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Comparison of natural histories and karyotypes of two closely related ant-eating spiders, *Zodarion hamatum* and *Z. italicum* (Araneae, Zodariidae)

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Abstract

Based on morphological characters, two species of the genus *Zodarion*, *Z. hamatum* and *Z. italicum*, were placed into the *italicum* group. The aim of this study was to evaluate similarity of these two species in respect of various aspects of their natural history and karyotypes. Both species had similar phenological patterns, being univoltine, but some specimens reached adulthood the same year before winter. Both representatives had nocturnal activity and were able to capture various ant species. *Zodarion hamatum* seems to be specialized on Myrmicinae ants, and *Z. italicum* on Formicinae ants. *Zodarion hamatum* showed more agile predatory behaviour than *Z. italicum* presumably due to specialization on Myrmicinae ants, which have lower population density. Both species are generalized mimics of bicoloured (orange–dark brown) ants, such as *Lasius emarginatus*; they performed similar courtship and mating. The two study species exhibited contrasting reproductive strategies. *Zodarion hamatum* spiders had higher fecundity than *Z. italicum* as a result of larger body size but *Z. italicum* had larger eggs than *Z. hamatum*. This is presumably an adaptation to different availability of prey ants. Both species had the same diploid chromosome number, sex chromosome system and pattern of X chromosome heteropycnosis in testes. Results support a very close relationship between these two *Zodarion* species.

Keywords: Araneae, mimicry, myrmecophagy, phenology, reproductive strategy, Zodariidae, *Zodarion*

Introduction

With 770 species, the family Zodariidae is moderately large (Platnick 2004). Nevertheless, little information about their biology is available for representatives of this group (Jocqué 1991). Attention has been paid mainly to the most advanced genus, *Zodarion* (e.g. Wiehle

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1928; Harkness 1976; Harkness and Harkness 1992), which nowadays includes 115 species (Platnick 2004). The main area of distribution of this genus is the Mediterranean.

Recent studies on various aspects of the natural history of *Zodarion* species revealed that all representatives investigated are obligatory ant-eaters (each species being specialized on a certain taxonomic group of ants), shelter themselves in igloo-shaped retreats and habitually imitate ants. In contrast to this, they differ in other aspects, such as phenology, circadian activity and reproductive behaviour. The karyotypes of *Zodarion* also vary remarkably: the male karyotype being composed of 24–29 acrocentric chromosomes, the sex chromosome system being X_1X_20 or $X0$ (Pekár and Král 2001, 2002; Pekár et al. forthcoming).

Based on the structure of the copulatory organs, Bosmans (1997) classified European species of the genus *Zodarion* into six groups. We expected species within one group to be more similar to each other in their natural history and karyotype than species from different groups. A comparative study on two representatives from distant groups, *Z. rubidum* (*rubidum* group) and *Z. germanicum* (*germanicum* group), revealed substantial differences in their natural history and karyotype (Pekár and Král 2001). Here, we focus on two species, *Z. hamatum* Wiehle, 1964 and *Z. italicum* (Canestrini, 1868), which are members of the same *italicum* group. These two species are very similar in appearance, size and morphology of the copulatory organs (Bosmans 1997). We investigated their phenology, circadian activity, mimicry, prey preference, reproductive behaviour and karyotype, and compared these data in order to see whether these two species are as closely related as suggested.

Zodarion italicum was first described from Italy in the second half of the 19th century. Nowadays it is known from western and central Europe (Bosmans 1997; Řezáč 2002). Apparently, the area of distribution of this species is still enlarging (Figure 1). *Zodarion hamatum* is found in the southern part of central Europe only (Bosmans 1997; Horak and Kropf 1999) (Figure 1). The distributions of both species overlap in northern Italy though we have no information on their syntopical occurrence.

Material and methods

Study areas

Zodarion italicum was observed and collected in Lochkovský profil (Prague 5–Radotín), the Czech Republic (49°60'N, 14°20'E, grid. no. 6052a). It is a small, open and dry area of rocky steppe with a dominant grass *Festuca valesiaca*, surrounded by old limestone quarries. Further, this species was collected on habitats of railway stations in Frankfurt am Main, Germany (see Bönsel et al. 2000 for further details). *Zodarion hamatum* was observed and collected on two sites in Graz (47°04'N, 15°25'E, 360 m), Austria: in the southern part of the city in the park along the river Mur, and along the main railway station. Both sites had ruderal character and were shaded with trees.

Specimens of spiders were identified after Bosmans (1997). Voucher specimens of spiders and ants are deposited at the Research Institute of Crop Production, Prague, Czech Republic.

Field and laboratory observations

The seasonal activity and sex ratio of *Z. italicum* was based on an intensive pitfall-trap sampling programme performed on railways in Frankfurt am Main (Malten, unpublished). The traps were emptied at fortnightly intervals from April 2000 to November 2001. The

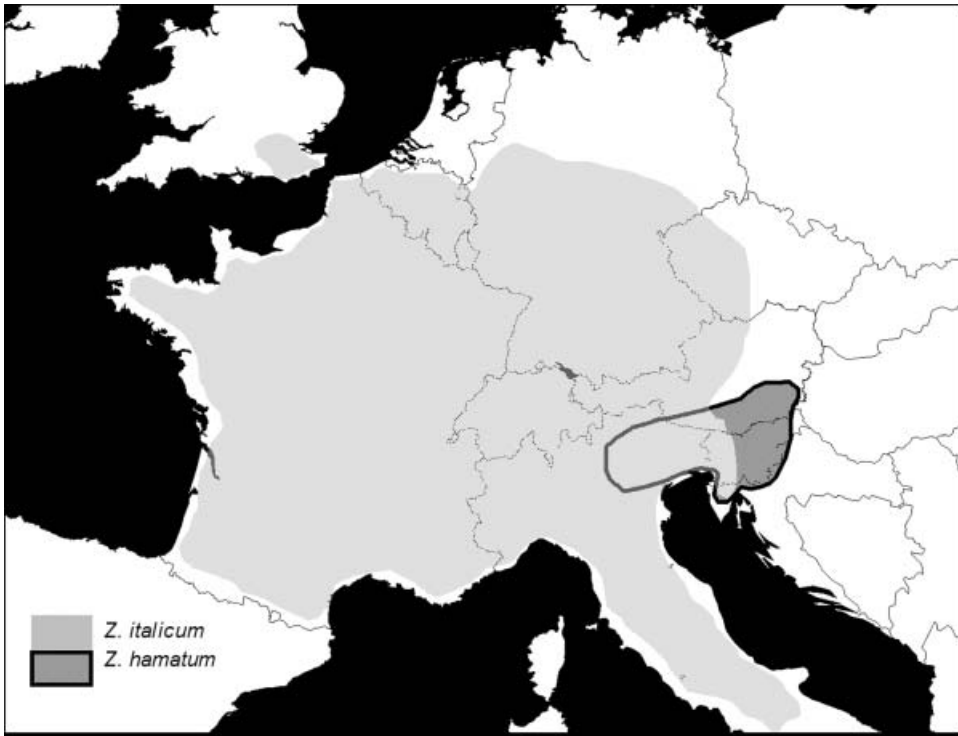


Figure 1. Distribution of *Zodarion hamatum* and *Z. italicum* in Europe. Distribution of *Z. italicum* in southern Italy is not shown.

phenology (i.e. proportion of adults at particular dates) was estimated from hand sampling at sites in Prague and Graz. In Prague the site was visited at monthly intervals between April and November 2002, and in Graz the study sites were visited four times in the same year.

In order to see whether overwintering adult females of *Z. hamatum* came from the spring or autumn generation, ovaries of five females collected from retreats in late October were investigated histologically. The spiders were fixed in modified Bouin–Dubosque–Brasil fluid (Smrž 1989), embedded in paraplast, sectioned (5–7 μm wide), and stained in Masson's triple stain. The preparations were investigated with a light microscope.

In the feeding experiments spiders were put singly in a Petri dish (diameter 40 mm, with a filter paper attached to the bottom) a day before the experiment started. Twelve females and 20 juveniles of each *Zodarion* species, collected at study sites, were used. Four ant species, namely *Formica cunicularia* Latreille, 1798, *Lasius niger* (Linnaeus, 1758) (both Formicinae), *Myrmica sabuleti* Meinert, 1860 and *Tetramorium caespitum* (Linnaeus, 1758) (both Myrmicinae), were offered to each *Zodarion* individual. The ants were offered to spiders randomly over a 4-day interval. Size (body length) of all ants was measured before the experiment. *Formica* ants were disabled by cutting off the distal parts of mandibles before releasing them in the dish. Other ant species were not disabled. An ant was released into a dish occupied by a spider. If the spider did not attack the ant within 15 min the experiment was terminated. Latency to the first attack, number of attacks and the paralysis latency (i.e. time to paralyse the ant) were recorded for each trial. The latency to the first

attack was estimated as the time from the first encounter between spider and ant to the first attack. The paralysis latency was estimated as the time between the first attack and complete immobilization, i.e. when an ant could not raise itself after being touched with forceps.

For observations of reproductive behaviour, 10 males and females of each species were brought to the laboratory. Spiders were kept singly in glass tubes (60 × 15 mm) under constant conditions (25 ± 2°C, 14 h light: 10 h dark) and were fed twice a week with various ant species. To observe courtship and mating, males were introduced into tubes occupied by females. After mating the males were separated from the females. The fecundity (total number of eggs) and the fertility (number of developing eggs) were observed from cocoons that were collected together with a guarding female at the study sites (12 cocoons in *Z. italicum* and 17 in *Z. hamatum*). For each female the length of the prosoma as well as the total body length were recorded.

For the karyological analyses, we used mainly males of the two last nymphal instars. Preparations were made from two specimens of *Z. hamatum* from Graz and four specimens of *Z. italicum* from Prague. The chromosome preparations were obtained from testes by a modification of the spreading technique described by Pekár and Král (2001). In *Z. italicum*, we obtained preparations also from embryos released from cocoons. Embryos were processed by the same method. We found that young embryos, before differentiation of legs, were optimal for preparation of chromosomes as their tissues contained the maximum number of mitoses.

Statistical analyses

Data were analysed using methods in R (R Development Core Team 2004), specifically by Generalized Linear Models (GLM) with an appropriate error and a link function. For proportions it was the binomial family (GLM-b), for counts the Poisson family (GLM-p), and for measurements the Gaussian family (ANOVA), all with their canonical link functions. If a Poisson model showed overdispersion the quasi-likelihood function with a logarithmic link and a squared variance was modelled instead. If data did not meet assumptions of normal distribution and homocedasticity in the Gaussian model they were transformed using logarithmic transformation. Measurements from the same individual (e.g. eggs from one egg sac) were treated as pseudoreplications and analysed using a nested design. The size of ants was used as a covariate in the analyses. The minimal adequate model was found using a deletion procedure based on the *F* test. The parameters were estimated from the minimal model and differences between them were compared using contrasts (Crawley 2002). Means and standard errors of parameters are given in the text.

Results

Phenology and circadian activity

Both study species had similar seasonal activity. Specifically, *Z. italicum* spiders become active in April, with maximum activity in June. Activity gradually declined until November (Figure 2A). During winter, December to March, both species were inactive, sheltered in igloo-shaped retreats attached mainly to the lower sides of stones. However, phenologies of the two species differed. In Prague, *Z. italicum* spiders were adult in May (Figure 2B), cocoons were laid in June and spiderlings hatched in the following month. All observed

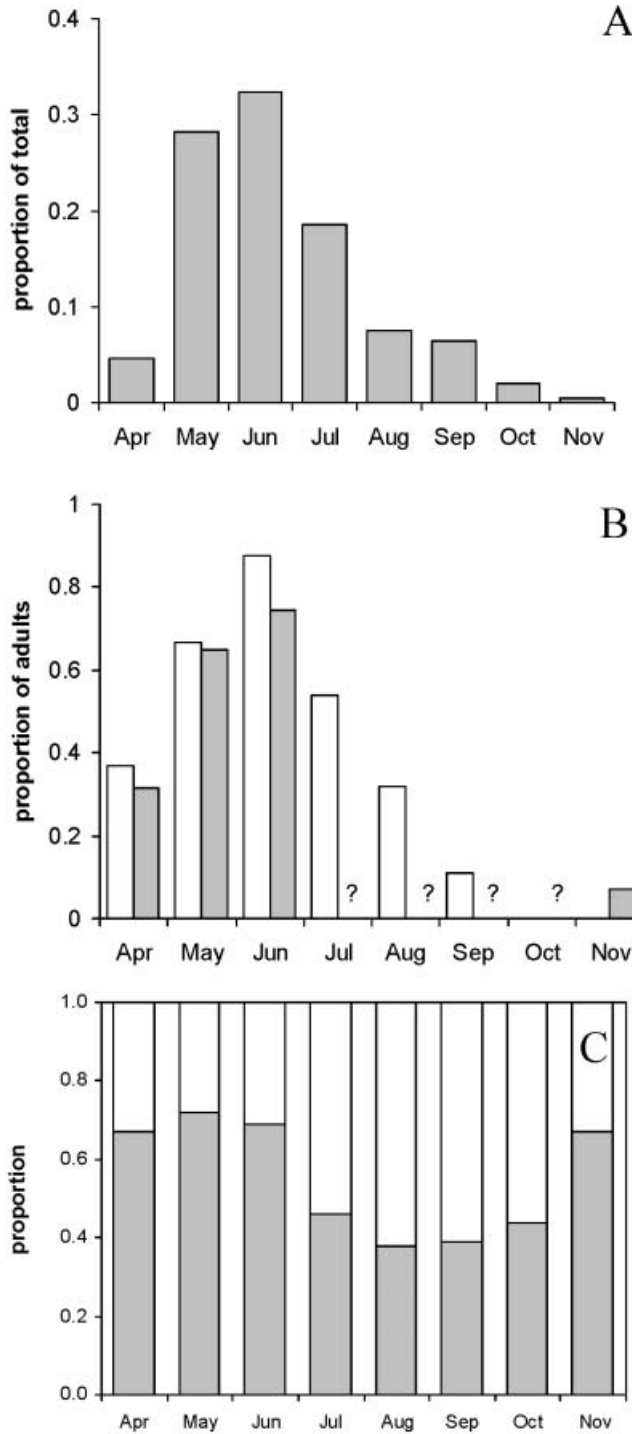


Figure 2. Phenology of study species. (A) Seasonal activity of adult individuals of *Zodarion italicum* (pitfall-trap data, $n=6266$); (B) proportion of adults in *Z. hamatum* (grey bar) and *Z. italicum* (empty bar) during season (hand collections, $n=121$), ? represents missing data; (C) seasonal variability in proportion of males (grey bar) and females (empty bar) of *Z. italicum* (pitfall-trap data, $n=6266$).

specimens ($n=34$) overwintered in a juvenile or subadult stage. In *Z. hamatum*, the spiders were already adult in April, and the cocoons were laid in May. The majority (99%, $n=200$) of specimens overwintered in a juvenile or subadult stage but a few females overwintered in the adult stage. Histological analysis showed that overwintering adult females came from a new (autumn) generation as their ovaries were filled with oocytes.

The sex ratio of *Z. italicum*, obtained from pitfall-trap data, changed with season (Figure 2C). In spring (April to June) and in late autumn (November) there were more males than females. But in summer and early autumn (July to October) the ratio was biased towards females. In total, there were significantly more males (0.61, $n=6266$) than females (binomial test, $P<0.0001$).

Prey

In the laboratory, spiders were able to catch all offered ant species, namely *F. cunicularia*, *L. niger*, *M. sabuleti*, and *T. caespitum*. The capture success, i.e. the ability to catch the ant, neither differed between *Zodarion* species studied nor among four ant species. The average capture frequency was 72% ($n=64$). But capture success was significantly higher for females (83%, $n=24$) than for juveniles (45%, $n=40$) in both *Zodarion* species (GLM-b, $P<0.0001$).

The latency to the first attack was different for each study species (ANOVA, $P=0.002$). It was longer for *Z. italicum* (mean=101.8 s, SE=10.0) than in *Z. hamatum* (mean=51.4 s, SE=8.6) for all ant species. There was no difference in the latency between females and juveniles but there were significant differences among four ant species (ANOVA, $P<0.0001$). The latency was largest for *Formica* followed by *Lasius*, *Tetramorium* and *Myrmica* ants (Figure 3).

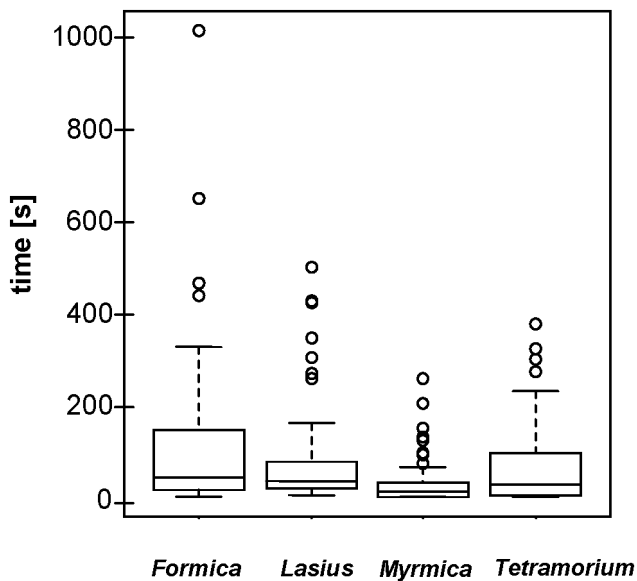


Figure 3. Latency to first attack for four ant species (pooled for females and juveniles of *Zodarion italicum* and *Z. hamatum*). Lines represent medians, boxes stand for 25 and 75 percentiles, respectively, bars are 1.5 times the interquartile range, circles are outliers.

To capture an ant, spiders often attacked it more than once. Significant differences were found in the number of attacks (contrasts, $P < 0.007$). For example, in *Z. italicum*, *Lasius* ants were attacked only once, *Formica* and *Tetramorium* twice, and *Myrmica* three times (Figure 4). Furthermore, the number of attacks differed for the two *Zodarion* species (GLM-p, $P = 0.01$). *Zodarion hamatum* attacked more ant species (mean = 2.81, SE = 0.2) than *Z. italicum* (mean = 2.27, SE = 0.2). The difference between these two spiders was mainly due to a significantly higher number of attacks by *Z. hamatum* on *Formica* and *Lasius* ants (contrasts, $P < 0.01$, Table I).

Spiders retreated after the attack and waited until the ant became paralysed. The mean paralysis latency was significantly different for both *Zodarion* species (ANOVA, $P = 0.003$). *Zodarion hamatum* was on average more effective than *Z. italicum*. The paralysis latency for the former species was 7.5 min (SE = 0.5), for the latter 10.9 min (SE = 1.1). There was no difference between females and juveniles, but there were significant differences in the paralysis latency of the ant species (ANOVA, $P < 0.0001$). *Myrmica* and *Tetramorium* had significantly longer latency than *Formica* and *Lasius* ants (contrasts, $P < 0.01$). *Zodarion hamatum* was particularly more effective in the paralysis of *Myrmica* ants (contrasts, $P = 0.006$; Table II). For the other three ant species there were no significant differences between two *Zodarion* species.

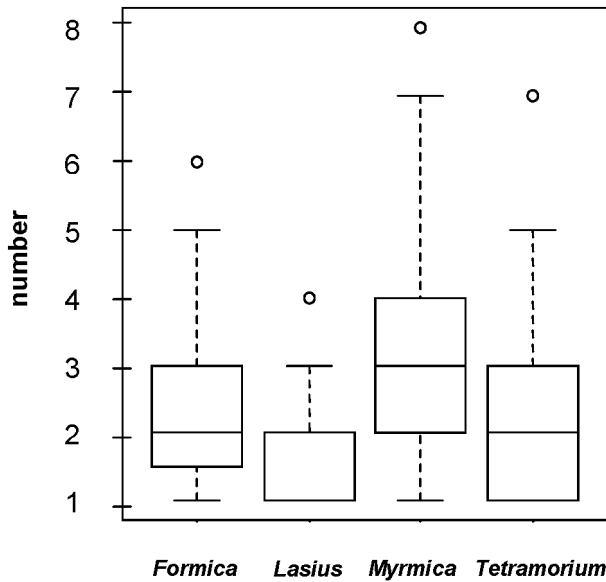


Figure 4. Number of attacks for four ant species (pooled for females and juveniles of *Zodarion italicum* and *Z. hamatum*). For description see Figure 3.

Table I. The mean (SE, n) number of attacks of studied *Zodarion* species on four ant species.

	<i>F. cunicularia</i>	<i>L. niger</i>	<i>M. sabuleti</i>	<i>T. caespitum</i>
<i>Z. hamatum</i>	3.11 (0.3, 19)	2.33 (0.3, 19)	3.21 (0.4, 20)	2.59 (0.4, 18)
<i>Z. italicum</i>	2.0 (0.2, 19)	1.45 (0.1, 17)	3.42 (0.3, 21)	2.05 (0.3, 19)

Table II. The mean (SE, *n*) paralysis latency (min) of four ant species after attack of studied *Zodarion* species.

	<i>F. cunicularia</i>	<i>L. niger</i>	<i>M. sabuleti</i>	<i>T. caespitum</i>
<i>Z. hamatum</i>	6.24 (0.7, 19)	3.19 (0.3, 19)	9.50 (0.6, 20)	10.99 (1.2, 18)
<i>Z. italicum</i>	7.08 (0.8, 19)	2.59 (0.2, 17)	18.63 (2.8, 21)	13.95 (1.4, 19)

Mimicry

A tentative mimicry model was found for *Z. hamatum* and *Z. italicum* (Figure 5). Both *Zodarion* species have similar appearance and seem to imitate bicoloured orange-dark brown ants, most closely *Lasius emarginatus* (Olivier, 1791). This ant species was found to occur together on the study sites with the two spider species. The spiders are 2.0–3.7 mm (*Z. hamatum*) or 1.6–4.1 mm (*Z. italicum*) long, with brown to orange-brown prosoma and dark brown abdomen, while legs are yellow to orange. The workers of *L. emarginatus* are on average 2.5–4.0 mm long with brown head and gaster, and orange-brown thorax and legs.

Reproduction

Courtship was similar for both *Zodarion* species. Usually it was very short (2–10 s), however it could last up to 2 min. Immediately after the first contact, the male began to vibrate the whole body, raised forelegs and drummed with the palps. In this position the male moved slowly towards the female. If the female was receptive she would allow the male, after sparring with palps, to climb over her body and copulate from each side. Copulation, i.e. insertion of a palp, was similar for both species, lasting on average 30 s for each side. It was



Figure 5. Mimics and the putative model (from left to right): *Zodarion hamatum*, *Lasius emarginatus* and *Z. italicum*. Scale bar: 1 mm.

interrupted two to four times so that it lasted 1.3 min (SE=0.3) in total. The female copulated with several males.

Females of both species produced the cocoon inside a retreat and guarded it until hatching. The mean fecundity of *Z. italicum* was 14 (SE=1.4, $n=12$) eggs per cocoon while that of *Z. hamatum* was 20.4 (SE=1.1, $n=17$). The difference was significant (ANOVA, $P=0.002$) and corresponds to the differences in size of the females. In *Z. hamatum* the length of the female prosoma (mean=1.26 mm, SE=0.05) was significantly larger than that of *Z. italicum* (mean=1.16 mm, SE=0.04) (t test, $P<0.02$). The relationship between the size of the prosoma and fecundity, combined for both species, is described by the following linear model: $y=17.6x-3.7$ ($R^2=0.14$, $P=0.04$). The size (diameter) of eggs was 0.7 mm (SE=0.01) in *Z. hamatum* and 0.8 mm (SE=0.01) in *Z. italicum*. The size was significantly different between both *Zodarion* species (nested ANOVA, $P=0.05$). Interestingly, the size of eggs did not increase with the size of the female prosoma in either species (linear regression, $P>0.61$). Fertility was similar for both species, being 97% ($n=29$).

Karyotypes

Both mitotic and meiotic phases were obtained from testes of the two last nymphal stages. The diploid chromosome number was 21 in males of both species (Figure 6). The same



Figure 6. Male karyograms. (A) *Zodarion italicum* (mitotic metaphase); (B) *Z. hamatum* (anaphase I).

number of chromosomes was found in male embryos of *Z. italicum* whereas mitoses of female embryos contained 22 chromosomes. Karyotypes of both species were formed by acrocentric chromosomes exclusively. Autosome pairs decreased gradually in size (Figure 6).

During diplotene and diakinesis, the majority of bivalents was unichiasmatic (Figure 7E). However, more than half of the plates counted contained one or two bivalents with two chiasmata. In *Z. hamatum*, one (in nine plates) or even two bivalents (in three plates) bore two chiasmata ($n=18$). A similar situation was observed in *Z. italicum*, one (in six plates) or two bivalents (in three plates) bore two chiasmata ($n=16$). Both types of bivalents (unichiasmatic and dichiasmatic) exhibited both terminal and intercalary location of chiasmata.

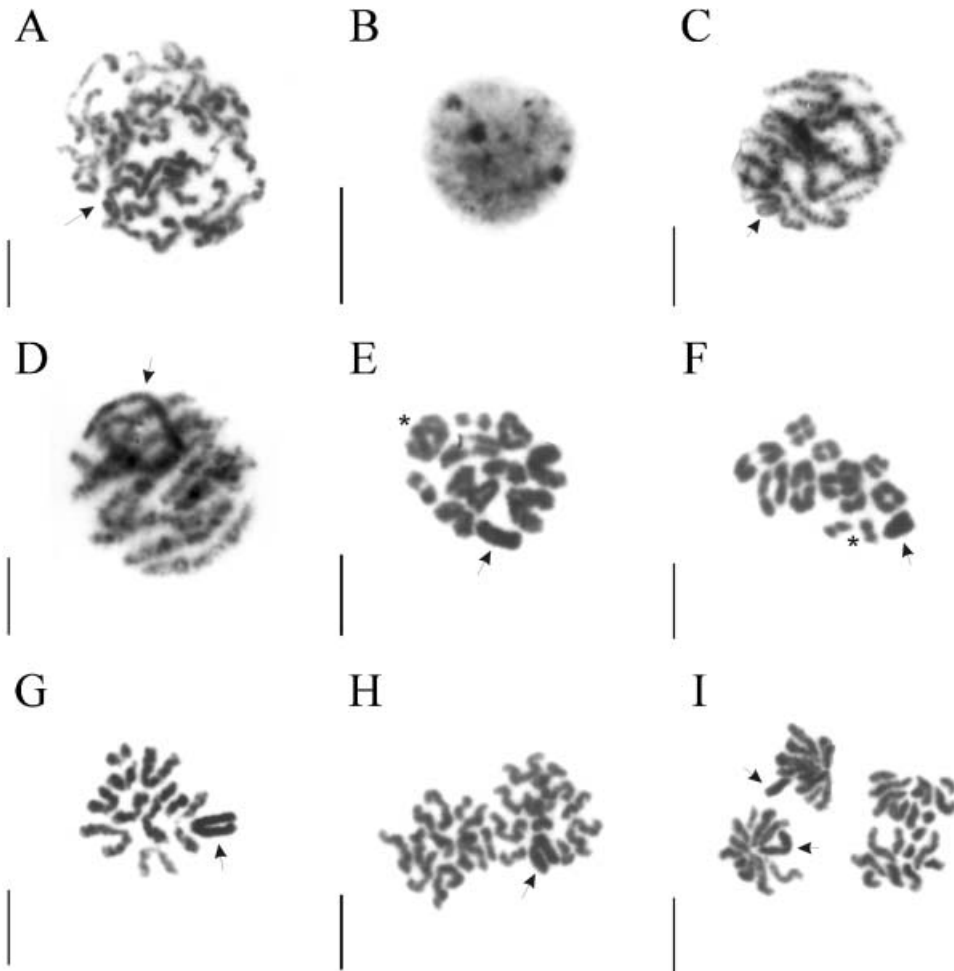


Figure 7. Behaviour of sex chromosome during spermatogonial mitosis and meiosis. (A, F) *Zodarion italicum*; (B–E, G–I) *Z. hamatum*. (A) Early spermatogonial prophase; (B) premeiotic interphase (two prominent heteropycnotic bodies represent segments of chromosome X); (C) pachytene (note that sex chromosome does not exhibit heteropycnosis); (D) late pachytene; (E) diplotene (*ring bivalent with two chiasmata); (F) metaphase I (*bivalent exhibiting precocious division); (G) anaphase I; (H) prometaphase II; (I) anaphase II. Arrow identifies sex chromosome. Scale bars: 10 μm .

Presence of a sole sex chromosome during male meiosis and comparison of mitoses of both sexes indicated an X0 sex chromosome system. The acrocentric sex chromosome was the longest chromosome of the karyotype. In both species, the X chromosome exhibited the same complicated pattern of heteropycnosis in testes. During the spermatogonial prophase, the X chromosome showed weak positive heteropycnosis (Figure 7A). Positive heteropycnosis of the X chromosome reappeared at interphase nuclei before the onset of meiosis. Despite the presence of only one sex chromosome in the male, we observed often two heteropycnotic bodies at interphase nuclei (Figure 7B). From leptotene to middle pachytene, the X chromosome was fibrous and did not exhibit heteropycnosis (Figure 7C). The last period of heteropycnosis started during late pachytene (Figure 7D) and lasted until the end of meiosis (Figure 7E–I).

Discussion

In this study we compared various aspects of the natural history, and the karyotypes, of two closely related European *Zodarion* species, *Z. italicum* and *Z. hamatum*.

Both species occur in similar habitats. *Zodarion italicum* appears to have some affinity to abandoned stone pits/quarries (Harvey and Murphy 1985; Řezáč 2002). Recent observations revealed that both species also occur on railway tracks (Bönsel et al. 2000; Komposch 2002; S. Pekár, personal observation; J. Gruber, personal communication) or close to it (Priester et al. 1998; Kindl-Stamatopoulos 2001). Adaptation to such an alternative type of habitat might have helped *Z. italicum* recently to extend its range in Europe. Only a few years ago this species was recorded for the first time in the Czech Republic (Řezáč 2002). It may take a similar course as *Z. rubidum* which is now recorded along railways across western and central Europe (Pekár 2002).

At present a few species of *Zodarion* spiders are often found syntopically in the neighbourhood of railways. In Germany (Hessen), *Z. rubidum* was found together with *Z. italicum* (see Bönsel et al. 2000) and in Austria (Styria) *Z. rubidum* occurs together with *Z. hamatum* (S. Pekár, personal observation). In northern Italy, where the distribution of *Z. hamatum* and *Z. italicum* overlaps, all three *Zodarion* species may occur syntopically on railways.

The population of *Z. italicum* from Prague was found to be univoltine, reaching adulthood in late spring, as other central European *Zodarion* species studied so far (Pekár and Král 2001). On the other hand, in southern and western Europe *Z. italicum* seems to be partly bivoltine as suggested by records of adults from southern France, Italy (Bosmans 1997) and Germany (this study) in early spring and late autumn. A similar situation was found in *Zodarion hamatum*. Adult males and females were already found in April in Graz. Due to early reproductive activity at least some newborn individuals of *Z. hamatum* finished their development before winter. We suggest that faster development and earlier reproductive activity of *Z. italicum* and *Z. hamatum* in southern parts of Europe are due to a warmer climate. For example, the average annual temperature is 1°C higher in Graz and Frankfurt am Main than in Prague.

Field observations on the ant-hunting behaviour of *Zodarion* species from the *italicum* group suggest that these spiders feed on Formicinae ants. *Zodarion italicum* was observed to run among *Lasius niger* (Formicinae) in Great Britain (Harvey and Murphy 1985). No observation on ant-predation exists for *Z. hamatum*, but another very closely related species, *Z. gallicum* (Simon, 1873), was found in association with *Lasius* ants (*L. niger* and *L. flavus* (Fabricius, 1781)) in Switzerland (Boevé 1992). Our laboratory experiments

showed that both species are able to feed on various ants. We expect that each *Zodarion* species is specialized on a certain taxonomic group of ants. This has been confirmed in a study on *Zodarion* spiders from Israel (Pekár et al. forthcoming). Previous laboratory experiments showed that some predatory characteristics are indirect indicators of prey specialization, particularly the low number of attacks and short paralysis latency. *Zodarion hamatum* made fewer attacks and had shorter paralysis latency with Myrmicinae ants; thus we infer it is specialized on the representatives of this subfamily, e.g. *Myrmica* ants. *Zodarion italicum* made fewer attacks and paralysed most quickly Formicinae ants; therefore we expect it is specialized on, for example, *Lasius* ants.

These two *Zodarion* species showed different predatory strategies. *Zodarion italicum* was rather prudent: it took a longer time to the first attack and attacked fewer times. In contrast to this, *Z. hamatum* attacked intentionally and more frequently. Such fiery behaviour might be more advantageous in the capture of slowly moving and rather non-aggressive Myrmicinae ants, whereas the prudent behaviour used by *Z. italicum* might be more advantageous in the capture of fast-moving and aggressive Formicinae ants. An alternative explanation is based on the different abundance of ants from these two subfamilies. Myrmicinae ants (e.g. *Myrmica*) are solitary foragers, less abundant on the surface than Formicinae ants, which forage in groups (e.g. *Lasius*). Thus the different attacking behaviour may be an adaptation to the abundance of ants. This is similar to results of Hedrick and Riechert (1989) on the feeding ecology of the desert spider *Agelenopsis aperta* (Gertsch, 1934) (Agelenidae). They found that populations inhabiting sites of low prey density showed a higher attacking rate than populations from sites of high prey abundance.

The two *Zodarion* species seem to mimic the same group of ants. We believe that both *Zodarion* species are generalized Batesian mimics of bicoloured (orange-brown and dark brown) ants. This includes *Lasius emarginatus* and several *Formica* species (e.g. *F. cunicularia*, *F. pratensis*). All these ants occur in central and southern Europe (Atanasov and Dlusskij 1992) thus both mimics are distributed within the range of their models. Other *Zodarion* spiders studied are general ant mimics too (Pekár and Král 2002; Pekár et al. forthcoming). In contrast to specific mimicry (imitation of a single ant species), generalized ant-mimicry (imitation of several ant species) allows the mimic to associate with different ants thus becoming more abundant and enlarging its distribution range (Edmunds 2000).

Zodarion hamatum and *Z. italicum* were found to differ in some reproductive parameters, each being a different example of the trade-off between egg size and fecundity (clutch size). Simpson (1995), in his analysis of reproductive characteristics in spiders, found that clutch size increases linearly with female body size. Results of our study on Israeli *Zodarion* spiders (Pekár et al. forthcoming) as well as the results of this study support the conclusion of Simpson: larger *Zodarion* species had higher fecundity. Simpson (1995) further showed that there is a negative relationship between egg and clutch size: species with higher fecundity produced smaller eggs. He proposed that large eggs might be adaptive where food for young is scarce. Eggs of *Z. hamatum* were larger than eggs of *Z. italicum* suggesting, as in the analysis of foraging behaviour, that its prey, Myrmicinae ants, are scarcer than *Lasius* ants, the prey of *Z. italicum*.

Comparison of karyotypes in both species did not reveal any difference in the number and morphology of chromosomes. We have not obtained sufficient numbers of mitotic metaphases or metaphases II in *Z. hamatum*, and therefore we could not compare lengths of individual chromosome pairs of studied species.

Species of the genus *Zodarion* possess either the X_1X_20 sex chromosome system that is considered ancestral in spiders (White 1973), or the derived $X0$ system, with X

chromosome(s) being acrocentric (Pekár and Král 2001; Pekár et al. forthcoming). We suppose that the two heteropycnotic bodies observed at premeiotic interphase of both species are segments of X chromosome that are equivalent to the original chromosomes X_1 and X_2 . Thus, it appears that meiotic superspiralization of sex chromosomes begins at centres that are equal to original sex chromosomes. The pattern of sex chromosome heteropycnosis found in meiosis of both species is unusual among spiders studied so far. Except for an interval from leptotene to middle pachytene, the sex chromosome is heteropycnotic throughout meiotic division. Absence of heteropycnosis during early prophase I is rare in spiders. Up to now, it has been found at pachytene of some theridiids only (Gorlov et al. 1995). The reason for the loss of heteropycnosis in the sex chromosome of study species during early prophase I is not known. It might be a consequence of an insertion of an autosome segment into the X chromosome. We believe that the complicated pattern of sex chromosome heteropycnosis observed in the study species evolved from that found in *Z. rubidum*. Our detailed study of *Z. rubidum* has shown that heteropycnosis of its sex chromosomes does not terminate during metaphase II as stated earlier (Pekár and Král 2001). Sex chromosomes of this species are heteropycnotic during all meiotic division except prometaphase and metaphase II when heteropycnosis is weak or even missing.

The diploid number of chromosomes in *Z. hamatum* and *Z. italicum* is the lowest number found in *Zodarion* spiders so far, suggesting that these species are the most derived known karyotype lineage of the genus. This idea is further supported by an unusual and derived pattern of sex chromosome heteropycnosis found in male meiosis of both species.

Observed data on natural history and karyotypes support a very close relationship between *Z. hamatum* and *Z. italicum*. The few differences are attributed either to occurrence in different climatic conditions (phenology) or adaptation to different prey ants (predatory and reproductive strategies). Classification of both *Zodarion* species into one group thus seems to be justified. Similar study of other species from the same and other groups is required to provide more data for an outline of the main evolutionary trends within the *italicum* group as well as within the genus *Zodarion*.

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