

A COMPARATIVE STUDY OF THE BIOLOGY AND KARYOTYPES OF TWO CENTRAL EUROPEAN ZODARIID SPIDERS (ARANEAE, ZODARIIDAE)

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ABSTRACT. A comparison of the biology and karyotypes of *Zodarion germanicum* and *Zodarion rubidum* (Araneae, Zodariidae) which occur in central Europe was carried out. Surprisingly, these species were found to differ in a number of characters such as pattern of activity, reproduction and karyotypes. *Zodarion germanicum* was observed to be diurnal, whereas *Z. rubidum* is nocturnal. Courtship and mating were markedly longer and more complex in *Z. germanicum* than in *Z. rubidum*. Females of *Z. germanicum* produced only one or two successive egg sacs including 17 eggs on average which they would guard, while females of *Z. rubidum* produced up to 5 egg sacs each having 4 eggs that they abandoned. The two species differ from each other also in number of chromosomes and the sex chromosome system. Results suggest these species belong to distant evolutionary lineages within the genus *Zodarion*.

Keywords: Araneae, Zodariidae, activity, reproduction, karyotype

About 500 species of Zodariidae have been described so far, most of which occur in the subtropical region (Jocqué 1991). In Europe, only one genus, *Zodarion*, including 47 species (Bosmans 1993, 1997), occurs. These species are well-known for being myrmecophilous and for constructing remarkable retreats from soil grains (e.g., Nielsen 1932). This remarkable behavior was observed for the first time more than 100 years ago (Simon 1864; Santschi 1908). Since then there have been seven studies concerning the biology of these spiders (Wiehle 1928, 1953; Schneider 1971; Harkness 1976, 1977a, b, 1995; Jocqué & Billen 1987; Couvreur 1990; Harkness & Harkness 1992). Nevertheless, a great majority of these investigations was centered upon the ant-eating behavior only. Thus, many other aspects of biology of these fascinating spiders, such as pattern of activity or reproduction, are poorly understood or even unknown.

In our study we focused on two species, *Zodarion germanicum* (C.L.Koch 1837) and *Zodarion rubidum* Simon 1914, the only representatives of the genus *Zodarion* in the Czech Republic and Slovakia. The former and larger species (body length 3.5–6.0 mm) oc-

curs abundantly in dry habitats associated with coniferous woodland only in central Europe. The latter and slightly smaller species (3–4 mm), was known only from southwestern France (Denis 1935). But in the last decades it has spread into central Europe, for example, onto sand dunes in South Moravia, Czech Republic (Pekár 1994). Both species show invasive tendencies as they often occur in secondary habitats. *Z. germanicum*, for instance, was recorded from heather rimming forested peat-bog (Mähringová 1993), and *Z. rubidum* on sandy substrates within the area of Berlin railway station (Germany) (Broen & Moritz 1987) or on mining dumps in Slovakia (Pekár 1994; Krajča 1996). At present, the ranges of the two zodariid species overlap in central Europe, but only in a few examples was sympatric occurrence proven at the ecological level (e.g., Jelínek 1999).

Based on morphological characters of copulatory organs, Bosmans (1997) classified 47 European species of the genus *Zodarion* into six groups. *Zodarion germanicum* was placed in “germanicum” while *Z. rubidum* was placed in “rubidum.” At the beginning of our observations, the two species appeared to be

very similar, both occurring in identical habitats and foraging on similar ant species (Pekár unpubl. data). However, later investigation showed that these species mimic different ant species (Pekár & Král unpubl.) and have different activity. Thus our aim was to focus in detail on aspects of their biology which have been insufficiently studied in order to clarify differences between the study species which could have significance for further study of evolution within the genus *Zodarion*.

STUDY AREA

The study sites are situated in Slovakia which is in the center of the distribution of *Z. germanicum* and at the northeastern edge of the distribution of *Z. rubidum*.

Zodarion rubidum was observed on a mining dump in Nováky town. The dump (about 25 years old) consists of Tertiary tuff and coal slate and is sparsely covered with vegetation, dominated by the grass *Calamagrostis epigeios* (L.) Roth. *Zodarion germanicum* was observed on a steep outcropping in a nearby village Opatovce nad Nitrou, about 6 km from Nováky. This study area is a former sand pit adjacent to a pine forest (*Pinus silvestris* L.). It was abandoned some 15 years ago. The Neogene conglomerate sands of this site are mostly barren, with many stones and the cover is sparse vegetation dominated by the grass *Dactylis glomerata* L. The elevation of both sites is 275–290 m. The average annual temperature of the area is 8.5 °C, and the average annual precipitation is 650 mm. Average bi-weekly temperatures for the sites are displayed in Fig. 1. Soil surface temperature of the study areas was measured under a clear sky (on 7 and 8 June 1997) by means of a THERM 2246-2 thermometer at 0600, 1000, 1400 and 1800 h. Obtained data showed that the temperatures of study sites were very similar.

METHODS

The investigation took place both in the field and under laboratory conditions. From April to October 1997, weekly visits were made to the study areas to assess the proportion of adult spiders which were either running on the ground or hidden in retreats. On one day in June 1997, the number of both spider species (seen during 5 min) and the number of ants (seen during 30 sec) in a 1 m²

circle drawn in the soil around three nest entrances was assessed every hour (between 0600 and 2200 h). In June the sun rises at about 0445 h and sets at about 2045 h in the study area. The frequency of ant species hunted by spiders was also recorded in June. A few egg sacs (3 in *Z. rubidum* and 2 in *Z. germanicum*) were collected, and the sizes of eggs were measured using a stereoscopic microscope.

Forty adult individuals (20♂ 20♀) of each species were brought into the laboratory in June to investigate their behavior. The individuals were kept in specimen containers (diameter 15 mm, 60 mm long) at 20 °C ± 2° and under natural LD regime (14:10). They were offered various substrates, such as soil, sand grains, paper, pine needles, leaves, and other plant material, all potentially useful for the construction of retreats. The relative frequency and size of retreats constructed was measured after three days. The substrate was moistened as it dried out, usually at three-day intervals. The reared specimens were fed in excess with ant workers of *Tetramorium caespitum* (L.).

Then all 40 specimens were moved in pairs (male and female) to a Petri dish (diameter 60 mm) with a filter paper attached to the bottom, and kept separated by a paper barrier in order to study their reproductive behavior. As soon as the male began to “search,” the barrier was removed. Style and duration of courtship and mating were observed under binocular stereomicroscope. After copulation males were removed. If the female was not receptive the males were immediately removed.

After females laid eggs, the number of egg sacs produced and the incubation periods were recorded. Individual fecundity was assessed by summing the number of hatched offspring with the number of undeveloped eggs which were left in each egg sac.

Data on the duration of mating, the number and size of eggs, and the incubation period for the two study species were compared using the permutation (exact) test since they did not meet the criteria required for parametric tests. A two-sided 2-sample randomization test after Manly (1997) was used. The simulation test procedure was constructed within RESAMPLING STATS program (Simon 1993).

Two different methods were used for chromosome preparations. The first method was

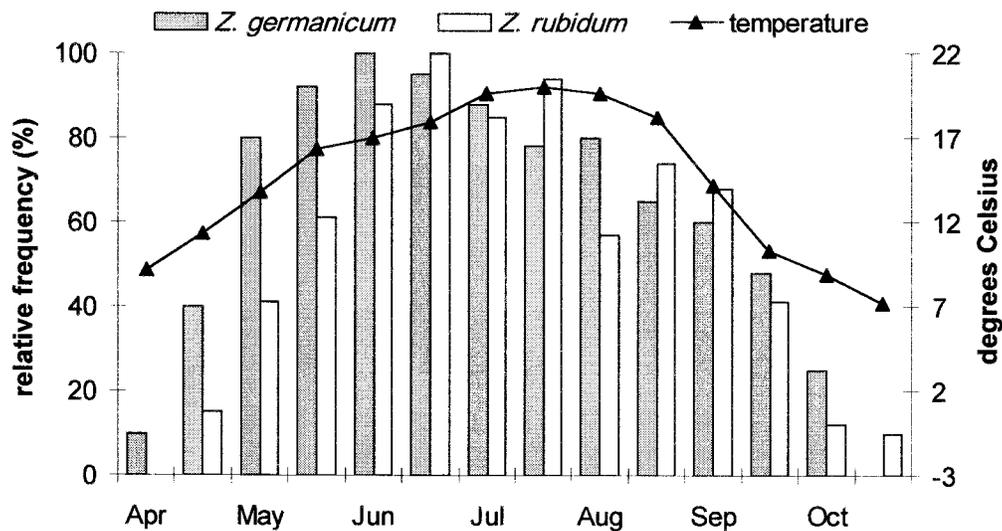


Figure 1.—Relative frequency of mature specimens of *Zodarion germanicum* and *Zodarion rubidum* compared with the average temperatures (▲) in the study region at biweekly intervals.

used for preparation of chromosomes from subadult and adult individuals. The entire contents of the abdomen were dissected out in a hypotonic solution (0.075 M KCl). After 20–25 min of hypotonic treatment, the tissues were placed into a small beaker with fresh fixative (a mixture of absolute methanol and glacial acetic acid, 3:1). The pieces of the tissues were incubated in a beaker in a refrigerator at 5 °C. During the first hour of incubation, the fixative was renewed twice (after 15 and 45 min of incubation). After 5–6 h the tissues were placed into a tube with new fixative, resuspended, and centrifuged at 2000 G for 5 min. The supernatant was discarded and the sediment was diluted in fresh fixative to an optimal concentration of fixed cells. The suspension was then dropped onto clean slides.

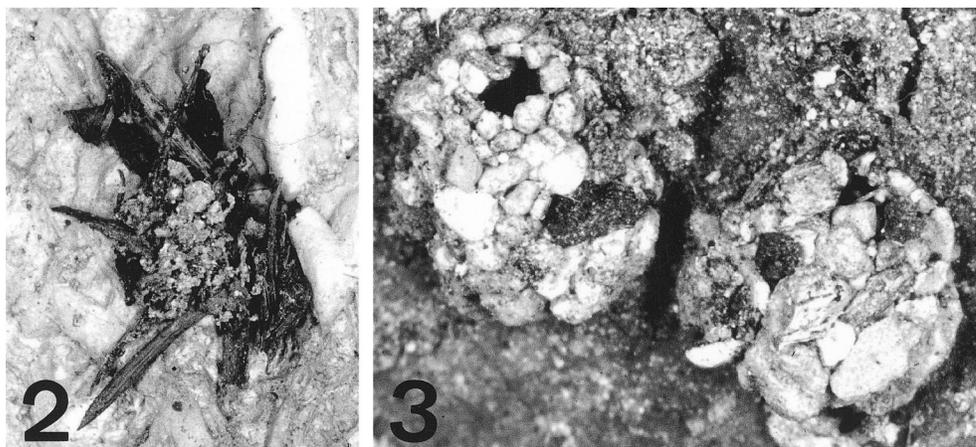
The chromosomes from first instar specimens were obtained by a modification of the spreading technique used by Traut (1976) as follows. The entire contents of the abdomen were dissected out and treated in hypotonic solution as in the former case. Following a 15–30 min fixation in freshly prepared Carnoy fixative (ethanol:chloroform:glacial acetic acid 6:3:1) the tissue was placed in a drop of 60% acetic acid on a clean slide. The tissue was quickly shredded as finely as possible with a pair of fine tungsten needles. The slide was then placed quickly on a warm histological plate (surface temperature of 40 °C) and

the drop of dispersed tissue was allowed to evaporate while keeping it moving constantly using a fine tungsten needle.

The slides obtained by both methods were air-dried at room temperature overnight, and stained with 5% Giemsa solution in Sørensen phosphate buffer (pH = 6.8) for 5–6 min (Cokendolpher & Brown 1985).

RESULTS

Phenology.—The phenology diagrams for the study species are shown in Fig. 1. Seasonal activity of spiders began in April when both juvenile and subadult specimens appeared on the ground and started hunting. Of the *Z. germanicum* specimens collected on 25 April 1997, 40% ($n = 15$) were adult, increasing to 80% ($n = 25$) within two weeks (11 May 1997). During that time, all individuals of *Z. rubidum* ($n = 17$) were still subadult. On 25 May 1997 92% ($n = 24$) of specimens of *Z. germanicum* and 61% ($n = 31$) of *Z. rubidum* were adult. In 1997, mating began in April (*Z. germanicum*) or at the end of May (*Z. rubidum*). The egg sacs were found on 17 June 1997. Examining cocoons the first free instar was found on 2 July for *Z. germanicum* and on 19 July for *Z. rubidum*. The last adults were recorded on 2 October for *Z. germanicum* and on 30 October for *Z. rubidum*. Both species overwinter as juveniles hiding in retreats.



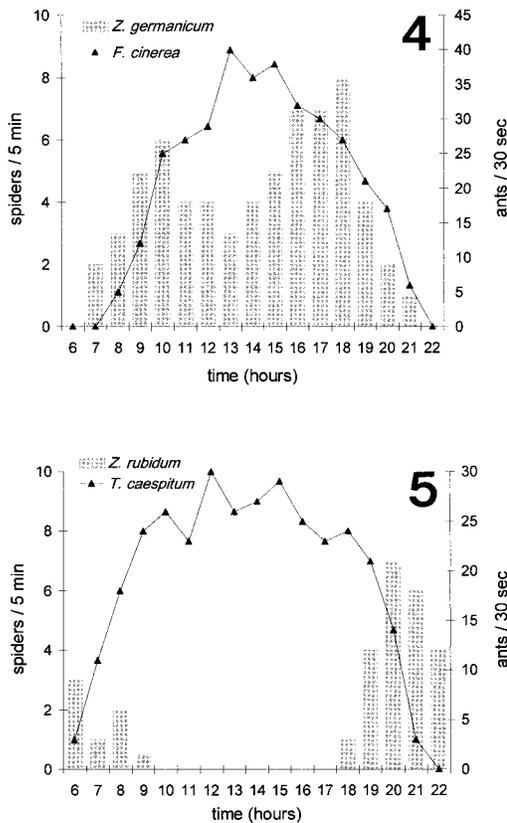
Figures 2, 3.—Igloo-shaped retreats. 2. *Zodarion germanicum* on the lower surface of a stone, constructed of soil and pine needles; 3. *Zodarion rubidum*, constructed of sand grains and attached to the lower surface of a stone.

Shelters.—The spiders rest and molt in retreats (Fig. 2). The retreats are closed solitary “igloo-shaped” shelters, usually attached to a solid substrate, such as the lower surface of stones, usually near an ant nest entrance. Often an aggregation of retreats attached to a stone was found (Fig. 3). In the field, the retreats were constructed with a wide variety of materials (e.g., soil or sand grains, plant material, pine needles) held together by webbing. In the laboratory, the retreats were also constructed of artificial material, e.g., paper. A new retreat was constructed when the old one was destroyed, or after molting. The material was collected by a spider from the vicinity of a retreat site. A spider brought a particle in its palps to a certain place, held it by a leg IV, attached it to the substrate with silk, and then continued this process until the retreat was complete. The construction of retreats lasted 0.5–2 h, depending on the availability of a suitable material. Nevertheless, in the laboratory 45% ($n = 40$) of specimens of *Z. germanicum* and 38% ($n = 40$) of *Z. rubidum* did not construct a retreat within 3 days. Such behavior was observed also in the field, where many individuals did not construct a retreat and were found to rest in soil holes or rock crevices and in other similar shelters. The diameter of retreats constructed by *Z. germanicum* was on average 5.6 ± 0.2 (S.D.) mm ($n = 8$) for adult males, 9.4 ± 0.2 mm ($n = 10$) for adult females and 4.1 ± 0.1 mm ($n = 12$) for the first instar. In *Z. rubidum* it was on

average 4.8 ± 0.2 mm ($n = 6$) for adult males, 5.3 ± 0.1 mm ($n = 9$) for adult females and 3.0 ± 0.1 mm ($n = 10$) for the first instar spiders. When no suitable material was offered, females usually spun a small sheet web (about 1 cm^2) to hide under, whereas males did not construct such a web.

Activity.—*Zodarion germanicum* was found to be active during the day. In June its activity began at about 0700 h and terminated approximately at 2100 h. The spiders were seen hunting and mating near the entrances of ant nests during all activity period, but before sunset they moved into an old retreat or constructed a new one. There was a slight decline in activity between 1000 h and 1400 h when the temperature of soil surface reached 40°C and the ants were most active (Fig. 4). During rainy or cool days (i.e., average day temperature about 15°C), the number of active spiders was approximately halved. Individuals of *Z. rubidum* were active in the morning (0600–0900 h) and in the evening (1830–2200 h) (Fig. 5). There was no spider active between 1000–1700 h. The nocturnal activity of this species was not investigated. The spiders were hunting and mating during both periods of activity; construction of retreats was recorded only in the evening. During these periods the surface temperature fell below 30°C .

Courtship and mating.—When a male of *Z. germanicum* approached a female, it began to move very slowly with the whole body vibrating, with waving raised forelegs and



Figures 4, 5.—Activity (mean number, $n = 3$) of spiders compared to the activity of ant species which the spiders most frequently hunted. 4. *Zodarion germanicum* and *Formica cinerea* in Opatovce nad Nitrou; 5. *Zodarion rubidum* and *Tetramorium caespitum* in Nováky.

drumming palps. When reaching a female, the male first lightly touched her with his forelegs, then followed by a “sparring” with palps. If the female was receptive she became passive, stayed in a normal position; and the male, still vibrating, moved across her and inserted palpal organs first from one side, then from the other side. This mating position is

classified by Foelix (1996) as ‘type 3.’ The courtship of *Z. rubidum* was much shorter. The male quickly approached the female with twitching raised forelegs and drumming palps. After a short period of palpation, they copulated in the same way as in *Z. germanicum*. The copulation lasted on average 11.9 ± 0.3 (S.D.) min ($n = 18$) in *Z. germanicum*, and 1.3 ± 0.1 min ($n = 15$) in *Z. rubidum*. The difference in duration is highly significant ($P < 0.001$; 2-sample randomization test, 4999 simulations). Soon after this primary, “long” copulation, the female of both species could copulate again with another male but the subsequent mating (which involved attempts to insert a palp from each side) lasted less than 15 sec. Before and after such short mating the female was vibrating/quivering.

Fertility and brood care.—The eggs were laid in woolly silken sacs (Fig. 6). There were on average only 4.2 eggs in a cocoon of *Z. rubidum* but 16.5 eggs in a cocoon of *Z. germanicum* (Table 1). The difference in number of eggs between the species is highly significant ($P < 0.001$; 2-sample randomization test, 4999 simulations). The eggs of both species were cream-colored and did not stick to each other but rolled freely. The mean diameter of eggs was 0.79 in *Z. rubidum* and 0.9 mm in *Z. germanicum*. The eggs of *Z. germanicum* were significantly larger ($P < 0.001$; 2-sample randomization test, 4999 simulations) than those of *Z. rubidum*.

Females of *Z. rubidum* produced an egg sac on average within 9 days after copulation whilst females of *Z. germanicum* produced an egg sac on average within 14 days (Table 1). Females of *Z. rubidum* produced up to 5 egg sacs within a month while females of *Z. germanicum* produced one or (in one case) two successive egg sacs, after hatching offspring from the first one. The female of *Z. rubidum* hid each egg sac in a separate retreat and kept on hunting ants without paying attention to

Table 1.—Comparison of differences (mean \pm standard deviation) found in the reproduction of the two study species.

	<i>Z. rubidum</i>	<i>Z. germanicum</i>
Number of eggs/cocoon	4.2 ± 0.1 ($n = 13$)	16.5 ± 0.3 ($n = 15$)
Diameter of eggs (mm)	0.79 ± 0.01 ($n = 12$)	0.9 ± 0.01 ($n = 24$)
Time to egg sac production (days)	5–13 ($n = 13$)	2–26 ($n = 15$)
Incubation period (days)	57.5 ± 1.1 ($n = 9$)	39.6 ± 1.9 ($n = 5$)

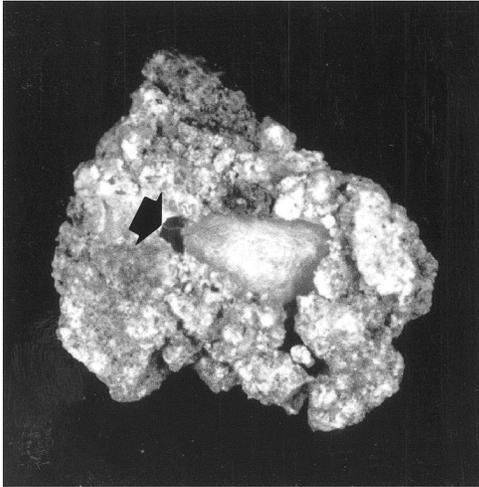


Figure 6.—Retreat of *Zodarion rubidum* including remnants of cocoon. Arrow points to the opening which spiderlings used to escape. The cocoon is the smooth-surfaced structure at the center.

the cocoons except for placing an occasional (31%, $n = 13$) dead ant in the retreat containing an egg sac. In contrast, the female of *Z. germanicum* built a large retreat in which the egg sac was placed and stayed on guard inside. She left the retreat approximately once during a four-day period to feed.

The first instar emerged from the egg sac on average 57.5 days after laying eggs in *Z. rubidum*, and after 39.6 days in *Z. germanicum* (Table 1). Nevertheless, the difference in the incubation period is not significant ($P = 0.17$; 2-sample randomization test, 4999 simulations). In the laboratory, the female of *Z. germanicum* died at last, and was fed upon by some of the first instar spiders. Spiderlings stayed in the remains of the cocoon until the first molt, which occurred within a few days of emergence. They then dispersed from the cocoon through a tiny opening on the side without assistance of the female (Fig. 6), and each specimen constructed its own tiny retreat.

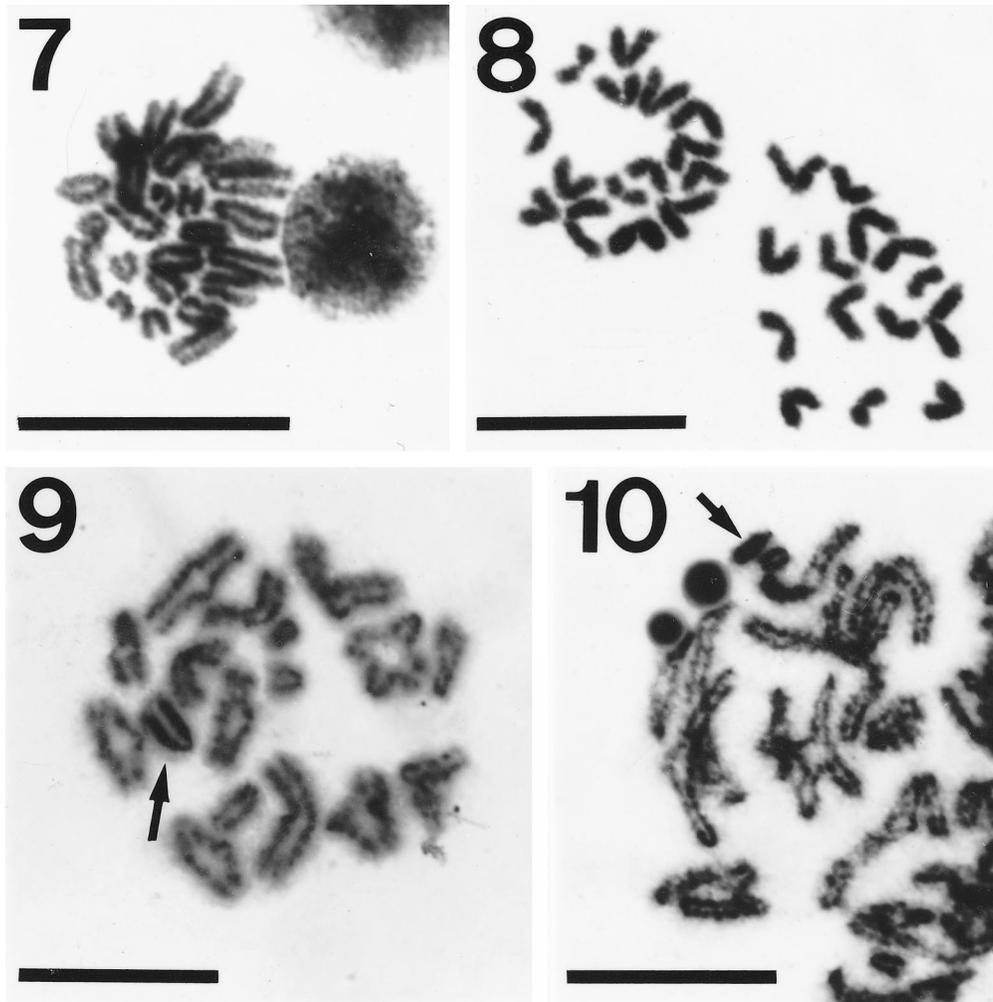
Karyotype.—Both mitotic and meiotic phases were obtained from subadult and adult males. The first instar and females gave only mitotic phases. Acrocentric chromosomes predominated in karyotypes of the both species but differences in the size of particular chromosomal pairs were apparent. The diploid chromosome number ($2n$) in *Z. germanicum* was 29 for males (Figs. 8, 10), and 30 for

females and in *Z. rubidum* 24 for males (Figs. 7, 9), and 26 for females. The comparison of meiotic male phases with mitotic metaphases of both sexes indicated an X0 type of sex chromosome system in *Z. germanicum*, with male X0 and female XX. The large X chromosome was acrocentric. *Z. rubidum* possesses sex chromosome system X_1X_20 with male X_1X_2 and female $X_1X_1X_2X_2$. Both X chromosomes were acrocentric but of different size. Similar to the majority of spiders analyzed so far, the X chromosome(s) in males of both species show greater condensation than autosomes during prophase I (positive heteropycnosis) and lie on the periphery of meiotic figures until metaphase II. In *Z. rubidum*, both X chromosomes are aligned closely to each other, not only during the first meiotic division, like the majority of species of spiders analysed so far, but even until metaphase II.

DISCUSSION

Because both species belong to the same genus, we expected that they might have similar life histories. Surprisingly, besides some similarities we also found several striking differences. Both species construct, like other species of the genus *Zodarion* studied so far, 'igloo-shaped' retreats. Observed building procedure was in agreement with the one given by Harkness (1977b) and Couvreur (1990). From an evolutionary point of view, we suppose the retreats are an apomorphy derived from simple burrowing behavior known from many other zodariid groups (Jocqué 1991) used for protection in an unusual environment of ground-living ants. Surprisingly, the construction of the retreats does not seem to be an obligatory habit of all specimens, as suggested by both laboratory and field observations. However, we suppose that even hiding in soil or in other similar places could be considered as a remnant of burrowing behavior.

Couvreur (1990) described two types of retreats, open and closed, constructed by *Z. rubidum*. According to him, the spiders hide in the open retreats when hunting but use closed retreats when resting. We have never observed open retreats either in a field or in a lab. In contrast to the laboratory findings of Harkness (1977b) on *Z. frenatum* Simon, we did not observe marked differences between the number of males and females which constructed retreats.



Figures 7–10.—7. *Zodarion rubidum*, mitotic metaphase of male; 8. *Zodarion germanicum*, two male daughter cells at metaphase II. Note differences in the size of particular chromosomes, especially in *Zodarion rubidum*; 9. *Zodarion rubidum*, diplotene of male; 10. *Zodarion germanicum*, diplotene of male. Arrow points to X chromosome(s) displaying still weak positive heteropycnosis. Scale line = 0.01 mm.

The onset of activity and maturity of *Z. rubidum* was delayed in comparison with *Z. germanicum* by about two weeks within which period the average temperature increased about 5 °C. This delay might be a consequence of the fact that the former species has spread to central Europe from southern Europe where the average day temperatures are considerably higher. The activity patterns of both species were clearly different. We observed *Z. rubidum* to be active in the evening and in the morning. We did not investigate its activity during the night since Couvreur (1990) studied the nocturnal activity of this

species in detail. Nocturnal activity was found also in other species of the genus *Zodarion*: *Z. frenatum* Simon 1884 (Harkness 1977a) and *Zodarion* sp. from Afghanistan (Schneider 1971). On the contrary, diurnal activity as observed in *Z. germanicum* has never been reported for any species of the genus *Zodarion*.

Until now, information gathered about mating and related behavior of the genus *Zodarion* has been very scarce and incomplete. Our observation revealed that although both species copulated in the same position, characteristic for “modern” wandering spiders (Foelix 1996), significant differences in courtship

and mating were observed. In *Z. germanicum*, courtship and mating took more time and were more complex than in *Z. rubidum*.

Except for the "long" copulation that we consider a true one, we also recorded multiple short copulations in both species. Such copulations were also noticed by Gerhardt (1928) who observed in *Z. elegans* (Simon 1873) multiple copulations, each lasting only a few sec. We consider this a pseudo-copulation. After the true copulation, the females became unreceptive and expressed this by a specific behavior (quivering) which threatened the male. A similar behavior was observed for the female of a thomisid spider, *Xysticus cristatus* (Clerck 1757) (Bristowe 1941).

Females of both species hid their egg sacs in retreats as observed by Harkness (1995) in *Z. frenatum* but showed different brood-care strategies. While females of *Z. germanicum* produced only one or two egg sacs of approximately 16 eggs each and guarded the egg sacs, females of *Z. rubidum* produced on average 5 egg sacs of approximately 4 eggs, and exhibited no further care. Wiehle (1953) found 25–50 eggs per egg sac in *Z. germanicum*. However, we found a maximum of 25 eggs per egg sac of this species. Regarding other *Zodarion* species, Harkness (1995) reported 9–12 eggs/egg sac of *Z. frenatum*. Unfortunately, he did not mention either how many egg sacs the female produced or whether the female guarded the egg sacs or not.

With respect to the karyology, the family Zadariidae appears to be practically an unknown group. Only one short note on the number of chromosomes in "*Storena*" *indica* Tikader & Patel 1975 (2n, male = 22; X_1X_2O) has been published (Datta & Chatterjee 1983). Males of the species examined possess a haploid number of chromosomes which is close to the mean male haploid number of chromosomes ($n = 14.09$) in spiders (Gowan 1985). Though both species studied are placed in the same genus, they differ considerably in the number of chromosomes as well as in the sex chromosome system. From an evolutionary point of view, *Z. rubidum* exhibited a sex chromosome system that seems to be an ancestral trait in spiders (Suzuki 1954; White 1973). This sex chromosome system was also found in the most primitive recent spider taxon, i.e., in Mesothelae (Suzuki 1954). Thus we hypothesize that the system XO in *Z. ger-*

manicum is derived from the X_1X_2O . The large acrocentric X chromosome of this species might have originated by tandem fusion between the ancestral acrocentric chromosomes X_1 and X_2 that are still conserved in the karyotype of "*S.*" *indica* and *Z. rubidum*.

Our comparative study revealed that although both species are placed in the same genus, they differ in a number of characters such as activity pattern, courtship, mating, brood care, karyotype and sex chromosome system. Our results support Bosman's (1997) separation of these species into two different groups and suggest they might belong to distant evolutionary branches of this genus. However, to understand further the evolution process within the genus *Zodarion*, we suggest additional research of these aspects of biology in other representatives of this genus. We assume such investigation might also contribute a clarification of the evolution of mimicry in the subfamily Zadariinae.

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