* (C. L. KOCH). These are species which mostly prefer beech-woods with a large quantity of dead wood. We have the

impression that, according to the first axis, soil texture is the most important parameter. In the future it would be useful to do research on deciduous forests with the same vegetation type and soil type and compare them with other results to reach a better conclusion on the reason why these forests are separated or grouped together from the rest. The second axis is probably a humid-dry gradient: dry forest stands mainly on top (e.g. Meerdaalwoud and Zoniënwoud) and more humid environments beneath (e.g. Koolhembos, Sevendonck and Bree), each associated with typical indicator species. Further analysis on a broader range of structural and other parameters should explain which parameter is most important for the division of the forest stands.

TWINSPAN-analysis yielded the same picture with the same indicator species. Habitat preferences of most of these indicator species, which appeared in the DCA-ordination as well as in the TWINSPAN-analysis, are similar to those generally found in the literature. Detailed information about distribution, phenology and habitat preferences of these species are discussed in Alderweireldt (1985), Seys (1985), Segers (1986), De Knijf (1993), De Bakker (1995), Van Waesberghe (1998), De Cock (1999) and D'Hert (1999).

When we look at the indicator species for dry forest stands on sandy soils, we note that almost all of them are not really typical (stenotopic) woodland species. They are, on the contrary, all species which prefer open, dry and exposed habitats like heathland and all kinds of grassland (e.g. *E. flavomaculata*, *T. terricola* and *P. uliginosus*). Indicator species which belong to forest stands on sandy loam /loam soils (e.g. *Coelotes terrestris* (Wider), *H. torpida*, …) are more typical (and stenotopic) woodland species in Belgium. Therefore it is difficult to interpretate the results obtained from the DCA-ordination. The difference between the two types of forest stands (sandy versus sandy loam /loam soils) can be the result of other reasons than those we have investigated here. Soils in the Campine Region (which are mostly dry, sandy and nutrient poor) were mostly planted with pine in the past, probably because this species is best adapted to this kind of soil and because pine wood was also frequently used in the mining industry. Pine forest stands have a more open vegetation, the soils are more exposed to the sun, are therefore warmer and all this resembles conditions of open habitats. This could explain the occurrence of several species that are not really bound to forests for their life-cycle. Comparison of these results with ordinations based on the most important litter and soil parameters strengthens our earlier findings. The ordination obtained based on the soil parameters seems to be similar to the one we derived on the basis of the most abundant species, but both ordinations (soil and litter) have very low eigenvalues and can therefore not be interpreted as being responsible for the difference. A Mann-Whitney U test between the litter and soil parameters of these two kinds of forest types confirmed the results already obtained, i.e. no significant difference between the two types of forest stands based on these parameters. The same result was obtained when using a (more formal) direct Canonical Correspondence Analysis (CCA) between litter and soil parameters and species frequencies: very low eigenvalues prohibits us to use even this ordination to explain the observed differences.

It can be concluded that the presented parameters are insufficient to explain the difference between the two kinds of forest stands. Other parameters, which are not available up to now, should give a clear picture of why these forests are separated. It is important in the

future that we also investigate deciduous forest stands in the Campine region on sandy, nutrient poor soils to explain the difference between these forests and those on nutrient rich sandy loam /loamy soils. We also remark that these results are based on only one month of data and that in the future, with a complete set of data, we will be able to make conclusions about the division of the stands and find suitable bio-indicators.

We can conclude that different spider communities are present in forests on nutrient-poor sandy soils (with mainly pine and birch (*Betula* sp.) as dominant tree species) and forests on nutrient-rich loam/sandy loam soils (oak (*Quercus robur*/*Q. petraea*), beech and mixed deciduous forest stands). This is also reflected in different main tree species and other vegetation which cannot be investigated up to now. It is important to emphasise that we are not dealing with a zoogeographical phenomenon because the species used in the analyses are the most abundant ones and are very common in the whole region.

Analysis of 8 forest stands from the region of the Flemish Ardens

Forests on the same soil type (loam) were compared with each other for the complete set of data (whole year cycle) with the most abundant species. The DCA-ordination of the 8 forest stands and distribution of the most important indicator species are shown in Fig. 3. The axes have eigenvalues of respectively 0.554 (axis 1) and 0.123 (axis 2) with a total explained variation of 35% (for both axes). The following axes (axis 3 and 4) have very eigenvalues so that further explained variation is minimal.

We see that Parikebos, Bos terrijst Edingen and Bos ter Rijst Schorisse are on the right while the other forest stands Neigembos, Brakelbos and Burreken are on the left. Indicator species on the right are *Robertus lividus* (Blackwall), *Pachygnatha listeri* Sundevall, *Saloca diceros* (O. P.-Cambridge), *Dicymbium tibiale* (Blackwall) and *Tapinocyba insecta* (L. Koch). These are species which prefer more humid environments (with a very thin litter layer) according to most literature. Detailed information about most of these species can be also found in the above-mentioned literature. Indicator species on the left are *Pardosa saltans* Töpfer-Hofmann, *Centromerus serratus* (O. P.-Cambridge), *Apostenus fuscus* Westring and *Lepthyphantes flavipes* (Blackwall). These are species which (according the literature) prefer dry forest stands with a very well developed litter layer. The difference along the first axis could thus be explained as a humid-dry gradient. The division based on the second axis is probably due to an open or closed type of vegetation (with corresponding main tree species). Neigembos 7bis (birch stand) and Neigembos 7 (beech stand) are the two extremes of this axis. That is explained by the fact that the beech stand is a lot more open (and it was also situated on a south directed slope) and receives more sunlight than the birch stand that has a more closed vegetation. Both stands were only a few meters apart. This is also shown in the indicator species. Species which appears more in the beech stand are *P. saltans*, *T. picta* and *Xysticus lanio* C. L. Koch (species which prefer open, dry habitats) and indicator species for the birch site are *C. serratus*, *Hahnia helveola* Simon and *Centromerus aequalis* (Westring) (which can also be found in dry forest stands with a more dense vegetation).The results of the TWINSPAN-analysis confirms these results (Van Waesberghe, 1998).

These results were compared with ordinations based on the most important litter and soil parameters. The ordination obtained based on the litter parameters seems to be similar to the one we derived on the basis of the most abundant species, but both ordinations (soil and litter) have very low eigenvalues and can therefore not be interpreted as being responsible for the difference. The same conclusion can thus be made as for the 50 forest stands. A Mann-Whitney U test between the litter and soil parameters of these 8 forest stands was done. Most significantly different values were seen within the litter parameters while only two parameters of the soil seemed to be significantly different, but these results were not sufficient to explain the difference between the forest stands. The analysis of other parameters (structural, vegetational,…) could not be done for the same reason as for the 50 forest stands (see above). The same results were obtained when using a (more formal) direct Canonical Correspondence Analysis (CCA) between litter and soil parameters and species frequencies: very low eigenvalues also prevented us from using this ordination to explain the observed differences. So differences in distribution of the forest stands in the ordination were mainly based on known habitat preferences of indicator species. Future investigations on other (probably more important) parameters should provide a more profound explanation of the observed differences.

As a conclusion the ordination of the spider communities that revealed the important character of a humid-dry gradient (along the first axis) is similar with the ordination of the litter parameters. This means that spider community composition on a subregional scale, with forests on the same soil type, correlates strongly with the abiotic characteristics of the litter layer, but because ordination based on the characteristics of the litter and soil layer could not give sufficient explanation (due to low eigenvalues) these conclusions still remain hypothetical and should be discussed more in detail in future when more information of other parameters becomes available.

Conclusions

We can conclude that the composition of soil-inhabiting spider communities on a Flemish scale seems to differ according to the soil type on which the forest is situated. They differ from nutrient-poor sandy and nutrient-richer sandy loam/loam soils. Other parameters which need further envestigation than these obtained from soil and litter seem to be responsible for the difference in species abundance. On a subregional scale, in forests which are situated on the same soil type, spider communities seem to vary mainly with the chemical and physical properties of the litter layer. That means that they are good indicators for the rate of litter breakdown. These first results indicate that, in the future, probably we will have to create two separate indicator-systems for the two most important soil types in Flanders. It will also be possible to evaluate forest soil quality on the basis of the spider communities if several types of forests on a same soil type are investigated. The low eigenvalues of certain analyses contradict these results. In the future the same analyses will be performed with a more complete set of parameters (structural, biotic and abiotic characters) to give a clearer

understanding of why these forests separate and to give a better indication of soil quality and the use of spiders as bio-indicators in forests.

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THE ENDEMIC SPIDERS (ARANEAE) OF THE BALKAN PENINSULA

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Abstract

DELTSHEV C.: The endemic spiders (Araneae) of the Balkan peninsula. In GAJDOŠ P., PEKÁR S. (eds): Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava), Vol. 19, Supplement 3/2000, p. 59-65.

The endemic taxa of spiders (Araneae) in the Balkan peninsula are represented by 348 species included in 30 families. Countries with the highest number of recorded endemic species are Greece (115), Croatia (68), Bulgaria (55), Bosnia (41), Crete (46). The distribution of the endemic spiders in the main geographic systems of the Balkan peninsula shows that they are best represented in the Pindus region – 150, Dinaric region – 145, Tracian-Macedonic region – 52, Balkanid region – 14, Danubian region – 4 and North Dobrudzha with 4 species. The largest proportion of endemics was encountered mainly in the mountains and islands, where they inhabit caves – 159, woodlands – 139, coastal sites – 48 and high altitude zones – 20 species. The extreme richness of troglobitic spiders in the Dinaric region (96) leads to the assumption that this was a major center of speciation and evolution of species. The same can be said for the forest of the Pindus region (74) and for the highest mountains (Rila, Pirin) of the Tracian-Macedonic region, where are found the greatest number of high altitude elements (15). The phenomenon can be regarded as a result of the relative isolation of the mountains compared with the lowland areas, in the context of paleo-environmental changes since the Pliocene. The high percentage of endemic spiders (25%) suggests an important process of autochthonous speciation. So the Balkan Peninsula can be considered as a main center of speciation in Europe.

Introduction

The first significant work concerning the spiders discovered and described on the Balkan peninsula was written by DRENSKY (1936). He reported 1066 species, 250 of them were found and described only from the territory of this region. More recent publications list the species described from Bulgaria, Greece, Serbia, Macedonia, Montenegro and part of Turkey (BRIGNOLI 1968, 1971, 1972, 1974a, 1974b, 1976, 1977, 1979, 1984, 1986; BUCHAR 1968; DEELEMAN 1976, 1978, 1988, 1993; DELTSHEV 1979a, 1979b, 1983a, 1983b, 1985, 1988, 1990, 1993, 1996, 1997a, 1997b; DELTSHEV, CURCIC 1997; DELTSHEV, PARASCHI 1990;

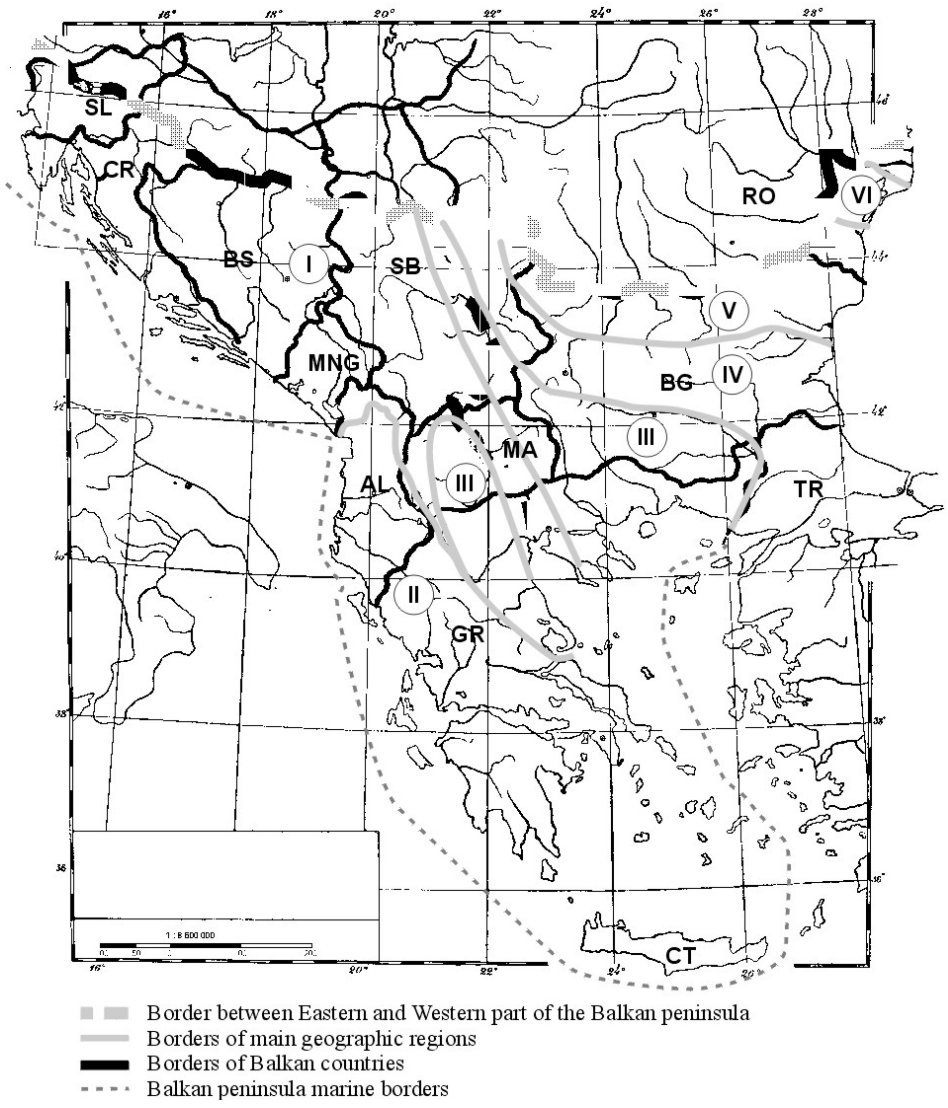

Fig. 1. Geographic division of the Balkan peninsula. I- Dinaric region, II- Pindus region, III- Tracian-Macedonic region, IV- Balkanid region, V- Danubian plain region, VI- North-Dobroudzha region, AL- Albania, BG- Bulgaria, BS- Bosnia, CR-Croatia, CT- Crete, GR- Greece, MA- Macedonia, MNG- Montenegro, RO- Romania, SB- Serbia, SL- Slovenia, TR-Turkey.

Thaler 1996; Thaler, Knoflach 1991, 1993, 1995; Wunderlich 1985, 1994a, 1994b, 1994c). The pooling of all available literature records and the accumulation of new data makes it possible to critically review all so called "endemic" taxa.

Study Area

The Balkan Peninsula is situated in the southeastern part of Europe. The northern border follows the rivers Danube (including its delta), Sava and Soca, and through Gorizia and Monfalcone reaches (the line of) the Gulf of Trieste. Its western border follows the (line of) Adriatic and Ionian coast including the islands. The eastern border passes to the east of the Aegean Islands Sirina, Astipalea, Amorgos, Miconos, Tinos, Andros, Skiros, continues along the Dardanelles, goes across the Marmara Sea and through the Bosphorus and then reaches the Black Sea coast. The southernmost point of the Balkan Peninsula region is Crete and the islands of Gavdos, Aiduronisi and Kufonisi (Fig. 1).

The question about the status and distribution of endemic spiders found in the Balkan peninsula is complicated. Some of them are found only in restricted areas (even in a single cave) while the others show wider distributions, sometimes even over the whole peninsula. Certainly, some of the widespread Balkan peninsula endemics can be found in neighbouring territories as well and can be placed in the Balkan, Asia Minor or to Southeast European spider fauna.

The geographical areas and their abbreviations used in the text, are as follows: AL – Albania: BG – Bulgaria; CT – Crete; CR – Croatia; GR – Greece; BS – Bosnia; MA – Macedonia; MNG – Montenegro; RO – Romania; SB – Serbia: SL – Slovenia; TR – Turkey.

Results and discussion

This contribution is the result of a critical revision of all data available for the endemic spiders of the Balkan peninsula territory and comprises 348 species from 30 families: Ctenizidae 5, Nemesiidae 4, Pholcidae 9, Leptonetidae 21, Segestriidae 2, Dysderidae 73, Oonopidae 1, Palpimanidae 1, Uloboridae 1, Nesticidae 6, Theridiidae 5, Anapidae 1, Mysmenidae 1, Linyphiidae 109, Tetragnathidae 2, Araneidae 1, Lycosidae 1, Agelenidae 29, Cybaeidae 1, Hahniidae 5, Dictynidae 1, Amaurobiidae 17, Liocranidae 4, Clubionidae 3, Zodariidae 8, Gnaphosidae 18, Zoridae 1, Philodromidae 2, Thomisidae 4, Salticidae 12. The established number is high and represents 25% of all spiders of the Balkan peninsula. The most characteristic families are: Linyphiidae s. l. (31.3%), Dysderidae (21%) and Agelenidae (8.3%). The genus *Troglohyphantes* is the most numerous and can be regarded as a faunistic phenomenon since from all 53 species established in the territory of the Balkans, 52 are endemics, distributed mainly in caves. Deeleman-Reinhold (1978) concluded that

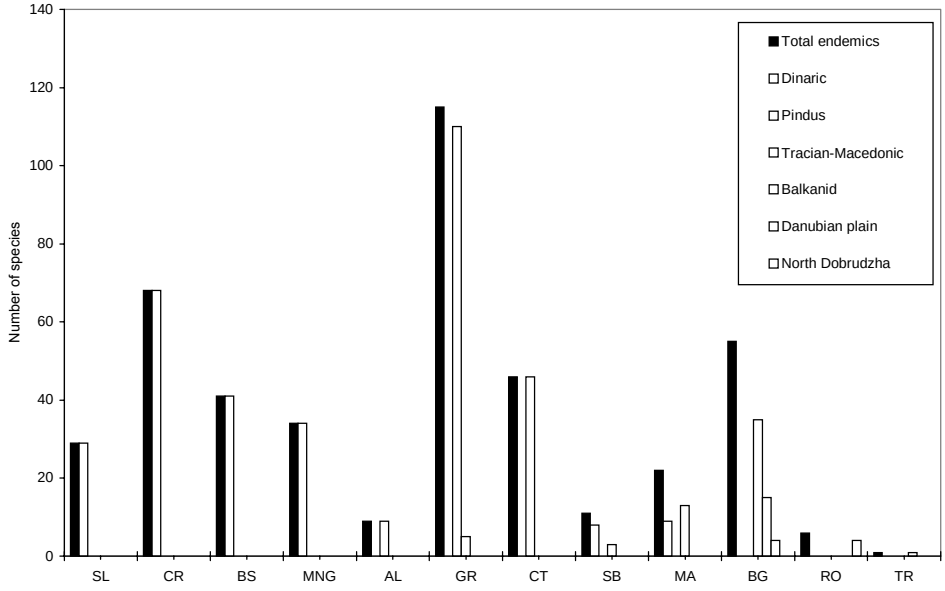

Fig. 2. Distribution of the endemic spiders into different countries and main geographic regions.

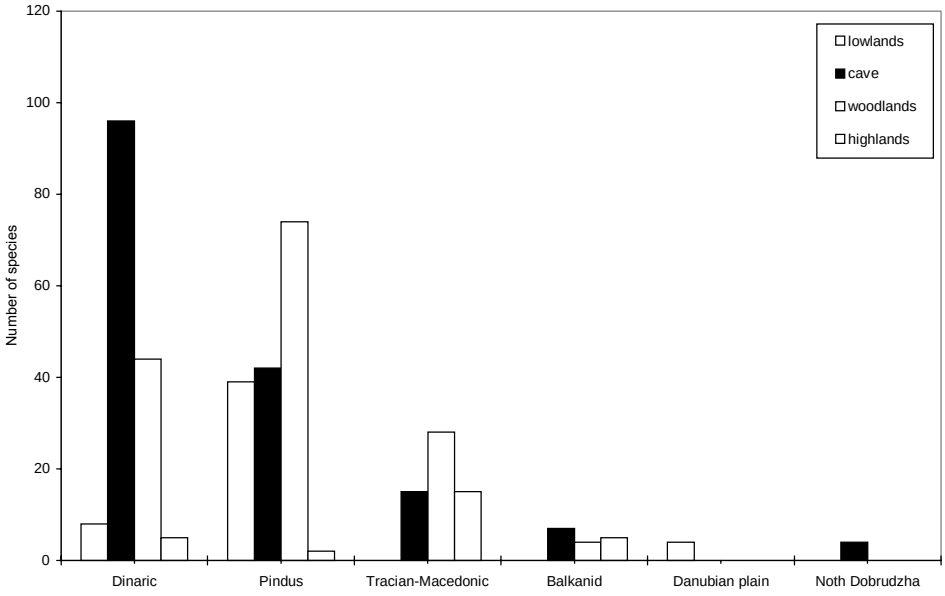

Fig. 3. Distribution of the endemic spiders into different altitude zones of the main geographic regions.

the present distribution and morphological diversity of *Troglohyphantes* in the Balkan Peninsula represents a repeated processes of expansion and contraction of its range. The representation of the genera *Dysdera* (28 endemics from 38 species), *Lepthyphantes* (18 endemics from 49 species) and *Tegenaria* (17 endemics from 31 species) is also due to expansion in caves, woodlands and highlands. Present day examples of cave penetration are the species *Lepthyphantes centromeroides* Kulczyński and *L. spelaeorum* Kulczyński, widespread in the Balkan peninsula. They occur in caves but also in the humus and ground detritus and indicate active subterranean colonisation (Deeleman-Reinhold, 1978). It should be emphasised that from the established 14 endemic genera (*Antrohyphantes*, *Barusia*, *Cryphoecina*, *Fageiella*, *Folkia*, *Icariella*, *Lasconia*, *Macedoniella*, *Minotauria*, *Protoleptoneta*, *Parastalita*, *Rhodera*, *Stalagtia*, *Sulcia*) for the Balkan Peninsula, only three (*Anthrohyphantes*, *Macedoniella*, *Protoleptoneta*) occur in the east of the Balkan Peninsula. Especially interesting is the distribution of the genera *Antrohyphantes* and *Fageiella.* The genus *Antrohyphantes* is found only at high altitude zones and caves of the eastern part of the region (Bulgaria). The genus *Fageiella* is endemic to the caves of the western part of the Balkan Peninsula (Bosnia, Montenegro). The two genera are closely related – their allopatric distribution indicates that they had been already separated before the establishment of the Vardar tectonic zone (Deltshev, 1996). This suggests that these two genera are paleoendemics.

The highest number of endemic species is recorded for the territories of Greece (115), Croatia (68), Bulgaria (55) and Crete (46) (Fig. 2). The picture concerning the distribution of the endemics in the main geographic systems of the Balkan peninsula, shows that they are best represented in the Pindus region – 150, Dinaric region – 145, Tracian-Macedonic region – 52, Balkanid region – 14, Danubian region – 4 and North Dobrudgha with 4 species (Figs 2, 3). The largest fraction of endemics was encountered mainly in mountains and islands, where they inhabit the caves – 159, woodlands – 139, coastal sites – 48 and high altitude zones – 20 species (Fig. 3). In the group of cave spiders, 51 are troglobites (blind or semi-blind) with the most numerous genera: *Troglohyphantes* – 15, *Folkia* – 6, *Stalagtia* – 5, *Leptonetella, Nesticus* and *Stalita* – 3 species. The recent cave spider fauna is formed after gradual changes in the fauna of the ancient humid Mediterranean forests. However, due to the lack of knowledge, it is difficult to determine with certainty which cave spider endemics of the Balkans are Tertiary and which are Quaternary elements. The extreme richness of endemic cave spiders in the Dinaric region (96) leads to the assumption that this was a major center of speciation and evolution of species. The same can be considered for the woodlands of the Pindus region (74) and for the highest mountains (Rila, Pirin) of the Tracian-Macedonic region, where the greatest number of high altitude elements (15) is found.

As a conclusion it should be noted that, according to their ranges, the endemic spiders of the Balkan peninsula belong to two different faunal complexes: Mediterranean and European. The Mediterranean elements are distributed in caves, forests, coastal sites and single species at high altitudes, while the European elements are distributed mainly in forests and high altitude sites. This phenomenon can be regarded as a result of the relative isolation of

the mountains compared with the lowlands, in the context of paleo-environmental changes since the Pliocene (Deltshev, 1996). The high percentage of endemic spiders (25%) suggests an important process of autochthonous speciation. So the Balkan Peninsula can be considered as a main center of speciation in Europe.

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THE EPISTOMO-LABRAL PLATE AND LATERAL LIPS IN SOLIFUGES, PSEUDOSCORPIONS AND MITES

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Abstract

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Solifugae and Pseudoscorpiones are accepted by most recent authors as sister taxa, forming a clade Haplocnemata. The sister group of Haplocnemata is less certain. Most recent authors have accepted Acari as monophyletic and placed them as sister group of Ricinulei, although a (Ricinulei + Trigonotarbida) relationship has also been proposed. In an attempt to resolve some of these phylogenetic questions, the mouthparts of Solifugae, Pseudoscorpiones and Acari were investigated. In these three orders the mouth is covered dorsally by a projecting epistomo-labral plate (a fused epistome and labrum), and ventrolaterally by a pair of finger-like lateral lips, probably derived from the coxae of the pedipalps. This character complex of a epistomo-labral plate + lateral lips is not seen in other arachnids, although similar, and perhaps homologous structures occur in Opiliones. The epistomo-labral plate + lateral lips are interpreted here as a possible synapomorphy for (Acari (Solifugae + Pseudoscorpiones)).

Introduction

On first appearances, solifuges and pseudoscorpions do not appear to be closely related. However, BÖRNER (1904, p. 156) placed both groups together in a taxon he called Haplocnemata, which he considered to be rather primitive arachnids whose legs lacked a patella. Most of the recent studies of arachnid phylogeny have also recognised this (Solifugae + Pseudoscorpiones) clade. VAN DER HAMMEN (1977, 1989) called it Apatellata, also interpreting the patella in both groups as absent based on the principal bend of the leg, or 'knee', in these orders occurring between a 'second femur' and the tibia, rather than the femur and patella as in other arachnids. He further noted that both solifuges and pseudoscorpions had mouthparts consisting of a rostrosoma and a pair of lateral lips (see below).

SHULTZ (1989) concluded that both these orders do in fact have a patella, homologising the musculature of the second femur in solifuges and pseudoscorpions with the patella musculature in other chelicerates. WEYGOLDT, PAULUS (1979), SHULTZ (1990) and WHEELER, HAYASHI (1998) also recognised this (Solifugae + Pseudoscorpiones) clade. The first two authors used Börner's older name, Haplocnemata and identified a number of convincing synapomorphies (Table 1). Haplocnemata therefore appears to be a well-supported group, although in the phylogenetic studies mentioned above there was less consensus about the position of Haplocnemata relative to the other arachnids.

Mites and ticks (i.e. Acari) have proved to be more controversial in studies of arachnid phylogeny. VAN DER HAMMEN (1989) summarised his hypothesis that Acari is diphyletic and consists of two, unrelated orders: Actinotrichida (i.e. 'mites') and Anactinotrichida (i.e. opilioacarids and 'ticks'). All mites have a gnathosoma, or capitulum (see also below). This basically consists of the labrum, epistome (or cervix), chelicerae and fused pedipalpal coxae which together form a movable, functional unit which articulates against the rest of the body, i.e. the idiosoma. VAN DER HAMMEN accepted that both mite groups have a gnathosoma, but noted that the muscles which move it originate in different places. In actinotrichids the muscles attach to an apodeme at the base of the epistome while in anactinotrichids they attach to the base of the gnathosoma. Based on this, VAN DER HAMMEN (1977, 1989) did not accept these gnathosomas as homologous, although it is evident that his conclusions were based primarily on autapomorphies for each of the two main mite lineages. LINDQUIST (1984) reviewed previous models of mite and arachnid phylogeny and concluded that mites are monophyletic and that Ricinulei are their sister group. WEYGOLDT, PAULUS (1979), SHULTZ (1990) and WHEELER, HAYASHI (1998) also regarded Acari as monophyletic, and also supported (Acari + Ricinulei). SHULTZ (1990) used the name Acaromorpha for this clade and presented two synapomorphies: (1) hexapodal larvae and (2) fused palpal coxae.

DUNLOP (1996) proposed two synapomorphies for Ricinulei and Trigonotarbida (an extinct order), namely: (1) opisthosomal tergites divided into medial and lateral plates and (2) a locking mechanism between the prosoma and opisthosoma. These characters have yet to be tested in a parsimony analysis of all arachnids, but provide explicit evidence against the Acaromorpha clade. Acari and Ricinulei both have fused palpal coxae, but then so do other arachnids (e.g. Uropygi). The mobility of the pedipalpal coxae plus the mouthparts as a gnathosoma supports Acaromorpha (e.g. LINDQUIST, 1984), but then coxal mobility is itself a plesiomorphic character state (SHULTZ, 1990). With respect to hexapodal larvae; the recent cladogram of WHEELER, HAYASHI (1998) placed pycnogonids (sea spiders) as sister group to other chelicerates. Pycnogonids show a pattern of development called anamery in which successive larval instars successively add appendages (e.g. BEHRENS, 1984), i.e. juvenile instars have fewer appendages than the adults. Taking pycnogonids as an arachnid outgroup, hexapodal larvae could be interpreted as a plesiomorphic, rather than an apomorphic, state.

Where does this leave the Acari? Most authors support a monophyletic Acari and LINDQUIST (1984, table 8) proposed eleven autapomorphies. A full discussion of all of these

is beyond the scope of this paper. Characters such as lack of well defined opisthosomal tergites and sternites provide strong support for a monophyletic Acari, but others may be symplesiomorphic, e.g. ingestion of solid food, which is also seen in Opiliones and Xiphosura. I want to stress one character in particular, 'A pair of subcapitular, bilobate lateral lips flanking mouth ventrolaterally.' (LINDQUIST, 1984, p. 40). In defence of mite diphyly, VAN DER HAMMEN (1989, pp. 99-100) presented counter-arguments to LINDQUIST's paper, which included the rejection of lateral lips as an autapomorphy of Acari on the grounds that they are present in Solifugae and Pseudoscopiones too. Evidently VAN DER HAMMEN regarded lateral lips as a convergent character (at least in mites), but why is it not a synapomorphy in all the arachnids where it is present? One of the difficulties with identifying the sister group of mites is that arachnology and acarology have developed almost as separate subjects and use different terms for homologous structures. This may conceal potential synapomorphies. In this paper I present a study of the mouthparts in Solifugae, Pseudoscorpiones and Acari in which I have tried to identify homologous elements. Based on this, I propose that all three groups have an epistomo-labral plate, a term used by SNODGRASS (1948) for a distinct, sclerotised projection, formed from a fused labrum and epistome, which is flanked by a pair of fleshy structures called lateral lips by GRANDJEAN (1936), which are derived from coxal endites. This character could be synapomorphic for an (Acari (Solifugae + Pseudoscorpiones)) clade.

Material and methods

Mouthpart morphology was studied in alcohol-preserved specimens. Solifugae were represented by a large specimen, probably of *Galeodes* sp. Pseudoscorpiones were represented by specimens of *Neobisium* (*Neobisium*) *sylvaticum* (C. L. KOCH). Opilioacari were represented by unidentified specimens kindly supplied by Prof. Bill Shear. Specimens were studied under a dissecting microscope and drawings were compared to descriptions in the literature, principally SNODGRASS (1948) and VAN DER HAMMEN (1989), but also PUNZO (1998) for solifuges, WEYGOLDT (1969) for pseudoscorpions and WITH (1904), GRANDJEAN (1936) and EVANS (1992) for mites. In an attempt to standardise nomenclature within this paper, alternative names for homologous structures, or structures interpreted here as homologous, are listed in Table 2 (see also VAN DER HAMMEN, 1980). These are discussed in more detail below.

Results

Solifugae (Fig. 1)

The solifuge mouthparts consist of two massive chelicerae set into a flexible membrane. Each chelicera has an anterolateral chelicerocarapacal articulation, a character SHULTZ (1990) identified as a synapomorphy of solifuges and pseudoscorpions (Table 1). The chelicerae are composed of two podomeres. The fixed ramus is larger, proximally bulbous, but narrows distally. The free ramus articulates ventrally against the fixed ramus. The free ramus

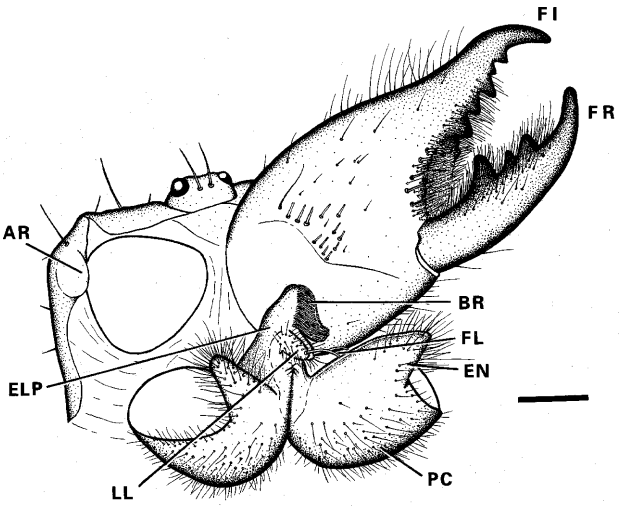

Fig. 1. Mouthparts in Solifugae (*Galeodes* sp.). Pedipalps and one chelicera removed for clarity. Abbreviations: AR- chelicerocarapacal articulation, BR- brush of setae in front of mouth, ELP- epistomo-labral plate, EN- coxal endite, FI- fixed ramus of chelicera, FL- flagellum projecting from lateral lip, FR- free ramus of chelicera, LL- lateral lip, PC- pedipalpal coxa. Scale bar = 2 mm.

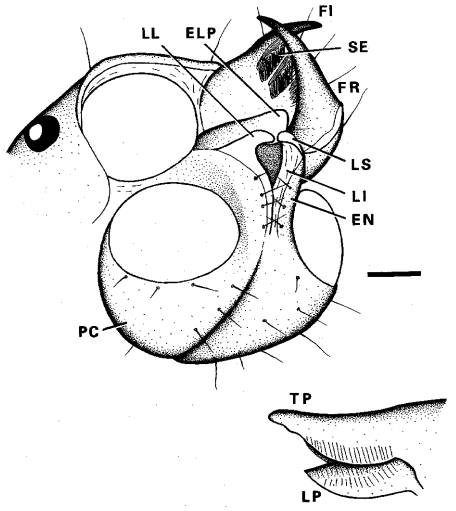

Fig. 2. Mouthparts in Pseudoscorpiones (*Neobisium* (*Neobisium*) *sylvaticum*). Pedipalps and one chelicera removed for clarity. Abbreviations: EN- coxal endite, ELP- epistomo-labral plate (alternatively intermaxilliary jugum), FI- Fixed ramus of chelicera, FR- free ramus of chelicera, LI- lamina inferior, LL- lateral lip (alternatively LS- lamina superior), PC- pedipalal coxa, SE- serrula exterior. Scale bar = 0.2 mm. Inset below: detail of pseudoscorpion epistomo-labral plate in lateral view after SNODGRASS (1948, fig. 12F) showing division into an upper lip, or taphrognath (TP), and a lower lip or lophrognath (LP); not to scale.

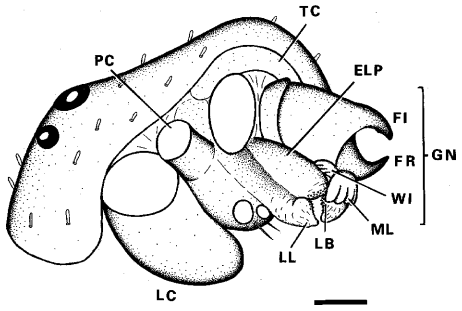

Fig. 3. Mouthparts in Acari (Opilioacarida, undetermined species), partly after GRANDJEAN (1936, fig. 1). Pedipalps, one chelicera and one set of maxilliary lobes and With's organ removed for clarity. Abbreviations: ELP- epistomo-labral plate (alternatively tentorium + subcheliceral plate + labrum), FI- fixed ramus of chelicera, FR- free ramus of chelicerae, GN- gnathosoma, LB- labellum, LC- coxa of first leg, LL- lateral lip, ML- maxilliary lobe, PC- pedipalpal coxa (part of gnathosoma), TC- tectum, WI- With's organ. Scale bar = 0.1 mm.

T a b l e 1. Synapomorphies of Haplocnemata (i.e. Solifugae + Pseudoscorpiones), derived primarily from WEYGOLDT, PAULUS (1979) and SHULTZ (1990).

1.	Two-segmented, chelate chelicerae
2.	A 'rostrum' (see text for details)
3.	An anterolateral articulation between the chelicerae and carapace
4.	Trachea with spiracles on the third and fourth opisthosomal segments

T a b l e 2. Alternative names for structures interpreted here as homologous. Names previously restricted to particular orders are indicated as follows: S- Solifugae, P- Pseudoscorpiones, A- Acari. Where the name refers to a component of the structure it is noted as (in part).

Name adopted here	**Likely synonyms**	**Author**
Epistomo-labral plate	Labrum + Epistome	various authors (e.g. SNODGRASS, 1948)
	Beak [S]	(e.g. BERNARD, 1895)
	Rostrum [S+P]	(e.g. SHULTZ, 1990)
	not Rostrum [A]	(e.g. WITH, 1904)
	Rostrosoma [S+P]	(e.g. VAN DER HAMMEN, 1989)
	Cervix (in part) [A]	(e.g. VAN DER HAMMEN, 1989)
	Intermaxilliary jugum [P]	(e.g. CHAMBERLIN, 1931)
	Taphrognath (in part) [P]	(e.g. CHAMBERLIN, 1931)
	?Lophrognath (in part) [P]	(e.g. CHAMBERLIN, 1931)
	Buccal cone (in part) [A]	(e.g. GRANDJEAN, 1936)
	Subcheliceral plate (in part) [A]	(e.g. EVANS, 1992)
	Tentorium (in part) [A]	(e.g. EVANS, 1992)
Lateral lips	Mouth lobes [S]	(e.g. SNODGRASS, 1948)
	Labium [S]	(e.g. PUNZO, 1998)
	?Hypopharynx [S]	(e.g. PUNZO, 1998)
	Lamina superior [P]	(e.g. SNODGRASS, 1948)
	Pedipalpal processes [S+P]	(e.g. SHULTZ, 1990)
	Maxilliary plates [A]	(e.g. WITH, 1904)
	Malae/Malapophyses [A]	(e.g. EVANS, 1992)

opposes the distal end of the fixed ramus, and together they form a highly sclerotised claw consisting of a number of smaller, opposable teeth. The fixed ramus is highly setose, and both the fixed and free rami have rows of long setae which overlie the distal claw. Mature male solifuges have a dorsal flagellum on the fixed ramus of the chelicerae (not present in the material examined which was presumably female).

An elongate, narrow, sclerotised structure projects between, and just below the chelicerae (Fig. 1). This structure has attracted a number of names (Table 2), although SNODGRASS'S (1948) term epistomo-labral plate is adopted here (see below). In his recent book on Solifugae PUNZO (1998) also referred to this structure as a labrum or rostrum, but labelled it in ventral view as a hypopharynx, while suggesting in the text that the ventral component of this

structure is a labium. SNODGRASS (1948) demonstrated quite convincingly that this structure in Solifugae is formed both from the labrum (the usually fleshy 'upper lip' overhanging the arachnid mouth), and the epistome (an adjacent, sclerotised plate, from which the labrum arises). The arachnid epistome can generally be distinguished from the labrum since the dorsal dilator muscles of the pharynx originate on the epistome (e.g. SNODGRASS, 1948, fig. 2D; SHULTZ, in press, fig. 2), and not the labrum. In Solifugae the labrum and epistome are strongly fused together such that both elements are sclerotised and there is no clear external division between them (Fig. 1), hence SNODGRASS's term epistomo-labral plate (Table 2). At the distal end of this structure, i.e. the labrum, there are two rows, or brushes, of dense setae, which probably filter the preorally masticated food. The mouth opens behind these setae.

Immediately below the labrum are a pair of fleshy projections which SNODGRASS (1948) called mouth lobes (see Table 2 for alternatives), but which I refer to here under GRANDJEAN'S (1936) term lateral lips (Fig. 1). Each lateral lip is highly setose and terminates in a flagellum. These lateral lips show a suture line suggesting fusion both with the palpal coxa and with the epistomo-labral plate and so could conceivably be derived as mesal endites from the palpal coxae. HEYMONS'S (1905) embryological studies showed that these lateral lips develop mesal from the large coxal endites and based on this Snodgrass saw no homology between the solifugae lateral lips and the coxal processes of other arachnids. However, HEYMONS (1905) concluded that the lateral lips, or 'Unterlippe', are derived from the pedipalpal segment and this is consistent with them being mesal palpal endites. VACHON (1958, fig. 3), though, figures these 'processus rostraux' as developing directly underneath the epistomo-labral plate. The palpal coxae are fused medially with a strongly developed and highly setose endite on the mesal surface (Fig. 1), a structure additional to the lateral lips.

Pseudoscorpiones (Fig. 2)

Like Solifugae, pseudoscorpions have chelate chelicerae composed of two podomeres, a fixed ramus and a free ramus. The articulation of the free ramus is primarily ventral, although not to the same degree as in Solifugae. The anterolateral chelicerocarapacal articulation was not strongly expressed in the pseudoscorpion material studied, although an articulation point in the same position as in solifuges was suggested by the way the chelicerae break off from the body during their removal. The free ramus bears a row of plate-like structures, the serrula exterior which is used for grooming (WEYGOLDT, 1969). Although not clearly visible in the preparation (which was not cleared in potassium hydroxide), the free ramus of the chelicera also bears the opening of the silk gland.

As in Solifugae, there is a sclerotised projection beneath and between the chelicerae (Fig 2). This has often been referred to as the jugum (Table 2), but again SNODGRASS (1948) indicated that it is formed from a fused labrum and epistome. I see no reason not to consider it homologous with the Solifugae epistomo-labral plate, as, for example, SHULTZ (1990) did. SHULTZ referred to this structure in both groups as a 'rostrum', but there is

a problem with using this term since 'rostrum' is (a) a crustacean term and (b) widely used for either the rostral tectum *above* the chelicerae in mites and specifically for the leading edge of the prodorsum in oribatids (WALTER, pers. com.). The mite 'rostrum' is clearly not homologous with SHULTZ's 'rostrum' and to prevent further confusion SNODGRASS's epistomo-labral plate is used here as a more neutral term for the projecting upper mouth lip. Some early derivative pseudoscorpions have a relatively long epistomo-labral plate, although HARVEY (1992, character 6), interpreted a long jugum as apomorphic for those taxa where it is present. The material studied here suggested that the distal, labral end of the pseudoscorpion epistomo-labral plate was more fleshy than in solifuges and that a slight demarcation between the labral and epistomal elements is present (Fig 2). There are no brushes of setae at the distal end of the labrum like those seen in Solifugae. Pseudoscorpions do differ significantly from solifuges in one important respect. The anterior part of their epistomo-labral plate can be divided into an upper lip, or taphrognath, and a lower lip, or lophognath (CHAMBERLIN, 1931) (Fig. 2). These elements are ridged, the lower one slots against the upper one and the mouth opens just behind them. There is no equivalent of this structure in solifuges, or in other arachnids, and this taphrognath-lophognath complex appears to represent a pseudoscorpion autapomorphy. Whether this lophognath element is homologous with the labium of other arachnids is not entirely clear and would merit investigation.

Adjacent to the pseudoscorpion epistomo-labral plate are two fleshy lobes, which in this case clearly are derived from the pedipalpal coxae. These coxae have medial flanges, or endites, which bear a number of anteriorly-projecting setae. These sclerotised endites are bordered mesally by more fleshy tissues which form the lateral walls of the preoral cavity (e.g. WEYGOLDT, 1969). These fleshy elements have been referred to as the lamina inferior, the broad ventral part, and the lamina superior, the finger-like dorsal part which lies alongside the epistomo-labral plate (Fig. 2). I suggest that these laminae superior are homologous with the lateral lips of solifuges, although perhaps they show a more plesiomorphic condition in which they are still, in effect, true coxal endites, and have not fused with the epistomo-labral plate directly below the mouth. Although not expressed in cladistic terminology, VAN DER HAMMEN (1989, fig. 118) interpreted both the laminae inferior and laminae superior in pseudoscorpions as lateral lips homologous with those in Solifugae, and treated this as a diagnostic (i.e. synapomorphic) for both orders.

Acari (Fig. 3)

Unlike the previous two orders, where the mouthparts are fairly similar in all members of the group, the variety among mouthparts of Acari can appear bewildering. This is partly due to their unnecessarily complicated terminology and also to specialisations for feeding in certain groups; e.g. parasitism by ticks. Polyphyly among the Acari could also explain this variability. As noted above, all mites have a gnathosoma (Fig. 3). This functional unit is formed from the chelicerae, the pedipalps, the labrum and the epistome. The

palpal coxae are fused to each other and to the labrum/epistome complex; and this whole structure below the chelicerae is usually referred to as the subcapitulum, infracapitulum or hypognathum (e.g. EVANS, 1992).

Oplioacarids are widely accepted as basal mites (e.g. NORTON et al., 1993) and their mouthparts are relatively simple compared to other mite groups. In opilioacarids the chelicerae are composed of three podomeres; a plesiomorphic state in arachnids (e.g. SHULTZ, 1990) compared to the two podomeres in Solifugae and Pseudoscorpiones. The chelicerae originate in a folded membrane and the area above the chelicerae has been referred to as a tectum. This structure forms a sclerotised plate between the carapace and chelicerae seen in some mites (EVANS, 1992) and sometimes referred to as a rostrum (e.g. WITH, 1904, see also above). GRANDJEAN (1936) found no evidence of sclerotisation above the chelicerae in opilioacarids and, although the area in question has been labelled (Fig. 3), the tectum may be absent in this group. The distal podomeres of the chelicerae form a small claw. As in solifuges, the claw has opposable teeth with the free ramus articulating ventrally against the fixed ramus.

As in Solifugae and Pseudoscorpiones, there is a sclerotised plate projecting beneath and between the chelicerae. This has been called the labrum (e.g. WITH, 1904; VAN DER HAMMEN, 1989) and WITH identified both a proximal and distal part. In a diagram of a generalised mite EVANS (1992) called the proximal part the subcheliceral plate and the distal part the labrum. SNODGRASS (1948) pointed out that the proximal part contains the muscles of the pharynx and so must unequivocally be the epistome. Therefore, as in Solifugae and Pseudoscorpiones, we essentially have an epistomo-labral plate (Fig. 3). In other, more derived, mite groups this structure appears to become more complicated as it forms a shelf over which the chelicerae slide, while the proximal region where prosomal muscles attach is often called a tentorium (see EVANS (1992) for a discussion). The distal, labral end of the epistomo-labral plate in opilioacarids appears somewhat fleshy and is ornamented with tiny triangular spines. There are no brushes of setae as in Solifugae.

Immediately below the epistomo-labral plate are a pair of fleshy projections which lie adjacent to it (Fig. 3). The mouth opens at their base beneath the labrum. WITH (1904) and SNODGRASS (1948) called these structures maxillary plates, but both GRANDJEAN (1936) and VAN DER HAMMEN (1989) called them lateral lips; the term adopted here. SNODGRASS felt that these, and the other lobes which develop around the mouthparts in mites, could not be homologised with structures in other arachnids, although he regarded the mouth lobes of pseudoscorpions as at least analogous. The lateral lips of opilioacarids have a distinct dorsal lobe which VAN DER HAMMEN (1989) called the labellum, and which also has small teeth like the epistomo-labral plate (Fig. 3). All authors accepted that these lateral lips in opilioacarids are derived as mesal endites from the pedipalpal coxae. In opilioacarids these coxae are fused together as the ventral part of the subcapitulum and each coxa has a more prominent, articulated, toothed lobe or endite which has variously been referred to as the maxilliary lobe (WITH, 1904), maxilliary organ (GRANDJEAN, 1936) or rutellum (VAN DER HAMMEN, 1989). Immediately mesal to this 'lobe' is a similar projection, usually referred to as WITH's organ. These structures have no obvious counter-

part in Solifugae and Pseudoscorpiones and Evans (1992) noted that they may be setal in origin. The mouthparts of mites are full of complicated, sclerotised projections and a full discussion of their terminology and likely homology with each other is beyond the scope of this paper, although further details can be found in Van der Hammen (1980). More significant is the basic morphology of a projecting epistomo-labral plate and an adjacent pair of lateral lips. This is present in basal mites such as opilioacarids, and can be seen in a modified form in other mite groups (Van der Hammen, 1989, fig. 14; Evans, 1992, figs. 5.1-5.6).

Discussion

Similar mouthparts in solifuges, pseudoscorpions and mites were noted as long ago as 1897 (Bernard, 1897, p. 16). Snodgrass (1948) recognised the basic labrum/epistome morphology in all three orders, but did not regard the various processes, i.e. solifuge mouth lobes, pseudoscorpion laminae and mite maxilliary plates, as homologous. Snodgrass's paper remains the definitive study, with excellent descriptions and constant efforts to standardise terminology. Yet I feel that he tended to use what are essentially autapomorphies of these three orders to reject relationships between them. There are significant differences between the three orders, e.g. fusion of the mouth lobes to the epistomo-labral plate in solifuges, the unfused laminae superior and the taphrognath-lophrognath complex in pseudoscorpions and the complex coxal processes as part of a gnathosoma in mites. However, none of these are clearly synapomorphic with any other arachnid order.

The epistomo-labral plate/lateral lip character identified here needs to be carefully defined. Referring to it as, say, a 'projecting labrum + epistome associated with coxal endites' is too broad and could apply to a number of arachnid orders. By its very nature the arachnid labrum projects forwards to a greater or lesser extent, though not always with a projecting epistome, while there are numerous examples of coxal endites (e.g. in labidognath spiders), not all of which are necessarily homologous with each other. I propose to define this character as: 'Epistome and labrum fused into a distinct, sclerotised projection which bears the mouth. Distal end of this epistomo-labral plate flanked ventrolaterally by a pair of fleshy, finger-like lateral lips derived as mesal endites from the pedipalpal coxae.'

This definition excludes groups such as Uropygi (whip scorpions), which have a large labrum, but which lack lateral lips. Opiliones (harvest spiders) present a more interesting case. Weygoldt, Paulus (1979) placed them close to Acari, while Shultz (1990) recognised a Dromopoda clade of the form: (Opiliones (Scorpiones (Solifugae + Pseudoscorpiones))). One of the characters defining Dromopoda was a stomatheca, a preoral cavity formed dorsally by the epistome and laterally by pedipalpal coxal endites. Shultz (1990) coded the stomatheca as secondarily lost in Haplocnemata, but in his discussion of the 'rostrum' he did note the presence of small processes from the pedipalps (i.e. lateral lips) and speculated that these might represent a highly reduced stomotheca.

The stomotheca has been criticised as a synapomorphy for Dromopoda (e.g. WEYGOLDT, 1998), since coxal endites are absent in early derivative scorpions which implies that the stomatheca is a convergent feature. However, in a recent study of opilionid anatomy, SHULTZ (in press) figured the epistome of a palpatore opilionid as a projecting, sclerotised structure with a small, ventral labrum. This is similar to the epistomo-labral plate as identified both by SHULTZ (1990) and this study. The coxal endites forming the opilionid stomatheca could be interpreted as 'lateral lips' too (WALTER, pers. com.). By contrast, the palpal endites in opilionids are fairly broad and plate-like, and not the finger-like structures identified here. However, these opilionid pedipalpal 'lips' are soft and fleshy SHULTZ (1990), like the lateral lips, and it easy to envisage a series of evolutionary steps by which lateral lips developed as projections from opilionid-like pedipalpal endites. In fact pseudoscorpions show this rather nicely (Fig. 2) with both a broad, fleshy opilionid-like 'lamina inferior' and a narrow, fleshy, solifuge-like 'lamina superior' (Fig. 2).

SHULTZ (1990) did not include Acari in Dromopoda, although on the basis of this study I think his 'rostrum' character (no. 15), i.e. the epistomo-labral plate, should not be restricted to Haplocnemata, but should also be coded as present in Acari; and conceivably in Opiliones too. A number of authors have suggested that mites and solifuges may be related; see EVANS (1992) and DUNLOP (1999) for reviews. Some rahagiid and palaeacaroid mites superficially show a remarkable resemblance to solifuges (DUNLOP, 1999), although LINDQUIST (1984) pointed out that neither group is widely accepted as basal mites and that the resemblance is most likely convergent. As in this present study, GRANDJEAN (1936) noted the presence of 'lèvres latérales' (= lateral lips) in solifuges and opilioacarids and the location of the mouth at the end of a 'rostre' in Solifugae and a 'cône buccal' in mites. GRANDJEAN (1936) mentioned a prelarval organ of Claparéde in actinotrichids and solifuges, although the character is not unique to these groups and may be plesiomorphic (WALTER, pers. com.). Interestingly, ALBERTI (1984) noted similarities in sperm structure between actinotrichid mites and solifuges, to the exclusion of anactinotrichids.

Similarities between mites and pseudoscorpions, other than small size, are less well documented. Acari appear more like Solifugae (Figs. 1, 3) in having a tight grouping of the epistomo-labral plate plus discrete lateral lips around a much more anteriorly located mouth. The lips in pseudoscorpions are less intimately associated with the mouth opening, which is more posterior, and it makes a certain amount of sense to interpret this as plesiomorphic (see above). However, the synapomorphies for Haplocnemata (Table 1), especially two-jointed chelicerae, argue strongly against a (Pseudoscorpiones (Acari + Solifugae)) relationship. Of course this epistomo-labral plate/lateral lips character must be weighed against other phylogenetic evidence and these observations are presented here for further discussion.

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SOLPUGIDS OF THE GENUS *EUSIMONIA* KRAEPELIN, 1899 (ARACHNIDA: SOLIFUGAE, KARSCHIIDAE) OF CENTRAL ASIA

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Abstract

GROMOV A.V.: Solpugids of the genus *Eusimonia* Kraepelin, 1899 (Arachnida: Solifugae, Karschiidae) of Central Asia. In GAJDOŠ P., PEKÁR S. (eds): Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava), Vol. 19, Supplement 3/2000, p. 79-86.

This paper presents a review of the genus *Eusimonia* in the fauna of Central Asia. Two valid species are found to occur in Central Asia: *E. divina* BIRULA, 1935 and *E. turkestana* KRAEPELIN, 1899. The type specimens of *Eusimonia* kept in the Zoological Museum (Berlin) and the Zoological Institute of the Russian Academy of Sciences (St. Petersburg) were re-examined. Four species names are newly synonymized: *Karschia (?) demokidovi* BIRULA, 1935 with *Eusimonia divina* BIRULA, 1935 syn.nov.; *Karschia (?) grombczevskii* BIRULA, 1935, *Barella birulae* ROEWER, 1933 and *Eusimonia celeripes* HIRST, 1908 with *Eusimonia turkestana* KRAEPELIN, 1899 syn.nov. Lectotypes are designated for the first time for the following species: *Eusimonia divina* BIRULA, 1935; *Barella birulae* ROEWER, 1933 and *Karschia (?) grombczevskii* BIRULA, 1935.

Introduction

To date, congeners of the genus *Eusimonia* KRAEPELIN, 1899 in Central Asia (Kazakhstan, Uzbekistan, Turkmenistan, N Iran, Afghanistan, W China and Mongolia) have been studied extensively and records of new species are hardly to be expected. KRAEPELIN (1899) described a new species, *E. turkestana,* from "Turkestan" without giving the precise locality. Within a few years, HIRST (1908) described another species, *E. celeripes,* from W China. In his monograph on the solpugids of the world, ROEWER (1933) assigned *E. turkestana* to the genus *Barella* HIRST, 1910 and also described *B. birulae* from China and Mongolia. Later, BIRULA (1935a) described a species *E. divina* from N Iran, as well as transferring both *Barella turkestana* and *B. birulae* to the genus *Eusimonia.* ROEWER (1941) did not support this idea and moreover transferred *E. divina* to the genus *Barella,* and later ROEWER

(1960) first recorded it for Afghanistan. Gromov, Kopdykbaev (1994) first recorded a representative of *Eusimonia* for SE Kazakhstan without its exact identification, and later (Gromov, 1999) first reported *E. divina* from N Turkmenistan. Thus, four *Eusimonia* species have so far been reported from Central Asia: *E. turkestana* Kraepelin, 1899, *E. celeripes* Hirst, 1908, *E. birulae* (Roewer, 1933) and *E. divina* Birula, 1935.

Material and methods

In the course of the present work, collections from the following museums have been re-examined: Zoological Museum in Berlin (Germany), Zoological Institute (St. Petersburg, Russia) and Zoological Museum of the Moscow State University (Moscow, Russia), as well as newly collected material from Central Asia.

Solpugids were mainly collected by the author during the night using an ultra-violet lamp (Sylvania F6T5/BLB), and some solpugids were collected also during the daytime under stones. Solpugids were preserved and studied in 70% alcohol using a MBS-10 stereomicroscope.

Abbreviations: AGC- private collection of the author; IASE- the Siberian Zoological Museum, Institute of Animal Systematics and Ecology, Novosibirsk, Russia, D.V.Logunov; ZISP- the Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia, V.A.Krivokhatsky; ZMB- the Zoological Museum, Museum fur Naturkunde, Berlin, Germany, J.A.Dunlop; ZMMU- the Zoological Museum of the Moscow State University, Moscow, Russia, K.G.Mikhailov.

All measurements are in mm.

Eusimonia Kraepelin, 1899

Type species: *Galeodes furcillatus* Simon, 1872

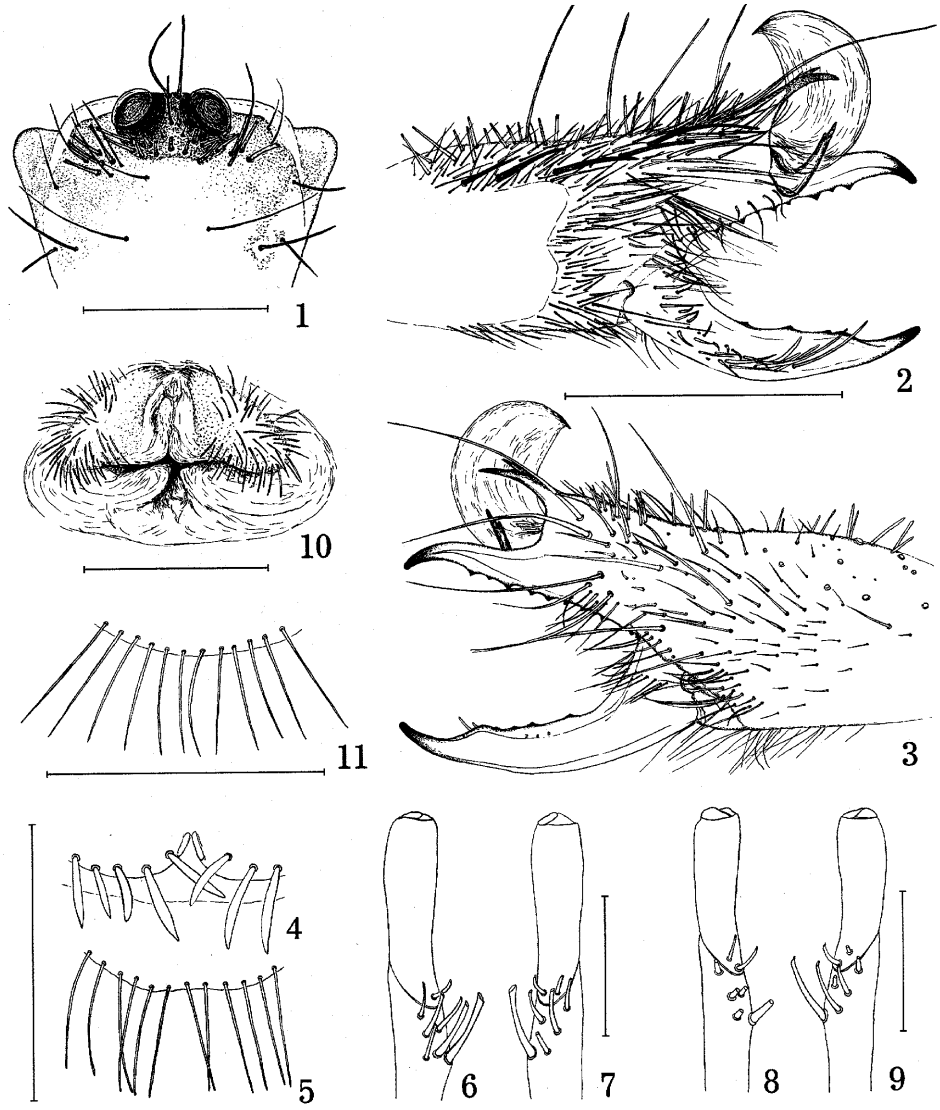
Eusimonia divina Birula, 1935 (Figs. 1-12)

Eusimonia divina Birula, 1935a: p. 1217, figs. 1, 2 (one male lectotype, designated here, and one female paralectotype from the ZISP; re-examined); Birula, 1938: p. 72, 76, figs. 49, 50; Gromov, 1999: p. 184.

Karschia (?) demokidovi Birula, 1935b: p. 305, fig. 3B (female holotype from the ZISP; re-examined); Birula, 1938: p. 43, 66, fig. 42; Roewer, 1941: p. 111, fig. 5; Gromov, 1999: p. 184, syn.nov.

Barella divina (Birula) Roewer, 1941: p. 112, figs. 69-73; Roewer, 1960: p. 8, fig. 1.

Material examined: Kazakhstan: 1 ♂ (AGC), Mangistau Area, Eraliev Distr., ca. 43 km E of Aktau [Shevchenko], Karagie Hollow, near Prokhlada Well, (43°35'N, 51°43'E), 19.05.1991, leg. Ye.Ye.Kopdykbaev; Uzbekistan: 42 ♂♂, 64 ♀♀, 2juv. (AGC), 1 ♂, 1 ♀ (IASE), 1 ♂, 1 ♀ (ZMB), Navoi Area, Tamdy Distr., Kyzylkum Desert, ca.1 km NW of Zarafshan, (41°36'N, 64°09'E), on *Artemisia*, 26-29.04.1998, leg. A.V.Gromov; Turkmenistan: 1 ♀ (ZMMU Tc-64), Tashauz Area, Tel'mansk Distr., Kaplankyr Nature Reserve, (41°12'N, 57°29'E), 23.04.1985, leg. L.A.Mitroshina; 1 ♂ (ZMMU Tc-63), same locality and collector, 3.05.1985; 1 ♂ (ZMMU Tc-74), Tashauz Area, Kalinin Distr, Karakum Desert, Kangakyr [Gangalykyr] Height, (41°22'N, 58°02'E), 12.05.1983, leg. O.S.Soyunov; 1 ♀ (ZISP 872, holotype of *K. demokidovi*), Mary Area, Bayram Ali Distr., near Bayram Ali, (37°37'N, 62°10'E), 8-10.04.1907, leg. K.Demokidov; Iran: 1 ♂ (ZISP 909, lectotype of *E. divina*), 1 ♀ (ZISP 909, paralectotype of *E. divina*), Semnan Ostan, E foothills of Elburz Mts., near Imamshekhr [Shakhrud], (ca. 36°25'N, 54°57'E), 21.05.1914, leg. A.Kirichenko.



Figs 1-11. *Eusimonia divina*, male [Zarafshan] (1), male [Kangakyr] (2-5, 8, 9), male [holotype] (6, 7) and female [Zarafshan] (10, 11): 1- propeltidium, dorsal view; 2 – left chelicera, internal view; 3 – same, external view; 4 – ctenidiae on III sternite of abdomen, ventral view; 5, 11 – ctenidiae on IV sternite of abdomen, ventral view; 6, 8 – spinulation of right palp, ventral view; 7, 9 – spinulation of left palp, ventral view; 10 – genital sternite, ventral view. Scale line = 1 mm.

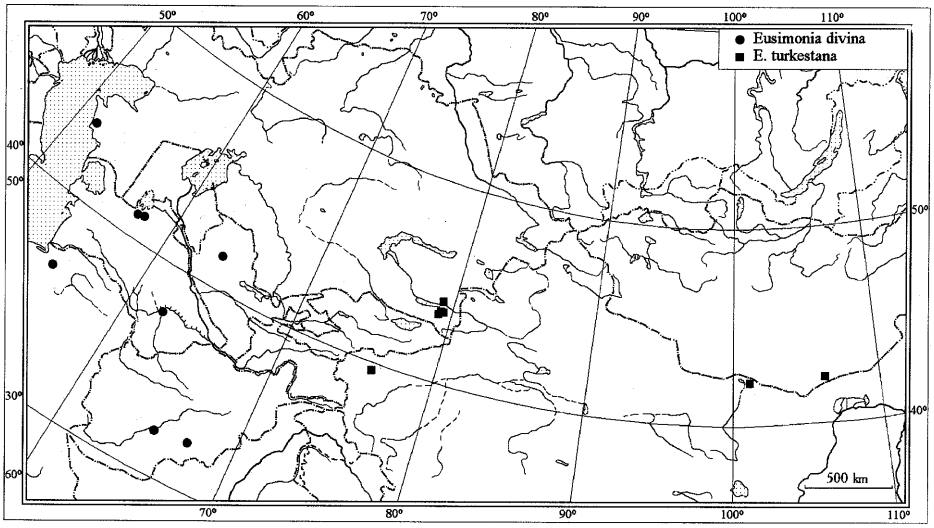


Fig. 12. Localities for *Eusimonia divina* and *E. turkestana.*

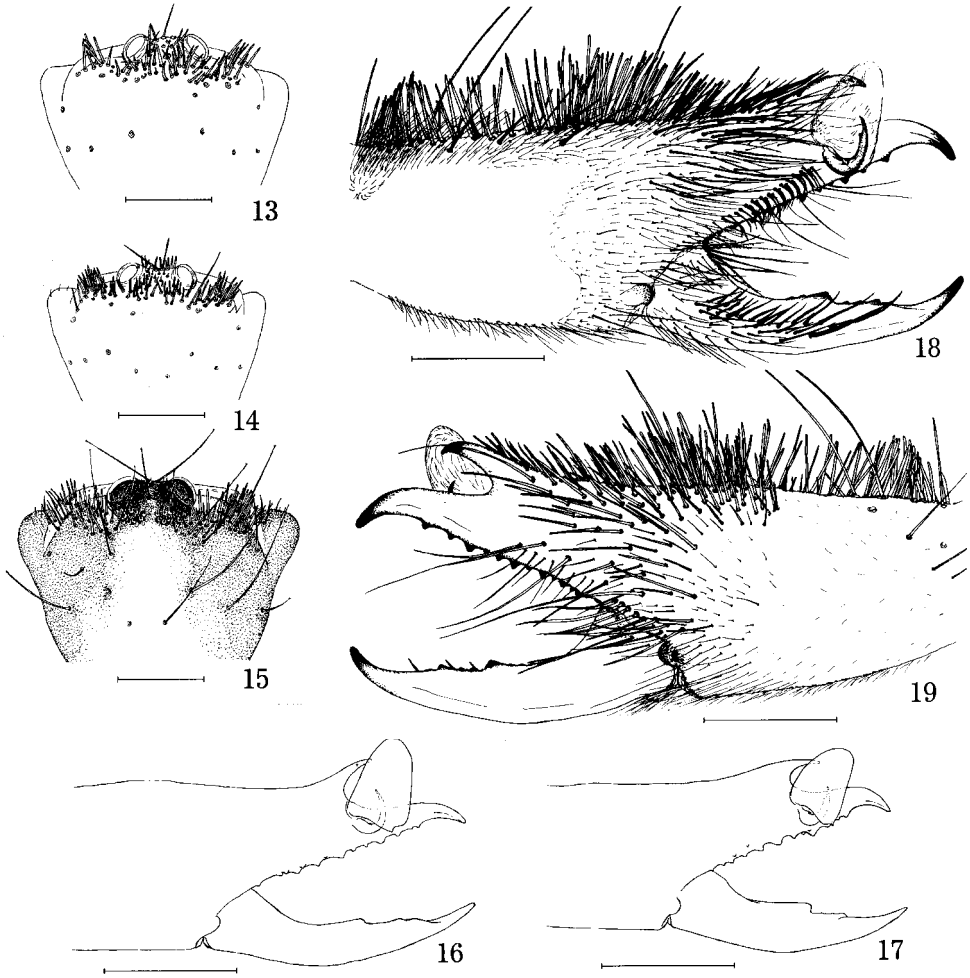
Material cited: Afghanistan: 1 ♂, 1 juv., Helmand Province, near Kadjahkai [Kajkai], (ca. 32°18'N, 65°05'E), stony slope, 29.04-1.05.1958, leg. K.Lindberg [Roewer 1960]; 1 juv., Zabul Province, near Gadjoui [Gadzhoi], (32°27'N, 67°20'E), under stones in steppe, 10.09.1957, leg. K.Lindberg [Roewer I960].

Description: See Birula (1935a, 1938) and Roewer (1941).

Variability: Male. Total length 8.1-11.4. Body coloration light yellow to yellow with infusion of brown as follows: propeltidium anteriorly on each side of ocular tubercle; abdominal tergites; entire palp except for the basal half of femur; entire femur excluding its base, and entire tibia IV. Dorsal cheliceral finger with 9-12 teeth, ventral one with 1 or 2 teeth. The number of teeth on the forked appendix of dorsal cheliceral finger =1-4. Third abdominal sternite with (3-5)+(3-6) ctenidiae, fourth one with 11-13 ctenidiae. Ctenidiae on the III sternite of abdomen club-shaped or thin and long. Right palpal metatarsus of the holotype with 6, left one with 5 spines; right palpal tarsus of the holotype with 1, left one with 2 spines. In other specimens, right and left palpal metatarsus with 5 spines; right and left palpal tarsus with 2 spines. Female. Total length 8.0-11.7. Variability of body coloration as in males. Dorsal cheliceral finger with 9-17 teeth, ventral one with 8-15 teeth. Fourth abdominal sternite with 11-13 ctenidiae.

Remarks: An examination of numerous specimens of *E. divina* from the vicinities of Zarafshan (Uzbekistan) has revealed that the number of cheliceral teeth is highly variable and cannot be considered a diagnostic character for the genus *Eusimonia.* Therefore, as the female holotype of *K. demokidovi* and female paratype of *E. divina* do not differ in the shape of the genital sternites, but in the number of cheliceral teeth only, these species names are to be treated as synonyms.

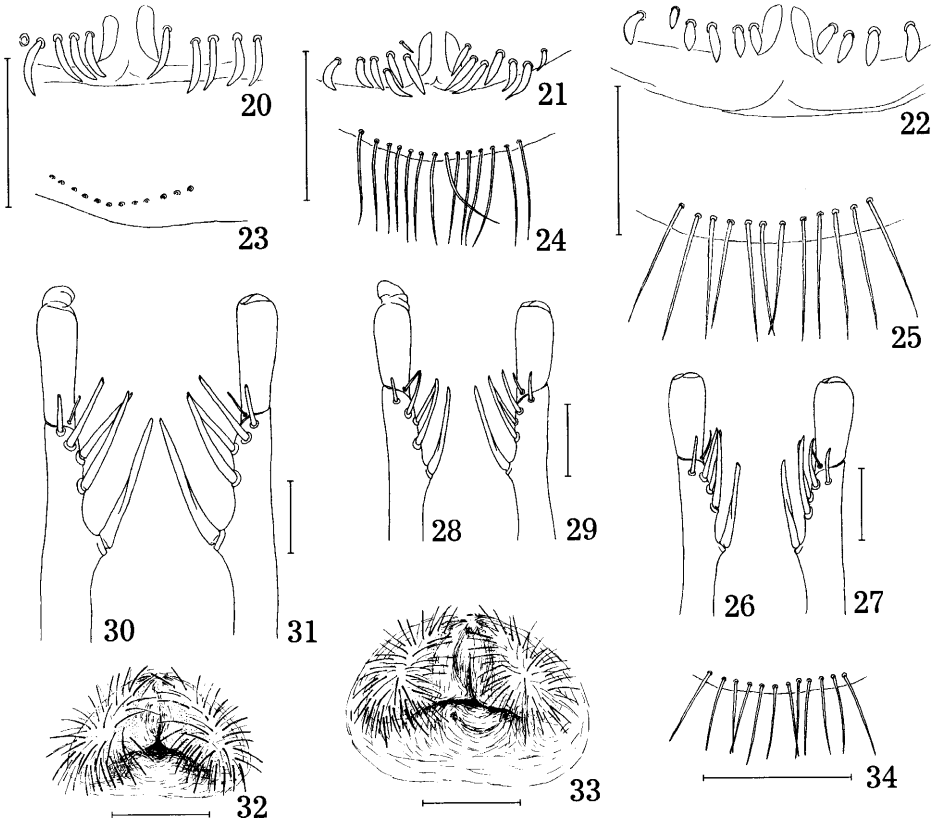
Distribution: From SW Kazakhstan (Karagie Hollow) and C Uzbekistan (Kyzylkum Desert) across Turkmenistan (Karakum Desert) to NE Iran (E foothills of Elburz Mts.) and



Figs 13-19. *Eusimonia turkestana*, male [holotype] (13, 16), male [lectotype of *Barella birulae*] (14, 17) and male [12 km NWW of Chundzha] (15, 18, 19): 13-15 – propeltidiums, dorsal view; 16-18 – left chelicerae, internal view; 19 – same, external view. Scale line = 1 mm.

to S Afghanistan (S foothills of Hindu-Kush Mts.) (Fig. 12). The record of *E. divina* in the basin of Ind River is quite doubtful, and hence the female from "grotto without name by Qal' eh-Malik" (Afghanistan, Nangarkhar Province, Siakh-Kokh Mt. Range, Sorkhab River valley, near Barinah Vill., (ca. 34°23'N, 70°11'E), 6.01.1958, leg. K.Lindberg) was identified by Roewer (1960) erroneously and does not actually belong to this species.

Ecology: This species prefers the clay deserts. Adults occur in April-May.



Figs 20-34. *Eusimonia turkestana*, male [holotype] (20, 23, 26, 27), male [lectotype of *Barella birulae*] (21, 24, 28, 29), male [12 km NWW of Chundzha] (22, 25, 30, 31), female [12 km NWW of Chundzha] (32, 34) and female [lectotype of *Karschia grombczevskii*] (33): 20-22 – ctenidiae on III sternite of abdomen, ventral view; 23-25, 34 – ctenidiae on IV sternite of abdomen, ventral view; 26, 28, 30 – spinulation of right palp, ventral view; 27, 29, 31 – spinulation of left palp, ventral view; 32, 33 – genital sternites, ventral view. Scale line = 1 mm.

Eusimonia turkestana Kraepelin, 1899 (Figs. 12-34)

Eusimonia turkestana Kraepelin, 1899: p. 250, fig. 23 (male holotype from the ZMB; re-examined); Kraepelin, 1901: p. 142, fig. 107; Birula, 1927: p. 210; Roewer, 1932: p. 132, figs. 117, 120, 141B; Birula, 1938: p. 72, 73; Gromov, Kopdykbaev, 1994: p. 21.

Eusimonia celeripes Hirst, 1908: p. 247 (three male syntypes from "Kashgar Steppe", probably lost); Roewer, 1933: p. 301, 302, fig. 224C; Birula, 1938: p. 72, 78; Zilch, 1946: p.123, syn.nov.

Barella turkestana (Kraepelin) Roewer, 1933: p. 303, 304, fig. 226d.

Barella birulae Roewer, 1933: p. 303, 305, figs. 226b, c, e, h, i (male lectotype, designated here, from China and one juvenile paralectotype from Mongolia, from the ZISP; re-examined), syn.nov.

Eusimonia birulai (Roewer) Birula, 1938: p. 72, 74, figs. 45B, 47, 48.

Karschia (?) grombczevskii Birula, 1935b: p. 306, figs. 4B, 5A (female lectotype, designated here, and two female paralectotypes from the ZISP; re-examined); Birula, 1938: p. 44, 67, figs. 43, 44; Roewer, 1941: p. 111, fig. 8, syn.nov.

Eusimonia sp. Gromov, Kopdykbaev, 1994: p. 21.

Material examined: Kazakhstan: l juv. (AGC), Taldykorgan Area, Zharkent [Panfilov] Distr., Kumkala Desert, ca. 37 km SWW of Aidarly, (43°51'N, 79°10'E), 2.06.1991, leg. A.V.Gromov; 1 ♂ (AGC), Almaty Area, Uigursky Distr., ca. 11 km NW of Chundzha, left riverside of Charyn [Sharyn] River, (43°37'N, 79°21'E), *Haloxylon* on loam, 12.06.1993, leg. Ye.Ye.Kopdykbaev; 1 ♂, 3 juv. (AGC), same locality, 27.05.1998, leg. A.V.Gromov; 1 ♂, 1 ♀ (AGC), Almaty Area, Uigursky Distr., ca. 12 km NWW of Chundzha, left riverside of Charyn [Sharyn] River, (43°35'N, 79°19'E), *Haloxylon* on loam, 18.06.1994, leg. A.V.Gromov; 1 juv. (AGC), Almaty [Alma-Ata] Area, Uigursky Distr., ca. 20 km SWW of Chundzha, left riverside of Charyn [Sharyn] River, (43°30'N, 79°12'E), clayey canyons, 26.04.1999, leg. A.V.Gromov; l juv. (AGC), Almaty Area, Uigursky Distr., W vicinities of Chundzha, (43°32'N, 79°26'E), 4.07.1996, leg. A.V.Gromov; China: 1 ♂ (ZISP 906, lectotype of *B. birulae*), Inner Mongolia, lower reaches of Edzin-Gol [Etszin-Gol] River, near Sogo-Nur [Sogo-Nor] Lake, (42°17'N, 101°17'E), expedition of P.K.Kozlov, 4.05-1.06.1926, leg. N.M.Przhevalsky; Mongolia: 1 ♂, 1 juv. (ZISP), South-Gobi Aimak, Gobi Desert, ca. 25 km SW of Khailastyn-Khuduk, Khushu-Sair, (ca. 42°17'N, 106°16'E), *Haloxylon* on sands, 21.06.1971, leg. M.A.Kozlov; Uncertain localities: 1 ♂ (ZMB 7973, holotype of *E. turkestana*), "Turkestan", leg. Conradt; 1 ♀ (ZISP 871, lectotype of *K. grombczevskii*), 2 ♀ (ZISP 870, paralectotypes of *K. grombczevskii*), "E Bukhara", 1889-1890, leg. B.L.Grombchevsky.

Material cited: China: 3 ♂♂ (syntypes of *E. celeripes*), "Kashgar Steppe", leg. C.Aris (Hirst, 1908).

Description: See Roewer (1933) and Birula (1938).

Variability: Male. Total length 13.2-18.7. Body coloration light yellow to yellow with infusion of brown as follows: dorsal surface of propeltidium; abdominal tergites; entire extremities except for the basal half of femur. Spines on the ocular tubercle short to long. Dorsal cheliceral finger with 10-13 teeth, ventral one with 1-5 teeth. The number of teeth on the forked appendix of dorsal cheliceral finger =1-2. Third abdominal sternite with (5-7)+(4-7) ctenidiae, fourth one with 10-14 ctenidiae. Ctenidiae on the III sternite of abdomen club-shaped, short or thin and long. Female. Total length 14.6-19.1. Variability of body coloration as in males. Dorsal cheliceral finger with 12-18 teeth, ventral one with 9-11 teeth.

Remarks: A comparison of the lectotype of *B. birulae,* as well as figure and description of the male syntypes of *E. celeripes* with the male holotype of *E. turkestana* and also its males collected from Kazakhstan and Mongolia has revealed that their diagnostic characters (i.e. the length of spines on the ocular tubercle, the number of spines on the anterior edge of propeltidium, the number of teeth on forked appendix of the dorsal cheliceral finger, the shape of flagellum, the shape of ctenidiae on the III sternite of abdomen and the number of ctenidiae on the IV sternite of abdomen) vary widely, and hence all the above species names are to be considered synonyms.

Roewer (1933) and Birula (1938) assigned two juvenile specimens to *B. birulae*, of which one was reported by Roewer as the female syntype: l juv. (ZISP 907), Mongolia, South-Gobi Aimak, Gobi Altai Mts., Noin-Bogdo [Noen-Bogdo] Mt. Range, (ca. 43°10'N, 101°45'E), expedition of P.K.Kozlov, 18-28.09.1925, leg. P.K.Kozlov; 1 juv. (ZISP 908, paralectotype of *B. birulae*), same locality, 29.09-13.10.1925, leg. N.M.Przhevalsky. An examination of these specimens has revealed them to be wrongly determined and to actually belong to the genus *Karschia.*

An adult female was simultaneously collected with a male of *E. turkestana* in the vicinities of Chundzha (Kazakhstan). This female cannot be separated by the shape of the genital sternites from the female lectotype and two female paralectotypes of *K. grombczevskii*, and therefore the latter name should be synonymized with *E. turkestana*.

Distribution: SE Kazakhstan (Charyn River valley), NW China ("Kashgar Steppe" and the Gobi Desert) and S Mongolia (Gobi Desert) (Fig. 12). Roewer (1933) erroneously recorded this species for Beluchistan (in SE Iran or SW Pakistan).

Ecology: This species prefers the clay deserts. Adults occur in May-June.

Acknowledgements

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POPULATION GENETIC EFFECTS OF FOREST FRAGMENTATION IN FLANDERS (BELGIUM) ON *COELOTES TERRESTRIS* (WIDER) (ARANEAE: AGELENIDAE) AS REVEALED BY ALLOZYMES AND RAPD

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Abstract

GURDEBEKE S., NEIRYNCK B., MAELFAIT J.-P.: Population genetic effects of forest fragmentation in Flanders (Belgium) on *Coelotes terrestris* (Araneae: Agelenidae) as revealed by allozymes and RAPD. In GAJDOŠ P., PEKÁR S. (eds): Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava), Vol. 19, Supplement 3/2000, p. 87-96.

Due to an ever-increasing urbanisation, industrialisation, development of road infrastructure and an intensive agriculture, forests in Flanders have become heavily fragmented. In general, organisms bound to small forest fragments have a reduced population size and are highly isolated from other populations. To assess the population genetic effects of forest fragmentation, we chose *Coelotes terrestris* (WIDER, 1834) as a model organism, because it is strongly bound to forest habitats. A first attempt to reveal the population genetic structure of this species was made by using allozyme electrophoresis. Only one enzyme (PGI) however showed good interpretable variation. This low degree of polymorphism together with the sometimes-questioned neutrality of allozyme markers made us choose genetic marker (RAPD). Ten forests, with a variable degree of isolation and a variable size were investigated. The majority (allozymes) and all (RAPD) pairwise comparisons of population allele/marker frequencies were significantly different, implying a very high degree of genetic isolation between the spider populations inhabiting the forests. No significant correlation could be found between the genetic diversity of the populations and the size of the forest in which they predominate.

Introduction

Natural ecosystems in Flanders (the northern part of Belgium) have become severely fragmented over the years. In general, the development of roads is known to be one of the causes of habitat fragmentation (SPELLERBERG, 1998), but also more intensive agricultural and industrial activities and increasing urbanisation are causative agents in this process. In

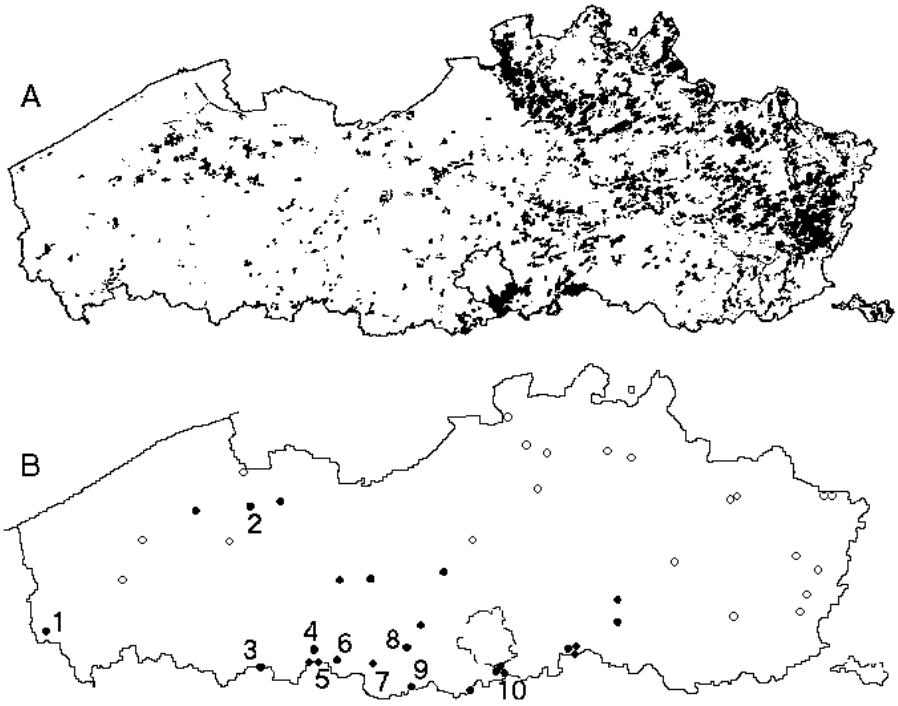

Fig. 1. A. Distribution of forests (shaded parts) in Flanders (Belgium), B. Geographic location of the sampled forests (open/filled circles represent absence/presence of *C. terrestris*, names of forests in Table 1).

the framework of the Flemish Impulse Program for Nature Conservation (VLINA) "Genetic-ecological research for nature conservation", a collaboration between several universities and institutes was started, to study the effects of habitat fragmentation in Flanders. This collaboration between research groups, each with their own specific area of expertise, will make it possible to assess fragmentation effects for different habitat types (e.g. dunes, marshes and forests), as well as for organisms belonging to different groups, ranging from invertebrates and vertebrates to plants. This can be useful since the effects of habitat fragmentation seem to differ between species, in relation to differences in their body size and vagility (Gaston, Blackburn, 1996; Desender et al., 1998).

In this study, genetic and ecological effects of forest fragmentation are investigated. Forests cover only about 10% of the total surface of Flanders and are highly fragmented (Fig. 1A). Only two forests possess a surface size that is larger than 800 ha, whereas 50% of the remaining forests are not larger than 60 ha (Van den Meersschaut, Lust, 1994). The high degree of forest fragmentation implies that populations of organisms bound to this habitat type are forced to live in several smaller and spatially isolated remnants (Young et

al., 1996). Especially in these fragments, population size is often reduced and a loss of genetic diversity may occur because of a lack of gene flow and/or the prevalence of inbreeding and genetic drift (GIBBS et al., 1994; SIMBERLOFF, 1998). This can result in a lowered adaptability to changing environmental conditions and in a higher risk of extinction (SIMBERLOFF, 1998). Belonging to a metapopulation structure (HOOPES, HARRISON, 1998) can be the answer to maintain sufficient genetic diversity.

The model organism we chose to conduct this study is *Coelotes terrestris* (WIDER, 1834) (Agelenidae, Araneae). Because of its method of prey capture and web building, it is strongly bound to forest habitats (SEGERS, MAELFAIT, 1990), rendering it suitable for this kind of research. This particular species was chosen because it is a rather large spider, which is highly abundant and easy to catch during the whole year. Furthermore, a large amount of literature is available concerning its ecology (e.g. TRETZEL, 1954; DE BLAUWE, BAERT, 1981; MAELFAIT et al., 1991; DE KNIJF, 1993; HÄNGGI et al., 1995) and its life cycle (SEGERS, 1986; SEGERS, MAELFAIT, 1990; DE BAKKER, 1995).

The population genetic structure of *C. terrestris* was studied by using two techniques: cellulose acetate electrophoresis and RAPD (WILLIAMS et al., 1990). RAPD has been used in arachnological studies only recently. A population genetic study was started on *Masoncus pogonophilus* CUSHING (Linyphiidae) by CUSHING (1998), whereas HETTLE et al. (1996) used it mainly to identify siblings and to discriminate between individuals of different broods of *Brachypelma albopilosa* VALERIO. A'HARA et al. (1998) focused on protocols and conditions for specimen and DNA storage, DNA extraction and RAPD profiling of spiders.

The goal of this project is 1) to contribute to the knowledge of the population genetic effects of forest fragmentation; 2) to try to develop a bio-indicating system which can be used to monitor the gains (or losses) of nature development measures that aim to connect otherwise isolated forest fragments. Connecting habitat fragments without any knowledge of the genetic structure of the inhabiting organisms may, indeed, lead to the occurrence of outbreeding depression if local adaptation has occurred in these specific forest fragments (TEMPLETON, 1986).

Material and methods

Sample collection

Individuals were caught by hand and, prior to analysis, stored at either –80°C or in liquid nitrogen (allozymes) or at –20°C (RAPD). For both techniques, a minimum of 30 individuals per population were investigated.

The sampled forests (Fig. 1B, Table 1) were chosen following a large inventory study conducted by the IBW (Institute of Forestry and Game Management). Those woodlands possessing a high abundance of *C. terrestris* were selected for allozyme analysis. Ten forests were chosen for RAPD analysis based on the results of a first study by MAELFAIT, HENDRICKX (1998). All forests occur on sandy loam and loamy soils and are mainly beech (*Fagus sylvatica*) forests.

For RAPD analysis, only adult females were used. This was necessitated partly by the timing of the sampling campaign: the life cycle of this species is such that mainly females occur in spring. Another reason was that, hitherto, there was no knowledge about any possible sex-specific bands.

T a b l e 1. Location and size of the sampled forests.

No.	Code	Name	Location	Size (ha)
1	HEL	Helleketelbos	Poperinge	42
2	DRO	Drongengoed	Knesselare	560
3	KLU	Kluisbos	Kluisbergen	295
4	BUR	Burreken	Zegelsem	16
5	BRA	Brakelbos	Brakel	205
6	PAR	Parikebos	Parike	9
7	RAS	Raspaillebos	Geraardsbergen	145
8	NEI	Neigembos	Ninove	77
9	EDI	Bos Ter Rijst	Edingen	280
10	ZON	Zoniën	Hoeilaart	4380

Allozymes

The cephalothorax was homogenised in distilled water. Cellulose acetate electrophoresis was performed following the procedures of HEBERT, BEATON (1989). Twenty enzymes were tested for polymorphism: adenilate kinase (AK), aldehyde oxidase (AO), alkaline phosphatase (ALP), arginine phosphokinase (APK), fumarate hydratase (FUM), glucose-6-dehydrogenase (G6PDH), glyceraldehyde-3-phosphate dehydrogenase (G3PDH), glycerol-3-phosphate dehydrogenase (GPDH), hexokinase (HEX), isocitrate dehydrogenase (IDH), lactate dehydrogenase (LDH), malate dehydrogenase (MDH), malic enzyme (ME), mannose phosphate isomerase (MPI), peptidase A (PEP-A), peptidase N (PEP-N), phosphoglucomutase (PGM), 6-phosphogluconate dehydrogenase (6PGDH), phosphoglucose isomerase (PGI), trehalase (TREH).

Enzyme allelic frequencies and deviances from Hardy-Weinberg equilibrium were tested with the software program TFPGA (MILLER, 1997). A Fisher exact test, using a contingency table approach (Fisher's RxC test) (see SOKAL, ROHLF, 1995), was performed to test for differences in allele frequencies between populations and an UPGMA dendrogram was constructed based on the genetic similarity index of NEI (1972), as implemented by the TFPGA program.

DNA extraction

Sterile needles were used to isolate muscle tissue from the spider's cephalothorax. The use of tissue was preferred over the whole cephalothorax to avoid any possible contamination by external parasites. This body part was also chosen over the spider's abdomen to avoid contamination by foreign DNA that could be present in the digestive organs. A similar approach was used by A'HARA et al. (1998).

Genomic DNA was isolated with the commercially available "Puregene" kit (Gentra Systems, Inc.). The instructions of the manufacturer were followed and yielded DNA of high molecular weight and good purity. Quantification of the DNA was performed with a Biospec 1601E Shimadzu spectrophotometer and the samples were diluted to a final concentration of 5 ng/µl.

RAPD procedures

Twenty RAPD primers (primer kit A – Operon Technologies Inc., Alameda, CA) were tested and a selection was made on the basis of the degree of polymorphism and the reproducibility of the banding profiles. This procedure yielded two primers to perform the population genetic analysis: OPA-01 and OPA-20 with respective sequences 5'-CAGGCCCTTC-3' and 5'-GTTGCGATCC-3'.

RAPD was performed on a TECHNE GENIUS thermal cycler, by using volumes of 25 µl containing 2.5 µl 10x PCR buffer (+ 1.5 mM $MgCl_2$) (Qiagen), 0.5 µl 25mM $MgCl_2$ (Qiagen), 100µM dNTP mix (Eurogentec), 25 picomoles of primer (Operon), 0.5 units *Taq*-polymerase (Qiagen) and 25 ng genomic DNA. Negative controls, in which the genomic DNA was replaced by water, were added during each PCR-reaction. The PCR-reaction consisted of an initial denaturation of 2 min at a temperature of 94°C, followed by 45 cycles of 1 min at 94°C, 2 min at 36°C (primer annealing step) and 2 min at 72°C (primer extension step). A final extension of the fragments was possible for 10 min at 72°C.

PCR products (5 µl) were size-separated on a 2 % TBE agarose gel for 53 min at 110 V and stained with ethidium-bromide. The banding profiles were visualised under ultraviolet light and the gel image was saved on computer with the ColorVision I software.

The interpretation of the banding pattern was conducted with the computer program GelCompar 4.2 (Applied Maths, Kortrijk, Belgium; VAUTERIN, VAUTERIN, 1992). The bands were sized against a Low Ladder (purchased from BIOzymTC BV, Landgraaf, the Netherlands) and scored as binary data: present (1) or absent (0).

RAPD data were analysed with the TFPGA program developed by MILLER (1997). Allele frequencies were estimated based on the square root of the frequency of the null (recessive) allele (WEIR, 1990) assuming that genotype frequencies were in Hardy-Weinberg equilibrium. UPGMA (Unweighted Pair Group Method using Arithmetic means) cluster analysis was performed using NEI's (1972) original distance. Like with the allozymes, a Fisher exact test showed the degree of differentiation between the studied populations. Geographical patterns in the data were tested with a Mantel test (MANTEL, 1967) of genetic distance versus log geographic distance. Pearson correlations were made with Statistica for Windows, release 5.1 (Statsoft, Inc., Tulsa, USA).

Results

Allozymes

A first attempt to unravel the genetic structure of C. *terrestris* populations in fragmented woodlands was made by using allozyme electrophoresis. Twenty enzymes were screened for possible polymorphism; only one (PGI) showed good interpretable allelic variation. UPGMA-clustering (Fig. 2) shows a deviant genetic structure of the two sampled sites (1 and 2) in the Zoniën forest. A second group is formed by the forests belonging to the Flemish Ardennes. Neigembos, although also being a forest of this geographic area is clustered together with the isolated forests Helleketelbos and Drongengoed in a third group. The pattern of this dendrogram can be explained by the allelic frequencies of PGI that occur in these forests. For this enzyme, three different alleles (S: slow, M: medium and F: fast) could be distinguished. By determining the genotype of a sufficiently large number of individuals per population, the allelic frequencies of these populations could be estimated (Fig. 3). The largest forest (Zoniën) possessed the three alleles in comparable amounts, whereas populations inhabiting the smaller forest fragments of the Flemish Ardennes had only two alleles. Populations in Neigembos, Helleketelbos and Drongengoed had also two alleles, of which one was present only in a very small amount.

A Fisher exact test showed that not all populations were significantly different from each other (Table 2). All populations were in Hardy-Weinberg equilibrium, so this assumption, made to analyse the RAPD data, was correct.

RAPD

The two primers yielded 30 good interpretable bands that were used in this analysis. Their sizes ranged between 400 and 1650 bp. 87% of the studied loci were polymorphic.

The constructed UPGMA-tree (Fig. 4) divided the forests into two clusters for which no geographic (or other) pattern could be found ($r=0.06$, $P=0.38$, Mantel test). All populations showed a highly significant genetic differentiation ($P<0.001$ in all pairwise combinations, Fisher exact test). Although these results are still preliminary, it appears that the patterns found with the allozymes are not supported by this molecular technique.

T a b l e 2. Genetic differentiation between the 10 populations based on allozyme data (with **: <0.01, *: <0.05).

	ZON1	ZON2	PAR	KLU	RAS	NEI	EDI	BRA	BUR	DRO	HEL
ZON1	X		**	**	**	**	**		**	**	**
ZON2		X	**	**	**	**	**	*	**	**	**
PAR			X	**	**	**	**		**	**	**
KLU				X		*	*	*		**	**
RAS					X	**	*	*		**	**
NEI						X	**	**	**		
EDI							X			**	**
BRA								X		**	**
BUR									X	**	**
DRO										X	
HEL											X

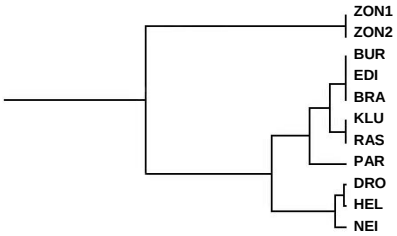

Fig. 2. UPGMA-dendrogram of *C. terrestris* populations based on allozyme data.

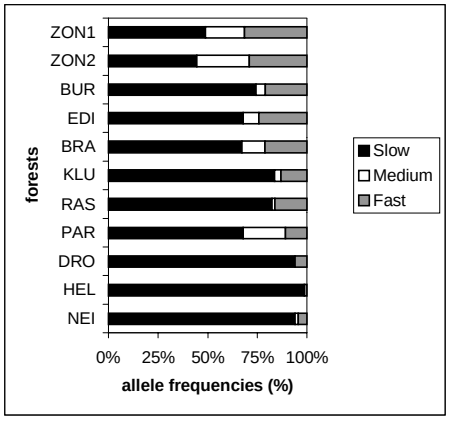

Fig. 3. Allele frequencies of the enzyme PGI in the 10 sampled populations.

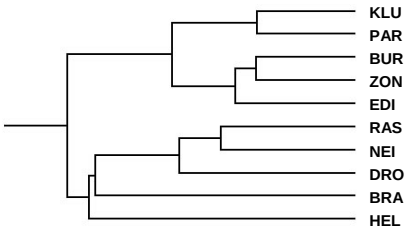

Fig. 4. UPGMA-dendrogram of *C. terrestris* populations based on RAPD data.

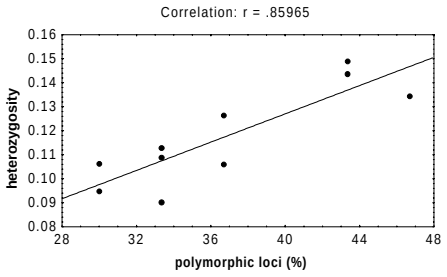

Fig. 5. Correlation between the percentage of polymorphic loci and heterozygosity.

Two different measures were used to study the genetic diversity of the sampled populations, namely the percentage of polymorphic loci and the average heterozygosity (Table 3). The lowest percentage of polymorphic loci (30%) was found in the populations of Burreken and Helleketelbos; the lowest average heterozygosity (0.09) was reached in Burreken and Parike. Based on these two measures, the spider population in Burreken had the lowest genetic diversity. The highest number of polymorphic loci were found in the population of Brakelbos (46.67%). The highest heterozygosity (0.15) appeared in the population of Raspaillebos. The percentage of polymorphic loci was correlated with the heterozygosity in all populations ($r=0.86$, $P<0.01$; Fig. 5). However, there appeared to be no correlation between the size of the forest and the degree of polymorphism in its populations ($r=0.43$, $P=0.21$).

T a b l e 3. Percentage of polymorphic loci and heterozygosity based on RAPD data.

Forest	Average heterozygosity	% polymorphic loci
KLU	0.11	36.67
PAR	0.09	33.33
BUR	0.09	30.00
ZON	0.14	43.33
EDI	0.11	33.33
RAS	0.15	43.33
NEI	0.11	33.33
DRO	0.13	36.67
BRA	0.13	46.67
HEL	0.11	30.00

Discussion

Although allozymes offer a quick and easy method to investigate the genetic structure in populations, the number of loci and alleles per locus is sometimes too low, rendering them only suitable to detect large-scale genetic patterns (GROSBERG et al., 1996). The low degree of polymorphism in *Coelotes terrestris*, together with the sometimes questioned neutrality of allozymes (e.g. RIDDOCH, 1993; CONGDON, 1994), made it necessary to search for another technique. BLACK (1993) noted that PCR techniques (SAIKI et al., 1988) have revealed polymorphisms in insect taxa that lacked allozyme polymorphisms. Apart from this higher degree of polymorphism, another advantage of PCR techniques is that they reveal variation on the DNA-level, whereas allozymes only offer variation on the gene-product level (STEWART, EXCOFFIER, 1995).

However, a lack of repeatability of the banding patterns is considered to be one of the drawbacks of the RAPD technique (HEDRICK, 1992; HARRY et al., 1998). Being a PCR-based technique, RAPD is very sensitive to the amplification conditions. Models of thermocyclers, changes in annealing temperatures, primer and template concentrations, dNTP concentration, Mg^{2+} concentration, are known to cause unreliable and inconsistent amplifications (see GROSBERG et al., 1996). Nevertheless, this technique is widely used and many authors stated that a standardisation of the reaction conditions is enough to ensure reproducibility of the amplification products (HADRYS et al., 1992; BLACK, 1993; HARRY et al.,

1998). We can confirm this statement since banding profiles were reproducible within, as well as between, different PCR reactions.

The higher degree of polymorphic markers generated by RAPD makes it possible to study the population genetic structure of our study species more thoroughly. However, in contrast with Buso et al. (1998) and De Wolf et al. (1998), RAPD and allozyme markers did not reveal the same or similar patterns. The populations of the ten sampled forests appear to have undergone a significant differentiation; furthermore, no geographical pattern could be found. This implies that they are not part of a metapopulation and that they each possess different gene pools.

In future, more populations will be investigated by RAPD analysis, by using more individuals per population, as well as more primers. A selected number of populations will be checked for temporal variation and also effects of forest fragmentation on a smaller scale will be assessed (e.g. between adjacent forest patches and within larger forest complexes that are subdivided by road infrastructure). Possible co-variation between genetic diversity and forest age or degree of isolation will be studied.

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INTERPRETATIONS OF ORB-WEB VARIABILITY: A REVIEW OF PAST AND CURRENT IDEAS

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Abstract

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The understanding of web-building behaviour in orb-web spiders has undergone several paradigm shifts. In the past, orb-web construction was assumed to be limited to genetically-controlled design patterns, suggesting that meaningful variation only existed at the species level. Subsequently, it was recognised that variation in web design also exists within species and that this variation was linked to the prey capture ability of webs. Another approach to interpreting individual variation is within a decision-making construct. The web-building decisions of spiders may thus be ruled by algorithms or mechanical constraints. Similarly, individual decisions may reflect foraging strategies aimed to maximise food intake. Our own work suggests that experience in web-building and prey capture may also contribute to individual variation of orb-web design. Using several key publications as well as recently collected data we discuss past and current ideas to interpret orb-web variability.

Orb-webs from a phylogenetic perspective

Orb-webs are constructed by more than 4200 spider species (LEVI, 1982; PLATNICK, 1997) and evolved over a period of about one hundred million years (SELDEN, 1989). They constitute the prey capture device for the Orbiculariae which include two distinct groups of orb-web spiders. The more ancestral Uloboridae, that along with the Deinopoidae form the superfamiliy Deinopoidea (OPELL, 1998), typically construct horizontally orientated orb-webs consisting of non-adhesive, cribellate silk. In contrast, the more derived araneoid orb-web spiders (Foelix, 1992) construct mostly vertical webs using ecribellate adhesive silk (e.g. OPELL, 1997; 1998). The vertical orientation of orb-webs has a number of advantageous consequences for prey capture: (1) they intercept more prey (CHACÓN, EBERHARD, 1980), (2) retain prey longer

(Eberhard, 1989), and (3) can absorb greater forces of prey impact (Craig, 1987a) which is facilitated by stronger axial fibres in the capture threads (Opell, 1997). The selective advantage of adhesive threads may be: (1) greater economy, since they are less costly to produce (Vollrath, 1992a; Opell, 1998), (2) lower visibility to insects (less UV-reflective), which enables araneoids to settle in a greater variety of habitats (Craig, Bernard, 1990; Craig et al., 1994), and (3) increased extensibility (flexibility) of the webs (Köhler, Vollrath, 1995; Lin et al., 1995). These synapomorphic characteristics within the araneoid spiders are considered to be key innovations, which led to a variety of orb designs, a greater radiation and an increase in species diversity (95 % all orb-web spider species) as opposed to the Deinopoidea (Coddington, Levi, 1991; Foelix, 1992; Bond, Opell, 1998).

The regular orb is no longer viewed as the evolutionary peak in orb-web evolution but as a basis. Some species of orb-web spiders construct webs, which deviated from the typical orb design (e.g. the sector webs constructed by *Hyptiotes* sp.). Others have lost the ability to construct webs altogether (e.g. *Celaenia* sp.). In general, the diversification of orb-web design has been attributed to changes in spider size. While both small (e.g. Anapidae, Theridiosomatidae) and large orb-web spiders (Araneidae and Tetragnathidae) construct orbs, only small ones build both planar and three-dimensional webs (Craig, 1987b). Therefore, the evolution of alternative web-designs may be the consequence of a general phyletic trend of small body size among the Araneoidea (Craig, 1987b).

The origin of the orb design is a topic that is still under active discussion. A monophyletic hypothesis suggests that the orb-web is not a derived character, but a plesiomorphic one which has evolved only once. This assumes that the uloborids and araneoids are close relatives, sharing a common, cribellate ancestor. This idea was first supported by Thorell (1886; cited in Shear, 1994), and Wiehle (1927), who did not believe that such complex web building behaviour could have evolved independently twice. Strong support for a common ancestor is provided through anatomical features that are shared by araneoids and uloborids (Coddington, 1990). A convergent hypothesis suggests the independent evolution of orb-webs in the Araneoidea and the Uloboridae. Accordingly, the orb-web evolved after the loss of the cribellum (e.g. Eberhard, 1982; 1990). Since the cribellum is a primitive character in the Orbiculariae, it is likely that the ecribellate Araneoidea originated independently, many times, by the loss of the cribellum (Shear, 1994). The orb-webs within the Araneoidea may be homologous in structure (Levi, 1978b) and araneoid species may be monophyletic with the orb as a primitive type of web (Coddington, 1986; Craig, 1987b). However, even if all orb-web spider species are derived from one ancestor, some design features may have evolved independently (Eberhard, 1990).

Interspecific variation

The interspecific variability in orb-web design was recognised at an early stage, and orb-webs of different species were described in great detail (e.g. Wiehle, 1928). Although the design was often viewed in context with its function, variations were attributed to geneti-

cally-controlled design patterns and often, extreme orb designs, such as ladder webs, attracted the most attention. For example, the ladder webs of the araneids *Scoloderus tuberculifer* (O. P.-CAMBRIDGE) (EBERHARD, 1975) and *Scoloderus cordatus* (TACZANOWSKI) (STOWE, 1978) are inverted with an extension above the hub which contrasts with the ladder web of *Herennia ornatissima* (DOLESCHALL), which is extended downwards (ROBINSON, LUBIN, 1979). These webs are thought to be specialised moth traps (EBERHARD, 1975; STOWE, 1978; FORSTER, FORSTER, 1985). In *Hyptiotes*, the triangle spider, the web consists of three sectors (OPELL, 1982; LUBIN, 1986) and in *Miagrammopes* (OPELL, 1990) only a few sticky threads make up the entire web. The bolas spider, *Mastophora*, reduced the web to a single line with a viscid ball at the end, which the spider twirls around. Male moths are attracted to the twirling ball by a pheromone that mimics attractants produced by female moths (EBERHARD, 1977a; 1980). Another curious deviation from the standard orb design is the reduced orb-web of *Wixia ectypa* (WALCKENAER) (STOWE, 1978), the so-called "asterisk web".

Orb-web function

The variety of orb designs has inspired numerous studies into their function. In general, the orb-web functions as a multi-purpose device, supporting the spider, transmitting mechanical impulses, and providing a substrate for it to move on. However, the main function of orb-webs is to trap prey. The traditional idea that orb-webs passively sieve prey from the surrounding air stream is no longer accepted. Instead, orb-webs must serve several functions and changes in orb-web design as well as web site selection will influence prey capture success (e.g. MURAKAMI, 1983). Web site selection may greatly affect the number and kind of prey captured. For instance, the nocturnal orb-web spider species *Larinioides sclopetarius* (CLERCK) constructs webs adjacent to artificial light, which also attracts high numbers of prey (HEILING, 1999). Similarly, feeding in conspecific aggregations may enhance capture success, when prey density is low or prey supply is unpredictable (UETZ, 1988; CRAIG, 1991). Web features which further influence prey capture include: web orientation (EBERHARD, 1989), web tension (CRAIG et al., 1985), silk strength (CRAIG, 1987a), web visibility or attractiveness to prey (e.g. CRAIG, BERNARD, 1990; CRAIG, FREEMAN, 1991) and web design (EBERHARD, 1986).

Web design includes the size of the web and the number and arrangement of radials and spirals. In general, a larger web is likely to encounter more prey (CHACÓN, EBERHARD, 1980). The distance between capture spirals (mesh height) may also be related to prey size and type. Orb-webs with a narrow mesh are thought to target small prey, which would otherwise fly through a larger mesh (MURAKAMI, 1983; SANDOVAL, 1994; HERBERSTEIN, HEILING, 1998; SCHNEIDER, VOLLRATH, 1998). However, a densely-meshed web may also be more visible and consequently more likely to be avoided by flying insects (CRAIG, 1986). The absorption of kinetic energy created by prey impact is facilitated by the mechanical properties of spider silk and the design of the web, which distributes the energy from the point of interception (CRAIG, 1986; GOSLINE et al., 1986). Accordingly, orb-webs with a higher number of

radii in relation to their number of capture thread turns can absorb the kinetic energy of large and fast-flying insects (Eberhard, 1986; Craig, 1987a).

Intraspecific variability in orb-webs

Ontogenetic shifts in web design

During the ontogeny of a spider, orb-webs generally undergo an increase in material investment, resulting in larger mature webs compared to small immature webs (e.g. Witt et al., 1972; Heiling, Herberstein, 1998). Various studies have demonstrated that web area gradually increases with the size and weight of a spider (Denny, 1976; Olive, 1980; Higgins, Buskirk, 1992; Ward, Lubin, 1992). This allometric growth of the orb during ontogeny does not necessarily include changes in the structural relationships. For example, the web design of *Argiope aurantia* (Lucas) (Witt et al., 1972) remains stable throughout the development of spiders. In contrast, other species show quite drastic changes in their web building behaviour. *Peucetia viridans* (Hentz) (Kaston, 1972) construct webs during immature stages only, while *Mastophora dizzydeani* Eberhard (Eberhard, 1980) only builds webs after the final moult. Similarly, most uloborid spiders construct different types of orb-web before and after the first moult, as the cribellum is not functioning during their first developmental stage (Eberhard, 1977b). All these ontogenetic variations are quite abrupt, without intermediary patterns of web design.

More gradual ontogenetic changes in orb-web design are characteristic in a number of araneid species, particularly with regard to the up/down extension of the orb. In general, young immature spiders tend to construct almost symmetric, less derived, orb-webs (Eberhard, 1990), which also show higher regularity (Witt et al., 1972). Adults construct asymmetric webs with the area above the hub reduced and the lower area enlarged, a phenomenon which is particularly common among the Nephilinae (see Japyassú, Ades, 1998 for summary) but also in other araneoid species.

Individual variation in orb-web design

Individual variation in orb-web design was first recognised in the early sixties, when Witt (1963) identified variation in web design in response to environmental prey conditions in the garden spider *Araneus diadematus* Clerck. When prey conditions were bad, thread production decreased but both web area and mesh height increased when spiders were starved (Witt, 1963). Since then, numerous studies have shown that variation in web-design also exists on the individual level and these variations were attributed to various biotic and abiotic factors. These include: available space (e.g. Leborgne, Pasquet, 1987) the presence of conspecifics (Gillespie, 1987; Heiling, Herberstein, 1999a), spider leg length (Vollrath, 1987), weather conditions (Cangialosi, Uetz, 1987; Ammitzbo, 1988),

presence of previously-spun lines (Gillespie, 1987), amount of available silk (Eberhard, 1989; Zschokke, 1997), prey size (Sandoval, 1994), spider weight (Herberstein, Heiling, 1999), gravity (Vollrath, 1992b), nutrition (Herberstein et al., 2000), and experience (Heiling, Herberstein, 1999b).

Approaches of interpreting orb-web variability

Morphological approach

Initially, it was assumed that orb-web construction was limited to genetically-controlled design patterns and that meaningful variation only existed at the species level (e.g. Levi, 1978a). Similarly, variation at the intraspecific level was formerly attributed to genetically-controlled morphological characteristics. For instance, ontogenetic changes in orb-web design were attributed to morphological changes during spider development. Accordingly, the 'Bauplan' of the web was interpreted as a projection of the animal's morphology (Peters, 1937). The resulting image of behavioural inflexibility in orb-web spiders and web building spiders in general remained unchallenged for another 30 years.

Mechanistic approach

The symmetric nature of orb-webs and the regularity in the arrangement of radials and spirals seems to imply that the process of web construction is based on strict physical and mathematical rules. Not surprisingly, one approach to understanding design variability is to place web building behaviour within a mechanistic context to identify algorithmic rules (e.g. Vollrath, 1992b; Vollrath et al., 1997). Accordingly, the placement of the sticky spirals may be based on leg length, which the spider uses as measuring tool. If leg length is reduced, so is the distance between the capture spirals (Vollrath, 1987). In contrast, the construction algorithm for the auxiliary spiral may be based on angles rather than distance (Vollrath, 1992b). Moreover, by loading these algorithmic rules into computer models, web building behaviour can be simulated (Krink, Vollrath, 1999).

Web building algorithms may be further modified by incorporating environmental cues, such as gravitational information. As orb-web spiders do not rely on visual cues during web construction, they may use gravity as a compass reference (Vollrath, 1992b; Zschokke, 1993). When *Araneus diadematus* were rotated in a vertical plane during web construction they appeared disoriented and constructed tangled and irregular capture spirals (Vollrath, 1992b). Similarly, web asymmetry may also be based on gravitational cues. Vertical orb-webs are often characterised by a top/bottom asymmetry, whereby the lower half of the web is larger than the upper. Orb-webs constructed in the absence of gravity are more symmetric, and the horizontal orb-webs built by uloborids, are also more symmetric (Vollrath, 1992b).

The extent of web-asymmetry may further be limited by physical factors such as the body weight of the spider. The position of a spider when it lays the capture spirals below the hub is carapace up or sideways. In contrast, when laying the threads above the hub, the spider has to lift and direct the abdomen with the spinnerets from sideways to above its carapace (VOLLRATH, 1986), which may be energetically more costly and time-consuming for larger or heavier spiders. Thus heavier *Argiope keyserlingi* KARSCH and *Larinioides sclopetarius* also produce more asymmetric webs than lighter individuals (HERBERSTEIN, HEILING, 1999).

Optimality approach

Another approach to understand orb-web variability is to interpret web building behaviour within the theoretical concepts of optimal foraging theory. Spiders benefit by maximising growth and reproductive output whilst minimising time of development and costs associated with foraging (e.g. HODGE, UETZ, 1996). Thus web building behaviour, and specifically web design, can be viewed as a trade-off between the costs and benefits associated with foraging, and individual variation in web design may reflect different trade-offs (HIGGINS, 1995). In one of the earlier studies, SHERMAN (1994) showed that *Larinioides cornutus* (CLERCK) varied its silk investment, and thus web dimensions, with changing energetic gains (from foraging) and energetic expenditures (from egg production). He found that satiated spiders constructed smaller webs containing less silk, presumably redirecting energy to egg production. In contrast, hungry spiders constructed larger webs in order to increase prey interception (see CHACÓN, EBERHARD, 1980) and energy gain, the prerequisite for egg production (SHERMAN, 1994). A similar relationship between foraging success and web design has since been found in other orb-web spiders, including *Argiope keyserlingi* (HERBERSTEIN et al., 2000).

Web asymmetry may also reflect a foraging strategy to optimise prey capture. Spiders are able to detect prey and travel to prey entangled in the lower half of the web more quickly than in the upper one (MASTERS, MOFFAT, 1983; AP RHISIART, VOLLRATH, 1994; LANDOLFA, BARTH, 1996). Thus by increasing the lower and decreasing the upper half of the web, spiders may increase the chance that prey will be intercepted and captured successfully (MASTERS, MOFFAT, 1983; AP RHISIART, VOLLRATH, 1994). Similarly, variation in mesh height may also be interpreted as a specific foraging strategy. By increasing mesh height, spiders may target larger prey, whilst smaller prey may pass between the spirals (SANDOVAL, 1994; SCHNEIDER, VOLLRATH, 1998; HERBERSTEIN, HEILING, 1998).

Individual experience

The role of experience and memory in web building behaviour has largely been neglected in favour for more mechanistic explanations (VOLLRATH, 1992b). In an early approach, to test the influence of prior experience on web-building behaviour, REED et al. (1970) confined *Araneus diadematus* in small tubes where they were unable to construct

a web, and tested the effects of this treatment on web design. The test revealed that inexperienced spiders built smaller webs, which was attributed to restricted silk production. Reed et al. (1970) found no indication for an influence of prior experience on orb design and concluded that 'web-building behaviour does not seem a fruitful ground for investigating plasticity in the spider nervous system'. We recently provided evidence for the influence of prior experience on the degree of orb-asymmetry (Heiling, Herberstein, 1999b). Our experiments revealed that *L. sclopetarius* with web-building experience constructed more asymmetric webs compared to inexperienced conspecifics. Moreover, web asymmetry was also influenced by previous prey capture experiences, as spiders increased the region of the web which intercepted most prey. *L. sclopetarius* and *A. keyserlingi* were able to monitor the success rate of different web regions and altered their web design accordingly (Heiling, Herberstein, 1999b). Thus, previous experience, in either web building or prey capture, may also affect intraspecific variation in orb-web design.

Conclusion

The surprisingly high degree of variability in orb-web design, particularly within individuals of the same species, has provided a fruitful ground for numerous investigations into factors that may influence this variability. However, to fully understand the complex nature of orb-web design variability, a combination of several different approaches is clearly necessary.

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IMPACTS OF SILVICULTURAL PRACTICE ON THE GROUND LIVING-SPIDER COMMUNITY (ARACHNIDA: ARANEAE) OF MIXED MOUNTAIN FORESTS IN THE CHIEMGAU ALPS (GERMANY)

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Abstract

JUNKER E.A., RATSCHKER U.M., ROTH M.: Impacts of silvicultural practice on the ground living-spider community (Arachnida: Araneae) of mixed mountain forests in the Chiemgau Alps (Germany). In GAJDOŠ P., PEKÁR S. (eds): Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava), Vol. 19, Supplement 3/2000, p. 107-117.

Investigations of long-term effects of clear-cutting, as well as slight and heavy shelterwood cutting, on soil-dwelling spiders were carried out in the mixed mountain forest of the Bavarian Alps. The experimental design included 4 plots (each of 0.5 ha): a control area (0) without intervention, and three plots, submitted in 1976 to different degrees of canopy opening. Slight (30) or heavy (50) shelterwood cutting resulted in a 30 or 50% reduction of basal area. On the clear-cut area (100) trees were completely removed. On each variant a subplot was fenced (Z) subsequently to silvicultural practice in order to prevent cattle and deer from entering. Spiders were collected 22 years after the management by pitfall traps (PT: n=9) from April 1998 to April 1999.
A total of 9750 spiders (97 species, 19 families) was collected, among them 23 Araneae listed in the Red Data Book of Germany and/or Bavaria. Small-sized species of Linyphiidae dominated the spider fauna on each plot. The portion of Lycosidae increased with increasing shelterwood cutting and reached maximum values (18.9%) on 50. The spider community reached its maximum biodiversity on clear-cuts, while the number of specimens as well as the biomass was lowest at these sites. Highest numbers of specimens were found on the unfenced slightly-cut shelterwood plot (30), and the highest biomass on the unfenced plot of heavily-cut shelterwood (50). The Quotient of Similarity (QS), according to Soerensen, decreased with increasing shelterwood cutting and was lowest between 0/Z and 100/Z. The highest similarity was reached between fenced and unfenced plots of the same intensity levels of forestry practice, as well as between the control area (0) and 30% shelterwood cut (30, 30/Z). Using niche width calculations 15 spider species were identified as being characteristic of the clear-cuts (Gnaphosidae: *Gnaphosa bicolor*, Liocranidae: *Agroeca brunnea*, Linyphiidae: *Agyneta ramosa*, *Ceratinella brevis*, *Gongylidiellum latebricola*, *Lepthyphantes flavipes*, *Lepthyphantes mansuetus*, *Lepthyphantes mengei*, *Micrargus herbigradus*, *Pocadicnemis pumila*, *Walckenaeria atrotibialis*, *Walckenaeria antica*, Zoridae: *Zora nemoralis*) and the heavily-cut shelterwood (Linyphiidae: *Diplocephalus picinus*, Lycosidae: *Alopecosa taeniata*). In addition *Micrargus apertus* was recorded for Bavaria for the first time.

Introduction

With respect to sustainable land use concepts in agriculture and forestry high priority is attached to maintaining the ecological integrity of ecosystems. In contrast to agricultural land use systems the effects of silvicultural methods on key biotic processes of ecosystem functioning are largely unknown today, apart from the clear-cutting system, fire application and mineral fertilisation (Beaudry et al., 1997; Hutto, 1995; Paquin, Coderre, 1997; Staddon et al., 1998). In this context measures for the regeneration of stands are particularly interesting, with the natural regeneration obtaining a high ranking, and not only for economic reasons (Otto, 1994). Regarding the Central European stands that have been mainly grown as high forests, natural regeneration can be controlled especially by operations in the shelterwood (Mosandl, 1991).

One of the most important faunistic key factors of ecosystem functions and processes operating in forests are predatory arthropods (e.g. Nyffeler, 1982). Species diversity, high abundance, and their sensitivity to alterations of environmental parameters designate the ground-living Araneae as a suitable indicator group (Ratschker, Roth, 1999).

The objective of this study consisted in assessing long-term effects of silvicultural practices of canopy density regulation (clear cutting, removal of 30 or 50% of the stand basal area) on spider assemblages and other predatory arthropods (Junker, Roth, 2000). Montane mixed forest systems were selected as investigation areas in the upper Bavarian lime alpine, which are endangered by an impoverishment of tree species composition (decline of fir) and the absence of natural regeneration (e.g. Burschel et al., 1990; Bernhart, 1988, 1990).

Material and methods

The assessment of the Araneae community was performed on four NW-exposed forest plots (71 x 71 m) in the Chiemgau Alps in 1998 (Forest District Ruhpolding, Rauschberg: 47°46' northern latitude – 13°39' eastern longitude, altitude a.s.l.: 890-920 m). The humus form was moder. In 1976 the plots were subjected to shelterwood cutting of various intensity (Table 1). The canopy opening on the plots of slightly- (30, 30/Z) and heavily-cut (50, 50/Z) shelterwood led to a tree species composition that largely resembled that of the control plot (percentages referring to the whole stand: *Picea abies*: 12-36%, *Abies alba*: 33-49%; *Fagus sylvatica*: 20-33%; *Acer pseudoplatanus:* 12-15%, cf. Ammer, 1996). Except for a core area (22 x 33 m) that was fenced (Z) on each subplot to exclude game species, all investigation areas were left to free succession after the silvicultural treatment. As was evident from a comparison of the relative slight intensity in the subplots, the silvicultural canopy density regulatory operations were still obvious 20 years after the practices (Table 1, Ammer, 1996).

The epigeal spider fauna was surveyed using pitfall traps (volume: 370 ml, diameter: 7 cm, number of replicates per variant: n=9) according to Mühlenberg (1993). Therefore the data (total of specimens, diversity, biomass) represent the activity of spiders on the ground. Saturated benzoic acid solution with detergent served as a preservative solution. The pitfall traps were placed in the plots each at a distance of 5.4 m in a grid-like pattern. Spiders were sampled at monthly intervals over the investigation period from April 23rd to November 4th 1998, with the winter trapping season lasting from November 5th 1998 to April 22nd 1999.

The Araneae were determined according to Heimer, Nentwig (1991), Roberts (1985, 1987, 1995), Wiehle (1956, 1960), Kronestedt (1990) and Relys, Weiss (1997). The nomenclature followed Platnick (1998) (in

T a b l e 1. Characterisation of the experimental plots (according to AMMER, 1996).

plot	Silvicultural operation	intensity of cut	altitude a.s.l. [m]	Slope inclination	relative light intensity [%]
0	control area	no intervention	890	22°	10.2
0/Z	control area	no intervention, fence	890	22°	10.2
30	slightly-cut	30 % reduction of basal area	910	24°	14.1
30/Z	slightly-cut	30 % reduction of basal area, fence	910	24°	14.1
50	heavily-cut	50 % reduction of basal area	920	21°	18.4
50/Z	heavily-cut	50 % reduction of basal area, fence	920	21°	18.4
100	clear-cut	100 % reduction of basal area	910	28°	39.1
100/Z	clear-cut	100 % reduction of basal area, fence	910	28°	39.1

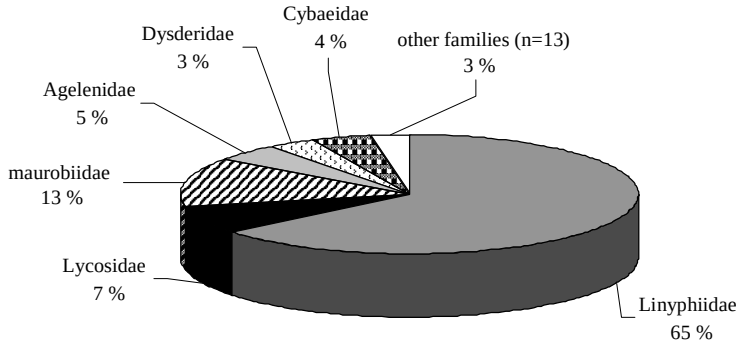

Fig. 1. Dominance structure of spider families in the total catch (n=6159 ind.), sampling period April 23rd 1998 to April 22nd 1999.

JÄGER, 1999). The data were statistically assessed (parameter-free tests: Mann-Whitney-U Test) using the program SPSS 8.0™ for Windows.

For the determination of characteristic species for various silvicultural variants only those species were used which according to ENGELMANN (1978) at least reached subrecedent proportions in the entire catch of spiders and had a niche width <0.3.

Results

As a whole, 9750 spiders were assessed; the juvenile proportion of which accounted for 36.8% (3591 ind.). The adult Araneae belonged to 97 species from 19 families; among them 23 species (23.7%) of the German Red List (PLATEN et al., 1998) or the Bavarian Red List (BLICK, SCHEIDLER, 1996) (Table 2). In addition *Micrargus apertus* (O.P.-CAMBRIDGE) was recorded for Bavaria the first time.

T a b l e 2. Compilation of the assessed species with indication of numerical abundance as well as the status of endangerment according to the German Red List (GRL: PLATEN et al., 1998) and the Bavarian Red List (BRL: BLICK & SCHEIDLER, 1996). 3: endangered, R: extremely rare species or endemic species; G: supposed endangerment, status, however, being unknown; 4S: questionable status, found rarely. * *Coelotes solitarius* was firstly recorded for Germany in 1994 (BLICK, 1994), *Micrargus apertus* was not published for Bavaria until now. Therefore they are not listed in the Bavarian Red List yet.

Species	**Red Data List**		**Study sites**								**Total**
	GRL	BRL	0/Z	0	30/Z	30	50/Z	50	100/Z	100	
SEGESTRIIDAE (1 species)											
Segestria senoculata (L.)					2		2				**4**
DYSDERIDAE (1 species)											
Harpactea lepida (C. L. K.)			14	14	23	20	40	24	41	23	**199**
THERIDIIDAE (3 species)											
Episinus angulatus (BL.)									1		**1**
Robertus lividus (BL.)						1	9	3	9	8	**30**
Robertus truncorum (L. K.)	**R**	**4S**	1	1	3	3	2			2	**12**
LINYPHIIDAE (51 species)											
Agyneta ramosa JACK.					1				33	7	**41**
Asthenargus perforatus SCHEN.	**R**	**4S**					2				**2**
Bolyphantes alticeps (SUND.)							1	12	6	9	**28**
Centromerus cavernarum (L. K.)		**4S**	9	11	18	19	26	8	5		**96**
Centromerus incilium (L. K.)									1		**1**
Centromerus pabulator (O. P.-C.)			84	44	33	51	7	11			**230**
Centromerus sellarius (SIMON)	**G**	**4S**	10	29	5	25	19	15	2	2	**107**
Centromerus silvicola (KULC.)	**3**	**3**	1	4	19	2	12		5		**43**
Centromerus sylvaticus (BL.)			1	2	2	3	11	39	11	43	**180**
Ceratinella brevis (WIDER)					1	1			19	2	**23**
Dicymbium tibiale (BL.)										1	**1**
Diplocephalus latifrons (O. P.-C.)			84	92	20	75	3	2		1	**277**
Diplocephalus picinus (BL.)					9	2	44	25		1	**81**
Diplostyla concolor (WIDER)			4		18	61	57	43	25	17	**225**
Drapetisca socialis (SUND.)			1								**1**
Erigone atra BL.						1		2			**3**
Erigone dentipalpis (WIDER)			1		1						**2**
Gonatium paradoxum (L. K.)	**3**	**4R**							3	4	**7**
Gongylidiellum latebricola (O.P.-C.)								1	4	10	**15**
Lepthyphantes alacris (BL.)			6	1	12	18	16	1			**54**
Lepthyphantes cristatus (MENGE)				3	8	8	49	147	34	75	**324**
Lepthyphantes flavipes (BL.)						1			13	8	**22**
Lepthyphantes fragilis (TH.)	**R**	**4S**			1	1					**2**
Lepthyphantes lepthyphantiformis (ST.)	**G**	**4S**	3	8	13	5	10	7	11	17	**74**
Lepthyphantes mansuetus (TH.)					1				21	1	**23**
Lepthyphantes mengei KULC.				2					5	3	**10**
Lepthyphantes montanus KULC.	**R**	**4S**	3	5	13	15	10	2	4	9	**61**
Lepthyphantes nodifer SIMON		**4S**		2	9	10	34	1			**56**
Lepthyphantes tenebricola (WIDER)			156	178	184	193	153	60	3	5	**4**
Linyphia triangularis (CL.)							1				**1**
Macrargus rufus (WIDER)			54	85	65	46	19	24	1		**294**
Maso sundevalli (WEST.)						1		1	1		**3**
Mecopisthes silus (O. P.-C.)						1					**1**
Meioneta innotabilis (O. P.-C.)		**4S**		1							**1**
Micrargus apertus (O. P.-C.)	**R**	*					4				**4**
Micrargus herbigradus (BL.)							2	1	10	43	**56**

Table 2. (cont.)

Species	Red Data List		Study sites								Total
	GRL	BRL	0/Z	0	30/Z	30	50/Z	50	100/Z	100	
Microneta viaria (BL.)			40	12	27	24	65	27	21	7	**223**
Neriene peltata (WIDER)					1			1			**2**
Neriene radiata (WALC.)									1		**1**
Oedothorax retusus (WEST.)							1				**1**
Pocadicnemis pumila (BL.)								10	12	13	**35**
Saaristoa firma (O. P.-C.)	**3**	**4S**			1	1					**2**
Saloca diceros (O. P.-C.)			49	19	17	34	19	7	14	14	**173**
Scotargus pilosus SIMON	**R**	**4S**			1	3					**4**
Tapinocyba pallens (O. P.-C.)			6	3	23	21	15	25	27	13	**133**
Thyreosthenius biovatus (O. P.-C.)	**G**	**4S**	1								**1**
Walckenaeria antica (WIDER)							3	14	13	28	**58**
Walckenaeria atrotibialis O. P.-C.				2	1	1	11	8	20	42	**85**
Walckenaeria cucullata (C. L. K.)									15	1	**199**
Walckenaeria furcillata (MENGE)									5	2	**7**
Walckenaeria obtusa BL.									1		**1**
TETRAGNATHIDAE (3 species)											
Metellina merianae (SCOP.)			1								**1**
Metellina segmentata (CL.)				1			1				**2**
Pachygnatha clercki SUND.										1	**1**
ARANEIDAE (1 species)											
Araneus diadematus CL.						1		1			**2**
LYCOSIDAE (6 species)											
Alopecosa taeniata (C. L. K.)		**4S**			1	1	5	48	9	2	**66**
Arctosa maculata (HAHN)	**2**	**3**								1	**1**
Aulonia albimana (WALC.)									1		**1**
Pardosa alacris (C. L. K.)				1	3	1	16	26	40	45	**132**
Pardosa riparia (C. L. K.)									1		**1**
Trochosa terricola TH.			9	10	26	12	45	80	38	36	**256**
AGELENIDAE (2 species)											
Histopona torpida (C. L. K.)			85	66	33	49	27	17	5	4	**1**
Tegenaria silvestris L. K.			2	1				1			**4**
CYBAEIDAE (1 species)											
Cybaeus tetricus (C. L. K.)	**G**	**4S**	42	22	45	53	25	25	28	22	**262**
HAHNIIDAE (2 species)											
Cryphoeca silvicola (C. L. K.)			3	3	1	1	2				**10**
Hahnia ononidum SIMON					1						**1**
DICTYNIDAE (1 species)											
Cicurina cicur (FABR.)			1	1	1				1	2	**6**
AMAUROBIIDAE (4 species)											
Amaurobius fenestralis (STRO.)				1	2						**30**
Callobius claustrarius (HAHN)			36	48	12	27	9	7			**139**
Coelotes inermis (L. K.)			73	73	82	89	51	60	35	70	**533**
Coelotes solitarius L. K.	**R**	*****	27	28	29	32	14	17	6	3	**156**
LIOCRANIDAE (2 species)											
Agroeca brunnea (BL.)				1				1	5	2	**9**
Phrurolithus festivus (C. L. K.)										1	**1**
CLUBIONIDAE (4 species)											
Clubiona caerulescens L. K.			2	1							**3**
Clubiona comta C. L. K.			3	2	3	2	1			1	**12**
Clubiona frutetorum L. K.		**4S**			1						**1**
Clubiona terrestris WEST.				1	1		1	1			**4**

Table 2. (cont.)

Species	Red Data List		Study sites								Total
	GRL	BRL	0/Z	0	30/Z	30	50/Z	50	100/Z	100	
CORINNIDAE (1 species)											**41**
Ceto laticeps (CANE.)		**4S**								1	**2**
GNAPHOSIDAE (8 species)											**28**
Drassodes pubescens (TH.)									1	1	**96**
Gnaphosa bicolor (HAHN)	**3**	**3**					1	1	6	1	**1**
Haplodrassus signifer (C. L. K.)								1			**230**
Haplodrassus silvestris (BL.)							2			2	**107**
Micaria fulgens (WALC.)									2		**43**
Zelotes clivicola (L. K.)							1	5	2	3	**11**
Zelotes petrensis (C. L. K.)			1								**1**
Zelotes subterraneus (C. L. K.)			2				4		3	2	**11**
ZORIDAE (2 species)											
Zora nemoralis (BL.)				2					6	1	**9**
Zora spinimana (SUND.)				1			1	1		4	**7**
THOMISIDAE (2 species)											
Xysticus cristatus (CL.)							1				**1**
Xysticus luctuosus (BL.)	**3**	**4R**						1	1		**2**
SALTICIDAE (2 species)											
Euophrys frontalis (WALC.)									1		**41**
Evarcha falcata (CL.)					1				1	1	**3**
Total	**17**	**21**	**815**	**781**	**774**	**915**	**854**	**814**	**589**	**617**	**6159**

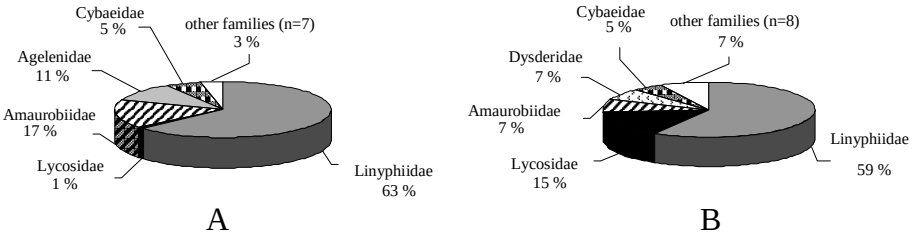

Fig. 2. Percentages of spider families in (a) plot 0/Z (n=815 ind.) and (b) plot 100/Z (n=589 ind.), sampling period: April 23rd 1998 to April 22nd 1999.

Table 3. Structural parameters of the spider assemblages of the study plots according to the catch-results of pitfall traps (n=9) - dominance classification according to ENGELMANN (1978); activity biomass [mg dry weight] according to HENSCHEL et al. (1996). Period of investigation: April 23rd 1998 – April 22nd 1999

	plot							
	0/Z	**0**	**30/Z**	**30**	**50/Z**	**50**	**100/Z**	**100**
number of specimens	815	781	774	915	854	814	589	617
number of species	34	39	46	41	48	45	54	52
number of main species	10	10	16	14	19	17	27	18
activity biomass [mg dry weight]	3109	3075	3194	3298	2715	3664	2343	2320
diversity index α (log series)	7.15	8.69	10.27	8.78	10.99	10.30	14.48	13.62

A	0/Z	0	30/Z	30	50/Z	50	100/Z	100
0/Z	xxx	xxx	xxx	xxx	xxx	xx	x	x
0	0.70	xxx	x	x	xxx	xxx	xx	xx
30/Z	0.65	0.71	xxx	x	xxx	xxx	xx	xx
30	0.65	0.71	0.76	xxx	xxx	xxx	xx	xx
50/Z	0.62	0.66	0.65	0.69	xxx	x	xx	xxx
50	0.53	0.62	0.63	0.67	0.71	xxx	xxx	xxx
100/Z	0.42	0.53	0.53	0.54	0.53	0.63	xxx	x
100	0.45	0.54	0.55	0.57	0.61	0.61	0.75	xxx

B	0/Z	0	30/Z	30	50/Z	50	100/Z	100
0/Z	xxx	xxx	xxx	xx	xxx	x	xxx	xxx
0	1.00	xxx	xxx	xx	xxx	xx	x	xx
30/Z	0.96	0.98	xxx	xx	xxx	xxx	xx	xx
30	0.83	0.86	0.84	xxx	xx	xx	x	xxx
50/Z	0.92	0.94	0.97	0.85	xxx	xxx	x	xx
50	0.77	0.88	1.00	0.82	0.97	xxx	x	xx
100/Z	0.67	0.76	0.84	0.75	0.75	0.76	xxx	xxx
100	0.62	0.81	0.84	0.65	0.84	0.85	0.99	xxx

legend:									
QS	0-0.1	>0.1-0.2	>0.2-0.3	>0.3-0.4	>0,4–0.5	>0.5–0.6	>0.6-0.7	>0.7–0.8	>0.8–0.9	>0.9–1.0
symbol		x	xx	xxx	x	xx	xxx	x	xx	xxx

Fig. 3. Trellis schematic outline for comparing the faunal similarity on the basis of species (A), using the Soerensen index (QS), and with inclusion of numerical abundance (B) according to BRAY & CURTIS (1957).

In the overall trapping, as well as in the catch results of all subplots, the Linyphiidae were dominant with proportions ≥359% (Fig. 1). Furthermore, the different shelterwood cutting intensities up to clear-cutting have led in the 22 years following the operations to a distinct shift in dominance structure. Thus, the proportion of Lycosidae increased with the intensity of opening up the canopy cover. Starting from the subrecedent dominance position (1%) on the control plot (0/Z), Lycosidae were the second most frequent spider family after the Linyphiidae on the heavily-cut shelterwood plot (50) (18.9%) and the clear-cut areas (100, 100/Z) (13.6%, 15.1%) (Fig. 2). Contrary effects were demonstrated for the Agelenidae and the Amaurobiidae: their dominance position decreased with increase in intensity of silvicultural measures (Fig. 2).

The highest relative abundance of Araneae was achieved on the slightly opened-up plot (30). The lowest population densities were found in the clear-cut areas (100, 100/Z), with, in part, highly significant differences to the other experimental variants ($P<0.01$, Mann-Whitney-U test). The increase in stand opening was accompanied by a rise in species richness, which was also reflected by the diversity indices. So, the clear-cuts (100, 100/Z) comprising 52 and 54 species, respectively, appeared to have the highest diversity values α (log series, Table 3).

Likewise, the number of leading species (according to ENGELMANN, 1978) increased with an enhancement of the opening-up of canopies (Table 3). While on 0/Z ten species accounted for 85% of the individuals, the equivalent figure for 100/Z was 27 species of which as many as 12 species (from the families Dysderidae, Lycosidae, Amaurobiidae, Cybaeidae and Linyphiidae) obtained dominant positions while only one species (*Lepthyphantes tenebricola* (WIDER)) reaching 19.1% in the fenced control plot.

T a b l e 4. Characteristic species for respective intensities of opening-up canopies: Niche width, number of individuals, dominance of individuals [%] and dominance classification according to ENGELMANN (1978) based on the catch-results of pitfall traps (n=9); sampling period: April 23rd 1998 – April 22nd 1999.

species	niche width	No. of individuals 0	30	50	100	dominance of individuals [%]	dominance classification
Walckenaeria atrotibialis O. P.-C.	0.24	2	2	19	62	1.40	subdominant
Diplocephalus picinus (BL.)	0.11	0	11	69	1	1.32	
Alopecosa taeniata (C. L. K.)	0.16	0	2	53	11	1.10	recedent
Micrargus herbigradus (BL.)	0.06	0	0	5	53	0.90	
Walckenaeria antica (WIDER)	0.24	0	0	17	41	0.90	
Agyneta ramosa JACK.	0.02	0	1	0	40	0.67	
Pocadicnemis pumila (BL.)	0.23	0	0	10	25	0.57	
Lepthyphantes mansuetus (TH.)	0.03	0	1	0	22	0.37	subrecedent
Ceratinella brevis (WIDER)	0.06	0	2	0	21	0.37	
Lepthyphantes flavipes (BL.)	0.03	0	1	0	21	0.36	
Gongylidiellum latebricola (O.P.-C.)	0.05	0	0	1	14	0.24	
Lepthyphantes mengei KULC.	0.16	2	0	0	8	0.16	
Gnaphosa bicolor (HAHN)	0.18	0	0	2	7	0.15	
Zora nemoralis (BL.)	0.18	2	0	0	7	0.15	
Agroeca brunnea (BL.)	0.20	1	0	1	7	0.15	

The highest activity biomass occurred in the unfenced heavily-cut shelterwood plot (50). Here too the clear-cuts significantly differed, with the lowest activity biomass being found in the control plots as well as in the unfenced opened-up areas (30, 50).

The estimation of the index of similarity using the Soerensen-quotient, according to MAGGURRAN (1988), yielded medium to high levels of coincidences between the plots (Fig. 3A). The clear-cut areas (100, 100/Z) were an exception. They clearly differed from the rest of the experimental variants, with the degree of faunal similarity decreasing with increasing levels of canopy opening. Thus, the lowest coincidence in species structure of spider assemblage was between 0/Z and 100/Z.

As it has been proven by the high Soerensen indices between the fenced and unfenced plots of the same management variant, the exclusion of game had hardly any effect on the faunal similarity of the plots. Also, the control (0) and the plots subjected to slightly-cut shelterwood (30, 30/Z) were largely congruent regarding species structure. Similar tendencies became apparent when including the activity densities of the species in the algorithm of the similarity index, according to BRAY, CURTIS (1957), with an overall trend of higher similarity values (Fig. 3B).

Out of the 15 characteristic species (Table 4) 13 taxa were specifically dependent on the clear-cut area (100, 100/Z). Only two species had high preferences for the heavily-cut shelterwood (50, 50/Z), whereas no characteristic species could be identified for the other plots.

Discussion

With a total of 97 species from 19 families the study plots were characterised by a spider assemblage of high species richness, with a dominance structure typical for forests (HUHTA, 1965). Using pitfall traps, STEINBERGER, MEYER (1993) sampled in similar studies carried out on comparable sites of Vorarlberg (beech mixed forest, northern aspect, elevation: 870 m a.s.l.) 40 species from nine families (diversity index α (log series): 7.93) – a result coinciding well with the species richness of the control plots (34 or 39 species). Thus, the high species diversity of the present investigation is chiefly attributable to plots with silvicultural operations and the resultant alterations in structural (vegetation layer) and microclimatic parameters. As compared with the control, opening-up canopies led to a denser and more structured ground vegetation as well as to an increase in irradiation intensity beneath the soil surface (Table 1, BURSCHEL et al., 1992). Species such as *Micaria fulgens* (WALCKENAER), *Xysticus luctuosus* (BLACKWALL) and *Lepthyphantes flavipes* (BLACKWALL), which, according to their autecological demands are classified as steno- or mesoxerophilic (MAURER, HÄNGGI, 1990), were largely found on the plots with a high degree of canopy opening, and thus preferred thermal relations (50, 50/Z, 100, 100/Z).

The structural parameters (total individuals, species richness) of the spider assemblage, as well as the data of the similarity indices, corroborate the results obtained by HUHTA (1965). This author found, subsequent to clear cutting measures in coniferous stands, a decrease in relative abundance as well as a change of the spider fauna, which correlated with the intensity of cut. This agrees in this study with the relationship that an increasing intensity of cut results in decreasing similarity values (according to Soerensen) between the control and the treated plots. As short-term effects, JENNINGS et al. (1988) ascertained both a higher numerical abundance and numbers of species on clear-cut areas as compared with forest stands. The significantly reduced activity biomass of the spiders on the clear cut plots (100, 100/Z) contrasts with the results obtained by HUHTA (1965, 1971), who found after an initial breakdown of the original spider population an increase in biomass due to an increased occurrence of wolf spiders on the clear-cuts. In this study the increased occurrence of Lycosidae on the plots with heavily-cut shelterwood (50, 100, 100/Z) could not compensate for the decline of Agelenidae and Amaurobiidae.

The absence of characteristic species in the control (0, 0/Z) or in the slightly opened-up plots (30, 30/Z) can be explained by the fact that silvicolous spider species in most cases are habitat generalists (VÄISÄNEN, BISTRÖM, 1990) which are also able to colonise open habitats, thus being likewise represented on the treated areas.

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PREDICTION OF SPIDER SPECIES OCCURRENCE: AN EXAMPLE USING THERIDIID SPIDERS (ARANEAE)

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Abstract

KASAL P., HLADÍKOVÁ M., HÄNGGI A.: Prediction of spider species occurrence: an example using theridiid spiders (Araneae). In GAJDOŠ P., PEKÁR S. (eds): Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava), Vol. 19, Supplement 3/2000, p. 119-124.

An attempt to predict spider species occurrence is described, using theridiid spiders as an example. Data from the database of Middle European spiders was evaluated to describe the relationships among the occurrence of spider species using the Jaccard coefficient and cluster analysis. Common "non-specific neighbour" species are eliminated in this way – they are often found with a spider in question but have a minimum indication value. The result of such an analysis is a list of the species occurring regularly with the given spider without any other relation to the features of the habitat. A possible use of such knowledge could be, for instance, the search for a certain species in the given place on the basis of the neighbour's occurrence discovered by previous collection.

Introduction

Numerous authors have described the relation between specific spider fauna and different biotopes. In this connection various efforts exist to classify the relations between species and phytocenosis, or even to define the spider community (LUCZAK, 1954; ŠMAHA, PĚNIČKA, 1989; VAN HELSDINGEN, 1997; GAJDOŠ, 1995). However, the same spider species are often found in different plant associations. Factors characterising plant ecological demands are often different from the factors affecting spider occurrence. In fact, the number of spider species is not strongly correlated with the plant species, but to a greater extent, depends on the spatial structure and microclimate of the environment (DUFFEY, 1966; CLAUSEN, 1986). The physical structure of the habitat also has a profound effect on habitat selection

(Robinson, 1981; Merkens, 1997). Thus these distributions may also reflect responses of the populations to competition for prey, or mates, rather than a pure preference for micro-habitat or microclimate (Snazell, 1982).

The main problem is that the factors influencing occurrence are very complex. For this reason it is very difficult to predict the presence of a species in a specific locality. The species typical for the appropriate habitat may or may not be present in such a locality. Finding a peatbog species in a peatbog is not surprising. On the other hand, a forecast of existence of a given species entirely in a particular peatbog is not at all certain to be true.

To solve the given question from this point of view, spider groups occurring together without a necessary relation with habitat features can be evaluated. The intention of the paper is the verification of the method of estimation of such groups. Possible use of the obtained knowledge could be, for instance, the forecast of the presence of a certain species according to the presence of other species of the mentioned group after previous collection in the given locality.

Material and methods

For solving the described problem, the evaluation of the theridiid spiders was performed using the database published in Hänggi et al. (1995). This database contains a list with the most abundant species collected together with the presented species. For brevity, we introduce the term „neighbour" for such species. However, the problem is that this list contains mostly common species, which we can call „non-specific neighbours". For example, *Trochosa terricola* (Thorell) is a very frequent species collected along with many different spiders. However, we search for specific neighbours, i.e. species that occur most frequently together with the spider in question but occur independently in few cases.

To search for a specific neighbour we used the Jaccard coefficient. Given two spiders, when A is an independent occurrence of the 1st spider, B an independent occurrence of the 2nd and C the occurrence of both together, then the Jaccard coefficient is equal to $C/(A + B + C)$. Cluster analysis was used to create dendrograms.

Results

An example of the result of Jaccard coefficient computing is shown in Fig. 1. The left part of the figure shows the most abundant species published in Hänggi et al. (1995), the right part is the result of computing (the rank order of spiders with highest Jaccard coefficients). The comparison shows that specific neighbours are species mostly different from the non-specific neighbours.

The co-occurrence of theridiids was evaluated by cluster analysis using all habitats in the database. In Fig. 2, discrimination into several groups was demonstrated: 1- Species living in trees and shrubs, 2- xerophilic spiders, 3- steppe spiders, 4- synanthropic species. Studying the first group, we can see large differences in terms of co-occurrence. For instance *Theridion pinastri* L. Koch and *Theridion tinctum* (Walckenaer), typical of pine forests, are very close. On the other hand, *Theridion pictum* (Walckenaer), which is found regularly on the banks of ponds, is distant from all others.

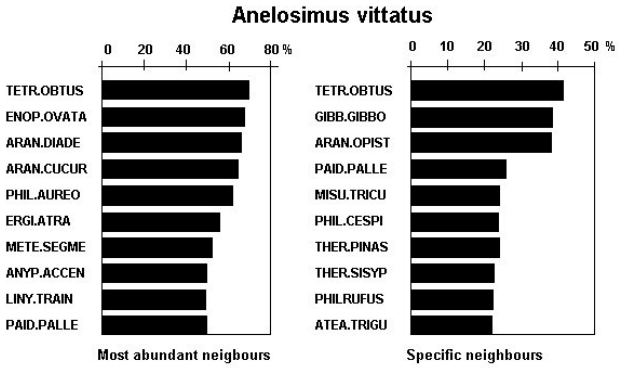

Fig. 1. Comparison of most abundant neighbours and specific neighbours.

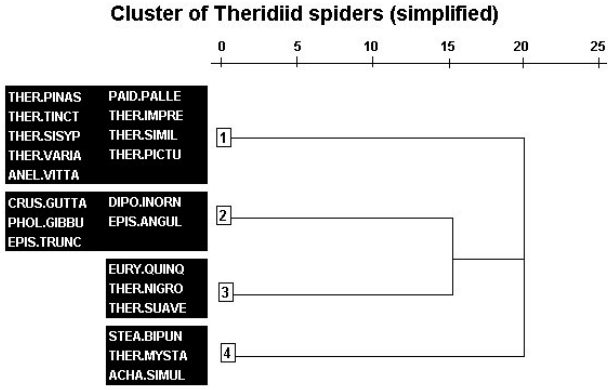

Fig. 2. Clusters of theridiid spiders (simplified).

To determine the specific neighbours of theridiid spiders living in trees and shrubs among all other spiders, it was necessary to eliminate those species that are common everywhere. For this purpose the specific neighbours were estimated by means of the Jaccard coefficient. In the second step, the first group from Fig. 2, with their specific neighbours, was evaluated using cluster analysis. These are the different spider communities characteristic of taller vegetation. Individual groups delimited in such a way are demonstrated in Fig. 3.

On the basis of evaluation of specific neighbours, an opportunity to estimate the probability of theridiid spider occurrence is presented. This probability is estimated as the highest frequency of combination of a given species with specific neighbours found in the database. We can see in Fig. 1 that there are several subgroups existing among specific neighbours of *Anelosimus vitatus* C. L. Koch.

Example: By data processing in the database, *A. vittatus* was found in combination with its specific neighbours (*Araniella opisthographa* (KULCZYŃSKI) and *Misumenops tricuspidatus* (FABRICIUS) in 95% of cases. The interpretation of this result: when we find *A. opistographa* and *M. tricuspidatus*, then *A. vitatus* should be expected in 95% of cases.

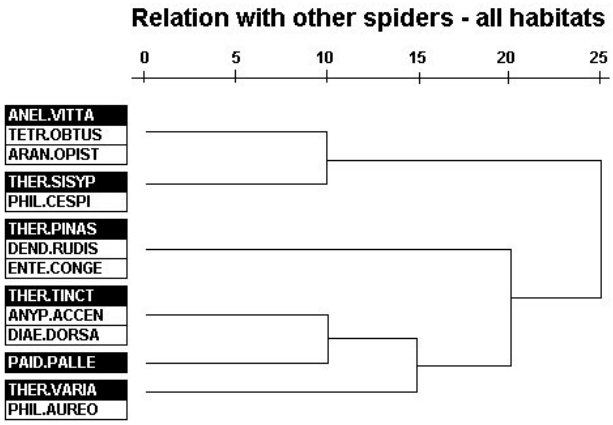

Fig. 3. Relations of theridiid spiders with other spiders in all habitats.

To verify the efficiency of predictions, the test of relevance was performed. To predict the occurrence of the species, the following sources were used: Czech faunal list RŮŽIČKA et al. (1996) and the data from the Swiss database HÄNGGI et al. (1995). The Swiss database was used as a training set of data for computing Jaccard coefficients. Czech species lists were used as a test set of data. We have tried to predict the presence of theridiid spiders (supposed to be unknown) according to the rest of the species in the lists. First, particular combinations of occurrence of individual theridiids in relation to a specific locality were inputted. Then we searched for the actual presence of the predicted species. In other words, using specific neighbours, the estimation was performed to ascertain if the present species could be really expected. The preliminary results of the test are as follows: in 13 localities 14 theridiid species were present. A successful prediction on the basis of computed combinations was 10 species, i.e. 71%. In all cases the list has to contain more than 30 species, because a lover number of species could influence the efficiency of computing probabilities.

Discussion

A spider community is a group of species which are often found together. Such a species group is usually composed of different kinds of species: Some species are found very frequently together in the specific type of habitat studied, but it is also possible to find them in other habitat types. Other species are found quite rarely, but exclusively in this particular habitat type and nowhere else Merkens (1997). The supposed reason for this fact is the very complex effect of individual ecological factors. In this connection Martin (1991) does not evaluate spider habitat preferences in relation to phytocenoses, but with more general features of habitat, which is similar to our concept. If phytocenosis is used in the last case for this purpose, then it is more often as the complex feature of habitat, for instance by means Ellenberg's method (Kropf, 1993).

Cluster analysis (in our paper in additional combination with the Jaccard coefficient) is actually often used for the evaluation of the complex relations between species and environment. Many papers evaluating occurrence of spider communities use multi-dimensional methods, which express the complexity of the factors in question more precisely – Finch (1997), Canard (1997). Bosmans (1986) created dendrograms based on the differences between individual habitats. The distinction into vegetation belts here is not necessarily coincident with the occurrence of spider communities. Similarly, according to multi-dimensional evaluation of heather arachnocenoses, the microclimate conditions are of the higher importance (Kleinmans, 1997).

Efforts to make a prediction of occurrence optimum, as described in Rushton (1991), are not so frequent. On the other hand, our preliminary results concerning prediction possibility show some positive facts, supporting the development of this approach using the described methods.

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CHECKLIST OF HARVESTMEN (OPILIONES) OF CZECHIA AND SLOVAKIA

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Abstract

Klimeš L.: Checklist of harvestmen (Opiliones) of Czechia and Slovakia. In Gajdoš P., Pekár S. (eds): Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava), Vol. 19, Supplement 3/2000, p. 125-128.

A checklist of harvestmen of Czechia and Slovakia is presented, with notes on selected species. Currently 28 species are known from Bohemia, 30 from Moravia (i.e. 33 from the Czech Republic), and 33 species from Slovakia.

Introduction

The first checklist of harvestmen of a region within the current Czech and Slovak Republics was published by Bárta (1869; a Czech version of this paper was published in 1870), who presented a list from the north of Bohemia. He named seven species, of which one was later synonymized with another species. After more than 30 years Nosek (1900) published an identification key for harvestmen in Bohemia and Moravia. Out of his taxa 20 are currently accepted species with 19 species known from Bohemia and one from Moravia. It took 34 years before the next attempt to summarise the knowledge on harvestmen of the territory of the former Czechoslovakia was published. It was Kratochvíl (1934), who presented the first critical account of harvestmen from Czechoslovakia. He was also the first who paid serious attention to the Slovak fauna. Kratochvíl (op. cit.) confirmed the occurrence of 50 "forms" (species and subspecies; p. 2) in the country. When synonymous taxa are removed, 26 species from Bohemia, 21 species from Moravia, and 32 species from Slovakia remain. During the following nearly 50 years the literature on the Czech and Slovak harvestmen was dominated by Vladimír Šilhavý. In 1956 he published a monograph on the harvestmen of Czechoslovakia (Šilhavý, 1956). The numbers of species confirmed by him for Bohemia, Moravia and Slovakia were 29, 24 and 32, respectively. These are not much higher estimates than those given in the previous treatment by Kratochvíl (1934),

T a b l e 1. Harvestmen (Opiliones) recorded from Czechia and Slovakia.

		Bohemia	Moravia (incl. Silesia)	Czech Republic (=Bohemia+ Moravia)	Slovakia
	EREBOMASTRIDAE				
1.	*Holoscotolemon jaqueti* (CORTI, 1905)[1]	-	-	-	*
	SIRONIDAE				
2.	*Siro carpaticus* RAFALSKI, 1956	-	-	-	*
	NEMASTOMATIDAE				
3.	*Mitostoma chrysomelas* (HERMANN, 1804)	*	*	*	*
4.	*Nemastoma bidentatum* ROEWER, 1914 subsp. *sparsum* GRUBER ET MARTENS, 1968	-	-	-	*
5.	*Nemastoma lugubre* (MÜLLER, 1776)	*	*	*	*
6.	*Nemastoma triste* (C. L. KOCH, 1835)	*	-	*	-
7.	*Paranemastoma kochi* (NOWICKI,1870)	-	*	*	*
8.	*Paranemastoma quadripunctatum* (PERTY, 1833)	*	*	*	*
	TROGULIDAE				
9.	*Dicranolasma scabrum* (HERBST, 1799)	-	-	-	*
10.	*Trogulus nepaeformis* agg.	*	*	*	*
11.	*Trogulus tricarinatus* (LINNAEUS, 1767)	*	*	*	*
	ISCHYROPSALIDIDAE				
12.	*Ischyropsalis hellwigi* (PANZER, 1794) subsp. *hellwigi*	*	*	*	-
13.	*Ischyropsalis manicata* L. KOCH, 1869	-	*	*	*
	PHALANGIIDAE				
	PHALANGIINAE				
14.	*Egaenus convexus* (C. L. KOCH, 1835)	-	*	*	*
15.	*Lophopilio palpinalis* (HERBST, 1799)	*	*	*	*
16.	*Opilio canestrinii* (THORELL, 1876)[2]	*	*	*	*
17.	*Opilio dinaricus* ŠILHAVÝ, 1938	-	-	-	*
18.	*Opilio parietinus* (DE GEER, 1778)	*	*	*	*
19.	*Opilio saxatilis* C. L. KOCH, 1839	*	*	*	*
20.	*Phalangium opilio* LINNAEUS, 1761	*	*	*	*
21.	*Platybunus bucephalus* (C. L. KOCH, 1835)	*	*	*	*
22.	*Platybunus pallidus* ŠILHAVÝ, 1938	-	*	*	*
23.	*Rilaena triangularis* (HERBST, 1799)	*	*	*	*
24.	*Zachaeus crista* (BRULLÉ, 1832)	-	*	*	*
	OLIGOLOPHIINAE				
25.	*Oligolophus tridens* (L. KOCH, 1836)	*	*	*	*
26.	*Lacinius dentiger* (C. L. KOCH, 1848)	*	*	*	*
27.	*Lacinius ephippiatus* (C. L. KOCH, 1835)	*	*	*	*
28.	*Lacinius horridus* (PANZER, 1794)	*	*	*	*
29.	*Mitopus morio* (FABRICIUS, 1799)	*	*	*	*
	GYANTINAE				
30.	*Gyas titanus* SIMON, 1879	*	*	*	*
31.	*Dicranopalpus* sp.[3]	-	-	-	*
	SCLEROSOMATINAE				
32.	*Astrobunus laevipes* (CANESTRINI, 1872)	*	*	*	*
	LEIOBUNUNAE				
33.	*Leiobunum blackwalli* MEADE, 1861	*	-	*	-
34.	*Leiobunum limbatum* L. KOCH, 1861	*	*	*	-
35.	*Leiobunum rotundum* (LATREILLE, 1798)	*	*	*	*
36.	*Leiobunum rupestre* (HERBST, 1799)[4]	*	*	*	-
37.	*Leiobunum tisciae* AVRAM, 1968[4]	*	*	*	*
38.	*Nelima gothica* LOHMANDER, 1945	*	-	*	-
39.	*Nelima semproni* SZALAY, 1951	*	*	*	*
	Total number of species	28	30	33	33

[1] A subadult specimen has recently been found in the Cerová vrchovina Mts. (FRANC, MLEJNEK, 1999). [2] Recently recorded also from Slovakia (KLIMEŠ, 1999). [3] Only immature specimens have been collected so far (KRATOCHVÍL, 1934; PEKÁR, in litt.). Two species of *Dicranopalpus* have been recorded in eastern Europe: *D. gasteinensis* DOLESCHAL, 1852 (WEISS, 1996) and *D. fraternus* SZALAY, 1950. They were tentatively synonymized by MARTENS (1978). More collecting is needed to revise the genus in the area. [4] ŠILHAVÝ (1981) was the first who distinguished in former Czechoslovakia within the *Leiobunum rupestris* aggregate two species. The species distributed in Slovakia, named *L. glabrum* by Šilhavý, is hardly conspecific with *Nelima glabra*, which was described from Tirol. Thus, the name *L. tisciae* AVRAM, 1968 should be used for the species distributed in Slovakia (see also WEISS, 1996).

Fig. 1. Map of Central Europe with Bohemia and Moravia (incl. Silesia) as historic countries within the Czech Republic. Total number of harvestmen species in individual neighbouring countries is given in brackets.

but numerous earlier errors were corrected. In the early 1970s Šilhavý published a key for the harvestmen of Czechoslovakia (ŠILHAVÝ, 1971), in which the number of confirmed species further decreased (23, 23 and 28, respectively, for the three regions). The critical account of Central-European harvestmen by MARTENS (1978) did not change the overall picture of our opilionid fauna. Two species were added to the Moravian fauna, whereas in Bohemia and Slovakia the number of confirmed species remained unchanged, in spite of a few corrections and new records.

During the last 20 years several more species have been found, so that at present 28 species of harvestmen are known from Bohemia, 30 from Moravia (33 together) and 33 species from Slovakia (Table 1, Fig. 1). This increase was partly caused by the recent spreading of two synanthropic species (*Leiobunum limbatum* L. KOCH and *Opilio canestrinii* (THORELL); nomenclature follows MARTENS, 1978; CRAWFORD, 1992 (*Zachaeus*); GRUBER, 1985 (*O. canestrinii*)) to Bohemia and Moravia (KLIMEŠ, ROUŠAR, 1998; KLIMEŠ, 1999, unpubl.), by new records of species expected in Slovakia by earlier authors (*Siro carpaticus* RAFALSKI (MAŠÁN, 1998); *Holoscotolemon jaqueti* (CORTI) (FRANC, MLEJNEK, 1999) as well as by a few other records (*Leiobunum tisciae* AVRAM in the Czech Republic (ŠILHAVÝ, 1981; KLIMEŠ, unpubl.; *Nelima gothica* LOHMANDER in Bohemia (ROUŠAR, in litt.); *Nelima semproni* SZALAY in Bohemia (ROUŠAR, 1998); *Egaenus convexus* (C. L. KOCH) in SE Moravia and the occurrence of *Zachaeus crista* (BRULLÉ) in south-eastern Moravia discovered by KRATOCHVÍL (1934) and neglected by later authors, was confirmed by KLIMEŠ, ROUŠAR (1998)).

In spite of the effort of harvestmen collectors and taxonomists there are still several problems to be solved. For example, a revision of the aggregate *Trogulus nepaeformis* in the whole distribution area is needed, occurrence of *Nemastoma bidentatum* subsp. *sparsum* GRUBER ET MARTENS in Slovakia should be confirmed, and *Dicranopalpus* sp. from Slovakia

should be identified. Several new species can be expected, such as *Opilio ruzickai* Šilhavý, 1938 in southern Moravia and southern Slovakia (synanthropic; see Gruber, 1964 and Komposch, 1993 for data from Austria), and possibly *Paranemastoma silli* (Herman, 1871) in eastern Slovakia. Among the old and never confirmed records, that of *Amilenus aurantiacus* (Simon, 1881) from central Slovakia (Kratochvíl, 1934) should be mentioned.

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COMPARATIVE HISTOLOGY OF THE VENOM GLANDS IN A LYCOSID AND SEVERAL OXYOPID SPIDERS (ARANEAE)

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Abstract

Kovoor J., Muñoz-Cuevas A.: Comparative histology of the venom glands in a lycosid and several oxyopid spiders (Araneae). In Gajdoš P., Pekár S. (eds): Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava), Vol. 19, Supplement 3/ 2000, p. 129-140.

The structure and histochemistry of the poison glands are described in *Lycosa tarentula* (Lycosidae), four *Peucetia* species and *Oxyopes lineatus* (Oxyopidae). All these species show two voluminous poison gland sacs which extend dorsally in the prosoma, over the central nervous system, their base reaching up to the central body of the brain. A muscle layer surrounds the gland sac; it is thicker in *Lycosa* than in the oxyopids and stops at the beginning of the excretory duct. The latter, rather narrow in *Lycosa*, starts at the base of the chelicera. It forms a secretory ampulla in the last third of the chelicera, then continues its way for about 400 µm to the entrance of the fang. In oxiopids, the gland sac itself enters the chelicera. An elongated ampulla appears at a quarter (*Peucetia*) or half (*Oxyopes)* the length of the cheliceral basal article) and reaches almost the extremity of the chelicera: the excretory duct proper runs only 40 µm before entering the fang. In all cases, the body of the glands presents two distinct regions secreting different substances. In *L. tarentula*, the main part of the poison gland secretes a complex protein product, with a fine granular appearance; a small accessory lobe, located ventrally in the proximal region of the gland sac, produces a glycoprotein. In oxyopids, the accessory portion of the gland is much more extensive; both regions produce protein; in the ventral proximal pouch, two substances are detected, one of which appears as flat square crystals, isolated inside the cells but stacked up in the gland lumen. The histological characteristics of the poison glands are examined from a phylogenetic point of view, as well as in relation to the behaviour of these species of hunting spiders.

Introduction

The contents of venom glands are better known than their structure and secretory process, especially in some species, such as *Atrax robustus*, *Latrodectus mactans*, *Loxosceles laeta* or *Phoneutria nigriventer*, the bites of which are dangerous to man. However,

Reese (1944), Smith, Russell (1967) and Smith et al. (1969) have published precise histological data on the venom glands of *Latrodectus mactans*. The microscopical anatomy of cheliceral glands in species belonging to 29 families of spiders, including two mygalomorphs living in France, was briefly described by Millot (1931). From this general work, the histophysiology of the venom glands of particular species could be studied. Legendre (1953), in an article treating the prosomal glands of *Tegenaria*, showed that the venom of the cheliceral glands was composed of two different secretory products. Much later, Wasowska (1969) followed the variation of the epithelium of these glands during the secretory cycle in *Tegenaria atrica.* The histochemical characteristics of agelenid venoms were furthermore reported by several authors (Gabe, 1959; Suomalainen, 1964; De Luca, 1965; Arvy, 1966).

Some cheliceral glands of spiders exhibit two or more regions secreting different products. This complexity has been demonstrated in *Latrodectus* (Barth, 1962; Smith, Russell, 1957), *Pholcus* (Kovoor, Zylberberg, 1971), *Scytodes* (Millot, 1930, 1931; Kovoor, Zylberberg, 1972), *Argyroneta*, *Gallieniella* (Lopez, Llinares, 1973; Lopez, 1977), *Desidiopsis* (Lopez, 1976) and also in several Salticidae and Thomisidae (Lopez, 1977).

In the present paper, we analyse and comment on the structure and histochemistry of venom glands that were never previously studied, in adult specimens of a lycosid and 5 oxyopid species. Developmental aspects of venom-, silk-gland and visual systems in two *Peucetia* species have been published earlier (Kovoor, Muñoz-Cuevas, 1995). Meanwhile, visual and behavioural activity rhythms of the same lycosid and oxyopid spiders have been under investigation for several years (Kovoor, Muñoz-Cuevas, 1998; Kovoor et al., 1992, 1995, 1999).

Material and methods

The burrowing lycosid spider, *Lycosa tarentula* (Linneus), was collected in Spain, in the vicinity of Canto Blanco (Madrid) University campus. Five oxyopid species were studied: *Peucetia cauca* Lourenço, 1990 (8 animals) from Colombia (Valle del Cauca); *P. gerhardi* van Niekerk et Dippenaar-Schoeman, 1994 (12 animals) from Nigeria (100 km from Port-Harcourt); *P. graminea* Pocock, 1900 (2 specimens) from Thailand (20 km from Bangkok); *P. viridis* (6 specimens) from Southern Spain (Altea); and *Oxyopes lineatus* Latreille, 1806 (12 specimens), found in the Réserve naturelle of Nohčdes (Pyrénées orientales, France). The prosoma of adult males and females was cut off and fixed in Bouin's fluid, dehydrated in 95% ethanol and preserved for three months in n-butanol before embedding in paraffin. Transverse and longitudinal sections (6 µm thick) were stained by classical general methods. Histochemical reactions and specific staining methods were used to visualize a) *anionic groups* and *polysaccharidic substances*: P.A.S. reaction, alcian blue, aldehyde fuchsin and toluidine blue staining; b) *proteins*: Danielli's coupled tetrazonium reaction, Morel and Sisley's reaction for tyrosin, aldehyde fuchsin, lead and phosphotungstic hematoxylin staining, and Adams's ferricyanide reaction for sulfhydryl and other reducing groups. Technical procedures are detailed in the handbooks of Gabe (1968) and Lillie, Fullmer (1976).

T a b l e 1. Main staining affinities and histochemical characteristics of the venom gland in *L. tarentula*, *Peucetia* species and *O. lineatus.* Technical references : (1) Danielli's coupled tetrazonium reaction (PEARSE, 1960); (2) Morel and Sisley 's reaction (LILLIE, 1965); (3) ferric ferricyanide reaction (ADAMS, 1956); (4) plumbic haematoxylin (SOLCIA et al., 1969); (5) P.A.S.- reaction (MAC MANUS, 1946); (6) aldehyde fuchsine (GABE, 1953).

	Acidophily Basophily	**Basic aminoacids Proline Tyrosine Tryptophan** (1)	**Tyrosine** (2)	**Reducing groups** (3)	**Carboxyl groups** (4)	**Polysaccharides Mucosubstances anionic groups** (5, 6)
L tarentula						
Part A	complex	++	/	±, +	±	0, +
Part B	cyanophilic, basophilic	+++, ++++	/	++	++, +, ±	+++, ++++
Peucetia sp.						
Part A	complex	+	0	±, +, ++	+	0, +
Part B :						
Background	complex	+	0	+	0	0
"crystalls"	basophilic	++	+	±	++	++
O. lineatus						
Part A	complex	+	0	+	0	0
Part B	basophilic	++	0	±	++	+++

Results

Microanatomical data

Cheliceral glands of the lycosid *Lycosa tarentula*, as well as those of the oxyopids *Peucetia* and *Oxyopes* comprise two voluminous sacs applied to the dorsal surface of the central nervous system; they frequently extend behind the central body of the brain, especially in adult females. The excretory duct of the gland begins at the base of the chelicera in *L. tarentula* (Fig. 1). In oxyopids, the gland sac penetrates into the chelicera and the excretory duct is therefore much shorter. It finally opens onto the upper surface of the fang, a little before the tip.

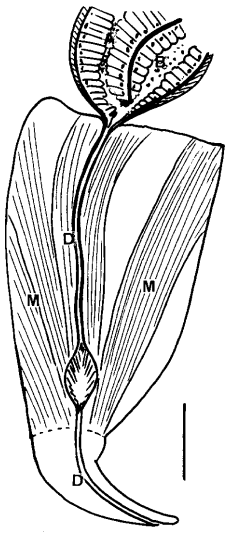

Fig. 1. Diagrammatic representation of a longitudinal section of a chelicera of *Lycosa tarentula* adult female. A, B: main and accessory pouches of the venom gland; D: excretory duct; M: cheliceral muscles. Scale line: 1 mm.

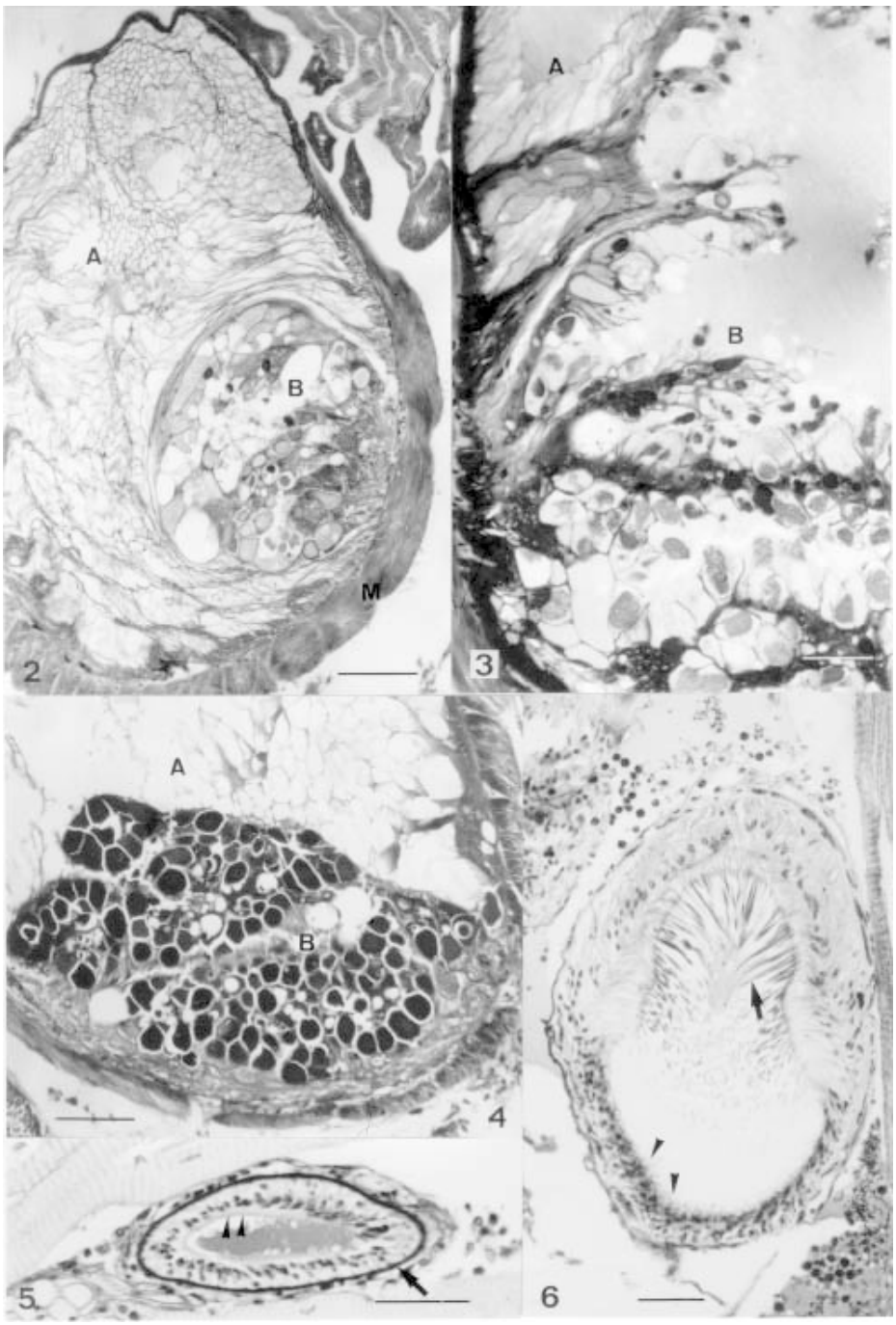
A
B
M
2
A
B
3
A
B
4
5
6

Fig. 2. Oblique section of the anterior part of the venom gland sac in *L. tarentula*. The ventral accessory pouch (B) shows a heterogeneous content: small granules and large vesicles are mixed in the gland lumen. Reducing groups (from *light grey* to *black*) are present in both products. In the main pouch (A), the secretory product, rather homogeneous, reacts weakly (*light grey*). Ferric ferricyanide reaction, orange filter. M: muscle. Scale line: 100 µm.

Fig. 3. Both regions of *L. tarentula* venom gland. In the main region (A), one substance appears homogeneous and cyanophilic; in the accessory pouch (B), one basophilic substance is granular, a second one looks like that of the main region. Masson-Goldner's trichrome, green filter. Scale line: 50 µm.

Fig. 4. B portion of *L. tarentula* venom gland. Strong positive PAS-reaction of the granular secretory product. PAS-reaction, green filter. Scale line: 100 µm.

Fig. 5. Oblique section of the venom gland duct in the frontal part of the basal article of the chelicera. Note the thick basal lamina (*arrow*) surrounding the epithelium of the duct lined by a cuticular intima (*arrow heads*). PAS-reaction, green filter. Scale line: 50 µm.

Fig. 6. Junction of the ampulla to the duct proper, and the end part of it, shortly before it enters into the fang. Note groups of very long microvilli at the apex of high ampulla cells (*arrow*), and short ones in the next portion (*arrow heads*). Phosphotungstic haematoxylin staining, green filter. Scale line: 50 µm.

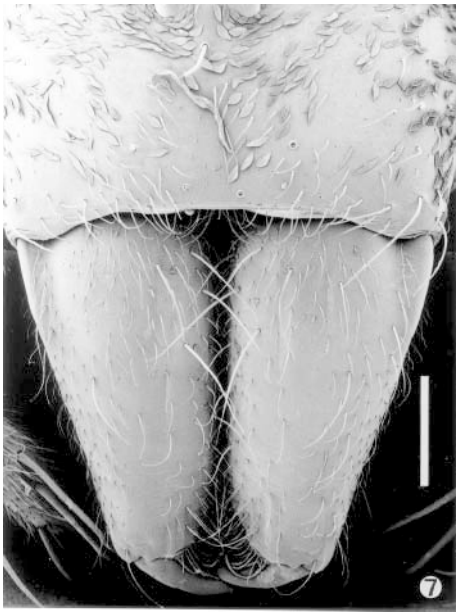

Fig. 7. Frontal view of the clypeus and chelicerae of *Oxyopes lineatus*. Scale line: 0.2 mm.

Gland sac

Venom components are produced in the large pouches of the poison glands. Each gland comprises two distinct regions secreting different substances. In *L. tarentula*, the distal pouch (A) is, by far, the widest. An accessory lobe (B) is appended to the main part in its proximal region, just before the collar of the gland (Figs 1, 2). A single festooned epithelial layer produces the venom which accumulates in the inflated apical part of the cells before being released into the lumen. A dense basal lamina ensures a link between the epithelium and a muscle fibre layer which surrounds the gland sac spirally (Fig. 3). Replacement cells (= substitution cells or qualified "auxillary" cells (Barth, 1962)) are present here and there at the base of the epithelium. The excretory duct is not provided with a muscle cover (Fig. 5), neither is the contact zone between the two pouches (Fig.

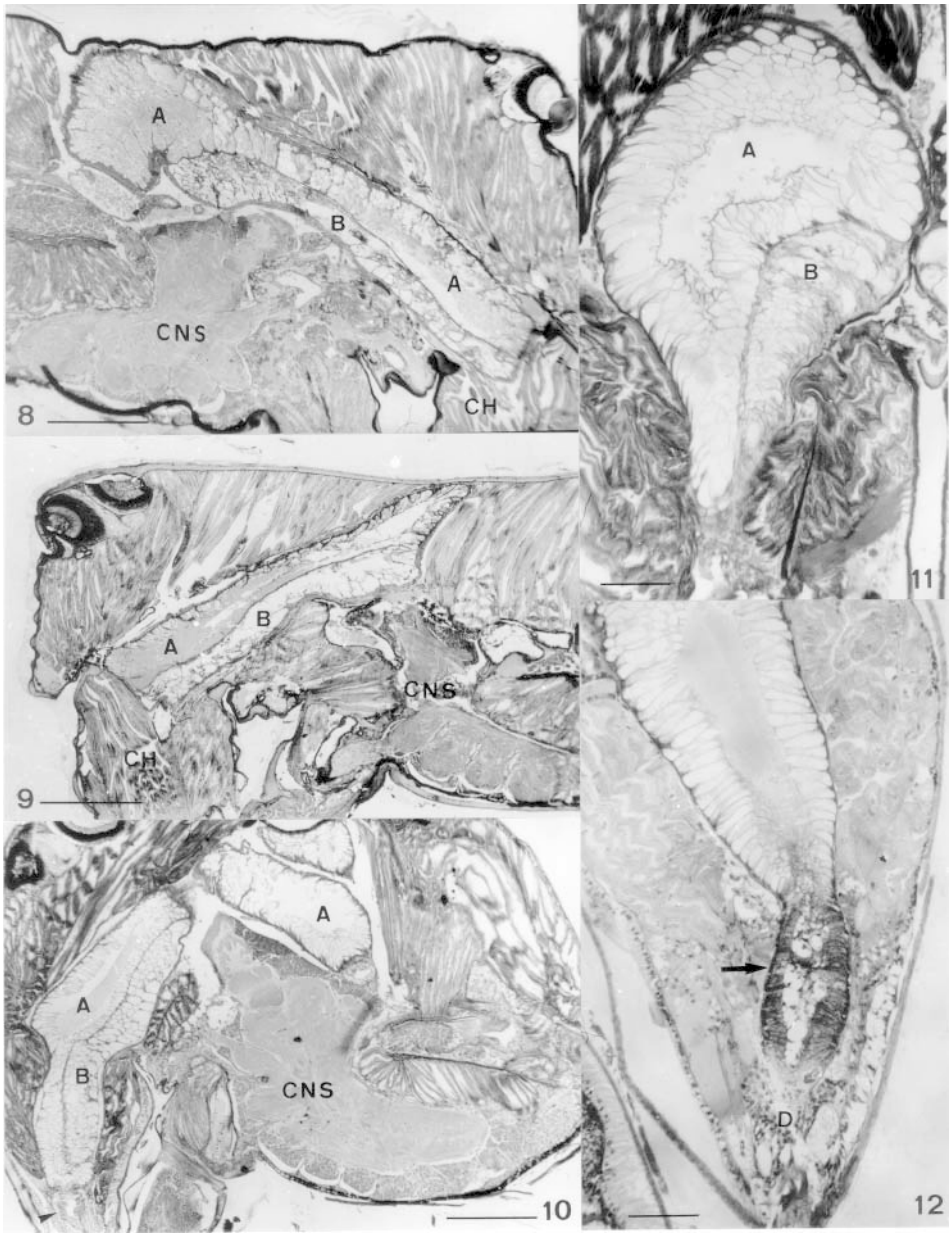

Fig. 8. Parasagittal section of the prosoma of *Peucetia gerhardi* adult female showing the extension of the poison gland sac, dorsally, above the central nervous system (CNS). A: main pouch, B: ventral accessory pouch of the poison gland. CH: chelicera. Ferric ferricyanide, orange filter. Scale line: 0.5 mm.

2). The basic histological structure of the venom glands in oxyopid species studied is the same as that in *L. tarentula*. The muscle layer surrounding the glands is half as thick as in *L. tarentula.* The general shape of the glands is quite irregular and the "accessory" lobe, much elongated, extends to the level of the optic lobes of the brain (Figs 8-10). The double gland sacs are prolonged inside the chelicerae (Fig. 11). Both pouches open into the excretory duct at the same level.

Three different substances have been distinguished from their staining affinities and histochemical characteristics in the venom of all species studied. The largest part of the glands (A) produces a single complex protein product, the staining affinities of which are double, i.e. acidophilic and basophilic. It is generally PAS-negative (Fig. 4), slightly reducing and does not contain histochemically detectable tyrosine. Histochemical differences in the above characters are noticeable in *Oxyopes lineatus*: in the main component of the venom, acidophily and reducing groups are more obvious (Table 1). The accessory pouches (B) secrete two different products in the six species studied, no matter what family they belong to. In *L. tarentula*, the B pouch is very small, but generally full of vesicles of different diameters bathed in a fine granular substance. Both products are proteinaceous with reducing groups and associated with a polysaccharidic fraction (Fig. 4). They are distinguished by their appearance, but also by their eosinophily or cyanophily (Table 1). The four *Peucetia* species obviously differ from *L. tarentula* in the appearance of the secretory products of the B pouch.. The epithelial cells of this pouch synthesise glycoprotein "crystals" and a granular protein substance accumulating in vacuoles (Figs 14-16). Crystals appear at first as short isolated sticks inside the cells (Fig. 15); they progressively enlarge up to a length of 20 µm, and are finally extruded into the lumen where they stack up, forming low piles (4µm) of three or four elements (Fig. 16). The corresponding region of the venom gland of *O. lineatus* secretes two substances showing the same histochemical characters as in *Peucetia* (Fig. 13); few differences appear in their general staining affinities (Table 1).

Fig. 9. Parasagittal section of the prosoma of *Peucetia gerhardi* adult male. Same labels and details as in fig. 7. PAS-reaction, green filter.

Fig. 10. The venom gland of an *Oxyopes lineatus* female entering the chelicera vertically; both regions of the gland run side by side until both open at the junction of the ampulla. One-step trichrome, green filter. Scale line: 100 µm.

Fig. 11. Poison gland sac of *Oxyopes lineatus* adult female, above the CNS, and penetrating the two third of the length of the chelicera where the duct starts as an ampulla (*arrow*). Danielli's coupled tetrazonium reaction, green filter. A: main pouch; B: accessory pouch; CNS: central nervous system. Scale line: 0.3 mm.

Fig. 12. *Oxyopes lineatus*. Proximal end of the poison gland sac, inside the chelicera; the ampulla (*arrow)* is followed by the terminal excretory duct (D) which reaches the fang. PAS-reaction, green filter. Scale line: 100 µm.

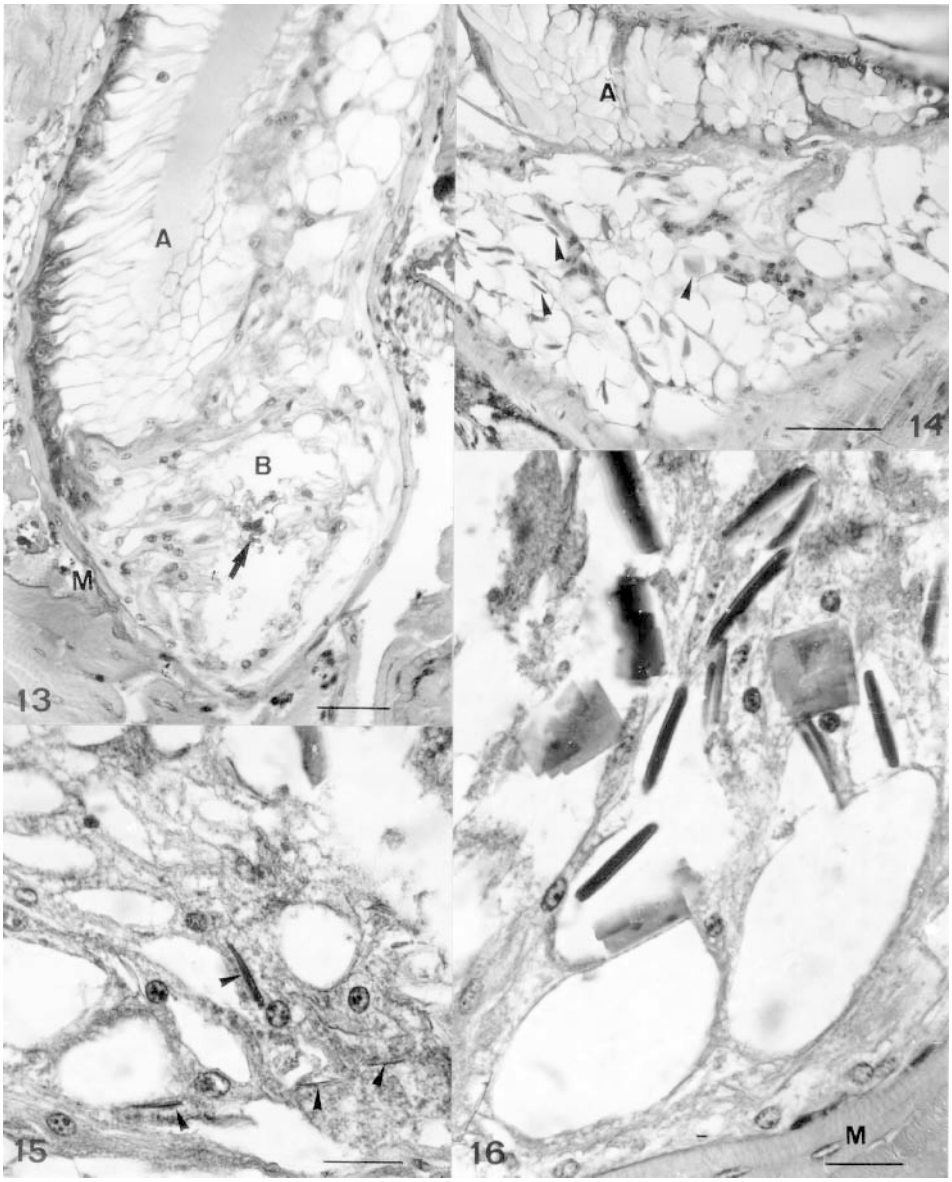

Fig. 13. Aspect of the anterior part of the venom gland of *Oxyopes lineatus*. Histological characteristics of the A and B regions of the gland are obviously different. One secretory product of the B region, granular or crystallised, is PAS-positive (*arrow*). M: muscle. PAS-reaction, green filter. Scale line: 50 µm.

Figs. 14. *Peucetia gerhardi*. A and B regions of the poison gland. One secretory product of B appears as PAS-positive crystals (*arrow heads*). Scale line: 50 µm.

Excretory duct

Lycosa tarentula. The excretory duct, lined by a cuticular intima, starts at the apex of the stout basal article of the chelicera, where the gland sac has narrowed in the shape of a funnel. Its total width varies from 50 to 70 µm, according to the age and size of the adult spiders (Fig. 1). *L . tarentula* adult females can live for more than one year. The duct runs laterally to the sagittal plane of the chelicera, along its frontal wall, for 3.4 mm. At this level, the duct diameter increases to 200 µm and an "ampulla" is formed. It is about 650 µm long and its epithelial cells, 50 µm high, bear long microvilli forming groups of several elements stuck together and almost completely filling the lumen (Fig. 6). Ampulla cells secrete a fine granular glycoprotein substance (PAS- and coupled tetrazonium reactions are positive). In the last third of the ampulla, microvilli progressively decrease in size and appear single (Fig. 6), fine granules still extrude from the cells but they do not react to PAS, and thus seem devoid of a polysaccharide component. From 380 µm to the fang, the last portion of the excretory duct, like its first part, is a narrow, thin-walled tube, internally covered by a cuticular intima.

Peucetia species and *Oxyopes lineatus*. Chelicerae of Oxyopidae are conical, long (*Peucetia*) or rather short (*Oxyopes*, Fig. 7) appendages, with a short but acute fang. The double sac of the poison gland enters the chelicera and fills its summit (Fig.11); it runs into one fifth or a third of the length of the basal article in *Peucetia*, and nearly two thirds in *Oxyopes lineatus* (Fig.12). The excretory duct starts with a secretory part, about 700 µm long and 120 µm wide in *Peucetia* species, shorter (from 260 to 300 µm long) and thicker walled (from 145 to 160 µm wide) in *Oxyopes* (Fig.12). This region corresponds to the "ampulla" present in *L. tarentula* and, similarly to the latter, secretes a glycoprotein substance (Fig.13). The narrow duct proper follows, it runs for 50 to 100 µm only before entering the fang.

Discussion and conclusion

Lycosa tarentula and the five oxyopid species of spider so far studied hunt their prey in the same way, whether at ground level (*L. tarentula*) or above, in foliage (Oxyopidae). When ambushing prey, at the opening of a burrow or on leaves of bushes, these spiders use visual cues along with chemical and mechanical signals to locate a possible prey.

Fig. 15. Aspect of the elaboration of both products in B cells of the venom gland in *P. cauca*. Native crystals are seen in the cytoplasm at different stages of their synthesis (*arrow heads*), together with light vesicles of different sizes. PAS-reaction, green filter. Scale line: 20 µm.

Fig. 16. Crystals, in profile and full face, and large vesicles representing both secretory products of the B pouch of the venom gland of *P. cauca*. M: muscle. PAS-reaction, green filter. Scale line: 20 µm.

They do not spin any web. The capture of prey is mainly dependent on eyesight, speed of movement and venom effectiveness. These three factors seem to be optimised in salticid spiders.

The cheliceral glands of the species studied are very large. The largest, in proportion to the size of the prosoma, are those of *Oxyopes lineatus*. As a whole, the visual performances of *L. tarentula* and *O. lineatus* are similar, but *O. lineatus* feeds on preys that are often larger than itself; and which may be subdued by a large quantity of venom or a very active venom. The shape of the venom glands in Oxyopidae, their thin muscle investment and their wide prolongation inside the chelicerae up to the secretory ampulla of the duct, indicate a massive flow of venom, which may be not only injected into the prey, but also sprayed over it. FINK (1984) observed that *Peucetia viridans* females expelled venom from their fangs straight at objects moving in front of them. This spitting behaviour "most likely serves a defensive function" which has not been described elsewhere.

Nothing of that sort was observed in *L. tarentula*. Anatomically, poison glands of *L. tarentula* resemble those of other Lycosidae, Agelenidae, Argyronetidae, Desidae (LOPEZ, 1977), and most probably of many other hunting or web building araneomorph spiders. The presence of a small anterior accessory pouch, although not indicated by MILLOT in his general work (1931), seems fairly common. It was found in the anterior part of the small cheliceral gland sac of even Salticidae (LOPEZ, 1977; KOVOOR, pers. obs.). In other evolutionary lines, such as in Theridiidae and Pholcidae, the whole anterior collar differs cytologically and histochemically from the rest of the gland. It was first described as the "lipocrine gland" by BARTH (1962) and then by SMITH, RUSSELL (1967) in *Latrodectus mactans*. Similarly, the venom gland of *Pholcus phalangioides* FUESSL. shows two secretory zones that differ both in the form of the cells and in the nature of the secretory products. The collar region secretes a glycoprotein instead of lipid substance (KOVOOR, ZYLBERBERG, 1971). Meanwhile, the extension of the accessory pouch up to a third of the gland length, and its crystallised secretory product, seems, at present, a characteristics of Oxyopidae. It should be noted that the venom filling the excretory duct always looks homogeneous: we could never detect any crystal in this last part of the gland. Crystals are likely to be solubilized in the mixture of the three substances present in the duct.

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We are indebted to Prof. J. Ortega-Escobar (Madrid), Dr W. Lourenço (Paris), Ms S. Jacobs (Berlin) who provided us with living specimens of all spider species needed.

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DESCRIPTION OF THE STRIDULATORY APPARATUS IN SOME SPECIES OF THE GENUS *RHOPALURUS* THORELL (SCORPIONES: BUTHIDAE)

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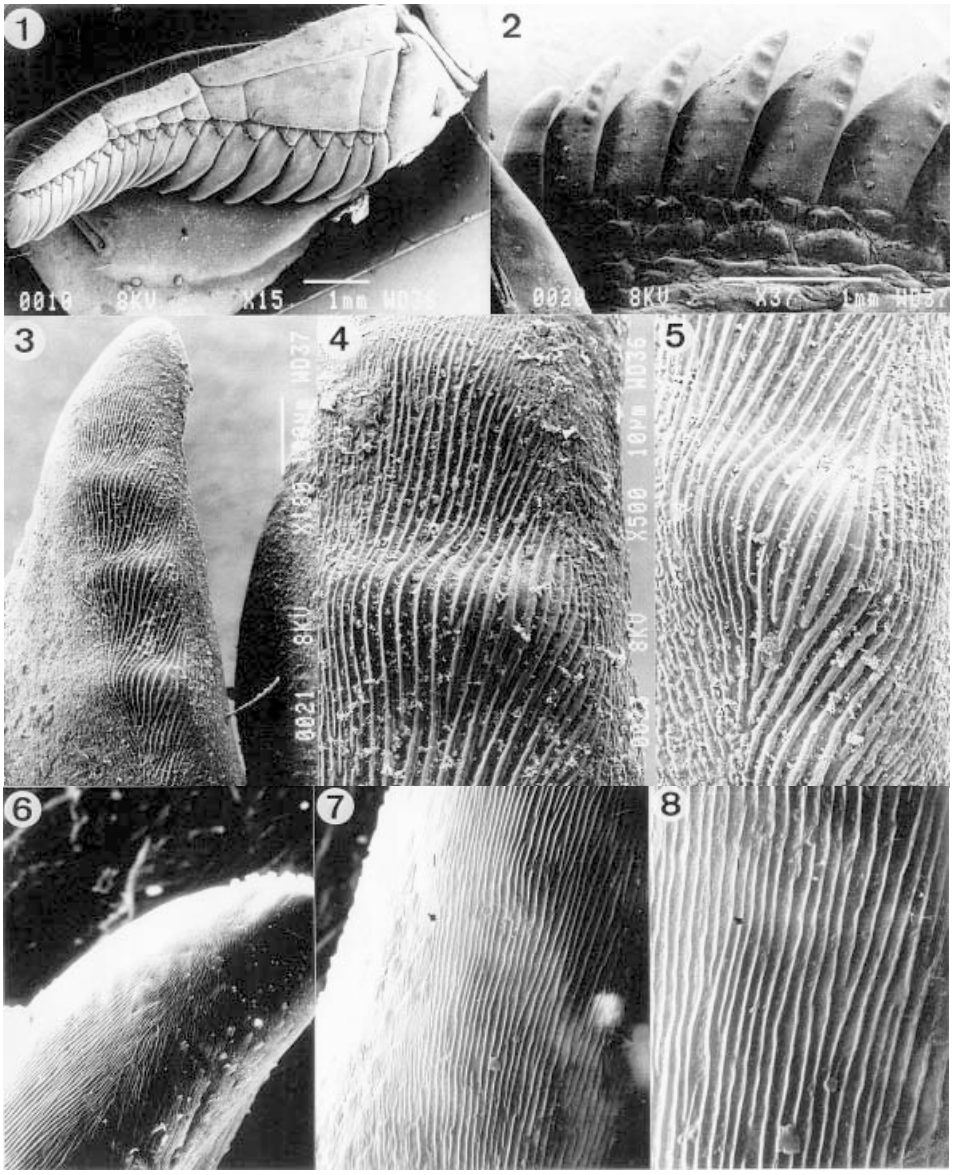
Lourenço W.R., Huber D., Cloudsley-Thompson J.L.: Description of the stridulatory apparatus in some species of the genus Rhopalurus Thorell (Scorpiones: Buthidae). In Gajdoš P., Pekár S. (eds): Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava), Vol. 19, Supplement 3/2000, p. 141-144.

The genus *Rhopalurus,* established by Thorell (1876), was based on a single species from Colombia, *Rhopalurus laticauda* Lourenço (1982) proposed a full revision of the genus *Rhopalurus* and reduced the number of species from 19 to 9. After this revision four new species have been described. In every case a stridulatory apparatus was found to be present.

All known species of the genus *Rhopalurus* have been examined and a detailed study carried out on *R. abudi* Armas et Marcano Fondeur and *R. princeps* (Karsch) using Scanning Electron Microscopy (S.E.M.) photography. The stridulatory surfaces were exposed by removing the pectines from freshly fixed specimens. These were then coated with gold, according to standard procedure, and photographed with the S.E.M. of the Muséum National d'Histoire Naturelle, Paris.

Stridulation has long been known to occur in scorpions of the genus *Rhopalurus*. It was first noted by W.J. Burcherl during a field trip to Brazil in 1828. Several decades later, Pocock (1904) described the phenomenon using more scientific terminology, but the structure of the stridulatory apparatus has only recently been observed with the use of Scanning



Figs 1-8. Scanning electron micrographs of the pecten of *Rhopalurus* species from the Caribbean area. 1-5. *Rhopalurus abudi* from the Dominican Republic. 1. Pecten, external aspect (x 15). 2. Pecten, internal aspect (x 37). 3. Tooth, internal aspect (x 180) showing three expanded zones over the stridulatory lyriform files. 4 and 5. Expanded zone in two different teeth (x 500). 6-8. *Rhopalurus princeps* from Haiti. 6. Tooth, internal aspect (x 600) showing the absence of expanded zones. 7 and 8. Detail of the internal aspect showing stridulatory lyriform files (x 1200 and x 2500, respectively).

Electron Microscopy for two species, *R. princeps* and *R. abudi*. In the case of another two species, *Rhopalurus agamemnon* (KOCH) and *Rhopalurus rochae* BORELLI, sonograms (spectrograms) of the stridulations have also been registered (LOURENÇO, CLOUDSLEY-THOMPSON, 1995).

POCOCK (1904) noted peculiarities in the structure of the stridulatory apparatus of different species. His initial observations concerned the size and shape of pectines. *Rhopalurus* species possess pectines which are quite broad in their proximal half (Fig. 1). In fact, this aspect of pectine structure has been observed in all known species of the genus.

The previous S.E.M. studies carried out on *Rhopalurus princeps* from Haiti (LOURENÇO, CLOUDSLEY-THOMPSON, 1995) associated with new work now carried out on *Rhopalurus abudi,* confirm many of Pocock's observations concerning the structure of the internal surface of the teeth. They confirm, in particular, the presence of two different patterns in the structure of the striated areas of the internal surface of the teeth which form the stridulatory apparatus. What Pocock defined as "tubercular elevations", correspond, in fact, to the expanded zones observed at the inner edge of each tooth. This pattern was reported by POCOCK (1904) only in the case of *R. junceus* (HERBST). Our observations show that a similar structure is present in *R. abudi* (Figs 2-5), but absent from *R. princeps* (Figs 6-8), which likewise is distributed hroughout the island of Hispaniola. Pocock made reference only to the pattern in *R. borelli* (=*R. agamemnon*), from which expanded zones are absent. The study of the other species present in South America reveals that this pattern is the usual one.

One question now can be addressed: What is the significance of the expanded zones observed in the two species from the Caribbean area ? From a morphological point of view, these expanded zones increase the surface of the area in which teeth are in contact with the granulated, depressed region of the third sternite which acts as a rasp. This presumably results in the production of a more intense and louder sound. This can be detected in both Caribbean species when they produce sounds. Those produced by *R. abudi* are much louder than the ones produced by *R. princeps*.

Although the function of stridulation in scorpions remains unproven, it is most probably to the deterrence of predators (LOURENÇO, CLOUDSLEY-THOMPSON, 1995). Stridulation has not been recorded as taking place during courtship in any species of scorpion. Indeed, scorpions appear to be deaf to airborne sounds (CONSTANTINOU, CLOUDSLEY-THOMPSON, 1984), although the pectines may, among their other functions, detect ground vibrations (CLOUDSLEY-THOMPSON, 1955).

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DESCRIPTION OF A NEW GENUS AND SPECIES OF SCORPION (BOTHRIURIDAE) FROM BRAZIL

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Abstract

Lourenço W.R., Monod L.: Description of a new genus and species of scorpion (Bothriuridae) from Brazil. In Gajdoš P., Pekár S. (eds): Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava), Vol. 19, Supplement 3/2000, p. 145-152.

The taxonomic difficulties which can be encountered in the study of scorpions belonging to the family Bothriuridae Simon are discussed briefly. Since the 1960s and 1970s several problems have been elucidated, in particular by San Martin and Maury. A new genus and new species *Brazilobothriurus pantanalensis* gen. nov. sp. nov., are described from Brazil. *Brazilobothriurus pantanalensis* is characterised by a unusual trichobothrial pattern of eight ventral trichobothria on each pedipalp chelae. Some information is given on the habitat of the new taxon and on the area where it originates, – the „ Pantanal " of Mato Grosso.

Introduction

Scorpions of the family Bothriuridae Simon, 1880 have always been considered difficult and complex taxa, and this, in particular, holds true for the genus *Bothriurus* Peters. This genus was described in 1861 and contained six valid species by the end of the 19th century. However, they were difficult to identify correctly as defined by Kraepelin (1899), who did not recognise many species which are regarded as valid today (Maury, 1981a).

Better characterisation of species in most bothriurid genera eventually became possible through new characters, such as those based on the structure of the hemispermatophores, trichobothrial patterns, and carinal morphology. This new approach was first attempted by San Martin (1963) and followed in the 1970s by Maury (1971), who described several additional bothriurid species and improved the classification at the subfamily and genus level. Maury (1975a) suggested that the genus *Bothriurus* was in fact composed of several

genera, and he described the genus *Orobothriurus* for several species from the Andean regions of Argentina, Chile, Bolivia and Peru.

Eighteen bothriurid specimens collected in the region of the „Pantanal“ in the State of Mato Grosso do Sul, Brazil, in 1963, belong to an additional new genus and species which are described below.

Brazilobothriurus gen.nov.

Diagnosis: General morphology similar to that of the genus *Bothriurus* Peters. *Brazilobothriurus* gen.nov. can be readily distinguished from all the other genera of the sub-family Bothriurinae by the following combination of characters: pedipalp chela with 8 ventral trichobothria (Fig. 3); inner margins of pedipalp-chela fingers furnished with a single row of granules (Fig. 4); male chela with an apophysis on inner surface near fixed finger (Fig. 3). Legs with very small pedal spurs present on legs III and IV. Other genera included in the sub-family Bothriurinae such as *Bothriurus*, *Orobothriurus* Maury, *Phoniocercus* Pocock and *Thestylus* Simon differ by having pedipalp chela with 5 ventral trichobothria (Fig. 6); *Cercophonius* Peters, *Centromachetes* Lönnberg and *Urophonius* Pocock, have the inner edges of their pedipalp-chela fingers lined with numerous granules arranged in 2 to 5 irregular rows (in some species, only the basal part of the dentate edge bears 2 rows of granules);.*Timogenes* Simon has a semicircular depression (Maury, 1975b) instead of an apophysis on the inner surface of the male chela.

Type and only known species: *Brazilobothriurus pantanalensis* n.sp.

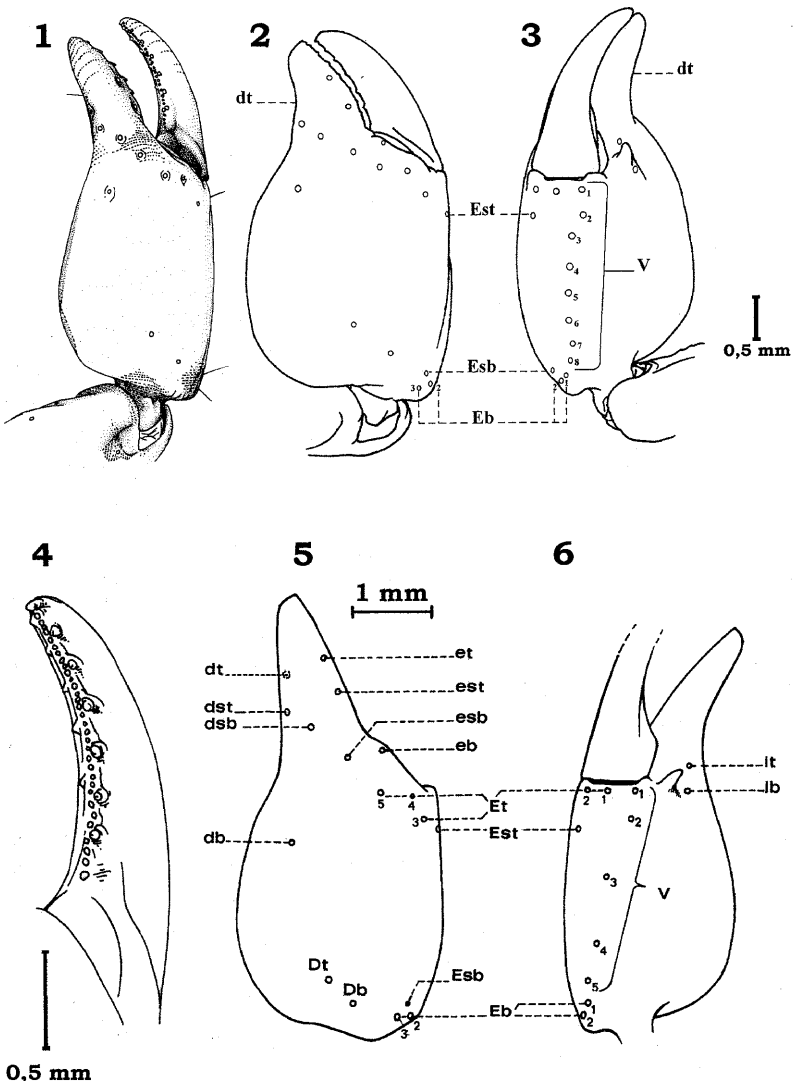
Etymology: The generic name is a combination of „Brazil“ and „Bothriurus“; its gender is male.

Brazilobothriurus pantanalensis sp.nov. (Figs. 1-4 & 7-14)

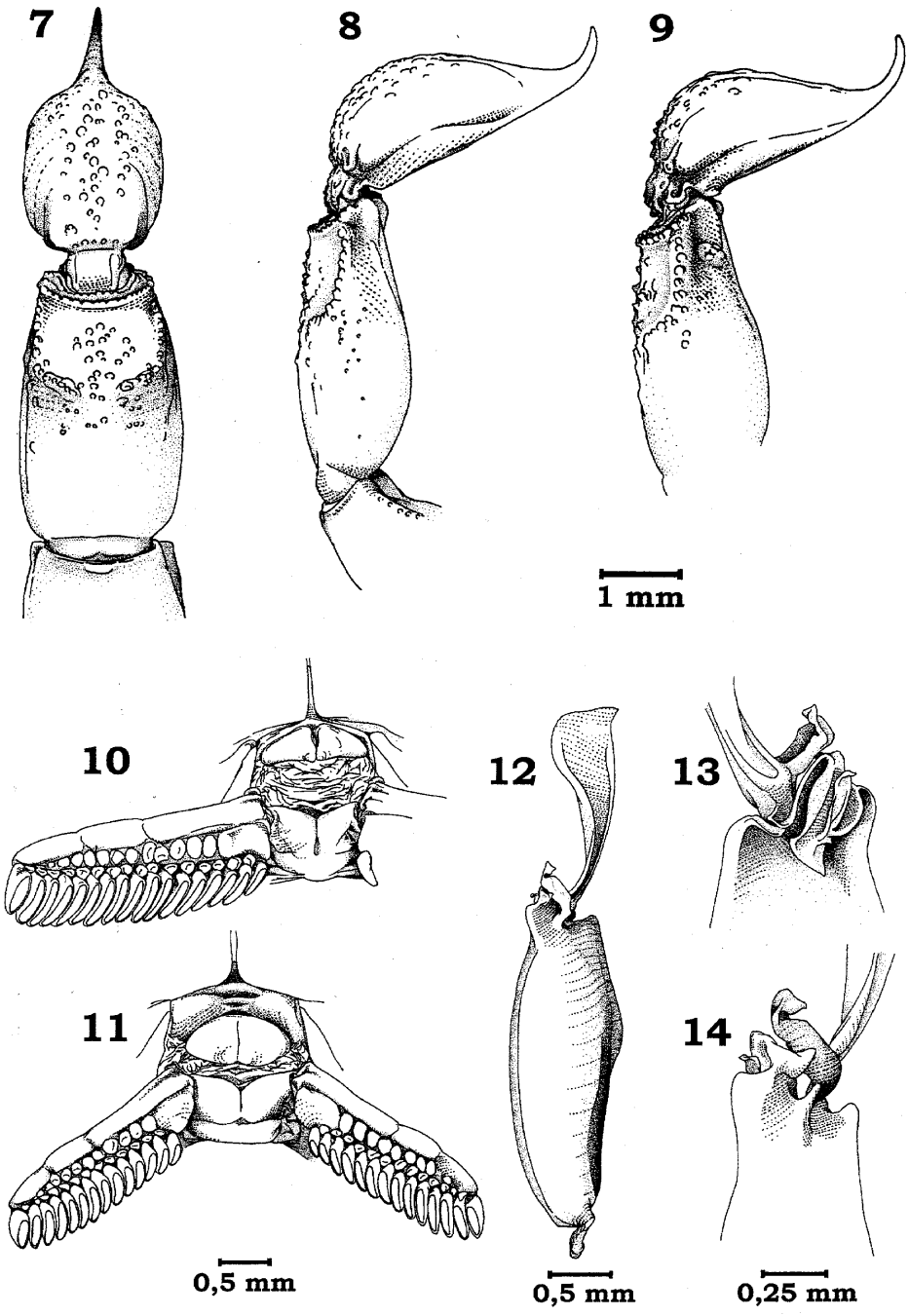
Type: Brazil, Mato Grosso do Sul, Corumbá, south of Fazenda Salina, 12-VI-1963 (E. Kleber, leg). Collected in association with *Tityus mattogrossensis*. Holotype ♂, allotype ♀, 12 paratype ♂♂ and 4 paratype ♀♀s. The holotype, allotype and two paratypes ♂♂ are deposited in the Muséum d'Histoire naturelle de Geneve, 8 paratypes (5 ♂♂ and 3 ♀♀) in the Muséum National d'Histoire Naturelle, Paris, 3 paratypes (2 ♂♂ and 1 ♀) in the Zoologisches Museum der Universität Hamburg and 3 paratypes (3 ♂♂) in the Museum Nacional, Rio de Janeiro.

Etymology: The specific name refers to the region of the „Pantanal“ in Brazil in which the species occurs (Fig. 15).

Description: Male holotype. Coloration: Body generally yellowish-brown. Prosoma: carapace brown with several yellowish spots, two on the anterior margin distinct and sometimes confluent; eyes surrounded by black pigmentation. Mesosoma: tergites brown with confluent vestigial yellowish spots and one median longitudinal yellow stripe; venter and sternites yellowish without spots; pectines and genital operculum pale yellow. Metasoma: all segments yellowish with longitudinal brown spots laterally and ventrally,



Figs 1-4. *Brazilobothriurus pantanalensis* gen.nov. sp.nov. 1. Pedipalp chela of female allotype, dorsal aspect. 2. Pedipalp chela of male paratype, dorsal aspect. 3. Idem, ventral aspect. 4. Edge of pedipalp-chela movable finger; Figs 5-6. *Bothriurus araguayae* VELLARD, 1934 (after LOURENÇO, MAURY, 1979). 5. Pedipalp chela of male holotype, dorsal aspect. 6. Idem, ventral aspect.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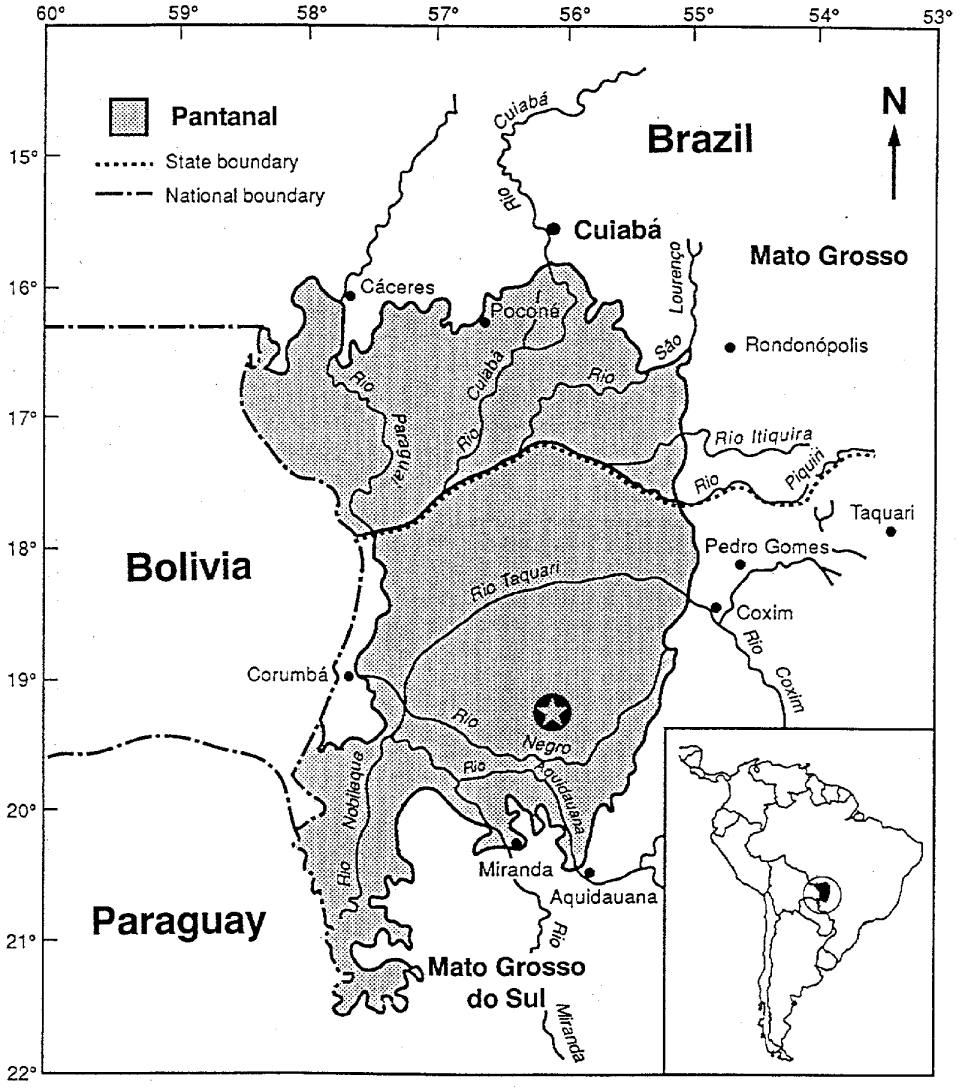

Fig. 15. Map showing the location of the „Pantanal do Mato Grosso", and the type-locality of *Brazilobothriurus pantanalensis* gen.nov. sp.nov. (white star in black circle; modified after Ponce, da Cunha, 1993).

Figs 7-14. *Brazilobothriurus pantanalensis* gen.nov. sp.nov. 7. Telson and metasomal segment V of male holotype, ventral aspect. 8. Idem, lateral aspect. 9. Telson and metasomal segment V of female allotype, lateral aspect. 10. Pectine and genital operculum of male holotype, ventral aspect. 11. Pectine and genital operculum of female allotype, ventral aspect. 12. Left hemispermatophore of male paratype. Global external aspect. 13. Capsular region of left hemispermatophore, internal aspect. 14. Idem, external aspect.

except on segment V where the spots are variegated and reddish brown; vesicle yellowish with very light brown spots; dark red. Chelicerae yellowish with some variegated brown spots; fingers dark reddish brown. Pedipalps reddish brown, with several diffuse brown spots, in particular on femur and tibia. Legs pale yellow with diffuse brownish spots on the proximal segments.

Morphology: Carapace punctate to smooth, weakly granular on the interocular area; anterior margin broadly rounded; keels absent; all furrows very weakly pronounced. Median ocular tubercle distinctly anterior to the center of the carapace. Three pairs of small lateral eyes, the posterior one being very much reduced. Sternum slit-like. Mesosoma: tergites punctate with only a few granules. Tergite VII with four indistinct keels. Venter: genital operculum divided longitudinally, each half with a roughly triangular shape. Pectines: pectinal tooth count 17-17 teeth (Fig. 10). Sternites smooth, with moderately elongated stigmata; VII without keels. Metasoma: segments I to IV with moderately to weakly pronounced dorsolateral and lateral keels moderately. Ventral keels absent on segments I to IV, present and shaped like an arc on segment V (Fig. 7). Intercarinal spaces smooth, with scattered granules on the lateral faces of segment V. Telson almost entirely smooth with only a few small granules on the ventral surface; aculeus short and weakly curved (Fig. 8). Cheliceral dentition characteristic of the family Bothriuridae (Vachon, 1963). Pedipalps weakly granular, almost smooth; femur pentacarinate with moderate keels and granular dorsal face; tibia and chela smooth and punctate, few granules on chela; keels vestigial; movable fingers with a line of granules not clearly divided into rows (Fig. 4). A moderately large apophysis is present on inner aspect of chela at the base of the movable finger (Fig. 3). Trichobothriotaxy of type C: neobothriotaxy (Vachon, 1973). Chela with a total of 30 trichobothria, 8 of them on the ventral aspect (Fig.3); tibia with 19, femur with 3 trichobothria. Legs: tarsi of legs III and IV with 2 rows of 3 spines and several very thin setae on the ventral surface. Hemispermatophore as shown in figures 12 to 14. The distal lamina is reduced whereas the trunk is large. This type of hemispermatophore being also found in *B. araguayae* (Lourenço, Maury, 1979).

Measurements (in mm): Carapace: length 3.1; anterior width 2.2; posterior width 3.4. Metasomal segment I: length 1.9; width 2.2. Metasomal segment V: length 3.7; width 2.0; depth 1.5. Vesicle: width 1.7; depth 1.3. Pedipalp: femur length 2.1; width 0.9; tibia length 2.3; width 0.9; chela length 4.4; width 2.3; depth 1.8; movable finger length 2.0.

Female (allotype): Coloration similar to that of male, but generally paler. Morphology: body more robust; genital operculum more oval in shape; pectines smaller and with 14-14 teeth (Fig. 11); telson proportionally shorter (Fig. 9); pedipalps smooth, with fewer granules on femur and pedipalp chela more elongated, narrower (Fig. 1). Pedipalp chela without apophysis on inner surface.

Measurements (in mm): Carapace: length 3.8; anterior width 2.6; posterior width 3.8. Metasomal segment I: length 2.0; width 2.3. Metasomal segment V: length 3.6; width 2.2; depth 1.7. Vesicle: width 1.7; depth 1.3. Pedipalp: femur length 2.0; width 1.0; tibia length 2.4; width 1.0; chela length 4.4; width 1.6; depth 1.6; movable finger length 2.2.

Variability of characters in paratypes: Paratypes, same data as holotype and allotype. There is no obvious variability of characters in paratypes, except in pectinial tooth count. The number of pectinial teeth varies between 16 and 20 (mostly 17-18) in males (n=13) and between 13 and 16 (mostly 14) in females (n=5).

Some ecological considerations about the „Pantanal"

The region of the Pantanal comprises an alluvial area of 150 000 km^2 in the upper Paraguay basin of central-western Brazil. This is one of the largest tropical wetland ecosystems in the world. The region has a seasonal climate with three to four dry months. During the rainy season from November to April, the precipitation is 1000-1400 mm. The average annual temperature is 25°C with maxima around 40°C during the dry season.

According to EITEN (1982), the Pantanal region is a complex of many vegetation types, a large proportion of which are inundated each year. The configuration of the area results in its isolation from surrounding formations, and endemics can be expected to occur in the region. A similar formation is found in the Bananal Island on the Araguaia River in west central State of Goiás. Some faunal associations can be seen between the two formations. In the case of scorpions, at least one species, *Ananteris mariaterezae* LOURENÇO (Buthidae) is present in both formations (LOURENÇO, 1982). As for the bothriurids, *Bothriurus araguayae* VELLARD is the only species known from Bananal Island (LOURENÇO, MAURY, 1979).

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EFFECT OF NUTRIENT BALANCE ON TOLERANCE TO LOW QUALITY PREY IN A WOLF SPIDER (ARANEAE: LYCOSIDAE)

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Abstract

MAYNTZ D., TOFT S.: Effect of nutrient balance on tolerance to low quality prey in a wolf spider (Araneae: Lycosidae). In GAJDOŠ P., PEKÁR S. (eds): Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava), Vol. 19, Supplement 3/2000, p. 153-158.

The tolerance of the wolf spider *Pardosa prativaga* to two low quality prey types, the aphid *Rhopalosiphum padi* (Aphididae) and the collembolan *Folsomia candida* (Isotomidae), was tested in spiders with different nutrient balance. Good and bad nutrient balance was achieved by feeding the spiders fruit flies raised in cultures of different nutrient content. Spiders with a good balance consumed three times more *R. padi* than spiders with a bad balance, whereas there was no effect of nutrient balance on the tolerance to *F. candida*. The rejection behaviour to *R. padi* and *F. candida* was tested in spiders of good nutrient balance. The spiders ate more *F. candida* than *R. padi* before they refused to attack more prey. Spiders that accepted a fruit fly after the rejection of a low quality prey item were considered to have an aversion against such prey. Of the spiders given *R. padi*, 76% had or acquired an aversion to them. Only 5% of the spiders had or acquired an aversion to *F. candida*.

Introduction

Generalist predators may experience large variation in the quality of prey. Some prey types are of high quality whereas others are so noxious that even a single item may have severe effects on the predator for several days after ingestion (TOFT, WISE, 1999b). Inferior prey types differ in the way they affect predators. They may be nutritionally insufficient, unpalatable or toxic. Examples of toxic prey are the collembolans *Folsomia candida* (WILLEM) and *F. fimetaria* (LINNAEUS). When fed to wolf spiders they produce negative effects, such as increased respiration, increased mortality and reduced fecundity (TOFT, NIELSEN, 1997; MARCUSSEN et al., 1999). The cereal aphid *Rhopalosiphum padi* (LINNAEUS) is a low quality prey for spiders when offered as a single-species diet. As a part of mixed

diets with fruit flies, however, *R. padi* may have positive synergistic effects (Toft, 1995), whereas *F. candida* and *F. fimetaria* retain their negative impact (Toft, Wise, 1999a; Marcussen et al., 1999).

Previous studies have indicated that spiders can experience nutrient deficiency when fed a monotypic diet of fruit flies or crickets in the laboratory (Miyashita, 1968; Uetz et al., 1992). In a field study, Greenstone (1979) found that the wolf spider *Pardosa ramulosa* (McCook) consumed three prey species in proportions that optimised the amino acid composition in their diet. Thus, nutrient deficiency in spiders may be possible at least in some habitats.

In this experiment, we studied the relationship between nutrient deficiency and tolerance to the two low quality prey types *R. padi* and *F. candida*. Tolerance indicates the degree to which the spiders can satisfy their food demand on one type of prey. We assume that the low quality of the two prey types is due to noxious chemicals that are costly to handle metabolically (Toft, Nielsen, 1997). Despite a possible toxic effect of both prey types, they may still provide essential nutrients to spiders with a bad nutrient balance. Over a short time scale, it may therefore be advantageous for spiders with a skewed nutrient balance to accept more low quality prey than spiders with a better nutrient balance, in order to restore their nutritional state. An alternative hypothesis would be that well-balanced spiders tolerate more defensive chemicals in the prey due to their better nutritional condition. In the latter case, nutrient imbalance would cause the spiders to eat less low quality prey.

We created two groups of wolf spiders with different nutrient balance by feeding them fruit flies raised on media of different nutrient content for several weeks. The tolerance to the two low quality prey was tested with spiders in good and bad nutrient balance. The tolerance of spiders to a specific prey item may depend on whether they develop aversions to the prey or not. The development of aversions to prey, however, is affected by the palatability, toxicity, and behaviour of the prey. Since the two prey types used in this study were quite different, at least in their toxicity and behaviour, we also tested the aversion/rejection behaviour of spiders to the two prey types.

Material and methods

The collembolan (*F. candida*) and the aphid (*R. padi*) used in this study were obtained from laboratory cultures. The collembolan was raised on baker's yeast and the aphid culture was maintained on wheat seedlings. The wolf spider *Pardosa prativaga* (L. Koch) was chosen as the test species. This is a common wolf spider in Danish agricultural fields and may naturally prey on *R. padi* and *F. fimetaria*. Females with egg sacs were collected in a garden at Skjoldhøj near to Århus, Denmark. They were kept in the laboratory at 20°C until hatching. By rearing the spiders from newly hatched spiderlings we could ensure a controlled feeding history of all spiders. Five days after hatching the spiderlings were transferred individually to small tubes (Ø 20 mm, height 60 mm) with a 1 cm base of plaster-of-Paris and charcoal that was wetted to maintain high humidity. All spiders were raised on wild type *Drosophila melanogaster* (Meigen). We cultured fruit flies of two different qualities. Flies of low nutrient quality (called Carolina-flies) were cultured in 4g of Carolina medium (Carolina Biological Supply Drosophila Medium Formula 4-24 Plain®) per culture

bottle. Higher quality flies (called dogfood-flies) were produced on a mixture of 1.8g crushed dog food (Techni-Cal® maintenance) and 2.2g Carolina medium per culture bottle. Earlier experiments have shown that *Pardosa* wolf spiders fed these fruit flies will have different growth and survivorship curves, i.e. different nutrient balance (MAYNTZ, TOFT, in prep.).

Effects of nutrient deficiency on the tolerance to R. padi and F. candida.

A 24 hour food consumption experiment was used to test whether the nutrient balance of the spiders affected the tolerance to the two low quality prey types.

Forty-three spiderlings were raised on Carolina-flies for 10 weeks. A pilot experiment had shown that the spiders after this period had a bad nutrient balance, indicated by a reduced growth rate compared to spiders fed dogfood-flies. The spiders were then randomly assigned to one of four treatment groups (between 8 to 10 individuals/group). Two of the groups were subsequently fed dogfood-flies for two weeks and were thereby allowed partly to recover a good nutrient balance. The two other groups continued on Carolina-flies in this period and were thus maintained in a bad nutritional state. To avoid creating a weight difference between spiders with good and bad nutrient balance we limited this treatment period to two weeks. The spiders were weighed at the start and at the end of the treatment period. The live weights of spiders in good and bad nutrient balance were compared and no significant difference was found (t-test, P=0.83). Thus, weight differences among treatments would not confound the results.

The ability to tolerate *R. padi* or *F. candida* was tested for spiders of good and bad nutrient balance. To ensure that the spiders would eat a measurable amount of food, they were starved for 7 days before the test. Each spider in the four groups was then offered either 10 *F. candida* or 10 *R. padi* (adults) for a 24-hour period. This amount was sufficient to ensure that live prey would be present throughout the test period. Prior to presentation, the wet weight of the 10 prey items was measured. At the end of the 24-hour test period surviving prey and the remains of those eaten were dried at 60°C for 48 hours in a vacuum oven. Five samples of 100 individuals of both prey types were also weighed and dried to obtain wet-weight-to-dry-weight conversion factors. The specific amount of prey eaten in dry weight was calculated as:

$$\frac{\text{Prey given (FW)} \times \text{Conversion factor - Remains (DW)}}{\text{Spider weight (FW)}}$$

Rejection behaviour of spiders offered R. padi or F. candida.

For this experiment, only spiders with a good nutrient balance were used. They were obtained by raising hatchlings on dogfood-flies for 14 weeks. After one week of starvation the spiders were divided in two groups (with 20 or 21 individuals/group). One group of spiders was used to test the rejection behaviour to *R. padi* and the other group to *F. candida*. Each individual spider was weighed and transferred to a test cup (Ø 100 mm) where the spider was allowed to acclimatise for 60 minutes. One prey item was weighed and dropped from about 100 mm height so that it landed just in front of the spider. When an aphid or a collembolan was presented in this way the spiders were more likely to attack and grab it. Subsequently, the spiders either started consuming the prey, or released it dead or alive. Whenever the spider had finished eating a prey the remains were collected and a new prey item presented. This procedure continued until the spider refused to accept new prey for a period of five minutes during constant presentation. This behaviour was defined as a rejection, and the number of test prey eaten until rejection, was noted. If a spider did not accept any prey at all, the experiment was terminated after five minutes. Immediately after rejection, a fruit fly was presented to the spider. Spiders accepting this fruit fly within a period of five minutes were considered to have an aversion to the test prey. If not accepted, the spiders might have been satiated or poisoned by the test prey. Remains of eaten prey were dried at 60°C for 48 hours and the specific food consumption was calculated in the same way as described for the previous experiment.

Results

Effects of nutrient deficiency on the tolerance to R. padi and F. candida.

Fig. 1 shows the consumption of Collembola and aphids in spiders with good and bad nutrient balance. There was a significant interaction between prey species and nutrient status in the relative prey consumption (Two-way ANOVA, $P<0.007$, log-transformed data). This interaction reflects the fact that well-balanced spiders consumed 3 times as many aphids as did deficient spiders (Fisher's LSD test, $P<0.05$) whereas there was no effect of nutrient balance on the consumption of Collembola (Fisher's LSD test, $P>0.05$). Collembola were in general eaten in larger quantities than aphids although this was not significant for spiders with good nutrient balance (Fisher's LSD test, $P>0.05$).

Rejection behaviour of spiders offered R. padi or F. candida.

Fig. 2 shows the specific food intake of *R. padi* and *F. candida* before the spiders rejected them. The spiders accepted significantly more *F. candida* than *R. padi* (t-test, $P<0.022$). *F. candida* was also eaten in larger numbers than *R. padi* before rejection occurred (Kruskal-Wallis Rank Sums, $P<0.0001$, Fig. 3). Of the spiders tested with *R. padi*, 86% did not eat any prey during the first five minutes of presentation whereas only 20% of the spiders in the other group completely refused *F. candida* (Fig. 3). Of the spiders fed *R. padi*, 76% accepted the fruit fly that was presented after the cessation of feeding. Those spiders had an aversion to the aphids or had developed one during the test. Among the spiders offered *F. candida*, however, 95% rejected the following fruit fly. Those spiders must have been either satiated or poisoned by the Collembola. Thus, aversions were much more frequently acquired to the aphids (76%) than to the Collembola (5%).

Discussion

The results of this study show that the nutrient balance of a spider influences its tolerance to the aphid *R. padi*. An earlier study with the same spider species found no influence of hunger level on the tolerance of *R. padi* (Toft, 1995). Thus, nutrient imbalance and hunger are two quite different types of stress factors to the spiders.

Changes in the spiders' physical condition as a result of nutrient deficiency may explain the reduced consumption of aphids. If aphids are chemically protected, negative post-digestive effects will be more serious in spiders suffering from nutrient deficiency and this may reduce consumption. Alternatively, if the threshold for developing an aversion is lowered by nutrient deficiency, spiders with a bad nutrient balance would develop an aversion earlier, and thus consume less aphids.

From other studies it appears that *F. candida* is potentially more harmful to spiders than is *R. padi* (Toft, Wise, 1999b). It was therefore surprising that the spiders had a higher con-

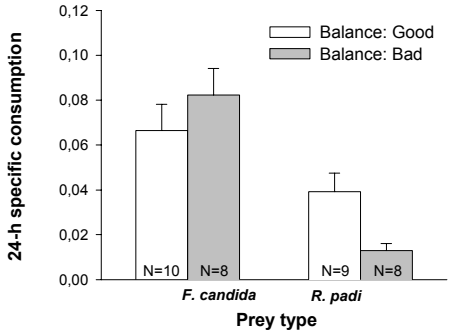

Fig. 1. Specific consumption [mg prey eaten (DW)/ mg spider (FW)] of *F. candida* and *R. padi* by wolf spiders *Pardosa prativaga* with good and bad nutrient balance.

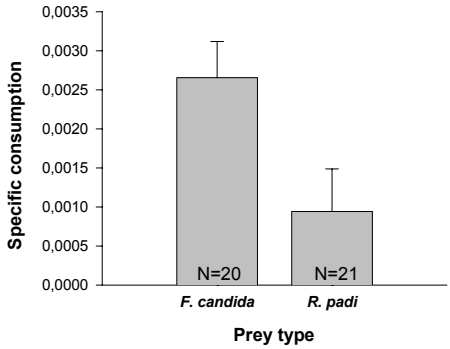

Fig. 2. Specific consumption [mg prey eaten (DW)/ mg spider (FW)] of *F. candida* or *R. padi* before rejection by the spiders. A rejection was realised when the spiders refused to attack and consume the prey for five minutes during constant presentation.

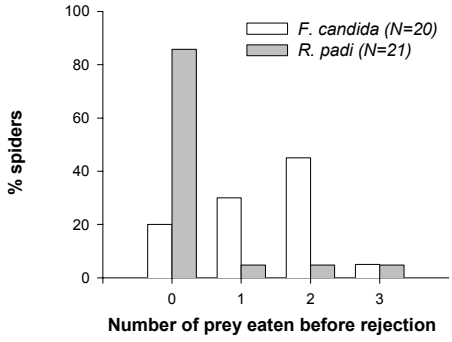

Fig. 3. Number of *F. candida* or *R. padi* eaten by the spiders before rejection. A rejection was realised when the spiders refused to attack and consume prey for five minutes during constant presentation.

sumption of *F. candida* than *R. padi*. One explanation could be that *R. padi* contains feeding deterrents (BILDE, TOFT, 1994) but *F. candida* does not. This would make *F. candida* more palatable to the spiders despite its increased harmfulness. It is still unclear, though, why so many spiders developed an aversion to *R. padi* but not to *F. candida*. The reason may be that slow-acting toxins cause the toxicity of *F. candida*. It would then be difficult for the spider to associate delayed post-digestive effects with the prey. Another possibility is that the spiders may be unable to develop aversions to palatable food items (LEE, BERNAYS 1990).

An earlier study has shown that spiders recently caught in the field, on average eat 2.6 *R. padi* before an aversion develops (TOFT, 1997). In the present study, however, most of the spiders completely avoided the aphids at the first encounter (cf. Fig. 3). This neophobia may be an effect of raising the spiders on a monotypic diet of highly palatable fruit flies. However, the spiders did feed on the aphids during the 24-hour food consumption study. The neophobia was therefore quickly overcome.

In conclusion, nutrient deficiency influences not only survival and growth of spiders (MAYNTZ, TOFT, in prep.) but also the acceptance of some low quality prey types.

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