Dietary specialisation and diversification of the spider genus *Dysdera* (Araneae: Dysderidae)

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CONTENTS

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1. INTRODUCTION

1.1. Dietary specialisation

Dietary specialisation as a driving force of morphological and behavioural diversification became a frequent subject of zoological studies since Darwin (1858) documented the adaptive diversity of finches in the Galapagos archipelago. Dietary specialists often evolve remarkable morphological and behavioural adaptations, which are absent in dietary generalists. Such adaptations increase the efficiency of capture of the principal prey but at the same time, constrain the ability to utilise other prey (Ferry-Graham, Bolnick & Wainwright 2002). It can be a fatal disadvantage when the principal prey resource becomes rare. As a result, Dietary specialisation has evolved rather on prey that is widely abundant (Emlen 1966).

The literature on specialised arthropod predators is biased towards aphid-specialists (*e.g.*,Hodek & Honěk 1996) and ant-specialists (*e.g.*, Hölldobler & Wilson 1990). On the other hand, we have only limited knowledge about specialised predators of other groups, for example of oniscoid isopods, i.e. woodlice, the dominant component of ground-dwelling fauna of many habitats (Sutton 1980). Woodlice are clumsy detritus-feeders, that possess almost insurmountable morphological, chemical, and behavioural defences. Their tegumental gland secretions make them evil smelling or indigestible for many predators (Sutton 1980). Heavily incrusted armour protects the majority of their body against a predator's mouth-parts. Moreover, the soft ventral side of the body is effectively protected either by rolling up into a ball (rollers) or by clinging strongly to the substrate (clingers) (Schmalfuss 1984).

Large vertebrate predators are able to overcome defences of woodlice (*e.g.*, Pernetta 1976, Lima, Magnusson & Williams 2000, Bureš & Weidinger 2003). Considering invertebrate predators (Gorvett 1956), only some groups of arthropods have been found to feed occasionally on woodlice (*e.g.*, Raupach 2005, Sunderland & Sutton 1980), namely scorpions (*e.g.*, Kheirallah 1979), harvestmen (*e.g.*, Sunderland & Sutton 1980), spiders of several different families (*e.g.*, Raupach 2005, Sunderland & Sutton 1980, Nentwig 1986, Pötzsch 1966, Barmeyer 1975), centipedes (*e.g.*, Sutton 1970), earwigs, ants (*e.g.*, Sunderland & Sutton 1980), true bugs (*e.g.*, Kott 2000), ant lions (Matsura & Kitching 1993), crickets (*e.g.*, Paris & Sikora 1967), and few beetles (*e.g.*, Dennison & Hodkinson 1983, Whitehead 1986).

Only one invertebrate group has been reported to be specialised on woodlices so far, namely most species of the ant genus *Leptogenys* from tropical Africa and America. Some *Leptogenys* ants specialised in woodlice are able to accept also other prey than woodlice (Whitcomb *et al.* 1972), others accepted only woodlice (Dejean 1997). Specialised species developed morphological as well as behavioural adaptations, which allow them to overcome regularly defensive tactics of woodlice. They have elongated, thin and curved mandibles which can grasp the rollers (Dejean 1997): when the woodlouse fits between the mandibles they grasp it by its whole body, when it is larger they grasp it by the edge of the shell (Dejean & Evraerts 1997).

Also spiders of the genus *Dysdera* are suspected to be specialised woodlice predators. These spiders are remarkable for an unusual morphological variability of the mouth parts, particularly chelicerae. The unique modifications of their mouth-parts are used as characters in infrageneric taxonomy (Deeleman-Reinhold & Deeleman 1988, Arnedo, Oromí & Ribera 2001), but little is known about their function.

Chelicerae are the most important mouth parts of spiders. They are used primarily for prey handling. Besides this, they are used also for burrow construction, courtship, and defence (Bristowe 1958). They are composed of two segments, a robust basal segment and thorn-like fang with a poison gland orifice on its tip. When inactive, the fang is compounded in the cheliceral groove on the medial side of the basal segment. In the majority of spiders the

chelicerae work synchronously against each other. They are extraordinarily morphologically uniform in the vast majority of spiders. This could be because spiders are usually nonselective predators; their mouth-parts must be generalized enough to allow them to capture a wide range of prey. Many of spider dietary specialists do not possess any cheliceral modifications. Instead, they developed various specialised hunting tactics and various types of silk and poison modifications to make the capture of their principal prey more efficient. Most of the cases of cheliceral modifications in spiders evolved under sexual selection as evidenced by sexual dimorphism in this character (*e.g.* in *Tetragnatha* – Wiehle 1963, *Enoplognatha* – Bosmans & Van Keer 1999, *Salticus* – Prószyński 2004). Only very few cases of cheliceral modifications are known to be associated with specialisation for prey capture. In two orb-web spiders (Orbiculariae) Olive (1980) showed a relationship between fang size, leg length, and web mesh size and placement. He suggested that combinations of these traits allowed orb-web spiders to specialize on larger or smaller flying insects and on insects differing in their defense abilities.
Cheliceral modifications in *Dysdera* cannot be explained by sexual selection as they are similar in both sexes and are present during the entire ontogenetic development. Thus the modifications have probably evolved in relation to the type of prey captured. It was suggested that one type of modification, namely elongated chelicerae, is an adaptation for an effective capture of armoured woodlice (Bristowe 1958, Pollard 1986). The first aim of my PhD. thesis was to find how is cheliceral variability of *Dysdera* spiders related to their prey and predatory behaviour.

1.1.1. Accepted prey and prey choice

Concerning prey, informations are available in two *Dysdera* species only. *Dysdera erythrina* and *D. crocata* possess elongated chelicerae and have been repeatedly observed to capture woodlice in nature (*e.g.*,Bristowe 1958, Hopkin & Martin 1985, Raupach 2005). Their woodlice-eating behaviour was also confirmed by detecting woodlice antigens in their digestive tract (Sunderland & Sutton 1980), and by a survey of remnants in their silk retreats (Cooke 1965*a*). However, these species were observed in the laboratory to catch almost all arthropods that were sufficiently small and slow moving (Cooke 1965*a, b, c*). Moreover, *D. crocata* did not prefer woodlice to other arthropods in the laboratory experiments (Pollard *et al.* 1995). Given these results their specialisation on woodlice was put into question. No information is available about the prey of the *Dysdera* species possessing other types of chelicerae.

The questions addressed in this part of my thesis are:
Which types of prey are accepted by *Dysdera* species with different types of chelicerae?
Which types of prey are prefered by *Dysdera* species with different types of chelicerae?
The results are presented in the chapter 2.1.

1.1.2. Metabolic adaptation

Prey choice experiments can result in misleading conclusions about prey specialisation due to unnatural conditions (*e.g.*, Stamp 2004). The ultimate evidence for dietary specialisation should provide analysis of the nutritional adaptations (Toft & Wise 1999). Such adaptation is a necessity allowing specialists to obtain all required nutrients from their exclusive prey. For specialists alternative prey is of inferior quality and has not a beneficial effect on their fitness, as has been demonstrated, for example, in aphidophagous predators (*e.g.*, Hodek & Honěk 1996, Short & Bergh 2004).

In spiders, the experimental evidence of nutritional specialisation has been performed only with an araneophagous and a myrmecophagous species so far. Li & Jackson (1997) showed that a diet made exclusively of spiders provides the araneophagous salticid *Portia* with a superior fitness compared to a monotypic insect diet and a mixed (insects and spiders) diet, which reduced the fitness. Similarly, Pekár *et al.* (unpublished) showed that myrmecopagous *Zodarion* spiders were able to develop only on monotypic ant diet. This is in contrast to generalists to which dietary mixing has a beneficial effect (*e.g.*, Oelbermann & Scheu 2002, Acharya, Kyle & Elser 2004). The results on *Portia* and *Zodarion* conform to those on the aphidophagous beetle *Coccinella septempunctata* Linnaeus (*e.g.*, Nielsen, Hauge & Toft 2002), and may thus represent a general response of specialised predators to a mixed diet.

I was mainly interested in the following question:
Are the prey preference experiments a reliable method to confirm specialisation on woodlice in *Dysdera* spiders?
The results are presented in the chapter 2.2.

1.1.3. Predatory behaviour

Predatory behaviour of only two *Dysdera* species, *D. crocata* and *D. erythrina* was observed. These species turn the prosoma sideways vertically to direct one chelicera against the ventral and the upper one against the dorsal side of the woodlouse. Elongation of their chelicerae was considered to be an adaptation allowing this grasping strategy (Bristowe 1958, Pollard 1986). However, my preliminary experiments shown that *Dysdera* species possessing other cheliceral modifications also readily captured woodlice.

The question addressed in this part of the thesis is:
Do the *Dysdera* species with different morphology of chelicerae capture woodlice using a different predatory tactics?
The results are presented in the chapter 2.1.

1.2. Diversification

The study of speciation has become one of the most active areas of evolutionary biology (Howard and Berlocher 1998). For different groups of organisms, various speciation modes were suggested. These modes have been often classified according to the geographical arrangement of populations undergoing the process, specifically allopatric, sympatric and parapatric mode of speciation (*e.g.*, Mayr 1963, Maynard-Smith 1966). Recently a different classification was proposed in which the first division separates those cases driven by selection from those in which speciation occurs primarily by genetic drift (Via 2001). In speciation by genetic drift the reproductive isolation evolves as a consequence of fixations of accidental mutations. In the speciation driven by selection, disruptive selection leads to reproductive isolation and consequent differentiation of speciesIt is in particular "ecological speciation" (*sensu* Schluter 2001) where reproductive isolation evolves ultimately as a consequence of divergent natural selection on traits in different environments. "Environment" refers to all biotic and abiotic elements of habitat, *e.g.*, climate or resource competition (Schluter 2001). Such speciation mode is suggested in cases when sister species differ in characters, which are influenced by natural selection, and currently live in sympatry, suggesting different niches. However, the reproduction barrier is supposed to evolve in allopatry. In this respect ecological speciation differs from the sympatric speciation, in which reproduction barrier evolves in sympatry (Maynard-Smith 1966). Among animals, ecological speciation was suspected to play a role in many herbivores, but in a few carnivores only (*e.g.*, Tauber *et al.* 1993).

Posible candidates of carnivores evolving by ecological speciation are just the *Dysdera* spiders as sister species of this genus often differ in the morphology of mouth parts and body size and occur sympatrically (*cf.* Deeleman-Reinhold and Deeleman 1988, Arnedo and Ribera 1999). Comprising more than 240 species (Platnick 2007), *Dysdera* is by far the largest genus in the family Dysderidae and one of the richest Palearctic spider genera. The number of species is probably much higher, which is documented by dramatic increase of the number of new species described in last decades (*cf.* Platnick 2007). Furthermore, the genus *Dysdera* is unique among other genera of the spider family Dysderidae by regular presence of aggregates of sibling species. To understand the evolution of *Dysdera* aggregates, a complex knowledge about their biology is necessary. Until now, we have only some information on the morphological differences, distribution (*e.g.*, Deeleman-Reinhold and Deeleman 1988), and mt DNA diversity (Arnedo *et al.* 2001) of only few aggregates.

To reveal the mechanisms generating interspecific barriers and reducing competition for prey, that might allow sympatric coexistence of closely related *Dysdera* species, I decided to perform an analysis of a selected aggregate. I concentrated on the *D. erythrina* aggregate. This aggregate, so far determined as a single species, is composed of several very similar species that have presumably diverged relatively recently. I assume that these young species differ mainly in characters that played an important role in the speciation process. Old taxa often do not provide clear signatures of speciation mode as these are already overdriven by following evolutionary processes (Jiggins & Mallet 2000). In order to get detailed information about morphological differences, habitat preference, phenology, and distribution of studied species, I analyzed i) an extensive material deposed in European museums, and ii) material collected myself during visits of locations of occurence. Furthermore, I analyzed karyotypes and diet in selected species, and performed crossing experiments between selected species of the aggregate. To supplement informations obtained by analysis of *D. erythrina* aggregate, I studied also natural history of the other *Dysdera* species occuring the central Europe that belong to several other aggregates.

1.2.1. Morphology

There has been much confusion concerning identification of *Dysdera* spiders because of the uniformity in both the shape and body color and lack of external female genitalic features (*e.g.*, Deeleman-Reinhold 1988). Moreover, sibling species of *Dysdera* display only minute morphological differences of copulatory organs – otherwise highly divergent structures among spider species.
Diagnostic characters of *Dysdera* spiders are the body size, colour of prosoma, shape and sculpture of carapace, leg spination, as well as the shape of chelicerae and copulatory organs (Deeleman-Reinhold & Deeleman 1988, Arnedo *et al.* 2001). The carapace length ranges between 1.5–8.3 mm. The prosoma is brown, red, ferruginous, orange, yellow or ecru. The carapace of particular species differ in relative width and height, it is smooth, smooth with pits or wrinkled. Spines are usually present only on hind legs, their number and position are species specific. In some species, leg spination is absent. Chelicerae differ in the shape of both basal segment and fang. The basal segment is either short or elongated. Furthermore, basal segment is either mediodorsally concave, covered by short bristles, or convex, covered by normal hairs. Fang can be normal, *i.e.* thorn-like, or dorsoventrally flattened. The male copulatory organ of *Dysdera*, bulbus, is composed of two segments, proximal tegulum and distal division, connected by haematodocha. Tegulum is smooth; its distal margin bears heavily sclerotised tooth-like posterior apophysis. Distal division bears lobes and apophyses of species specific shape. The openning of the sperm duct is located on the apical part of distal division. The female copulatory organ, endogyne, is positioned within an abdomen. It is relatively complex, holding two types of "cul-de-sac" sperm storage organs (Cooke 1966). Anteriorly it is composed of heavily sclerotised spermatheca and bursa copulatrix. Behind the epigastric furrow there is an unsclerotised structure called posterior diverticle.
Despite minute morphological diffrences between particular *Dysdera* siblings in aggregates, these details could play an important role in the speciation process.

The question addressed in this part of my thesis is:
In which morphological characters do the *Dysdera* sibling species differ?
The results are presented in the chapters 2.3 and 2.4

1.2.2. Distribution

The genus *Dysdera* is a Palearctic taxon; most species are restricted to small areas in the western part of Palaearctic region, mainly in the Mediterranean basin (Platnick 2007, Deeleman-Reinhold & Deeleman 1988). Remarkably small distribution areas of most species are probably caused by inability of *Dysdera* to disperse to a long distance. These spiders are characterised by a long life and relatively low fecundity (*cf.* Cooke 1965*a*). Thus they belong to K-selected species which do not undergo high-risk dispersal behaviors such as ballooning. Balloon dispersal has never been reported in *Dysdera* spiders, and they have never been recorded in aerial samples (Duffey 1956). For example, not a single specimen was captured among 10,000 spider specimens collected in Switzerland (Blandenier & Fürst 1998). A single ballooning dysderid recorded in Blandenier & Fürst (1998) turned out to be juvenile of *Harpactea* (Řezáč, unpublished).
Nevertheless, *Dysdera* species are prone to passive accidental transport with human material due to their tendency to attach silken retreats to large objects lying on the ground. Chance to disperse by such transport is frequent among species with affinities for synanthropic habitats. The most remarkable case represents *Dysdera crocata,* which was introduced to synantropic habitats of almost all continents (Cooke 1967). Beside *D. crocata*, four other *Dysdera* species

were recorded from outside Palearctic region, but their identity was put into question (Cooke 1965*c*). Similar, yet less extensive (within the Mediterranean basin), expansions to synanthropic habitats have also been recorded for several other species, namely *D. aculeata, D. lata, D. spinicrus, D. westringi* (Deeleman-Reinhold & Deeleman 1988), and *D. kollari* (Gasparo 2004).
Interestingly, closely related *Dysdera* species often occur sympatrically (*e.g.*, Deeleman-Reinhold and Deeleman 1988). On the other hand, some species avoid to occur in the same sites in areas of sympatric occurence, that could be a consequence of competition. Such case are probably *D. erythrina* and *D. crocata* in England (Cooke 1967).
A special preadaptation for migration might be thelytokous parthenogenesis found in *D. hungarica*. As each adult specimen can produce eggs, thelytokous reproduction is twice as fast as sexual one where half of the population is formed by males. Moreover, new localities can be colonized more quickly as a single individual can give rise to a new clone (Suomalainen *et al.* 1987). However, we have almost no information about the distribution of sexual populations and parthenogenetic clones of *D. hungarica*.

The questions addressed in this part of my thesis are:
Are there any other *Dysdera* species beside *D. crocata* occuring outside Palearctic region?
What is the overall distribution of the *Dysdera* species occuring in the central Europe?
Do the selected *Dysdera* sibling species occur sympatrically or allopatrically?
Do the selected *Dysdera* species occur in the same sites in areas of sympatric occurence?
What is the distribution of sexual populations and parthenogenetic clones of *D. hungarica*?
The results are presented in the chapters 2.3 and 2.4.

1.2.3. Habitats

Dysdera spiders are non-web building clumsy predators foraging on the ground at night. During the day they shelter themselves in silk retreats in gravel covered by organic material, under stones or woods (Cooke 1965*a*). The majority of *Dysdera* species occur mainly in xerothermic forests (see Deeleman-Reinhold & Deeleman 1988).
Ecological plasticity can be expected in parthenogenetic clones of *D. hungarica*. Thelytoky may enable the clones to survive even in suboptimal habitats, which are, however, not suitable to harbour the high abundance necessary for sexual reproduction. However no information is available about the habitats of parthenogenetic clones and sexual populations of this species.

I was mainly interested in the following questions:
Do the *Dysdera* sibling species prefer different habitats?
Do the parthenogenetic clones of *D. hungarica* occur in wider range of habitats than the sexual populations of this species?
The results are presented in the chapters 2.3 and 2.4.

1.2.4. Phenology

Phenology of only two *Dysdera* species, namely *D. crocata* and *D. erythrina*, has been studied so far. Cooke (1965*b*) concluded that females of both species lay eggs in May–June and that it takes juveniles one and half year to mature. According to these data both species have biennal life cycle.
The sympatrically occuring *Dysdera* species probably possess some mechanisms of precopulatory barrier which prevent them from vasting their reproduction potential. Such barrier could be different phenology preventing nonspecific partners to meet in the same time.

The question addressed in this part of my thesis is:
Do the sympatrically occuring *Dysdera* species possess different phenologies?
The results are presented in the chapters 2.3 and 2.4.

1.2.5. Genetics

Karyotype of only one *Dysdera* species has been studied so far. The male karyotype of *D. crocata* is composed of five autosome pairs and a single sex chromosome (Benavente & Wettstein 1980, Benavente 1982, Rodríguez Gil *et al.* 2002). Thus it possesses the sex chromosome system X0. Four autosome pairs were recorded in the population called *D. magna* from Uruguay (Díaz & Sáez 1966a, b). The karyotypes of both forms are composed of holocentric chromosomes (Díaz & Sáez 1966a, b, Benavente & Wettstein 1980, Rodríguez Gil *et al.* 2002). In contrast to normal (monocentric) chromosomes, holocentric chromosomes possess kinetochore along the major part of their length. Therefore, products of breakages (fragments) or fusions (fused chromosomes) often segregate regularly to the poles during divisions. In this way, fragments and fused chromosomes are more easily tolerated than in organisms with more common monocentric chromosomes (Jacobs 2004). Thus, holocentric structure of chromosomes can facilitate diversification of karyotypes.
If chromosome rearrangements played important role in speciation, the karyotypes of closely related species should be more diversified than karyotypes of unrelated species.
Despite sympatric occurrence of some closely related *Dysdera* species, hybrids have never been observed. Cooke (1965*a*) observed in the laboratory that *D. crocata* and *D. erythrina* are not ready to mate, however rarely they do so.
Absence of mating between closely related species with overlapping areas indicate some recognition mechanisms preventing them to cross.

The questions addressed in this part of my thesis are:
What is the degree of karyotype diversification of the *Dysdera* spiders?
Do the *Dysdera* sibling species differ remarkably in their karyotypes?
Do the *Dysdera* spiders recognise nonspecific partner belonging to the sympatrically occuring sibling species?
The results are presented in the chapters 2.3, 2.4 and 2.5.

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2. RESULTS

All the results, including discussion of results obtained, are presented in the following section as a collection of already published or submitted papers.

1) **Řezáč M.**, Pekár S. & Lubin Y.: Morphological and behavioural adaptations for oniscophagy in *Dysdera* spiders (Araneae: Dysderinae). Accepted by *Journal of Zoology*[*].
2) **Řezáč M.** & Pekár S.: Evidence for woodlice-specialisation in *Dysdera* spiders: behavioural *versus* developmental approach. Accepted by *Physiological Entomology*.
3) **Řezáč M.**, Král J. & Pekár S.: Revision and speciation mode of the spider aggregate *Dysdera erythrina* (Araneae: Dysderidae): sibling species with sympatric distribution. Submitted to *Invertebrate Systematics**.
4) **Řezáč M.**, Král J. & Pekár S.: The spider genus *Dysdera* (Araneae, Dysderidae) in central Europe: revision and natural history. Accepted by *Journal of Arachnology*.
5) Král J., Musilová J., Šťáhlavský F., **Řezáč M.**, Akan Z., Edwards R. L., Coyle F. A., Ribera C. (2006): Evolution of the karyotype and sex chromosome systems in basal clades of araneomorph spiders (Araneae: Araneomorphae). *Chromosome Research*, 14: 859–880.

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Morphological and behavioural adaptations for oniscophagy in *Dysdera* spiders (Araneae: Dysderinae)

A short title: Adaptations for oniscophagy in *Dysdera* spiders

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Abstract
Very little information is available about predators feeding on woodlice. Spiders of the genus *Dysdera* (Dysderidae) were long suspected to be oniscophagous, but evidence for their diet specialisation is lacking. *Dysdera* spiders are characterised by an unusual morphological variability of their mouth-parts, particularly the chelicerae. We investigated the relationship between mouthpart morphology, prey preference and predatory behaviour of five species representing different cheliceral types. The species with unmodified chelicerae readily captured various arthropods but refused woodlice while species with modified chelicera captured woodlice. *Dysdera erythrina* and *D. spinicrus* captured woodlice as frequently as alternative prey types. *Dysdera abdominalis* and *D. dubrovninnii* significantly preferred woodlice to alternative prey. Cheliceral modifications were found to determine the grasping behaviour. Species with elongated chelicerae used a 'pincers tactic', i.e. inserted one chelicera into the soft ventral side and placed the other on the dorsal side of woodlouse. Species with dorsally concave chelicerae used a 'fork tactic': they tucked them quickly under woodlouse in order to bite the ventral side of woodlouse body. Species with flattened chelicerae used a 'key tactic': they inserted a flattened chelicera between sclerites of the armoured woodlouse. Our results suggest that prey specialisation for woodlice differs among *Dysdera* spiders.

Key words: chelicerae, defence tactics, diet specialisation, *Dysdera*, Isopoda, mouthparts, predatory behaviour, woodlice

INTRODUCTION

Diet specialisation as a driving force of morphological and behavioural diversification became a frequent subject of zoological studies since Darwin (1858) documented the variability of beaks of finches in the Galapagos archipelago. Diet specialists often evolve remarkable morphological and behavioural adaptations, which are absent in diet generalists. Such adaptations increase the efficiency of capture of the principal prey but at the same time, constrain the ability to utilise other prey (Ferry-Graham, Bolnick & Wainwright, 2002). Specialization can be a great disadvantage when the principal prey becomes rare. As a result, diet specialisation has evolved mainly on prey that is abundant (Emlen, 1966).

The literature on specialised arthropod predators is biased towards aphid-specialists (e.g. Hodek & Honěk 1996) and ant-specialists (e.g. Hölldobler & Wilson 1990). We have

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only limited knowledge about specialised predators of woodlice, the dominant component of ground-dwelling fauna of many habitats (Sutton, 1980). Woodlice are clumsy detritus-feeders that possess almost insurmountable morphological, chemical and behavioural defences. Their gland secretions make them evil smelling or indigestible for many predators (Sutton, 1980). Heavily incrusted armour protects most of their body against a predator's mouth-parts. The soft ventral side of the body is effectively protected either by rolling up into a ball (rollers) or by clinging strongly to the substrate (clingers) (Schmalfuss, 1984). These defence mechanisms are particularly effective against small predators (Gorvett, 1956) as only a few groups of arthropods have been found to feed occasionally on woodlice, namely scorpions (e.g., Kheirallah, 1979), harvestmen (e.g., Sunderland & Sutton, 1980), spiders of several different families (e.g., Raupach, 2005; Sunderland & Sutton, 1980; Nentwig, 1986; Pötzsch, 1966; Barmeyer, 1975), centipedes (e.g., Sutton, 1970), earwigs, ants (e.g., Sunderland & Sutton, 1980), true bugs (e.g., Kott, 2000), ant lions (Matsura & Kitching, 1993), crickets (e.g., Paris & Sikora, 1967), and few beetles (e.g., Dennison & Hodkinson, 1983; Whitehead, 1986). A single woodlice-eating specialist has been observed so far. Ants of the genus *Leptogenys* from tropical Africa and America developed morphological as well as behavioural adaptations, which allow them to overcome woodlice defensive tactics. These ants have elongated, thin and curved mandibles by which they grasp the rollers (Dejean, 1997): if the woodlouse fits between the mandibles they grasp it by its whole body, if it is larger they grasp it by the edge of the shell (Dejean & Evraerts, 1997).

Spiders of the genus *Dysdera* (Dysderidae) are suspected to be specialised predators of woodlice as well. This genus is composed of 250 described species; almost all of them are restricted to small areas in the western Palaearctic, mainly around the Mediterranean basin (Platnick, 2006). These spiders are non-web building predators that search for prey on the soil surface at night. During the day they are hidden in silk retreats under stones or wood. This spider genus is remarkable for an unusual morphological variability of the chelicerae. The unique modifications of their mouth-parts are used as characters in infrageneric taxonomy (Deeleman-Reinhold & Deeleman, 1988; Arnedo, Oromí & Ribera, 2001), but little is known about their function.

Spider chelicerae are composed of two segments, a robust basal segment and a thorn-like fang with a poison gland orifice near its tip. They are used primarily for prey handling but function also in burrow construction, courtship and defence (Bristowe, 1958). In the majority of spiders the chelicerae work synchronously against each other. Chelicerae are extraordinarily morphologically uniform in the vast majority of spider species. This could be because spiders are usually nonselective predators and their mouth-parts must be generalized enough to allow them to capture a wide range of prey. Many of the dietary specialists in spiders do not possess any cheliceral modifications. Instead, they developed various specialised hunting tactics and various types of silk and poison to make the capture of their principal prey more efficient. Very few cases of cheliceral modifications are known to be associated with functional specialisation for prey capture. Olive (1980) showed a relationship between fang size, leg length and web mesh size and placement. He suggested that combinations of these traits allowed orb-web spiders to specialize on larger or smaller flying insects and on insects differing in their defence abilities. Most of the cases of striking cheliceral modifications in spiders evolved under sexual selection as evidenced by sexual dimorphism in this character (e.g. in *Tetragnatha* – Wiehle, 1963; *Enoplognatha* – Bosmans & Van Keer, 1999; *Salticus* – Prószyński, 2004).

Cheliceral modifications in *Dysdera* cannot be explained by sexual selection as they are similar in both sexes and are present during the entire ontogenetic development. Thus we suggest that the modifications have evolved in relation to the type of prey captured. There are observations on the predatory behaviour of only two *Dysdera* species so far. Both, *Dysdera*

erythrina and *D. crocata*, possess elongated chelicerae and are known to feed regularly on woodlice (Bristowe, 1958; Sunderland & Sutton, 1980; Hopkin & Martin, 1985; Raupach, 2005). Analysis of prey remnants found in their silk retreats and choice experiments indicated that these species do not prefer any particular woodlouse species (Cooke, 1965a; Pollard *et al.*, 1995). The capturing technique of these two species is similar. Elongation of their chelicerae was considered to be an adaptation allowing them to grasp woodlice (Bristowe, 1958; Pollard, 1986).

Given that elongated chelicera allow *Dysdera* spiders to capture woodlice efficiently, why have other modifications evolved in sister species? We hypothesised that *Dysdera* species with different chelicerae either (1) possess different prey specificity, with some being oniscophagous while others preying on alternative prey, (2) feed on different types of woodlice or (3) feed on woodlice using different capture tactics. In order to test these hypotheses we performed prey preference experiments and observed predatory behaviour of five *Dysdera* species possessing different cheliceral types.

METHODS

Five *Dysdera* species representing different types of chelicerae (Table 1) were selected for the prey choice experiments and observations of predatory behaviour.

Assessment of prey preference

Two experiments were performed to reveal prey preferences of each *Dysdera* species. The first experiment was design to reveal the range of prey taken. Ten adults of each *Dysdera* species were placed singly in Petri dishes (diameter 30 mm) with moistened filter paper covering the bottom of the dish. For two weeks the individuals were kept at 20°C and deprived of prey. In previous experiments we found that two weeks without food is an optimal period to make spiders moderately hungry (M. Řezáč, unpubl. data). Then they were offered ground-dwelling arthropods abundant in the dry forest habitats of the studied spider species. In particular we used woodlice (*Armadillidium vulgare* (Latreille, 1804)), centipedes (*Lithobius* sp.), millipedes (Julidae), ants (*Lasius niger* (Linnaeus, 1758)), beetles (various Carabidae), spiders (*Pardosa* sp.), earwigs (*Forficula auricularia* Linnaeus, 1758) and springtails (large Entomobryidae). We also offered them few non-epigaeic arthropods, namely true bugs (various Miridae), flies (*Musca domestica* Linnaeus, 1758) or *Drosophila melanogaster* Meigen, 1830), and moths (*Ephestia kühniella* Zeller, 1879). All prey offered were alive and given one at a time. The order of prey presentation was random. The prey never exceeded the spider in size. If the prey was not captured within 30 minutes after being offered, it was replaced by another prey item chosen randomly until a prey item was accepted. We prevented the spiders from consuming the prey in order to keep them hungry. Refusal of prey was recorded only when followed by an acceptance of other prey on the same day. If the spider did not accept any other prey from the remaining types, we offered it the same prey it had already accepted to confirm the preference.

In the second experiment we tested whether *Dysdera* species are able to catch woodlice species with different defence tactics versus alternative prey. We used 50 individuals of each *Dysdera* species. As prey we used a rolling woodlouse *A. vulgare,* a clinging woodlouse *Porcellio scaber* and an alternative prey *M. domestica*. The length of the prey corresponded approximately to the length of spider's prosoma. The Petri dishes of the same size as in the previous experiment were with a piece of moistened filter paper attached to the bottom to provide humidity. The three prey types were offered simultaneously to each spider individual. We checked the dishes after 24 hours and replaced dead prey by a fresh one

when necessary. We recorded cases when only one prey was eaten, which was determined by observing if the prey had been sucked out. In total we had fifty replications with every tested spider species.

Data were analysed with Generalised Linear Models within R (R Development Core Team 2004). As all data were proportions, binomial error structure with cannonical link function was used (GLM-b). The maximal model of the two-way analysis of deviance (ANODEV), including the interaction between *Dysdera* species and prey species, was simplified by combining *Dysdera* species with a similar response, as the interaction was significant. Each simplification was tested with χ^2 statistics. Combining continued until a minimal adequate model was achieved (Crawley, 2002). This procedure is in accordance with the principle of parsimony. Differences at species level were then tested using *a posteriori* contrasts.

Observation of predatory behaviour

To compare predatory behaviour of *Dysdera* species we used the woodlouse *A. vulgare* as prey since this species was generally accepted. The prey length was between half and full body length of the spider. We recorded on video twenty attacks for each species performed by different individuals of both sexes and various ontogenetic stages. As before, the spiders were starved for two weeks before the experiment. In four out of five species tested the spider usually attacked immediately after the encounter with the prey. We waited for an attack for a maximum of two hours. We focused on the role of the chelicerae in grasping the woodlouse. The grasping behaviour was drawn based on the frames from the video-sequences.

RESULTS

Prey preference

We found a significant difference in the capture frequency between species with unmodified and modified chelicerae (ANODEV, GLM-b, $\chi^2_{10}=97$, $P<0.0001$). The species with unmodified chelicerae avoided woodlice and readily captured only rather small, mainly soft-bodied arthropods, such as flies, spiders, centipedes, moths and springtails (Fig. 2). All the species with modified chelicera showed similar capture preference for prey (simplification, $\chi^2_{22}=20.8$, $P=0.53$). They all readily captured woodlice and sometimes some other arthropods, such as flies, spiders and centipedes. For the species with very elongated chelicerae woodlice were the only prey accepted.

In the second experiment five *Dysdera* species showed significantly different preferences for flies, clinging and rolling woodlice (ANODEV, GLM-b, $\chi^2_4=135.3$, $P<0.0001$). Only the species with unmodified chelicerae preferred flies to either of the woodlice (contrast, $\chi^2_2=66.4$, $P<0.0001$, Fig. 3). In comparison with all other species, the species with very elongated and flattened chelicerae captured significantly more rolling than clinging woodlice and flies (contrast, $\chi^2_2=69.5$, $P<0.0001$).

Predatory behaviour

The species with unmodified chelicerae, *Dysdera* sp. n., attacked all prey types using a standard attack tactic (n=20): both chelicerae grasped the prey synchronously from above. They rarely attacked woodlice. When they did so, they failed to capture them. By contrast, species with modified chelicerae captured woodlice quickly and effectively and the prey was

paralysed quickly. As soon as the prey was paralysed they transported it either with the chelicerae inserted in the ventral side of the cephalic part of the woodlouse (Fig. 5a), or by dragging the prey using the tarsal scopulae (Fig. 5b). Depending on type of cheliceral modification they used one of three grasping tactics. These tactics were used uniformly by adult males and females, as well as by juveniles.

Pincers tactic

This tactic was used exclusively by the two species with elongated chelicerae, *D. erythrina* (100%, n=20) and *D. abdominalis* (100%, n=20). Both species approached slowly, very close to the woodlouse, turned the prosoma sideways (vertically) to be able to insert one chelicera underneath the woodlouse and the other over the dorsal side of the woodlouse (Fig. 4a). Then the spider gripped the woodlouse rapidly, in a grasp similar to that of pincers. While the fang of the lower chelicera penetrated the soft ventral side, the upper chelicera did not penetrate the hard dorsal side, but rather provided an anchor. In *D. erythrina* the fang of upper chelicera was usually stretched, while in *D. abdominalis* it was folded in the cheliceral groove. Spiders could use either the left or right chelicera for the attack. As the insertion of the lower fang was the first sudden motion of the attacking spider, the woodlouse usually did not have time to defend itself by rolling up. If it managed to roll up, spiders would wait motionless for less than a minute with chelicerae ready for attack until the woodlouse finally unrolled itself. Alternatively they rotated a woodlouse with their front legs and pedipalps and actively searched with one fang for an interstice between the sclerites. We observed this alternative tactic also in species using other grasping tactics.

Dysdera abdominalis rhythmically tapped the woodlouse with its frontal legs before an attack. The fang penetration was quick and the spider then retreated before the woodlouse could finish defensive rolling

Fork tactic

This tactic was used exclusively by the species with concave chelicerae, *D. spinnicrus* (100%, n=20). It approached a woodlouse at a distance of a half-body size, then attacked abruptly, getting under woodlouse quickly with both chelicerae and inserting its fangs into the soft ventral side before the woodlouse could roll up (Fig. 4b). About 50% of the attacks were directed towards head. The concave shape of the dorsal side of the basal cheliceral segment helped to get beneath the ventral side of woodlouse in a movement similar to scooping up a bite with a fork.

Key tactic

This tactic was used exclusively by the species with flattened chelicerae *D. dubrovninnii* (100%, n=20). The spider approached a woodlouse, searched with one fang for an edge of some sclerite on woodlouse's dorsal side and then slid the fang under the sclerite (Fig. 4c). The fangs are able to penetrate between sclerites only because they are both flat and dorsoventrally relatively elastic. Neither rolling nor clinging to the substrate provided protection against this hunting tactic. Spiders could use either chelicera for the insertion. We called this a 'key tactic' as it reminded us of skilful opening a closed safe using a key.

DISCUSSION

The five species of the genus *Dysdera* investigated here possessed chelicerae with different morphology and showed different prey preference and predatory behaviour. Interestingly, all three hypotheses suggested to explain the variation in cheliceral morphology were supported by our observations.

The species with unmodified chelicerae used standard capture behaviour similar to other spiders. It refused woodlice but readily captured various arthropods. In nature, we observed it to feed on a staphylinid beetle and a dysderid spider (M. Řezáč, unpubl. data). In contrast to this, all of the studied species with modified chelicerae readily captured woodlice. The species possessing different cheliceral modifications use different grasping tactics to capture woodlice. The two species with elongated chelicerae, *D. erythrina* and *D. abdominalis*, penetrated the unprotected ventral side of woodlouse with one chelicera and held the dorsal side of woodlouse by the other one. We expect these two *Dysdera* species to capture mainly clumsy rollers. In order to accurately direct a fang against the ventral side of woodlice, the spider has to come into close contact with the prey before grasping. Such an approach could alert fast woodlice.

The concave shape of the dorsal side of chelicerae allowed *D. spinicrus* to tuck both chelicerae under a woodlouse and consequently bite into the ventral side. This is a quick attack without previous contact, which should be effective even for fast clingers, which are able to quickly find a substrate to cling onto. Flattening of the cheliceral fang allowed *D. dubrovninnii* to insert the fang between the sclerites on the dorsal side of a woodlouse. Thus protecting of ventral side by rolling or clinging to the substrate does not protect woodlice against such attack. This study thus reveals that the cheliceral modifications and capture tactics allowed *Dysdera* spiders to overcome the unusual defence tactics of woodlice – heavy armour protecting most of their body and behavioural defences protecting their soft ventral side.

Another adaptation for oniscophagy seems to be the mode of prey transportation. Polyphagous spiders transport their prey holding it in their chelicerae (Foelix, 1996). But some *Dysdera* species transported woodlice by holding the prey with scopulae hairs present on the legs and pedipalps (Fig. 5b). It is possible that the cheliceral modifications for prey capture constrain other functions of chelicerae, including their usage during transport of prey.

According to our observations of prey preference, the grasping tactic and the related cheliceral modification are constant characters found in both sexes and all ontogenetic stages of each species. As these characteristics are obviously tightly linked, cheliceral morphology can be used to predict the prey preference and the grasping tactic in species whose diet and behaviour are unknown. Results of prey preference suggest that there are three main groups of prey-specificity in *Dysdera*: (1) prey generalists represented by the species with unmodified chelicerae, (2) facultative woodlice-specialists represented by species with moderate cheliceral modifications, and (3) obligatory woodlice-specialists represented by species with extreme modifications. The prey generalist, *Dysdera* sp. n., refused woodlice. Facultative woodlice-specialists, *D. erythrina* and *D. spinicrus*, captured other prey beside woodlice and were not choosy with regard to the type of woodlouse. We believe these species capture mainly woodlice in nature. *Dysdera crocata*, possessing elongated chelicera, and being the only *Dysdera* species whose diet ecology has been studied so far, seems to belong to this category. It was observed in the laboratory to eat almost all prey that was sufficiently small and slow moving (Cooke, 1965a, b, c). Moreover, it did not prefer woodlice to other arthropods in the laboratory experiments (Pollard *et al.*, 1995). This species might be ecologically very plastic; as it is the only species of the family Dysderidae that has colonised most parts of the world (Cooke 1967). The obligatory woodlouse-specialists, represented by *D. abdominalis* and *D. dubrovninnii*, captured virtually only woodlice; moreover they significantly preferred rollers to clingers.

To our knowledge *Dysdera* spiders are the only specialised woodlice predators occurring outside tropical zones. With the striking variability of morphological adaptations and grasping tactics described here, these spiders are a highly diversified clade of oniscophagous feeders.

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Table 1. *Dysdera* species used in this study, with a description of cheliceral characters.

Species	Locality	Chelicerae
Dysdera sp. n.[1]	Israel: Mt. Meron	"Unmodified": both basal segment and fang short and robust (Fig. 1a–b)
Dysdera erythrina Walckenaer, 1802	Czech Rep.: Prague	"Slightly elongated": both basal segment and fang slightly elongated (Fig. 1c–f)
Dysdera abdominalis (Deeleman-Reinhold, 1988)[2]	Israel: Bet Guvrin	"Very elongated": both basal segment and fang very elongated (Fig. 1c–f)
Dysdera spinicrus Simon, 1882	Israel: Mt. Meron	"Concave": basal segment dorsally concave, fang elongated, protruding forwards when opened (Fig. 1g–h)
Dysdera dubrovninnii Deeleman-Reinhold, 1988	Slovakia: Humenné	"Flattened": basal segment short, fang dorsoventrally flattened (Fig. 1i–j)

[1]Undescribed species, related to *Dysdera dentichelis* Simon, 1882 (Řezáč, in prep.).
[2]Platnick (2006) presents this species as a representative of the genus *Tedia* Simon, 1882. However, according to molecular phylogeny *Tedia* is an ingroup of the genus *Dysdera* (Arnedo, pers. com.).

Fig. 1. Chelicerae of the studied *Dysdera* spiders: (a, b) unmodified chelicerae, *Dysdera* sp. n.; (c, d) elongated chelicerae, *Dysdera erythrina*; (e, f) very elongated chelicerae, *Dysdera abdominalis*; (g, h) concave chelicerae, *Dysdera spinicrus*; (i, j) flattened chelicerae, *Dysdera dubrovninnii*. (a, c, e, g, i) lateral view; (b, d, f, h, j) frontal view.

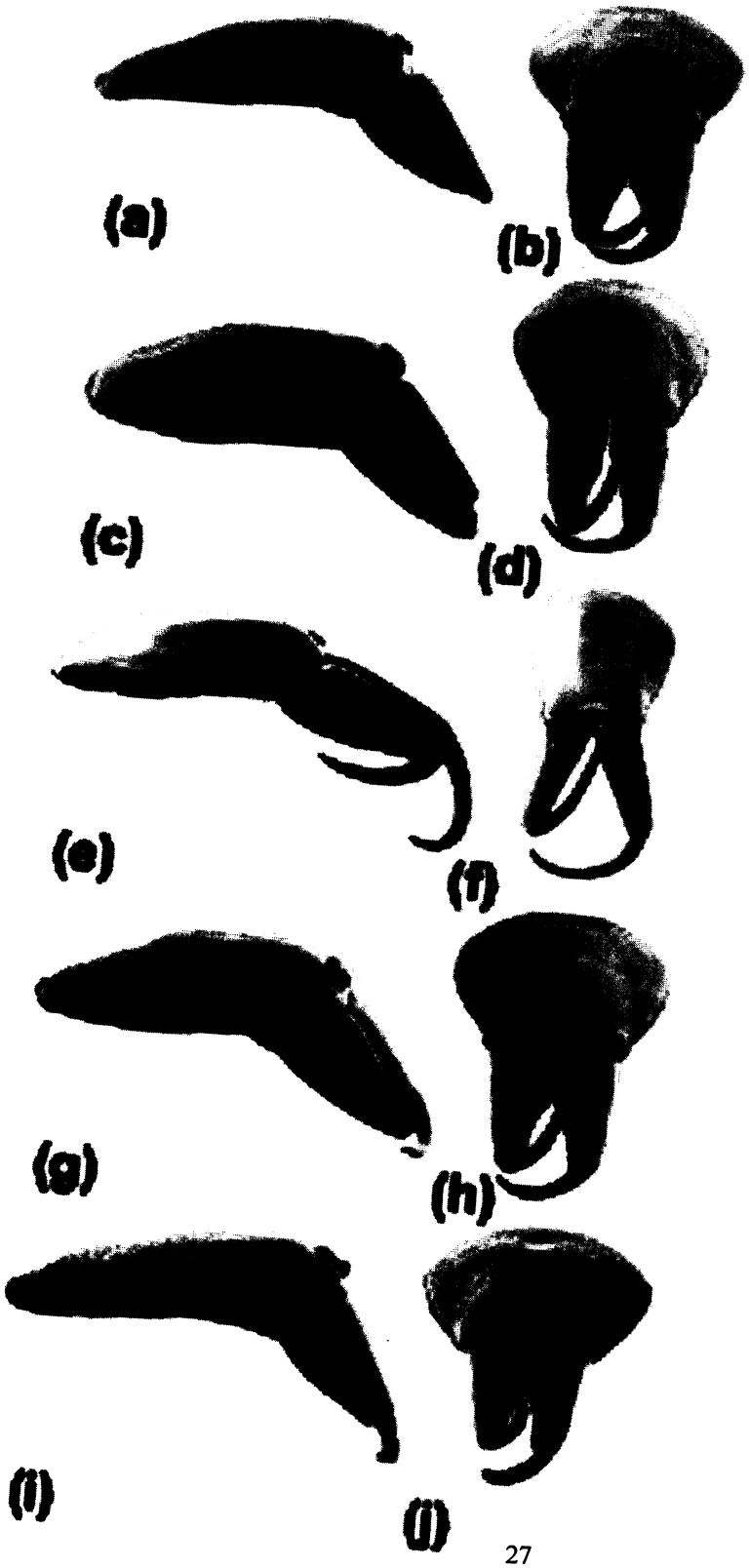

(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)

Fig. 2. Proportion of 11 arthropod taxa accepted as prey by five *Dysdera* species tested (for each species, N=10).

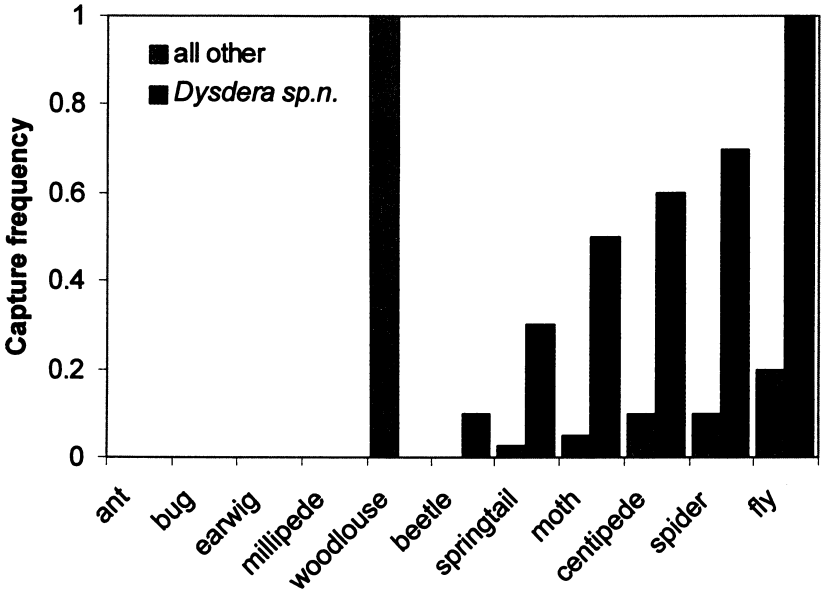


Fig. 3. Capture preference of five *Dysdera* species for three prey species (for each species N=50).

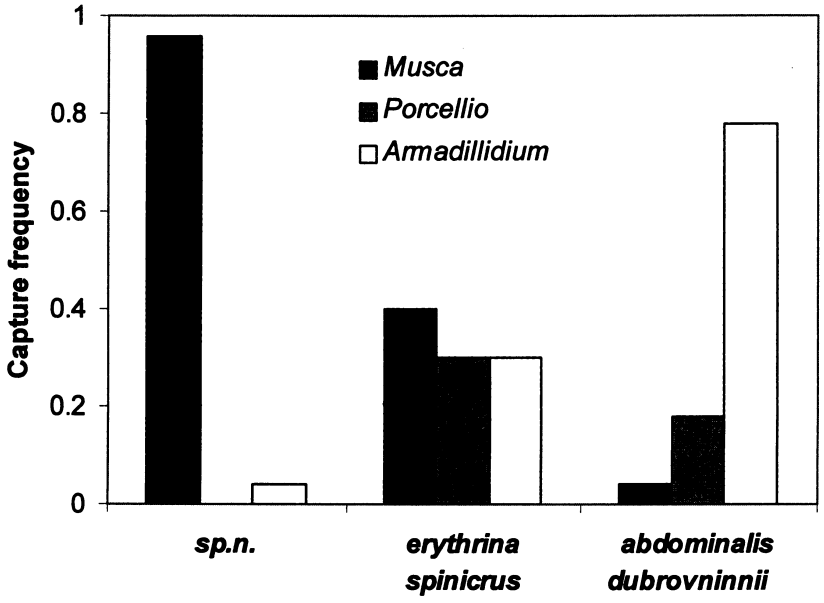


Fig. 4. Grasping tactics used by *Dysdera* spiders to capture woodlice: (a) "pincer" tactic of the *Dysdera* species with elongated chelicerae; (b) "fork" tactic of the *Dysdera* species with concave chelicerae; and (c) "key" tactic of the *Dysdera* species with flattened chelicerae.

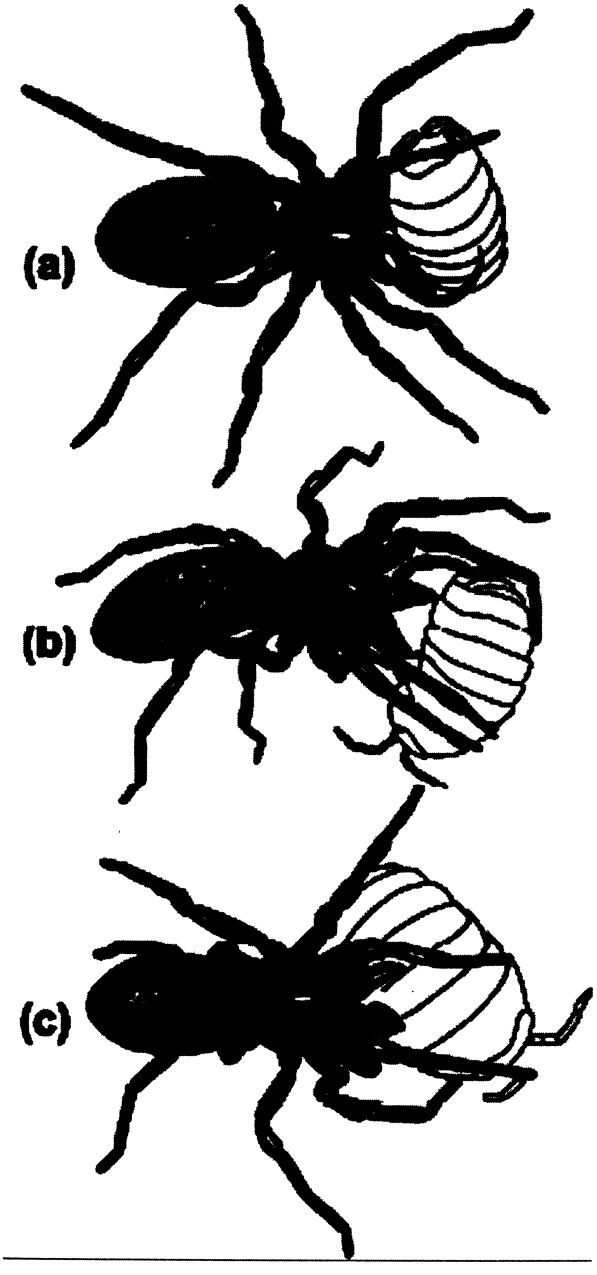
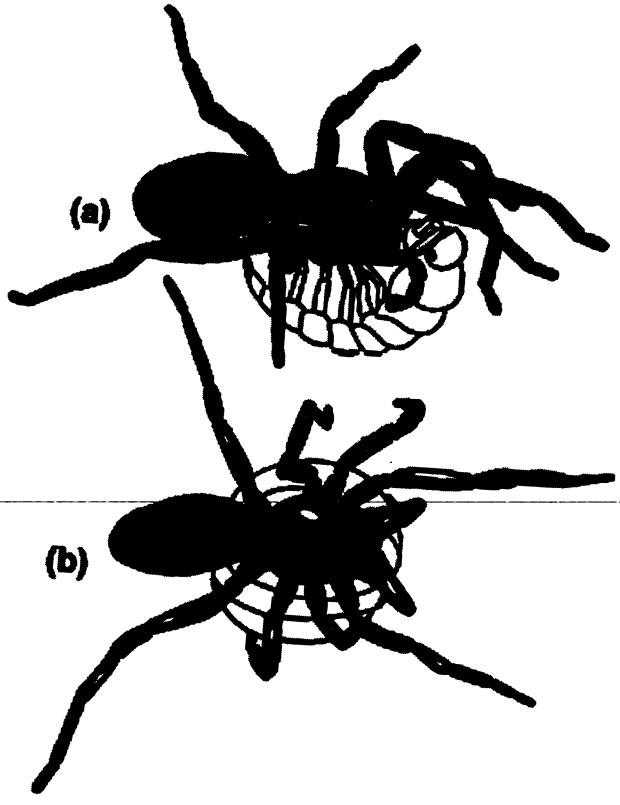


Fig. 5. Grasp used for transportation of attacked woodlouse *Armadillidium vulgare* by (a) *Dysdera dubrovninnii*, (b) *Dysdera abdominalis*.


(a)
(b)

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Evidence for woodlice-specialization in *Dysdera* spiders: behavioural versus developmental approaches

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Abstract. The dietary specialization in a woodlouse-eating spider *Dysdera hungarica* Kulczyński (Araneae: Dysderidae) is studied using two types of laboratory experiments. In the first experiment, the rate of development of spiderlings reared on one of three diets: pure woodlice [composed of two species *Oniscus asellus* Linnaeus and *Armadillidium vulgare* (Latreille)]; pure flies (*Drosophila melanogaster* Meigen); and a mixed woodlouse-fly diet, is studied. Spiders develop significantly faster on the woodlice-containing diets (i.e. pure woodlice and mixed diet) than on the fly diet. In the second experiment, the prey-choice for two woodlice species (*O. asellus* and *A. vulgare*) and a fly (*D. melanogaster*) is investigated. *Dysdera hungarica* spiders capture significantly more often flies than woodlice. These contrasting results reveal the different value of developmental and behavioural experiments. The dietary studies are assumed to provide better evidence of specialization than behavioural experiments, which might be misleading due to unnatural conditions. It is concluded that *D. hungarica* is a metabolically adapted woodlice specialist. The present study thus provides the first evidence of nutritional specialization on woodlice.

Key words. Generalist, metabolic adaptation, nutritional value, oniscophagy, specialist, woodlice.

Introduction

Woodlice are very abundant ground-dwelling arthropods in many habitats (Sutton, 1980). To protect themselves from predators, they have evolved morphological (heavily incrusted armour), chemical (gland secretions) and behavioural defences (rolling into a ball or clinging to the substrate) (Sutton, 1980; Schmalfuss, 1984). Large predators are able to overcome these defences (Pernetta, 1976; Lima *et al.*, 2000; Bureš & Weidinger, 2003). However, small predators are not (Gorvett, 1956); therefore, only some arthropods are found to feed occasionally on woodlice (Sunderland & Sutton, 1980; Raupach, 2005).

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To date, only two groups of animals are considered as woodlice-eating specialists; ants of the tropical genus *Leptogenys* and spiders of the Palaearctic genus *Dysdera*. *Leptogenys* ants are either generalist predators (Maschwitz *et al.*, 1989), termite specialists (Maschwitz & Schönegge, 1983), or earwig specialists (Steghaus-Kovac & Maschwitz, 1993), but most species appear to be woodlice specialists (Dejean, 1997). Some ants are observed to feed also on prey other than woodlice (Whitcomb *et al.*, 1972), others accept only woodlice (Dejean, 1997). The ants have evolved morphological (elongated mandibles) as well as behavioural adaptations allowing them to grasp woodlice that protect themselves by rolling into a ball (Dejean & Evraerts, 1997; Dejean, 1997).

The spider genus *Dysdera* (Dysderidae) is composed of 250 described species; almost all of them being restricted to small areas mainly in the Mediterranean (Deeleman-Reinhold & Deeleman, 1988). They are nonweb building predators, searching for prey on the soil surface at night and hiding in

silk retreats under stones or wood during the day (Cooke, 1965a). Two species of this genus, namely *Dysdera erythrina* (Walckenaer) and *Dysdera crocata* Koch, are repeatedly observed to capture woodlice in nature (Bristowe, 1958; Hopkin & Martin, 1985). Their woodlice-eating behaviour is also confirmed by the detection of woodlice antigens in their digestive tract (Sunderland & Sutton, 1980), and by a survey of remnants in their silk retreats (Cooke, 1965a). Although these data show that *Dysdera* spiders feed on woodlice, it is not known whether this is their exclusive prey. It is suggested that their remarkably elongated mouth parts, particularly chelicerae, are an adaptation for the effective capture of armoured woodlice (Bristowe, 1958; Pollard, 1986); thus the spider should be specialized. On the other hand, in the laboratory, they are observed to catch almost every arthropod that is sufficiently small and slowly moving (Cooke, 1965a,b; Pollard *et al.*, 1995). Given these results, their woodlice-specialization is questionable.

Various experimental approaches are used to identify prey specialization. Some of these, such as prey preference, can result in misleading conclusions (Stamp, 2004). Better evidence for dietary specialization should allow studies on nutritional adaptation (Toft & Wise, 1999). Such adaptation is a necessity, allowing specialists to obtain all their required nutrients from an exclusive prey. For specialists, the alternative prey is of inferior quality and has no beneficial effect on their fitness, as has been demonstrated, for example, in aphidophagous predators (Hodek & Honìk, 1996; Short & Bergh, 2004).

The present study aimed to reveal the level of specialization in a species with elongated chelicerae, namely *Dysdera hungarica* Kulczyński and to compare the results of two types of approaches, a behavioural and a rearing experiment. Specifically, it was of interest to determine whether the spiders choose to catch any of two woodlice species in preference to flies, and also the effect of three different diet types, including woodlice and alternative prey, on the ontogenetic development of spiderlings.

Materials and methods

Dysdera hungarica is characterized by elongated chelicerae (cheliceral length/carapace length ≥ 1). The ratio cheliceral length/carapace length is in the range 0.5–1.5 in the genus (M. Řezáč, unpublished data). The distribution of this species stretches from Caucasus and Crimea to the Balkan Peninsula and central Europe (Řezáč *et al.*, 2007). It occurs in xerothermic woods and bushes, often semirural ones (Řezáč *et al.*, in press). Fully developed spiderlings (first-free instar) resting in the maternal silk retreats were collected under stones or wood in oak forest near the town Vranov nad Topl'ou in Slovakia in the middle of August. They were stored at 5°C for 2 months without food to slow down their development during the preparation for the experiment. Afterwards, they were fed with woodlice until the first moulting. Then they were randomly assigned to one of three diet groups so that there were 11–13 individuals in each treatment. Spiderlings were placed singly into glass vials of an appropriate size (diameter 9 mm, length 55 mm) with a strip of paper to provide a dry place on which to sit. The tubes were plugged with a fabric gauze, and kept in a controlled chamber at 29 ± 2 °C under an LD 16 : 8 h photoperiod. The gauze plug was moistened at a 6-day interval to provide sufficient humidity.

Three different diets were used in the experiment: woodlice, including *Oniscus asellus* Linnaeus and *Armadillidium vulgare* (Latreille), which were offered on alternate days; flies (i.e. wingless form of *Drosophila melanogaster* Meigen); and a mixed diet consisting of two woodlice species and flies offered alternately. Woodlice were raised in plastic boxes (17 × 12 × 6 cm) with a layer of regularly moistened sand and decaying *Acer platanoides* Linnaeus leaf litter. Flies were raised on an agar medium (87 g of fine maize semolina, 50 g of sugarcane, 25 g of dried yeast, 12 g of agar, 1000 mL of water).

Spiderlings were fed *ad libitum* for 1 day every 6 days. On each feeding date, an excess of prey was offered (two to five prey specimens) to assure the spiders' satiation. The length of the prey corresponded approximately to the length of the spider's prosoma. Discarded prey was removed on the next day.

Spiders were weighed before each feeding using an analytical balance (Sartorius AG, Germany) with a precision of 0.01 mg. Moulting was checked daily. The experiment was terminated after approximately 3 months when the vast majority of tested specimens passed the second moulting.

In the second experiment, the preference of *D. hungarica* with respect to the capture of woodlice (*O. asellus* and *A. vulgare*) and a fly (*D. melanogaster*) was tested. The spiders were collected in the same place as mentioned above. For 2 weeks, the individuals were maintained at 25 °C and deprived of prey to make them moderately hungry. Fifty juvenile spiders were placed singly in Petri dishes (diameter 30 mm) with a piece of moistened filter paper attached to the bottom to provide water for the animals. The length of offered prey corresponded approximately to the length of spider's prosoma. To each individual spider, all three prey species were offered at the same time. After 24 h, the dishes were checked and the dead prey was replaced with a fresh one. Cases were recorded when only one prey was eaten (sucked out).

Data were analysed using R software (R Development Core Team, 2006). The longitudinal data on body weight were analysed with linear mixed effect models (LME) using the nlme package (Pinheiro *et al.*, 2006), which is a modern and more powerful method than repeated measures analysis of variance (ANOVA) (Pinheiro & Bates, 2000). In this analysis, diet and time were fixed and time was a random effect to take account of the temporal pseudoreplication. Heteroscedasticity among treatment groups was tested by comparing a model with and without the variance function (varIdent). The presence of temporal autocorellation was investigated by inclusion of autocorrelation structures (corCAR1). Slopes of linear models were compared between treatment groups using *a posteriori* linear combination analysis. The instar durations and the comparison of weight at

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the beginning of the experiment were analysed using a one-way ANOVA. Differences between treatments were investigated using Tukey's honest significant difference (HSD) test. The McNemar test was used to compare observed capture frequencies (Crawley, 2002).

Results

The three types of diet affected the developmental rate differently. There was a significant difference in the duration of the first instar among diets (ANOVA: $F_{2,25} = 7.02$, $P = 0.0038$; Table 1). This instar lasted significantly longer in spiders fed a pure diet of flies than in those fed diets containing woodlice (Tukey's HSD, $P < 0.028$).

For body weight, at the beginning of the experiment, the mean weight of spiderlings was 2.57 mg (range 1.69–3.90 mg) and it did not differ between treatments (ANOVA: $F_{2,34} = 0.82$, $P = 0.45$). On the whole, the growth rate differed significantly among groups (LME: $F_{2,421} = 4.6$, $P = 0.011$; Fig. 1). Those feeding on pure woodlice or mixed diet increased their weight significantly more than those feeding on flies (*a posteriori* contrasts, $P < 0.018$). There was no significant difference between the growth of spiders fed on pure woodlice and a mixed diet (*a posteriori* contrasts, $P = 0.5$). Although the trends of weight change were nearly linear for the woodlice diets, the trend broke off after 37 days for the fly diet, after which additional growth ceased in these spiders.

The spiders had a different prey-choice. The majority of individuals ($n = 37$) captured the fly, seven individuals captured *Oniscus* and six individuals captured *Armadillidium*. Thus, they captured flies significantly more frequently than any woodlice (McNemar test: $\chi^2 > 19$, d.f. $= 1$, $P < 0.0001$).

Discussion

Dysdera spiderlings reared on a fly diet develop slower and grow less than those reared on woodlice-containing diets. The lack of woodlice in the fly diet has an immediate negative effect on development and growth and the difference becomes apparent within one stadium. The results thus support strongly the hypothesis that woodlice are an essential component of the optimal diet of *D. hungarica*. They also suggest a nutritional woodlice-specialization in *D. hungarica*, which is further supported by the fact that the fly diet is found to be a prey of intermediate to high quality to polyphagous predators (Mayntz & Toft, 2001).

Table 1. Mean ± SE duration of the instar for *Dysdera hungarica* spiders reared on three diets.

Diet	Duration (days)
Woodlice	48.0 ± 2.4 ($n = 11$)^a
Mixed diet	51.6 ± 6.2 ($n = 10$)^a
Flies	68.5 ± 2.7 ($n = 8$)^b

Significant differences between diets (at $P = 0.05$), based on Tukey's honest significant difference test, are indicated by different superscript letters.

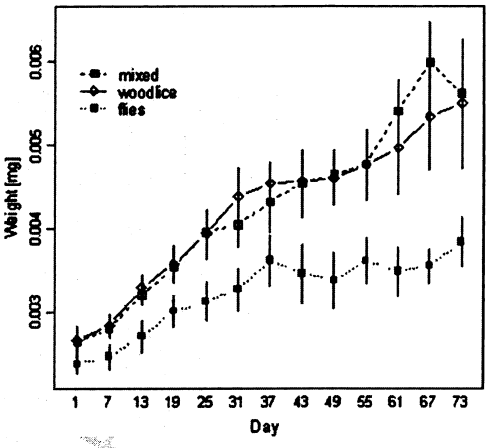

Fig. 1. Mean ± SE body weight of *Dysdera hungarica* spiders reared on three diet types.

To date, the experimental evidence on nutritional specialization in spiders has been performed only with an araneophagous and a myrmecophagous species. Li & Jackson (1997) show that a diet comprised exclusively of spiders provides the araneophagous *Portia* with a superior fitness compared with a monotypic insect diet and a mixed diet (insects and spiders), which reduced the spiders' fitness. Similarly, S. Pekár *et al.* (unpublished data) show that myrmecophagous *Zodarion* spiders are able to develop only on monotypic ant diet. This is in contrast to generalists to which dietary mixing has a beneficial effect (Oelbermann & Scheu, 2002; Acharya *et al.*, 2004). The results obtained for *Portia* and *Zodarion* conform to those for the aphidophagous *Coccinella septempunctata* Linnaeus (Nielsen, Hauge & Toft, 2002), and may thus represent a general response of specialist predators to a mixed diet.

In the present experiment, *D. hungarica* show similar response to monotypic woodlice and the mixed diet during one stadium. It is possible that a difference between these two diets might become apparent in later stadia, for which additional studies are necessary.

The results from the prey preference experiment are in contradiction with the results from the diet experiment: *D. hungarica* prefers to catch flies rather than woodlice. This is, however, consistent with previous experiments with other *Dysdera* species: *D. crocata* does not prefer woodlice to other arthropods (Pollard *et al.*, 1995). However, fruit flies, as well as houseflies (*Musca domestica*), moths (Psychidae), bugs (Miridae) and mealworm larvae (*Tenebrio molitor*), tested by Pollard *et al.* (1995) are not available to *Dysdera* in nature.

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Dysdera is a clumsy predator, foraging on the ground at night (Cooke, 1965a), and able to capture only other clumsy, ground dwelling and nocturnally active invertebrates, mainly woodlice. The capture of flies in the laboratory is the result of the artificial set-up. *Dysdera* might prefer to attack more active arthropods simply due to experiencing more encounters in small experimental spaces, thus leading to a higher chance of capture (Sih & Christensen, 2001). Laboratory studies with other invertebrate predators often reveal a failure to distinguish a beneficial prey from an unfavourable one (Stamp, 2004; Rickers, Langel & Scheu, 2006).

In a previous study (M. Řezáč *et al.*, unpublished data), the degree of diet specialization correlated with the degree of modification of *Dysdera* mouth parts, particularly chelicerae. *Dysdera* species, with short chelicera, refused woodlice and fed only on the alternative prey, whereas species with very elongated chelicera captured only woodlice. Species with elongated chelicera, such as *D. hungarica*, captured both woodlice and the alternative prey (M. Řezáč *et al.*, unpublished data). Thus, behavioural experiments are able to reveal prey specialization only in those species in which morphological modifications control their behavioural abilities.

Dysdera hungarica possess elongated chelicerae but their elongation is not as extreme as in some other species. The intermediate elongation allows *D. hungarica* to capture other prey than woodlice, although it appears to be nutritionally adapted to woodlice. It is concluded that *D. hungarica* is nutritionally specialized on woodlice and that nutritional adaptation experiments can provide more accurate information on diet specialization than prey preference experiments.

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Running head: Revision and speciation mode of the spider aggregate *Dysdera erythrina*

Revision and speciation mode of the spider aggregate *Dysdera erythrina* (Araneae: Dysderidae): sibling species with sympatric distribution

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Abstract. Dysdera spiders are specialised predators of woodlice. This extremely rich genus is composed mainly of aggregates of sibling species. Interestingly, species of the aggregate often occur sympatrically. To understand the evolution of the aggregates, we performed an analysis of *D. erythrina* aggregate. We distinguished six morphologically very similar species, two of them are new. Areas of all species include southern France and northeastern Spain, which are thus probably the speciation center of the aggregate. We did not find any obvious differences in habitat preferences of study species; they occured together in some locations. All species fed on woodlice, but they exhibit differences in karyotype, sculpture of carapace, morphology of the groove accessing the spermatheca for sperm, morphology of mouth-parts, and body size. Experimental crossing showed a partial precopulatory behavioral barrier between two species. We hypothesize chromosome rearrangements played a primary role in *Dysdera* speciation. The secondary contact of allopatrically evolved cryptic species likely led to evolution of recognition mechanisms. Carapace structure and the shape of endogynal medial groove might be involved in interspecific barrier. Sympatric occurrence of these species might be allowed by diet specialisation on different size or species of woodlice, documented by displacement of body size and shape of chelicerae.

Additional keywords: character displacement, diet specialization, interspecific recognition, karyotype, Mediterranean, new species, precopulatory barrier, sibling species, speciation, woodlice.

Introduction

The study of speciation has become one of the most active areas of evolutionary biology (Howard and Berlocher 1998). For different groups of organisms various speciation modes were suggested. These modes have been often classified by the geographical arrangement of populations undergoing the process, specifically allopatric, sympatric and parapatric mode of speciation (e.g., Mayr 1963; Maynard-Smith 1966). Recently a different classification was proposed in which the first division separates those cases driven by selection from those in which speciation occurs primarily by genetic drift (Via 2001). In speciation by genetic drift the reproductive isolation evolves as a consequence of fixations of accidental mutations. In the speciation driven by selection, disruptive selection lead to differentiation of species and their reproductive isolation. It is in particular "ecological speciation" (*sensu* Schluter 2001) where reproductive isolation evolves ultimately as a consequence of divergent natural selection on traits in different environments. "Environment" refers to all biotic and abiotic elements of habitat, e.g., climate or resource competition (Schluter 2001). Such speciation mode is suggested in cases when sister species differ in characters, which are influenced by natural selection, and currently live in sympatry, suggesting different niches. However, the reproduction barrier is supposed to evolve in allopatry. In this respect ecological speciation differs from the sympatric speciation, in which reproduction barrier evolves in sympatry (Maynard-Smith 1966). Among animals, ecological speciation was suspected to play a role in many herbivores, but in a few carnivores only (e.g., Tauber *et al.* 1993). Posible candidates of carnivores evolving by ecological speciation are the *Dysdera* spiders as sister species of this genus often differ in the morphology of mouth parts and body size and occur sympatrically (*cf.* Deeleman-Reinhold and Deeleman 1988; Arnedo and Ribera 1999).

Dysdera spiders are ground dwellers characteristic of xerothermic forests. At night they search for prey while during the day they shelter themselves under stones (Cooke 1965). This genus is a Palearctic taxon with vast majority of species being endemics of small areas in the Mediterranean. Beside frequent sympatric occurrence of sibling species this group is exceptional among other genera of the family Dysderidae also in other aspects, which could be related to speciation. Firstly, *Dysdera* is by far the richest genus of the family. Almost 250 species have been described (Platnick 2007). However, the number of species is probably much higher, which is documented by dramatic increase of the number of new species described in last decades (*cf.* Platnick 2007). Secondly, large portion of *Dysdera* species belongs to aggregates of sibling species, which display only minute morphological differences of copulatory organs – otherwise highly divergent structures among spider species. Finally, *Dysdera* spiders were found to be prey specialists feeding on woodlice (Cooke 1965; Řezáč M, unpublished data). In fact, they are the only known specialised predators of woodlice outside tropics (*cf.* Sutton 1980).

To understand the evolution of *Dysdera* aggregates, a complex knowledge about their biology is necessary. Until now, we have only some information on the morphological differences, distribution (e.g., Deeleman-Reinhold and Deeleman 1988), and mt DNA diversity (Arnedo *et al.* 2001) of only few aggregates. To reveal the processes that might have been responsible for the evolution we decided to perform an analysis of a selected aggregate. We concentrated on *D. erythrina* aggregate, composed of hardly morphologically distinguishable species that have presumably diverged relatively recently. We assume that these young species differ mainly in characters that played an important role in the speciation process. Old taxa often do not provide clear signatures of speciation mode as these are already overdriven by following evolutionary processes (Jiggins and Mallet 2000).

Heterogenity of the taxon *D. erythrina* was recognised already by Simon (1882). He distinguished three new species, very similar to *D. erythrina* (Walckenaer, 1802), namely *D.*

fervida, D. lantosquensis, and *D. provincialis*. However, he later degraded these taxa to "local forms" of *D. erythrina* (Simon 1914). Since then nobody has distinguished these taxa; they were even neglected in the modern revision of the genus (Deeleman-Reinhold and Deeleman 1988). Nevertheless, they have never been formally synonymised (*cf.* Platnick 2007).

In order to get information about morphological differences, habitat preference, phenology, and distribution of species of the *D. erythrina* aggregate we analyzed all the material available and visited locations of occurence of particular species. Furthermore, we analyzed karyotypes and diet in selected species of the aggregate. Moreover, we performed crossing experiments between two species. As a result we verified the Simon's species and discovered two new species, *D. catalonica* and *D. montsenensis*. The character of detected differences allowed us to hypothesize about the pattern of speciation process responsible for the origin of *Dysdera* aggregates.

Material and methods

Morphology

Diagnostic characters of studied *Dysdera* spiders appear to be the body size, colour of prosoma, shape and sculpture of carapace, leg spination, as well as the shape of chelicerae and copulatory organs. The carapace length of studied species ranges between 2.0–5.3 mm. The prosoma is dark brown, brown, reddish brown or ferruginous. The carapace of particular species differ in relative width and height, it is either gently or roughly wrinkled. Leg spination of particular species differs in the number of spines on ventral side of ti IV. Chelicerae differ in the shape of the basal segment; it is either mediodorsally concave, covered by short bristles, or convex, covered by normal hairs.

The male copulatory organ of *Dysdera* (Fig. 1*A*), bulbus, is composed of two segments, proximal tegulum and distal division, connected by haematodocha. Their bottom margins are in retrolateral view angled or almost straight. Tegulum is smooth; its distal margin bears heavily sclerotised tooth-like posterior apophysis. In some species this apophysis is equipped with additional tooth (PAT) on its proximal side. Proximally from posterior apophysis, there is a lump, which can be smooth or wrinkled. Distal division is terminated by apical lobe enclosing the fossette. In its apicalmost end apical lobe is interrupted by membranous patch. Opposite of apical lobe there is a fissure bordered by two lamelas, laterally by upper border of the lateral sheet (UBLS) and medially by lower border of the lateral sheet (LBLS). The openning of the sperm duct is located beneath the apical part of LBLS.

Dysdera females possess no external copulatory organ. Their copulatory organ (Fig. 1*B*), endogyne, is positioned within an abdomen. It is anteriorly composed of heavily sclerotised spermatheca and bursa copulatrix. In some species lateral parts of spermatheca are retroventrally equipped with lobes (RL). Behind the epigastric furrow there is an unsclerotised structure called posterior diverticle. The dorsal part of bursa copulatrix is composed of sclerotised dorsal arch, distally unfolded towards uterus by dorsal fold. On the ventral side of dorsal arch, there is a sclerotised coriaceous lamina. The bursa is ventrally enclosed by a ventral wall. The dorsal side of the ventral wall is longitudinally divided by the medial groove, which proximally continues as a duct leading to the spermatheca. Laterally ventral wall forms flexuous ventral archs, which are dorsally bordered by major fold.

Nomenclature of structures of the *Dysdera* copulatory organs (Figs 1*A–B*) was mostly adopted from Arnedo *et al.* (2000).

Light microscopy

To investigate the morphology of female genitalia, endogyne was dissected, brightened using concentrated glycerol and observed under a light microscope.

Scanning electron microscopy

Alcohol-preserved specimens were used for scanning electron microscopy. The prosomas and male copulatory organs were removed for study. The female genitalia were dissected, macerated by 5% KOH until the tissues were dissolved, and washed in distilled water. Samples were then dried at room temperature, mounted on a stub, coated with gold and examined using scanning electron microscope.

Distribution and habitat preferences

The data on distribution and habitat preferences were obtained from the material reposited in the revised collections and from surveys of 25 locations of particular species. Vegetation of inspected localities in the Czech Republic and Slovakia was characterized after Chytrý *et al.* (2001) and Moravec (1995).

Phenology

The data on phenology were inferred from our observations in the visited localities. At least ten individuals were checked for developmental stage during inspection of locality. Some Czech and Slovak localities of *D. erythrina* and *D. lantosquensis* were inspected repeatedly to ascertain the differences of population structure in different seasons. Additional data were obtained from the material in collections by comparing sampling dates.

Prey preference

Prey preference of ten adult specimens of each *D. erythrina* (Czech Rep.: Prague-Ruzyně, 50°05′N, 14°18′E), *D. lantosquensis* (Czech Rep.: Pardubice, 50°04′N, 15°48′E), *D. provincialis* (Spain: Montseny, 41°46′N, 2°23′E), and *D. montsenensis* (Spain: Montseny, 41°46′N, 2°23′E) was studied. In our previous experiments, we found that two weeks without food is an sufficient period to make *Dysdera* spiders moderately hungry (M. Řezáč, unpublished data). Therefore, the specimens were kept at 20°C deprived of prey for this period. As a woodlouse we used *Armadillidium vulgare* (Latreille, 1804). As a controll prey we chose fly *Musca domestica* Linnaeus, 1758, which is frequent prey of many polyphagous spiders (Nentwig 1987). Size of both woodlouse and fly corresponded approximately to the length of spider's prosoma. We put woodlouse into the Petri dish occupied by the spider. When the spider did not capture the woodlouse in 30 minutes, we removed it and offered a fly for another 30 minutes. Refusal *versus* acceptance of the prey was recorded. Specimens that refused both prey items were tested during consequent days.

Karyological analysis

The most appropriate ontogenetic stage for the karyological analyses was found to be the young adult male, which occurs from the end of the summer to the spring in all species studied. Testes of this stage contained numerous dividing cells suitable for karyotype study, such as spermatogonial mitoses as well as various meiotic stages. Four species were studied karyologically:

D. erythrina: 3#, Czech Rep.: Prague-Ruzyně, 50°05′N, 14°18′E, 5.ix.2002, 17.ix.2002; #, Spain: Montblanc, 41°22′N, 1°08′E, 5.iii.2007
D. lantosquensis: 2#, Slovakia: Hrušov, 48°34′N, 20°37′E, 28.viii.2003; 2#, Hungary: Balatonfüred, 46°55′N, 17°52′E, 2.x.2006
D. provincialis: 2#, Spain: Montseny, 41°46′N, 2°23′E, 14.ix.2006
D. montsenensis: 1#, Spain: Montseny, 41°46′N, 2°23′E, 14.ix.2006
The chromosome preparations were obtained by the method described in Řezáč *et al.* (2006).

Crossing experiments

To conduct the crossing experiments, ten adult specimens of each sex of *D. erythrina* (Czech Rep.: Prague-Ruzyně) and *D. lantosquensis* (Czech Rep.: Pardubice) were collected in April. Five specimens of one species were coupled with partners of other species and five specimens with conspecific partners as the control. Thus, 20 couples were tested in total. Particular pairs were put in a Petri dish (diameter 31 mm) for an hour and the resulting behaviour (mating or avoidance) was recorded.

Abbreviations

Collections

AMS	Australian Museum, Sydney, Australia
BMNH	British Museum of Natural History, London, U.K.
JL	J. C. Ledoux, Solignac sur Loire, France
MNHN	Muséum national d'Histoire naturelle, Paris, France
MR	M. Řezáč, Prague, Czech Republic
NHRS	Naturhistoriska Riksmuseet, Stockholm, Sweden
RICP	Research Instiute of Crop Production, Prague, Czech Republic
UB	Universitat de Barcelona, Barcelona, Spain
ZMHB	Museum für Naturkunde, Humbold Universität, Berlin, Germany

Legs

ta	tarsus
mt	metatarsus
ti	tibia
pa	patella
fe	femur
cx	coxa

Results

Taxonomy

Genus ***Dysdera*** Latreille

Dysdera Latreille, 1804
Type species *Dysdera erythrina* (Walckenaer, 1802), by original designation.

Dysdera (erythrina) agg. nov. Řezáč

This aggregate contains six species.

Key to species of the *Dysdera (erythrina)* aggregate

1. Mediodorsal margin of basal cheliceral segment concave, covered by short bristles (Fig. 2*B*); ventral side of ti IV with usually three spines 2
Mediodorsal margin of basal cheliceral segment convex, covered by normal hairs (Fig. 2*A*); ventral side of ti IV with usually four spines 3

2(1). Carapace dark brown, roughly wrinkled (Figs 2*B, D*); maximum carapace length/width less than 1.2; bottom margins of tegulum and distal division in retrolateral view angled; LBLS at 45° angle with UBLS (Fig. 3*B*); lateral edges of spermatheca not incurvated backwards (Fig. 4*B*) *D. lantosquensis*
Carapace ferruginous, gently wrinkled (Fig. 2*F*); maximum carapace length/width more than 1.2; bottom margins of tegulum and distal division in retrolateral view are in line; LBLS almost parallel with UBLS (Fig. 3*D*); lateral edges of spermatheca incurvated backwards (Fig. 4*D*) *D. fervida*
Carapace brown, roughly wrinkled (Fig. 2*H*); maximum carapace length/width more than 1.2; bottom margins of tegulum and distal division in retrolateral view angled; LBLS at 35° angle with UBLS (Fig. 3*F*) *D. montsenensis* sp. nov.

3(1). Carapace reddish brown, often longer than 4 mm; bottom margins of tegulum and distal division in retrolateral view angled (Fig. 3*C*); medial groove with sclerotised teeth (Figs 4*C*, 5); anterior margin of dorsal arch usually almost straight (Figs 4*C*, 5) *D. provincialis*
Carapace ferruginous, usually shorter than 4 mm; bottom margins of tegulum and distal division in retrolateral view are in line (Figs 1*A*, 3*A, E*); medial groove simple; anterior margin of dorsal arch regularly round (Figs 4*A, E*) 4

4(3). Carapace gently wrinkled (Figs 2*A, C*); membranous patch conspicuous; lump smooth (Fig. 3*A*); PAT usually present; anterior margin of spermatheca in ventral view usually convex (Figs 1*B*, 4*A*) *D. erythrina*
Carapace roughly wrinkled (Fig. 2*G*); membranous patch inconspicuous; lump pronounced and remarkably wrinkled (Fig. 3*E*); PAT absent; anterior margin of spermatheca in ventral view concave (Fig. 4*E*) *D. catalonica* sp. nov.

Dysdera (erythrina) catalonica Řezáč, sp. nov.
(Figs 3*E*, 4*E*, 5*E*, 7)

Holotype. 1#, Spain: *Catalonia:* Serra de Prades, Barranc de la Font d'en Garro, 41°21′18″N, 1°5′9″E, 28.v.2003 (M. A. Arnedo), (UB).
Paratypes. 1#, Spain: *Catalonia:* Montserrat, 41°36′N, 1°48′E (RICP); the same data as holotype, 1@; 3#, France (MNHN).

Description
Carapace (Fig. 3*E*). # 3.3–3.9 mm (holotype 3.5 mm), @ 3.5 mm long; maximum length/width = 1.26, maximum height/length = 0.29. Frontal, lateral and posterior lateral margins rounded; notch shallow; cephalic part wide as 1/2 carapace length. Gently wrinkled; uniformly ferruginous; with tiny black spots mainly in front of fovea.
Eyes. AME diameter 1.3 mm, PLE 1.2 mm, PME 1.0 mm. AME slightly back from frontal border, separated from one another by about an eye diameter, close to PLE. PME very close to each other, less than 1/4 of PME diameter from PLE.
Sternum. Gently wrinkled, mainly between legs; yellow-orange; uniformly covered with slender black hairs.
Labium. Trapezoid, longer than wide at base, with a triangular groove at the tip.

Gnathocoxae. 1.4 mm long.
Chelicerae. Basal segment length/carapace length = 0.44, fang length/carapace length = 0.37. Cheliceral inner groove with three teeth and lamina at base; basal tooth > medial tooth > distal tooth, distal tooth located roughly at center of groove, basal tooth close to basal lamina, medial tooth close to basal tooth. Basal segment mediodorsally convex, covered with piligerous granulation with normal hairs, ventral side smooth.
Legs. For lengths of leg segments see Table 1. Spines on ti III, mt III, ti IV and mt IV (Table 2); claws hardly longer than wide. All segments ferruginous-yellow (originally probably darker), but forelegs darker.
Abdomen. 4.5 mm long, cylindrical, whitish. Abdominal dorsal hairs 0.3 long.
Bulbus (Fig. 4*E*). 1.20–1.44 mm long, distal division length/bulbus length = 0.60. bottom margins of tegulum and distal division in retrolateral view almost straight. Distal half of tegulum in retrolateral view wider than its proximal half. UBLS is partially covering fissure, UBLS almost parallel with LBLS. LBLS is bended down in its apical part. Membranous patch inconspicuous. Lump pronounced and remarkably wrinkled. PAT absent.
Vulva (Fig. 5*E*). Spermatheca approx. 0.42 mm long, anterior margin in ventral view concave, lateral edges remarkably incurvated backwards, RL not developed; unequal sclerotized muscle anchors on the proximal side inconspicuous. Anterior margin of dorsal arch with median and two additional lateral lobes. Transverse furrows on ventral wall slightly developed; medial groove is simple.

Remarks
Some females from mountain ranges in northeastern Spain (Montseny: Vallès Oriental, Turó de l'Home; Pyrenées: Riu), characterized by remarkably brownish prosoma, possess relatively short chelicerae, similar to *D. catalonica*. However, they have a different vulva (Fig. 5*F*), thus they probably represent another species.

Etymology
Named after Catalonia, the Spanish region to which the distribution range of the species is probably restricted.

Habitat
Dysdera catalonica was found in the pine *(Pinus sylvestris)* forest at the elevation of 1030 m.

Distribution (Fig. 7)
This species is known from northeastern Spain. Its occurence in France is dubious.

Dysdera (erythrina) erythrina (Walckenaer)
(Figs 1*A–B*, 2*A*, 3*A*, 4*A*, 5*A*, 6*A*, 7, 8*A*)

Aranea erythrina Walckenaer, 1802: 224 (unspecified sex).
Dysdera erythrina: Blackwall 1864: 370, pl. 28, fig. 266 (#@); Becker 1896: 314, pl.17, figs 22, 22a (#@); Simon 1914: 99, 112, fig. 168 (#@); Roewer 1928: 50, pl. 7, fig. 562 (#); Locket and Millidge 1951: 84, figs 42A, 42D (#); Wiehle 1953: 16, figs 36–43 (#@); Charitonov 1956: 26, fig. 18 (#); Alicata 1964a: 6, fig. 4 (@); Cooke 1966: fig. 3 (@); Muller 1967: 122, fig. 9 (#); Dresco 1973: 245, fig. 2 (#); Schult 1983a: 72, figs 1–3, 10 (#); Schult 1983b: 17, fig. 6 (#); Roberts 1985: 60, figs 19a, c, e, g (#@); Deeleman-Reinhold and Deeleman 1988: 164, figs 8, 50 (#@); Heimer and Nentwig 1991: 44, figs 95.4–95.6 (@); Roberts 1995: 94–95, fig. p. 95 (#); Mcheidze 1997: 78, fig. 72 (#); Roberts 1998: 98 (#); Uhl 2000: 163, figs 1, 2A (@); Bellmann 2001: 56 (#@).

Dysdera cambridgii Thorell, 1873: 465 (#@); Chyzer and Kulczyński 1897: 268, pl. 10, figs 40, 45 (#@).

Doubtful

Dysdera erythrina: Dufour 1820: 38, pl. 73, fig. 7 (#); Audouin 1826: 380, pl. 5, fig. 3 (@); Hahn 1831: 7, pl. 1, fig. 3 (@); Koch 1838: 76, fig. 389 (#); Fage 1913: 499, figs 3–6 (unspecified sex); Drensky 1938: 93, fig. 8e (#).
Dysdera cambridgii: Bösenberg 1902: 320, pl. 30, fig. 473c (#@).

Syntypes. Dysdera erythrina: unspecified number of specimens (not available), France: surroundings of Paris (C. A. Walckenaer), (repository unknown, probably lost as it could not be found in MNHN). *Dysdera cambridgii:* 4@1juv. (examined), Germany: Bad Pyrmont, 24.ix. (T. Thorell), (NHRS); 2#1@7juv. (examined), Germany: Kissingen (T. Thorell), (NHRS); 1# (examined), Great Britain: England (O. P. Cambridge), (NHRS).
Other material examined. **France:** Haute vienne (many #@, MNHN, *D. erythrina* – det. E. Simon); Rhône, Lyon, Fay le Noyer (1@ iv.1916, K. Verhoeff, ZMHB); Côtes d'Armor, Saint Quay Portrieux (3#1@ 1858–91, H. Lucas, MNHN); Pyrénées Orientales, Banyuls (1#19@ iv.1931, 3#3@1juv. 26.v.1931, MNHN); Pyrénées Orientales, Valmanya (many #@, viii.1912, MNHN); (5#4@, MNHN); (many #@, MNHN); (many #@, MNHN); (2#2@, MNHN); (1#, MNHN); Ariège, Cazavet (1# iii.1962, Salege, MNHN); Dordogne, Plazac (2#1@4juv. 25.ix.1976, J. C. Ledoux, JL); Gard, Redessan, road to Meynes (3# 17.iv.1970, J. C. Ledoux, JL); Hérault, Grabels near Montpellier (2#2@1juv. 2.xi.1961, J. C. Ledoux, JL); Hérault, Saint-Gély, puech de Caucaliès (2#3@ 16.x.1984, x.1988, JL); Corrèze, Brive la Gaillarde (1# ix.19?75, BMNH). **Great Britain:** England, Box Hill Surry (1@ viii.1989, M. R. Gray, AMS); Swanaye (1@, O. Thomas, BMNH); Surrey, Mickleham Downs (1#1@ 30.v.1983, P. Hillyard, BMNH); Salcombe, Devon (3@3juv., R. R. Stebbing, BMNH). **Mauricius:** (1#, MNHN). **Spain:** Catalonia, Garraf, Begues (1@ 28.iv.2005, M. A. Arnedo, UB); Tarragona province, Montblanc (3juv. 3.ix.2006 [matured in January 2007], M. Řezáč & J. Dolanský, CMR); Pyrenées, San Juan de L'Hum (many #@, vii.1914, MNHN); Pyrenées, Mujjunda (2#1@ 1.vi.19?14, L. Baviere, MNHN).
For numerous examined material from **Austria**, **Czech Republic**, **Germany**, **Hungary,** and **Slovakia** see Řezáč *et al.* in press).

Description

Carapace (Figs 2*A*, 3*A*). # 2.6–4.0 mm, @ 2.8–4.1 mm long; maximum length/width = 1.29, maximum height/length = 0.29. Very gently wrinkled; ferruginous.
Chelicerae. Basal segment length/carapace length = 0.51, fang length/carapace length = 0.41. Basal segment mediodorsally slightly convex, covered by normal hairs.
Legs. Beside a pair of apical spines, the ventral side of ti IV is usually armed with two more spines. All segments ferruginous-yellow.
Bulbus (Figs 1*A*, 4*A*). 1.11–1.60 mm long, distal division length/bulbus length = 0.54. Bottom margins of tegulum and distal division in retrolateral view almost straight. Distal half of tegulum in retrolateral view wider than its proximal half. UBLS is not even partially covering fissure, UBLS almost parallel with LBLS. LBLS is suddenly bended down in its apical part. Membranous patch conspicuous. Lump smooth. PAT usually present.
Vulva (Figs 1*B*, 5*A*, 6*A*). Spermatheca approx. 0.55 mm long, anterior margin of spermatheca in ventral view convex, lateral edges incurvated backwards, RL not developed; unequal sclerotized muscle anchors on the proximal side often conspicuous. Anterior margin of dorsal arch regularly round. Transverse furrows on ventral wall remarkably developed; medial groove is simple.

Remarks

The identity of *D. erythrina* seems to be clear as the type locality is situated in the region where only one species from *D. erythrina* aggregate occurs. The name *D. cambridgii* is the junior synonym of *D. erythrina* as the examined type material of *D. cambridgii* is identical with *D. erythrina*.

Bulbi illustrated in Dufour (1820) and Koch (1838) do not seem to belong to any species of the *D. erythrina* aggregate. However, their schematic drawings, as well as drawings in Hahn (1831) and Fage (1913), do not allow more accurate identification. The drawing in Drensky (1938) is perhaps redrawn after Chyzer and Kulczyński (1897) and Simon (1914). In this case, however, the shape of bulbus rather resembles that of *D. lantosquensis*. The bulbus illustrated in "Die Spinnen Deutschlands" (Bösenberg 1902) resembles *D. provincialis* by shape. However, *D. provincialis* probably does not occur in Germany. The drawings in Charitonov (1956) and Mcheidze (1997) are redrawn after Chyzer and Kulczyński (1897). The drawing in Dresco (1973) is adopted from Simon (1914).

Habitat

In the Czech Republic, this species occurs in xerothermic forests on slopes (e.g., plant communities *Carpinion, Quercion pubescenti-petraeae, Quercion petraeae, Genisto germanicae-Quercion*, less often *Fagion*) and their fringes (*Geranion sanguinei*), in bushes (*Berberidion*) and in shaded parts of dry grasslands and heaths (*Festucion valesiacae, Bromion erecti, Euphorbio-Callunion*). It is also common in planted forests and semirural woods and bushes (often with *Hedera helix* on the ground), especially in surroundings of ruins overgrown by bushes. Its occurence is mainly concentrated in habitats enriched by calcium (the element essential for woodlice).

Phenology

Mating takes place probably from April to June, eggs are laid in June and July. Spiderlings disperse from maternal retreat in August and September. The spiders mature mainly in September of the following year, overwinter as adults and mate in the next spring. Thus, this species has a biennal life cycle.

Distribution (Fig. 7)

Dysdera erythrina has probably the largest distribution of all species of the aggregate. The coherent area stretches from Spain to the western parts of the Czech Republic and Austria. It reaches as far north as England, Belgium, Netherlands, northern Germany, and Poland. The species is probably able to disperse by means of human transportation to semirural habitats outside its coherent distribution. Such introduction is documented by material from Beľanské Tatry in Slovakia and Mauritius (in this case also mislabeling has to be taken into consideration). The occurence of this species in the Middle East (Audouin 1826) is probably based on misidentification.

The map of distribution of *D. erythrina* for Slovakia (Gajdoš *et al.* 1999) includes in fact *D. lantosquensis*; the map for the Czech Republic (Buchar and Růžička 2002) combines *D. erythrina* and *D. lantosquensis*, and the map for Serbia (Deltshev *et al.* 2003) is perhaps based on material of *D. lantosquensis*. The maps of distribution in Spain (Ribera *et al.* 1989; Romano and Ferrández 1983) may depict any species of the aggregate.

Dysdera (erythrina) fervida Simon

(Figs 3*D*, 4*D*, 5*D*, 7)

Dysdera fervida Simon, 1882: 216 (#@).
Dysdera erythrina fervida: Simon 1914: 99, 113 (#@).

Doubtful
Dysdera pumila Thorell, 1873: 580 (#).

Syntypes. Dysdera fervida: 1#1@ (examined), France: Corsica, 1882 (E. Simon), (MNHN); unknown number of specimens (not available), France: Provence (E. Simon), (probably mixed with other specimens of the aggregate – examined material labeled "*D. erythrina*, France" reposed in MNHN). *Dysdera pumila:* 1# (not available), Spain: Balearic Islands: Formentera (F. Söderlund), (repository unknown, missing in the NHRS – T. Kronestedt, personal communication).
Other material examined. **France:** Les Manies, Taynes? (1# 1914, MNHN); (5#, MNHN); (1#, MNHN); Var, Agay near Saint Raphaël (1# 25.ix.1862, L. Berland, MNHN); Provence, Alpes, Cote d'Azur, Iles d'Hyères, Ile de Port Cros (1@, S. Carranza, UB); (3#1@, MNHN); (1#1@, MNHN). **Spain:** Catalonia, Delta de l'Ebre, Illa de Buda (1@ iv.2002, E. De Mas , UB).

Description
Carapace (Fig. 3*D*). # 2.0–3.5 mm, @ 2.8–4.3 mm long; maximum length/width = 1.26 maximum height/length = 0.32. Roughly wrinkled; redish brown to ferruginous.
Chelicerae. Basal segment length/carapace length = 0.55, fang length/carapace length = 0.48. Basal segment mediodorsally concave, densely covered by short bristles.
Legs. Beside a pair of apical spines the ventral side of ti IV is usually armed with only a single spine. All segments ferruginous-yellow.
Bulbus (Fig. 4*D*). 0.95–1.24 mm long, distal division length/bulbus length = 0.59. Bottom margins of tegulum and distal division in retrolateral view almost straight. Distal half of tegulum in retrolateral view as wide as its proximal half. UBLS is partially covering fissure, UBLS almost parallel with LBLS. LBLS forms a lobe in its proximal part, which partly covers fossette, and forms lamella protruding forward apical part of bulbus. Membranous patch inconspicuous. Lump gently wrinkled. PAT absent.
Vulva (Fig. 5*D*). Spermatheca approx. 0.40 mm long, anterior margin in ventral view concave, lateral edges remarkably incurvated backwards, RL slightly developed; unequal sclerotized muscle anchors on the proximal side inconspicuous. Anterior margin of dorsal arch with median and two additional lateral lobes. Transverse furrows on ventral wall inconspicuous; medial groove is simple.

Remarks
Original description of *D. fervida* does not include drawings, however, verbal description (Simon 1882) and diagnosis (Simon 1914) is sufficient for reliable identification. It has not been reported ever since. *Dysdera pumila* might be a senior synonym of this species judging from the small body size. The original description of *D. pumila* lacks drawings and the type material are probably lost. However, *D. pumila* probably is not a junior synonym of *D. erythrina* as stated in Platnick (2007). Thorell obviously knew *D. erythrina* very well because he described *D. pumila* and *D. cambridgii* (a junior synonym of *D. erythrina*) in the same paper. The nomenclature of *D. fervida* may change in the future after revision of *Dysdera* from Balearic Islands.

Distribution (Fig. 7)

Dysdera fervida is known from southern France, particularly Provence, French Pyrénées, Corsica, and northeastern Spain, particularly Catalonia. *D. pumila*, perhaps identical with *D. fervida*, is known from the island of Formentera (Balearic Islands).

Dysdera (erythrina) lantosquensis Simon
(Figs 2*B*, 3*B*, 4*B*, 5*B*, 7, 8*B*)

Dysdera lantosquensis Simon, 1882: 215 (#).
Dysdera erythrina lantosquensis: Simon 1914: 99, 113 (#).
D. rubicunda C. L. Koch, 1838: 79, figs 390a–b (#).
Dysdera erythrina: Loksa 1969: 75, figs 52C–D, 53F (#@); Miller 1971: 74, pl. 5, fig. 7 (@); Schult 1983b: 17, fig. 4 (@); Deeleman-Reinhold and Deeleman 1988: 164, figs 12, 44–49 (#@); Heimer and Nentwig 1991: 44, fig. 95.1 (#).

Syntypes. Dysdera lantosquensis: unknown number of males and females (not available), France: Alpes Maritimes: Saint Matrin Vésubie near Lantosque (E. Simon), (probably mixed with other specimens of the aggregate – examined material labeled "*D. erythrina*, France" reposed in MNHN). *D. rubicunda:* unknown number of males (not examined), Germany (C. L. Koch), (perhaps BMNH); unknown number of males (not examined), Czech Rep.: Bohemia (C. L. Koch), (perhaps BMNH).
Other material examined. **France:** (2#, MNHN); (1#, MNHN). **Italy:** Ancona, citadel in the city (1#1@ 27.iii.1999, F. Šťáhlavský, MR); Genova, S. Sirodi Struppa (1#1@ 6.iv.–8.v.1993, S. Firullo, MR); Pesaro, S. Leo (2#2@ 15.x.1991, F. Gasparo, MR); Pezolo Valle Uzzone, Cuneo (1@ 13–18.viii.1970, L. Zunino, MNHN), Tuscany, Monte Argentario (1@ 2004, S. Carranza, UB). **Spain:** delta of Ebro river, Tarragona town, La Tankada lake (2# 11.vi.1999, J. Dolanský, MR).
For numerous examined material from **Austria, Czech Republic, Hungary,** and **Slovakia** see Řezáč *et al.* in press).

Description
Carapace (Figs 2*B*, 3*B*). # 2.1–3.3 mm, @ 2.3–3.6 mm long; maximum length/width = 1.17, maximum height/length = 0.33. Very roughly wrinkled; dark brown to ferruginous.
Chelicerae. Basal segment length/carapace length = 0.49, fang length/carapace length = 0.48. Basal segment mediodorsally concave, densely covered by short bristles.
Legs. Beside a pair of apical spines, the ventral side of ti IV is usually armed with only a single spine. All segments ferruginous-yellow.
Bulbus (Fig. 4*B*). 0.98–1.15 mm long, distal division length/bulbus length = 0.64. Bottom margins of tegulum and distal division of tegulum and distal division in retrolateral view angled. Distal half of tegulum in retrolateral view as wide as its proximal half. UBLS is partially covering fissure, UBLS at 45° angle with LBLS. LBLS is suddenly bended down in its apical part. Membranous patch inconspicuous. Lump smooth. PAT usually absent.
Vulva (Fig. 5*B*). Spermatheca approx. 0.45 mm long, anterior margin in ventral view concave, lateral edges not incurvated backwards, RL remarkably developed; unequal sclerotized muscle anchors on the proximal side inconspicuous. Anterior margin of dorsal arch with median and two indistinct additional lateral lobes. Transverse furrows on ventral wall slightly developed; medial groove is simple.

Remarks
The type material of *D. lantosquensis* probably do not exist any more. The only vial in MNHN labeled *D. lantosquensis* (Martigues, xi.1913, AR5877, 25195) was empty. Original

description of this species does not include drawings, however, its identity can be deduced from the verbal description (Simon 1882) and diagnosis (Simon 1914). Although this species has been collected several times, it has been confused with *D. erythrina* (e.g., Deeleman-Reinhold and Deeleman 1988, Heimer and Nentwig 1991).
The male of *D. lantosquensis* was probably described already by C. L. Koch in 1838 as *Dysdera rubicunda*. He coupled male of *D. lantosquensis* with a female obviously belonging to the genus *Harpactea*. In the introduction of the description he emphasized eye arrangement which is present only in *Harpactea* female. In order to stabilise nomenclature, the species name *rubicunda* should be henceforward used for this common central European *Harpactea* species. Thaler and Knoflach (2002) also noted this confusion but they erroneously applied the Koch's description to *D. erythrina*.

Habitat and phenology
Similar to that of *D. erythrina*.

Distribution (Fig. 7)
Dysdera lantosquensis can be found in the area stretching from northeastern Spain to central Europe. It does not reach as far to the north as *D. erythrina* but it occurs further to the east. In central Europe, it occurs in the east part of Austria, east part of the Czech Republic, in Slovakia and in Hungary. It may also occur in southern Poland and easternmost Ukraine. Further spreading can be expected due to its affinity for semirural habitats.

Dysdera (erythrina) montsenensis Řezáč, sp. nov.
(Figs 3*F*, 4*F*, 5*F*, 7, 8*D*)

Holotype. 1#, Spain: *Catalonia:* Montseny Mts., Can Cervera near Montseny town, 41°46'N, 2°24'E, 9.ix.2006 (M. Řezáč), (RICP).
Paratypes. 2#, the same data as holotype.

Description
Carapace (Fig. 3*F*). # 2.8 mm long; maximum length/width = 1.32, maximum height/length = 0.25. Frontal, lateral and posterior lateral margins rounded; notch shallow; cephalic part wide as 1/2 of carapace length. Roughly wrinkled; uniformly brown; with dense black spots mainly in front of fovea.
Eyes. AME diameter 0.15 mm, PLE 0.13 mm, PME 0.11 mm. AME slightly back from frontal border, separated from one another by about an eye diameter, close to PLE. PME very close to each other, less than 1/4 of PME diameter from PLE.
Sternum. Roughly wrinkled; yellow-orange; slender black hairs only on sides.
Labium. Trapezoid, longer than wide at base, with a U-shaped groove at the tip.
Gnathocoxae. 1.0 mm long.
Chelicerae. Basal segment length/carapace length = 0.59, fang length/carapace length = 0.42. Cheliceral inner groove with three teeth and lamina at base; medial tooth > basal tooth > distal tooth, distal tooth located roughly at basal third of groove, basal tooth close to basal lamina, medial tooth close to basal tooth. Basal segment mediodorsally concave, covered with short bristles, ventral side smooth.
Legs. For lengths of leg segments see Table 3. Spines on ti III, mt III, ti IV and mt IV (Table 4); claws hardly longer than wide. All segments yellow.
Abdomen. 3.1 mm long, cylindrical, whitish. Abdominal dorsal hairs 0.02 long.
Bulbus (Fig. 4*F*). 1.2 mm long, distal division length/bulbus length = 0.50. Bbottom margins of tegulum and distal division in retrolateral view angled. Distal half of tegulum in retrolateral

view slightly wider than its proximal half. UBLS is partially covering fissure, UBLS at 35° angle with LBLS. LBLS is bended down in its apical part. Membranous patch small. Lump slightly pronounced and smooth. PAT absent.

Etymology
Named after Montseny, the Spanish mountain range to which the distribution range of the species is probably restricted.

Habitat
Dysdera montsenensis was found in the humid *Platanus* forest in the bottom of a deep valley of mountain brook in the elevation 650 m.

Distribution (Fig. 7)
Known only from the type locality in northeastern Spain.

Dysdera (erythrina) provincialis Simon
(Figs 3*C*, 4*C*, 5*C*, 6*B*, 7, 8*C*)

Dysdera provincialis Simon, 1882: 214 (#@).
Dysdera erythrina provincialis: Simon 1914: 99, 113 (#@); Berland 1912: 47, fig. 1 (#@).

Doubtful
Dysdera corallina Risso, 1826: 161 (unspecified sex).

Syntypes. Dysdera corallina: unknown number of specimens (not available), France: surroundings of Nice (A. Risso), (probably do not exist any more as they could not be found in the MNHN). *Dysdera provincialis:* unknown number of males and females (not available), France: Ile de Porquerolles in Var (E. Simon), (probably mixed with other specimens of the aggregate – examined material labeled "*D. erythrina*, France" reposed in MNHN).
Other material examined. **France:** (many #@, MNHN); Gard, Mount Aigoual (3@ vi.1911, MNHN); Languedoc-Roussillon, Canigou mountain between Valmanya and La Bastide (1#1@ 18.x.2004, M. A. Arnedo, UB); Languedoc, Montagne Noire (1@ 1993, UB); *Pyrénées Orientales:* Argelès, forest Massane (1#1@ 11.iii.1995, J. C. Ledoux, JL); Banyuls (3#3@ 25.ix.1862, L. Berland; 1#1juv. 29.iii.1964; 4#3@; MNHN); Banyuls, Cap l'Abeille (many #@ xii.–ii., MNHN); Banyuls, Fontaine Jassal (1#1@1juv. 21.vii.1963, J. C. Ledoux, JL); Conat (2#1@ 13.iv.1994, J. C. Ledoux, JL); Nohèdes, Montillá (2# 15.ix.1993, J. C. Ledoux, JL); Cerbère (7#1@, BMNH). **Spain:** *Girona:* Colera, Ermita Sant Miquel de Colera (1@ 21.iv.2004, M. A. Arnedo, UB); southern Pyrenées, Maćanet de Cabrenys (1# 15.vi.1999, J. Dolanský, MR); Pyrenées, San Juan de l'Herm, Mujjunda (4@ 1.vi.1914, L. Baviere, MNHN); Rosas near Port Vendres (2#5@1juv., MNHN); Ripollès, Setcases (1#1@ 20.x.2004, M. A. Arnedo, UB). *Catalonia:* Conca de Barberà: Serra de Prades, Barranc de la Font d'en Garro (1#1@ 28.v.2003, M. A. Arnedo, UB); Alt Emporà: La Jonquera (1#1@ 16.iv.2005, S. Carranza, UB).

Description
Carapace (Fig. 3*C*). # 3.7–4.9 mm, @ 3.3–5.3 mm long; maximum length/width = 1.32, maximum height/length = 0.26. Very gently wrinkled; redish brown to ferruginous.
Chelicerae. Basal segment length/carapace length = 0.50, fang length/carapace length = 0.40. Basal segment mediodorsally convex, covered by normal hairs.

Legs. Beside a pair of apical spines, the ventral side of ti IV is usually armed with two more spines. All segments redish-ferruginous.
Bulbus (Fig. 4*C*). 1.29–1.78 mm long, distal division length/bulbus length = 0.55. Bottom margins of tegulum and distal division of tegulum and distal division in retrolateral view angled. Distal half of tegulum in retrolateral view wider than its proximal half. UBLS is not even partially covering fissure, UBLS almost parallel with LBLS. LBLS is regularly bended down, forming characteristic lobe in its apical part, visible in ventral view. Membranous patch very variable in size, but always conspicuous. Lump smooth. PAT usually present.
Vulva (Figs 5*C*, 6*B*). Spermatheca approx. 0.60 mm long, anterior margin in ventral view straight or convex, lateral edges slightly incurvated backwards, RL not developed; unequal sclerotized muscle anchors on the proximal side inconspicuous. Anterior margin of dorsal arch almost straight. Transverse furrows on ventral wall slightly developed; medial groove with sclerotised teeth (Fig. 6*B*).

Remarks
Original description of *D. provincialis* does not include drawings, however, its identity is unambigouesly given by the verbal description (Simon 1882) and diagnosis (Simon 1914). Since the period of its description, *D. provincialis* was neglected. *D. corallina* might be a senior synonym of this species based on the red coloration of chelicerae. Unfortunately, the original description is too brief and the type material could not be traced.

Habitat
Dysdera provincialis occurs in various Mediterranean forests and bushes (*Quercus, Pinus, Fagus, Corylus*).

Distribution (Fig. 7)
Dysdera provincialis is known from northeastern Spain, southern France, and Apennines in Italy.

Karyotypes

The male karyotype contained nine autosome pairs in *D. erythrina* (Fig. 8*A*), five autosome pairs in *D. lantosquensis* (Fig. 8*B*) and *D. montsenensis* (Fig. 8*D*), and four autosome pairs in *D. provincialis* (Fig. 8*C*). Analysis of male meiosis showed the sex chromosome system X0 in all species. The sex chromosome is remarkably longer than autosomes in *D. erythrina* and *D. lantosquensis*, as long as the longest autosome pairs in *D. montsenensis*, and as long as medium autosomes in *D. provincialis*.

Prey Preference

All specimens of *D. erythrina*, *D. lantosquensis, D. provincialis*, and *D. montsenensis* readily captured woodlice. In cases when they refused woodlice, they also refused flies.

Crossing Experiments

All five males and females of the same species (*D. erythrina, D. lantosquensis*) did copulate. In interspecific crosses, all males of *D. lantosquensis* and females of *D. erythrina* mated. In contrast to this, none female of *D. lantosquensis* mated with any male of *D. erythrina*.

Discussion

The genus *Dysdera* is unique among other genera of the spider family Dysderidae by regular presence of aggregates of sibling species. Trying to understand the evolution of these aggregates we focused on a model aggregate of *D. erythrina*. We analyzed wide range of aspects assuming that particular taxa will differ mainly in characters, which played an important role in speciation process. We distinguished six morphologically very similar taxa that fit the phenetic species concept (Winston 1999). Areas of all species of the aggregate include also southern France and northeastern Spain. This region is thus suspected to be the speciation center of the aggregate. We did not find any obvious differences in habitat preferences of particular species; in some localities they even lived together. However, we found remarkable differences in their karyotypes (Table 5), sculpture of carapace, shape of endogynal medial groove, shape of chelicerae, and body size. This brings us to the question, why these hardly distinguishable species differ so remarkably right in these characters. Sympatric coexistence of closely related species requires effective mechanisms generating interspecific barriers and reducing competition for prey (Otte and Endler 1989). We suppose that observed differences between the species reflect the action of such mechanisms.

Chromosome rearrangements might have played a primary role in the evolution of interspecific barriers in the genus *Dysdera*. These spiders are characterized by holocentric chromosomes (Díaz and Sáez 1966; Benavente and Wettstein 1980; Rodríguez Gil *et al.* 2002). We suggest that due to the structure of holocentric chromosomes, karyotypes can easily differentiate in *Dysdera*. In contrast to normal (monocentric) chromosomes, holocentric chromosomes possess kinetochore along the major part of their length. Therefore, products of breakages (fragments) or fusions (fused chromosomes) often segregate regularly to the poles during divisions. In this way, fragments and fused chromosomes have higher probability to be fixed in a population in comparison with normal chromosomes (Jacobs 2004).

Rapid divergence of karyotypes might have been facilitated by inability of *Dysdera* to disperse to a long distance. In contrast to majority of other spiders, *Dysdera* has never been observed to balloon (e.g., Blandenier and Fürst 1998; Duffey 1956). Moreover, *Dysdera* spiders are usually associated with forest habitats (Deeleman-Reinhold and Deeleman 1988), which were periodically fragmented during Quarternary climatic oscillations (Iversen 1964). Without efficient migration ability, habitat fragmentation might have led to separation of populations. In small isolated populations, chromosome rearrangements could have been easily fixed by the genetic drift. Chromosome races lost the ability to hybridize with the ancestral form and gave rise to a new species.

Secondary contact of new and ancestral species likely gave rise to recognition mechanisms that would prevent them from wasting their reproduction potential (reinforcement, *sensu* Rundle and Nosil 2005). An example of the recognition might be the observed one-sided precopulatory barrier between *D. erythrina* and *D. lantosquensis*. We assume the different sculpture of the carapace might facilitate intraspecific recognition in this case. Nevertheless, interspecific copulations do occur in *Dysdera* species (Cooke 1965; our observation of copulation of *D. lantosquensis* males and *D. erythrina* females), however, it may not necessarily lead to production of non-viable eggs. Both *Dysdera* sexes copulate repeatedly (Jackson and Pollard 1982; our observations), thus females are probably provided by sperm from different males. Copulatory organ of *Dysdera* females is relatively complex, holding two types of "cul-de-sac" sperm storage organs (Cooke 1966). Such structure of copulatory organ

gives females an opportunity to manipulate sperm before fertilisation (see Uhl 2000). It encourages us to expect that in an environment with high chance of interspecific copulation, *Dysdera* females have developed mechanisms for recognition and elimination of non-specific sperm that prevent decrease of fertility. From this point of view the species-specific anatomy of medial groove, through which the sperm has to pass to spermatheca, could be suggestive.

We suppose that closely related *Dysdera* species can occur sympatrically due to diet specialisation avoiding competition for prey. The results of our experiments document that all tested species readily capture woodlice. However, we found remarkable interspecific differences in body size and the morphology of mouth parts, particularly chelicerae, among the species of the *D. erythrina* aggregate. All these findings suggest their specialisation on different species or size of woodlice. Observed differentiation of characters determining potencial prey, particularly mouth parts and body size, resembles character displacement accompanying species radiation in islands (e.g., Darwin 1859). We suppose that such island-like radiation was caused by woodlice being an island-like prey: they are badly accessible, being protected by effective defences. Particularly, they are protected by tegumental gland secretions, incrusted armour, and behavioural defences protecting soft ventral side of the body. However, those predators which once evolved adaptations necessary for overcomming these defences, gained rich food source as woodlice belong to most abundant ground dwelling invertebrates in many habitats (Sutton 1980). Moreover, woodlice are very variable prey similar to the habitats on an island: some species defend themselves by rolling up into a ball, others cling to the substrate (Schmalfuss 1984). Each species shows extraordinary polymorphy of size due to epimeric ontogeny (Sutton 1980). Thus, single invertebrate predator is not able to utilize the whole range of their variability so that they provide food source for several potential predators. Particular *Dysdera* species could start to specialise on specific woodlice already during initial, allopatric stage of speciation, when food resources were more restricted in a small area. Such specialisation could have been reinforced after the contact with other species when natural selection favored specialised specimens which did not compete for prey.

Sympatric occurence of closely related species has been documented also in other *Dysdera* aggregates (e.g., Deeleman-Reinhold and Deeleman 1988). Interestingly, the species of these aggregates differ in the same characters as the representatives of the *D. erythrina* aggregate. These characters may represent interspecific barrier: karyotype differences (Řezáč and Král, unpublished data), sculpture of carapace (Arnedo and Ribera 1999); or niche division: body size (Deeleman-Reinhold and Deeleman 1988), shape of chelicerae (Arnedo and Ribera 1999). Therefore, other *Dysdera* aggregates might have probably evolved in the same way as the *D. erythrina* aggregate.

According to the suggested mode, the initial causes of speciation in *Dysdera* aggregates were incompatible chromosome mutations that were fixed by genetic drift (speciation by genetic drift *sensu* Schluter 2001). Following sympatric coexistence of particular species was likely allowed by further ecological/morphological differentiation driven by natural selection. In contrast to the ecological hypothesis of speciation (Schluter 2001) the suggested mode predicts existence of cryptic species possessing karyological but not morphological differences in case they remained geographically isolated.

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Table 1. *Dysdera catalonica* sp. n., holotype, lengths of appendage segments (mm)

appendage	ta	mt	ti	pt	fe	cx	total
I	0.6	2.3	2.5	1.9	3.2	1.7	10.5
II	0.6	2.2	2.3	1.7	2.8	1.4	9.7
III	0.6	1.9	1.4	1.2	2.2	0.8	7.3
IV	0.7	2.6	2.2	1.5	2.8	1.0	9.7
pedipalp	0.8		0.8	1.0	1.8		4.5

Table 2. *Dysdera catalonica* sp. n., spination on leg segments (N=3)

Leg segment	prodorsal	proventral	ventral	apical ventral	retroventral	retrodorsal
ti III	2		1	2		1
mt III	3–4	1–2		2	1–2	2–3
ti IV	0–1	0–1	1	2		2
mt IV	4	2–3		2	2	3

Table 3. *Dysdera montsenensis* sp. n., holotype, lengths of appendage segments (mm)

appendage	ta	mt	ti	pt	fe	cx	total
I	0.5	1.6	1.8	1.3	2.1	1.2	8.5
II	0.5	1.5	1.6	1.2	1.9	1.1	7.8
III	0.4	1.2	1	0.8	1.5	0.6	5.5
IV	0.5	1.8	1.6	1.1	2	0.7	7.7
pedipalp	0.7	0	0.7	0.7	1.3	1	4.4

Table 4. *Dysdera montsenensis* sp. n., holotype, spination on leg segments

Leg segment	prodorsal	proventral	ventral	apical ventral	retroventral	retrodorsal
ti III	2		0–1	2		
mt III	2–3	1–2		2		1–2
ti IV	0–1		1	2		1
mt IV	4	2		2	1	2

Table 5. List of karyotyped species of the aggregate *D. erythrina*

Species	Diploid number of chromosomes	Sex chromosome system
D. provincialis	# 9	X0
D. lantosquensis	# 11	X0
D. montsenensis	# 11	X0
D. erythrina	# 19	X0

Figures

Fig. 1. *Dysdera erythrina*, drawing of the copulatory organs showing the morphological characters. *A*, bulbus, retrolateral view; *B*, vulva, ventral view. AL: apical lobe, BM: bottom margin, CL: coriaceous lamina, DA: dorsal arch, DD: distal division, DF: dorsal fold, FI: fissure, FO: fossette, L: lump, LBLS: lower border of lateral sheet, MF: major fold, MG: medial groove, MP: membranous patch, PA: posterior apophysis, PAT: tooth of posterior apophysis, RL: retroventral lobe, S: spermatheca, T: tegulum, UBLS: upper border of lateral sheet, VA: ventral arch, VW: ventral wall.

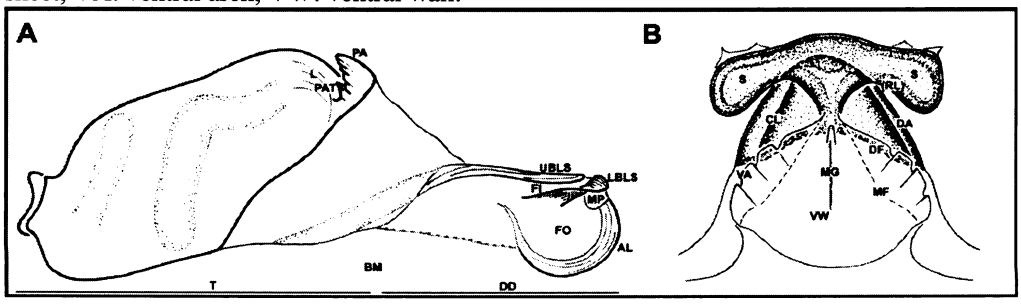


Fig. 2. Male prosomas, lateral view. *A*, *Dysdera erythrina*, Czech Republic: Prague; *B*, *Dysdera lantosquensis*, Slovakia: Hrušov. Scale bars = 1 mm.

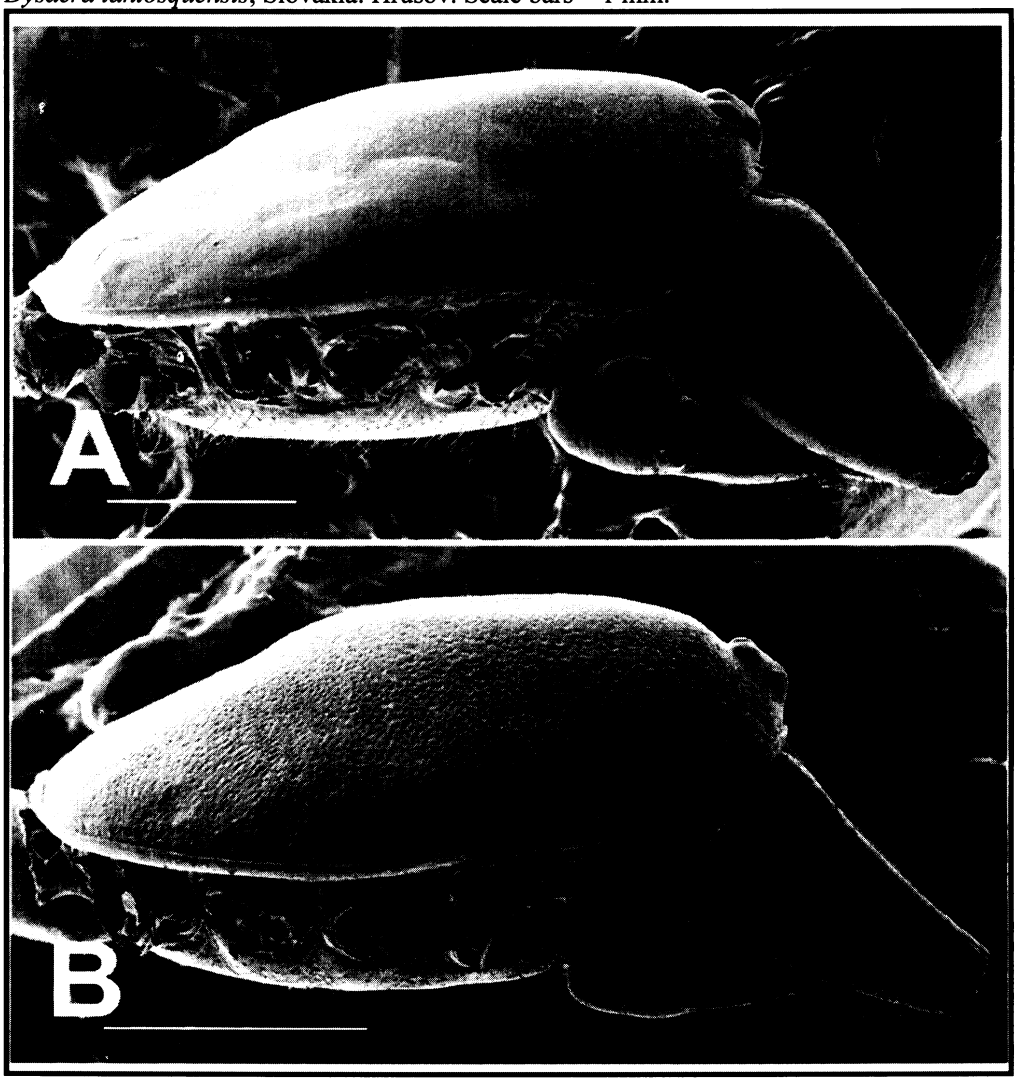


Fig. 3. Male prosomas, dorsal view. *A*, *Dysdera erythrina*, Czech Republic: Prague; *B*, *Dysdera lantosquensis*, Slovakia: Hrušov; *C*, *Dysdera provincialis,* France: Provence; *D*, *Dysdera fervida,* France: Agay; *E*, *Dysdera catalonica*, Spain: Montserrat; *F*, *Dysdera montsenensis*, Spain: Montseny. Scale bars = 1 mm.

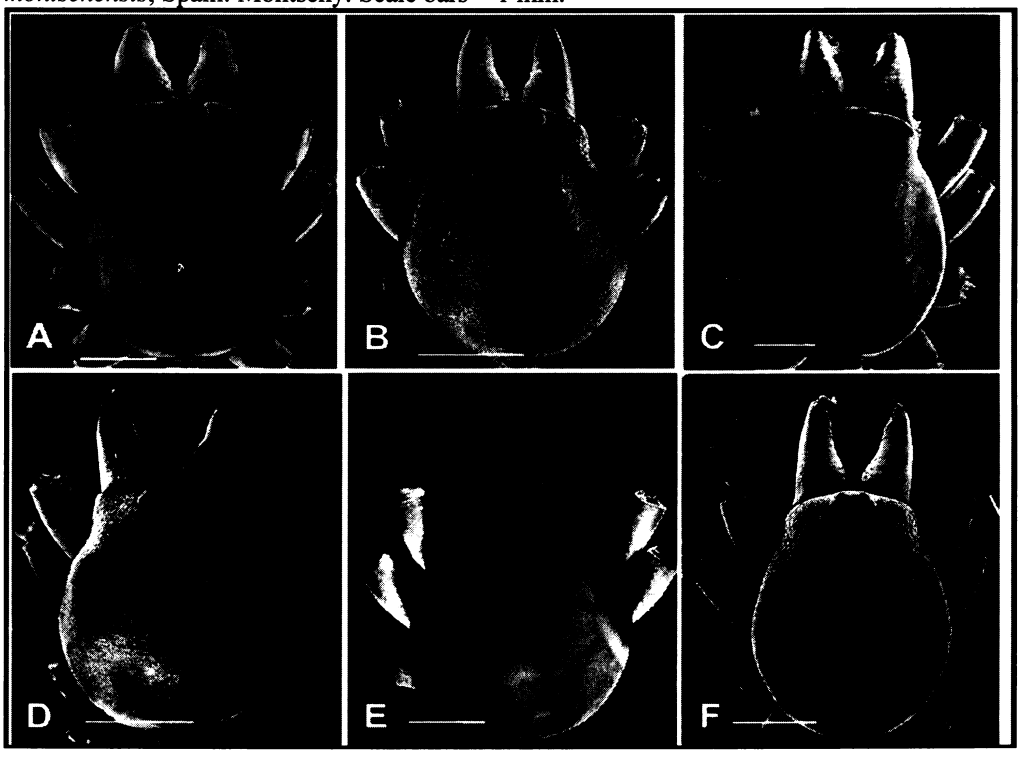


Fig. 4. Left male bulbus, retrolateral view. *A*, *Dysdera erythrina*, Czech Republic: Prague; *B*, *Dysdera lantosquensis*, Slovakia: Hrušov; *C*, *Dysdera provincialis,* France: Provence; *D*, *Dysdera fervida,* France: Agay; *E*, *Dysdera catalonica*, Spain: Montserrat; *F*, *Dysdera montsenensis*, Spain: Montseny. Scale bars = 0.1 mm.

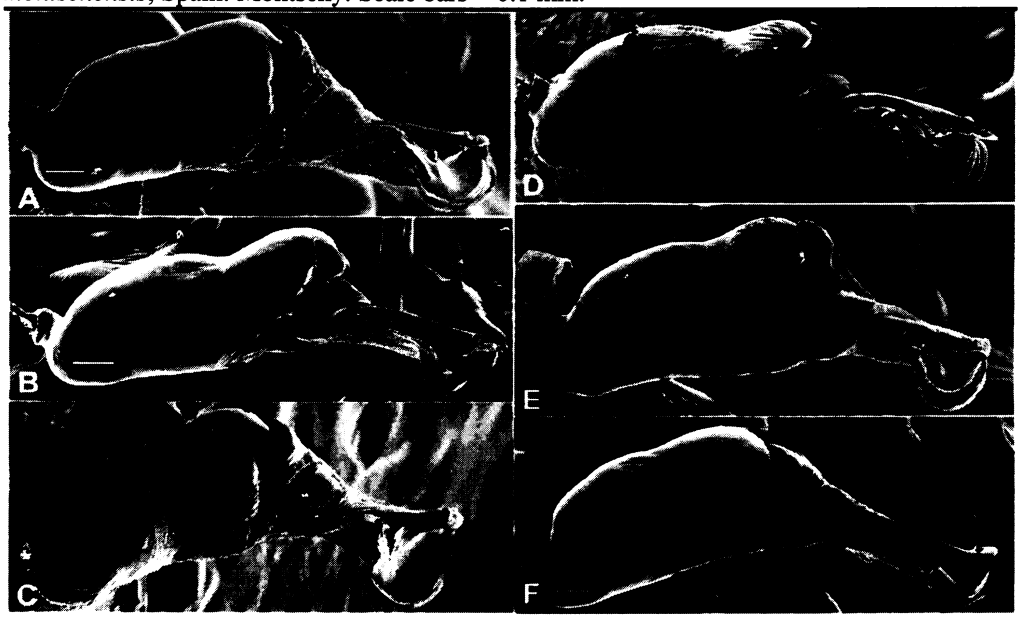


Fig. 5. Vulva, ventral view. *A*, *Dysdera erythrina*, Czech Republic: Prague; *B*, *Dysdera lantosquensis*, Slovakia: Hrušov; *C*, *Dysdera provincialis,* France: Provence; *D*, *Dysdera fervida,* France: Agay; *E*, *Dysdera catalonica*, Spain: Montseny; *F*, *Dysdera* sp., Spain: Serra de Prades. Scale bars = 0.1 mm.

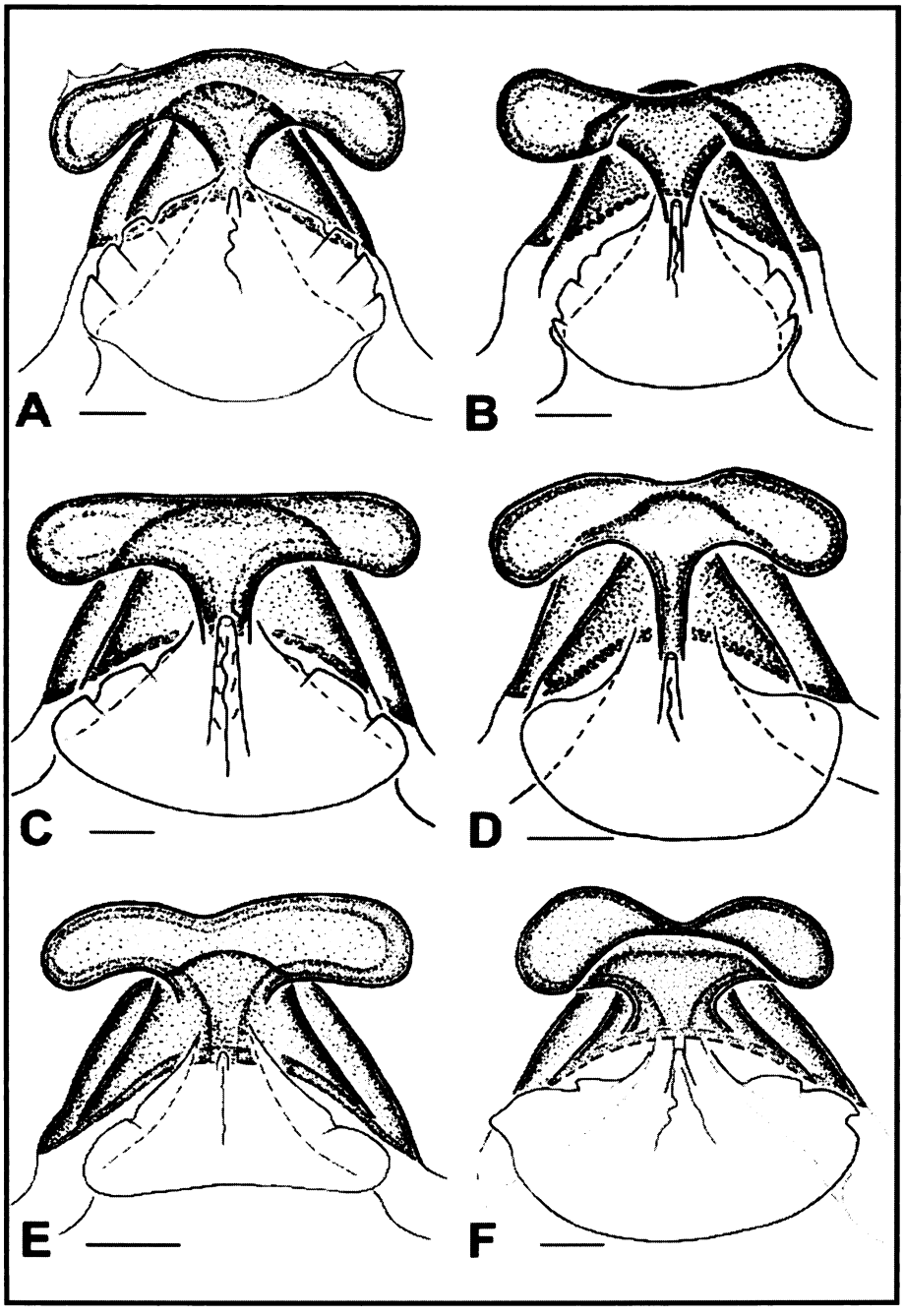


Fig. 6. Vulva, dorsal view. *A*, *Dysdera erythrina*, Czech Republic: Prague; *B*, *Dysdera provincialis*, France: Provence.

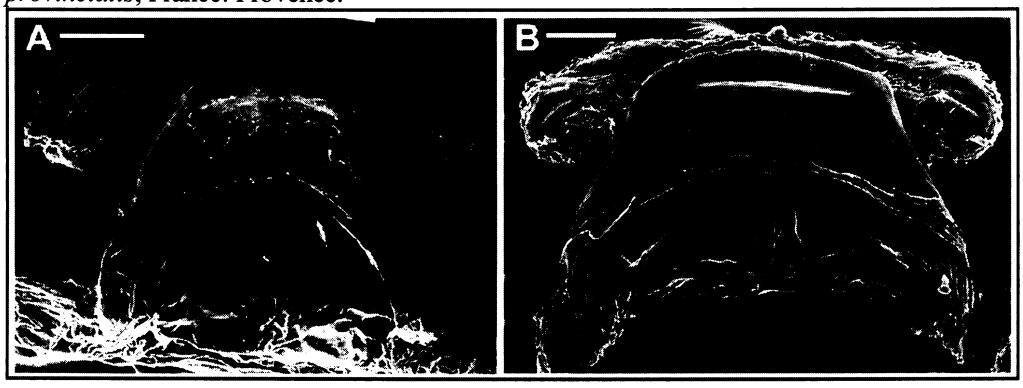


Fig. 7. Distribution of the *Dysdera (erythrina)* aggregate. ? identifies inaccurate or dubious record.

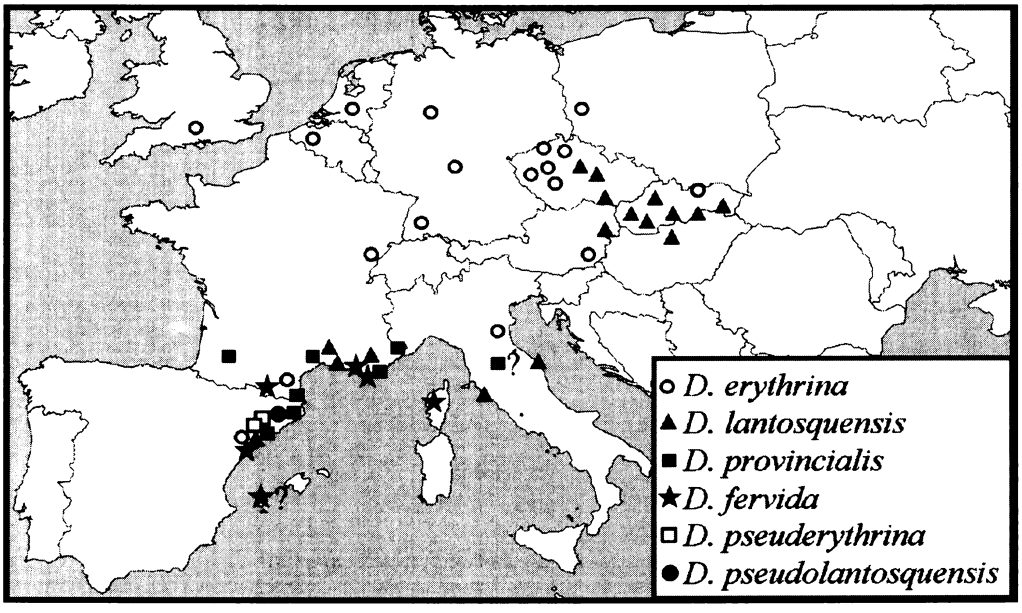
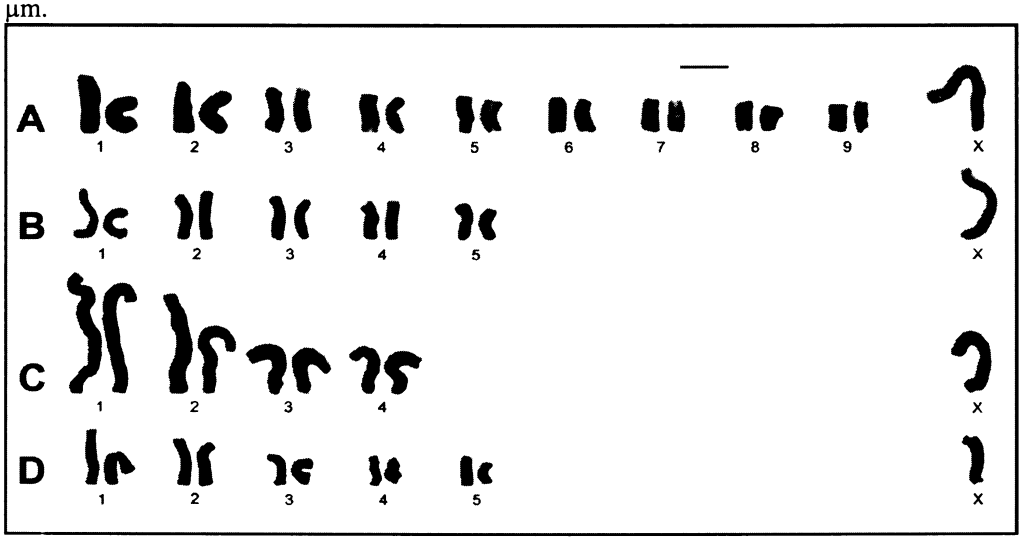


Fig. 8. Male karyotypes (based on spermatogonial metaphases). *A*, *Dysdera erythrina*; *B*, *Dysdera lantosquensis*; *C*, *Dysdera provincialis*; *D*, *Dysdera montsenensis*. Scale bar = 10 μm.



THE SPIDER GENUS *DYSDERA* (ARANEAE, DYSDERIDAE) IN CENTRAL EUROPE: REVISION AND NATURAL HISTORY

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ABSTRACT. Nine species of the genus *Dysdera* were found to occur in central Europe: *D. adriatica* Kulczyński 1897, *D. crocata* Koch 1838, *D. dubrovninnii* Deeleman-Reinhold 1988, *D. erythrina* (Walckenaer 1802), *D. ninnii* Canestrini 1868, *D. hungarica* Kulczyński 1897, *D. lantosquensis* Simon 1882, *D. longirostris* Doblika 1853, and *D. taurica* Charitonov 1956. Two species, *D. dubrovninnii* and *D. lantosquensis*, are newly recorded from central Europe. The original description of *D. hombergi* (Scopoli 1763), the name used for a common species of the genus *Harpactea*, probably refers to *D. ninnii*. We retain the name *D. ninnii* as a *nomen protectum*. *Dysdera hamulata* Kulczyński 1897 appears to be a junior synonym of *D. maurusia* Thorell 1873. This North African species probably does not occur in central Europe, and a previous record from Slovakia is probably based on mislabeled material. A review of all species of *Dysdera* named from outside the Palearctic region demonstrated that *D. australiensis* Rainbow 1900 and *D. magna* Keyserling 1877 are junior synonyms of *D. crocata*, and that *D. bicolor* Tatzanovski 1874 and *D. solers* Walckenaer 1837 are erroneously placed in the genus *Dysdera*; the former is likely to be an oonopid and the latter a caponiid. In central Europe, *Dysdera* spiders prefer xerothermic forests, particularly sites enriched by calcium. All species probably have biennal life-cycles. The male karyotype of seven species were examined, and diploid chromosome numbers were found to be extraordinarily variable, ranging from 9 (*D. crocata*) to 40 (*D. longirostris*). Karyotypes consist of holocentric chromosomes.

Keywords: Sibling species, karyotype, geographic parthenogenesis, taxonomy, thelytoky

Spiders of the genus *Dysdera* (Dysderidae) are ground dwellers characteristic of xerothermic forests of the Mediterranean and adjacent areas. During the day, they shelter in gravel covered by organic material or under stones, and at night they search for woodlice, their principal prey (Cooke 1965).

Comprising more than 240 species (Platnick 2007), *Dysdera* is currently the largest genus in the family Dysderidae and one of the richest Palearctic spider genera. Interestingly, the vast majority of species appear to be endemic to only small areas of the Mediterranean region, and only nine representatives appear to have colonized central Europe after the last

glacial period. Although the species diversity in this region is low, there has been much confusion concerning their identification because of the uniformity in both the shape and body color, similarity in external female genitalic features and the presence of sibling species (e.g., Deeleman-Reinhold & Deeleman 1988).

A modern revision of the genus was initiated by Deeleman-Reinhold & Deeleman (1988), focusing on species from the eastern part of the Mediterranean. The genus was redefined and divided into different species-groups. This paper revises central European species of the genus *Dysdera*, based mainly on analysis of material from the Czech Republic and Slovakia. We solve some nomenclatural problems and summarize data on the distribution, habitat preferences, phenology and karyotypes of the species. We recognize eight species representing five groups within central Europe: *D. crocata* C. L. Koch 1838 (*crocata* group); *D. ninnii* Canestrini 1868, *D. dubrovninnii* Deeleman-Reinhold 1988 (*ninnii* group); *D. hungarica* Kulczyński 1897, *D. adriatica* Kulczyński 1897, *D. longirostris* Doblika 1853 (*longirostris* group); *D. taurica* Charitonov 1956 (*lata* group); *D. erythrina* (Walckenaer 1802) and *D. lantosquensis* Simon 1882 (*erythrina* group). -

MATERIAL AND METHODS

Distributional data and habitat preferences were obtained by analysis of extensive material from collections and during our field work. Selected localities were visited mainly in the summers of 1999–2005. Vegetation of inspected localities was characterized following Chytrý *et al.* (2001) and Moravec (1995).

Morphology of specimens was examined using a Nikon SMZ 645 stereomicroscope and an Olympus BX51 light microscope. Before examination, female vulvae were dissected and cleared by glycerol. The prosoma, chelicerae and bulbi of selected males were removed, placed on a stub, coated with gold and examined using a scanning electron microscope JEOL JSM 6400. To describe structures of the male pedipalp and the female vulva, we used the terminology of Arnedo *et al.* (2000).

Phenology was studied both on selected localities and by processing data on labels of the revised material. Phenological observations were performed on data from the following localities: Rokštejn [49°19'N, 15°43'E], Czech Republic (*D. ninnii*); Vinné near Michalovce [48°48'N, 21°58'E], Slovakia (*D. dubrovninnii*); Hrušov [48°36'N, 20°40'E] and Vinné near Michalovce, Slovakia (*D. hungarica*); Plitvička jezera [44°54'N, 15°36'E], Croatia (*D. adriatica*); Rilski monastir [42°07'N, 23°20'E] and Kranevo [43°20'N, 28°02'E], Bulgaria (*D. longirostris*); and Kranevo, Bulgaria (*D. taurica*).

For the karyological analyses, the most appropriate ontogenetic stage was found to be the adult male shortly after molting, which occurs at the end of the summer in all species studied. Testes at this stage contained numerous dividing cells suitable for karyotypic analysis, namely spermatogonial mitoses as well as various meiotic stages. The chromosome preparations were obtained by the method described in Pekár & Král (2001). Localities of karyotyped species were as follows: *D. crocata* – Kranevo near Varna, Bulgaria, 1 ♂; Çaytepe near Ordu, Turkey, 1 ♂; Mitra near Évora, Portugal, 4 ♂; Bloemfontein, South Africa, 1 ♂; Taborno, Tenerife, Spain, 2 ♂; *D. ninnii* – Rokštejn near Brtnice, Czech Republic, 2 ♂; *D. dubrovninnii* – Vinné near Michalovce, Slovakia, 2 ♂; *D. hungarica* – Hradisko near Hrušov, Slovakia, 2 ♂; *D. adriatica* – Korana near Plitvička jezera, Croatia, 1 ♂; *D. longirostris* – Kranevo near Varna, Bulgaria, 4 ♂; and *D. taurica* – Kranevo near Varna, Bulgaria, 2 ♂. Chromosome preparations were examined under immersion lens using an Olympus BX 50 light microscope.

Specimens are lodged in the following institutions: private collection of Aleš Jelínek, Telč, Czech Republic (AJ); Australian Museum, Sydney, Australia (AMS); Museum of Natural History, London, England (BMNH); private collection of F. Gasparo, Trieste, Italy

(FG); Magyar Természettudományi Múzeum, Budapest, Hungary (HNHM); private collection of J. Dolanský, Pardubice, Czech Republic (JD); private collection of J. Svatoň, Martin, Slovakia (JS); private collection of L. Kubcová, Prague, Czech Republic (LK); private collection of M. Antuš, Prague, Czech Republic (MA); Muséum d'Histoire Naturelle, Genève, Switzerland (MHNG); Muséum National d'Histoire Naturelle, Paris, France (MNHN); private collection of M. Řezáč, Prague, Czech Republic (MR); Naturhistoriska Riksmuseet, Stockholm, Sweden (NHRS); Národní Muzeum, Prague, Czech Republic (NMPC); Naturhistorisches Museum, Vienna, Austria (NMW); private collection of P. Gajdoš, Nitra, Slovakia (PG); South Australian Museum, Adelaide (SAM); Naturmuseum Senckenberg, Frankfurt am Main, Germany (SMF); Univerza v Ljubljani, Slovenia (UL); Universidad de La Laguna, Spain (ULCI); private collection of V. Bryja, Brno, Czech Republic (VB); private collection of V. Hula, Brno, Czech Republic (VH); Vihorlatské múzeum, Humenné, Slovakia (VMH); private collection of V. Růžička, České Budějovice, Czech Republic (VR); Western Australian Museum, Perth, Australia (WAM); private collection of Z. Majkus, Ostrava, Czech Republic (ZM); Museum für Naturkunde, Humboldt Universität, Berlin, Germany (ZMHB).

TAXONOMY

Family Dysderidae C.L. Koch 1837

Genus *Dysdera* Latreille 1804

Type species.—*Dysdera erythrina* (Walckenaer, 1802).

Remarks.—Comprising more than 240 named species (Platnick 2007), *Dysdera* is currently the largest genus in the family Dysderidae. The vast majority of species appear to be endemic to the Mediterranean region, only nine representatives appear to have colonized central Europe.

KEY TO THE SPECIES OF CENTRAL EUROPEAN *DYSDERA*

1. Carapace smooth with rounded pits ..... 2 (*ninnii* group)
   Carapace wrinkled, without rounded pits 3
2. Cheliceral fang not flattened ..... *Dysdera ninnii*
   Cheliceral fang dorsoventrally flattened ..... *Dysdera dubrovninnii*
3. Tibiae III and IV with one or more dorsal spines ..... *Dysdera taurica* (*lata* group)
   Tibiae III and IV without dorsal spines 4
4. Femur IV with one or more dorsal spines ..... *Dysdera crocata* (*crocata* group)
   Femur IV without dorsal spines 5
5. Lateral anterior margins of carapace parallel (dorsal view), inner margin of basal cheliceral segment concave ..... 6 (*erythrina* group)
   Lateral anterior margins of carapace convergent (dorsal view), inner margin of basal cheliceral segment straight ..... 7 (*longirostris* group)
6. Mediodorsal margin of basal cheliceral segment concave, covered by short bristles; length of cheliceral fang/length of carapace more than 0.45; ventral side of tibia IV usually with three spines ..... *Dysdera lantosquensis*
   Mediodorsal margin of basal cheliceral segment convex, covered by normal hairs; length of cheliceral fang/length of carapace less than 0.45; ventral side of tibia IV usually with four spines ..... *Dysdera erythrina*
7. Ratio of the length of cheliceral fang and the length of carapace approximately 0.75 ..... *Dysdera longirostris*
   Ratio of the length of cheliceral fang and the length of carapace approximately 0.5 8

8. Male: bulbus with relatively parallel finger-like lateral sheet apophysis (Figs. 28, 29). Female: paired chitinized bands on the ventral wall of the copulatory bursa large and parallel (Fig. 30).....*Dysdera hungarica*
   Male: bulbus with relatively protruding finger-like lateral sheet apophysis (Figs. 32, 33). Female: paired chitinized bands on the ventral wall of the copulatory bursa narrow and anteriorly convergent (Fig. 34) ..... *Dysdera adriatica*

Dysdera crocata species-group

Remarks.—This species-group was first recognised by Deeleman-Reinhold (1988). Only one species of the group, *D. crocata* Koch 1838, has been found in central Europe. The other species, *D. hamulata* Kulczyński 1897 described from Slovakia (a junior synonym of *D. maurusia* Thorell 1873) probably does not occur in central Europe.

Dysdera crocata C. L. Koch 1838
Figs. 1–4, 17

Dysdera crocata C. L. Koch 1838: 81, figs. 392–394; Doblika 1853: 119; Becker 1896: 316, plate 17, fig. 21; Chyzer & Kulczyński 1897: 268, plate 10, fig. 41; Bösenberg & Strand 1906: 118, plate 16, fig. 445; Simon 1910: 320, fig. 9K; Simon 1914: 95, 111; Kaston 1948: 62, figs. 7–10; Locket & Millidge 1951: 84, figs. 41A, 42B–C, E; Wiehle 1953: 19, figs. 44–48; Charitonov 1956: 24, fig. 8; Grasshoff 1959: 217, fig. 10; Cooke 1966: 36, figs. 2, 4–6; Braendegaard 1966: 71, figs. 59–61; Loksa 1969: 78, figs. 54A–C; Tyschenko 1971: 71, fig. 101; Cooke 1972: 90, fig. 1; Dresco 1973: 247, fig. 4; Roberts 1985: 60, figs. 19b, d, f, h; Forster & Platnick 1985: 214, figs. 831, 841, 860, 864; Yoshikura 1987: 153, fig. 20.10A; Deeleman-Reinhold & Deeleman 1988: 157, figs. 23–27; Heimer & Nentwig 1991: 44, fig. 94; Wunderlich 1992: 292, figs. 28–31; Dunin 1992: 62, fig. 1; Roberts 1995: 94; Wunderlich 1995: 407, figs. 6–9; Dippenaar-Schoeman & Jocqué 1997: 155, figs. 73e, f; Mcheidze 1997: 74, figs. 61–62; Roberts 1998: 97; Song *et al.* 1999: 68, figs. 27F–I; Arnedo *et al.* 2000: 281, figs. 35, 37; Planet 1905: 61, plate 4, fig. 1 (identification doubtful).

Dysdera interrita Hentz 1842: 223; Emerton 1902: 22, figs. 70–72; Comstock 1940: 109, fig. 99.

Dysdera gracilis Nicolet 1849: 340, plate 2, fig. 5.

Dysdera rubicunda: Blackwall 1864a: 371, plate 28, fig. 371; Menge 1872: 297, plate 54, fig. 171.

Dysdera wollastoni Blackwall 1864b: 179 (identification doubtful).

Dysdera balearica Thorell 1873: 581 (identification doubtful).

Dysdera coerulescens Koch 1874: 203 (identification doubtful).

Dysdera magna Keyserling 1877: 230 [considered to be a synomym by Cooke (1967), however not accepted by Platnick (2007)]. **New synonymy.**

Dysdera maurusia: Dahl 1883: 41.

Dysdera australiensis Rainbow 1900: 485, plate 23, fig. 1 [considered to be a synomym by Cooke (1967), however not accepted by Platnick (2007)]. **New synonymy.**

Dysdera erythrina: Planet 1905: 61, plate 4, fig. 2.

Dysdera sternalis Roewer 1928b: 94.

Dysdera cretica Roewer 1928b: 95, plate 1, fig. 1.

Dysdera menozzii Caporiacco 1937: 58, fig. 1.

Dysdera palmensis Schmidt 1982: 395, fig. 3.

Dysdera inaequuscapillata Wunderlich 1992: 295, figs. 42–46.

Type material.—*Dysdera australiensis:* AUSTRALIA: *New South Wales:* female holotype, Sydney (33°52'S, 151°06'E) (AMS, examined).

Dysdera balearica: SPAIN: male holotype, Mallorca, Balearic Islands, F. Söderlund (repository unknown, not examined).

Dysdera coerulescens: GERMANY: syntypes: males and females, Lorsbacher near Nassau (50°23'N, 7°50'E), L. Koch, May 1871 (repository unknown, not examined); 1 specimen, same locality, O. Böttger, April 1873 (repository unknown, not examined).

Dysdera cretica: GREECE: juvenile holotype, Rethymnon (35°22'N, 24°28'E), Crete, C.F. Roewer, June 1926 (SMF, not examined).

Dysdera crocata: GREECE: syntypes: unknown number of adult specimens, Morea peninsula (37°30'N, 22°15'E), Peloponnesos, Schuh (perhaps BMNH, not examined).

Dysdera gracilis: CHILE: juvenile holotype, Santiago (33°28'S, 70°38'W) (repository unknown, not examined).

Dysdera inaequuscapillata: SPAIN: male holotype, Punta Hidalgo (28°31'N, 16°15'W), Tenerife, Canary Islands, 14 December 1986, R. Wis (ULCI, not examined). Paratypes: 1 male, 2 females, 1 juvenile, collected with holotype (ULCI, not examined); 1 female, same locality, 23 December 1986, C. Campos (ULCI, not examined); 1 male, Mercedes (28°31'N, 16°17'W), Tenerife, Canary Islands, Spain, May 1984, S. Morales (ULCI, not examined).

Dysdera interrita: U.S.A.: *Massachusetts*: syntypes: 1 male, 1 female, May, T.W. Harris (repository unknown, not examined).

Dysdera magna: BRAZIL: syntype: 1 female, Rio Grande do Sul (32°02'S, 52°06'W), W. Bösenberg (Uruguay is indicated in original description) (BMNH, examined).

Dysdera menozzii: LIBYA: syntypes: 3 males, 1 female, Tagiura (32°52'N, 13°21'E), C. Menozzio (repository unknown, not examined).

Dysdera palmensis: SPAIN: holotype female, Mazo (28°36'N, 17°45'W), La Palma, Canary Islands, G.E.W. Schidt (repository unknown, not examined).

Dysdera sternalis: GREECE: holotype female, Akrotiri, Crete, May 1926, C.F. Roewer (SMF, not examined).

Dysdera wollastoni: PORTUGAL: syntypes: 2 males, 3 females, 2 juveniles, Madeira (32°44'N, 16°59'W), T. V. Wollaston (repository unknown, not examined).

Other material examined.—ALGERIA: 1 ♂, M'sila area, Bou Saada [35°12'N, 4°10'E], (MNHN). AUSTRALIA: *Lord Howe Island* [31°33'S, 159°05'E]: 1 ♂, R. Baxter (AMS). *New South Wales:* 2 ♂, 4 ♀, Botany [33°56'S, 151°11'E], 1964–1965, 18 October 1978 (AMS); 1 ♂, 1 ♀, same location, 20 September 1966, R.E. Mascord (AMS); 1 ♂, 1 ♀, Sydney [33°52'S, 151°05'E], 22 April 1930, W.M. Pratt (AMS); 1 ♀, same location, 4 January 1955, A. Musgrave (AMS); 1 juvenile, North Sydney [33°44'S, 151°07'E], 4 June 1944, R. Virgona (AMS); 1 ♀, Mosman [33°49'S, 151°14'E], 29 November 1947, L.S. McKern (AMS); 1 ♀, Randwick [33°55'S, 151°14'E], 4 September 1951, T. Riding (AMS); 1 ♀, Moss Vale [34°33'S, 150°22'E], 2 October 1987, (AMS); 1 ♀, Northbridge [33°48'S, 151°13'E], 29 February 1972, J. Watson (AMS); 1 ♀, Mudgee [32°36'S, 149°34'E], 21

August 1989, J. McQuiggin (AMS); 1 ♀, Chippendale [33°53'S, 151°11'E], 11 February 1994, L. Bonsheck (AMS); 1 ♂, Forbes [33°23'S, 148°00'E], 16 September 1993, M.C. Daniel (AMS); 1 ♀, Pyrmont, Darling Island [33°51'S, 151°11'E], 6 December 1933 (AMS); 1 ♂, Pyrmont [33°52'S, 151°11'E], 1 February 2001, B. Dancs (AMS); 1 ♀, Surry Hills [33°53'S, 151°12'E], August 2001 (AMS); 1 ♂, East Lindfield [33°46'S, 151°11'E], 17 July 1956, D. MacMichael (AMS); 1 ♀, Bathurst [33°25'S, 149°34'E] (AMS); 1 juvenile, Clovelly [33°55'S, 151°15'E], 24 February 1944, R. Crapp (AMS); 1 ♂, 1 ♀, Enfield [33°53'S, 151°06'E], May 1949, L. Jarrett (AMS); 1 ♀, same location (AMS); 1 ♀, Canterbury [33°54'S, 151°07'E] (AMS); 1 ♀, Carlton [33°58'S, 151°08'E], July 1928, J. McClure (AMS); 1 ♀, Waverley [33°53'S, 151°15'E], B.W. Stevens (AMS); 1 ♂, Paddington [33°53'S, 151°13'E], 8 June 1971, P. Hutchings (AMS); 1 ♀, Kirribilli [33°50'S, 151°12'E], 1 August 1974 (AMS); 2 ♀, Kyeemagh [33°57'S, 151°09'E], October 1964, W.R. Macpherson (AMS); 1 ♂, 1 ♀, Rose Bay [33°52'S, 151°16'E], August 1963, A.L. Ironside (AMS); 1 ♂, Lakemba [33°55'S, 151°04'E], E.A. Brack (AMS). *Norfolk Island* [29°01'S, 168°02'E]: 1 ♀, 20 April 1993, H. Sampson (AMS); 1 ♂, 1 ♀ (AMS); 1 ♀, December 1915–January 1916, A.M. Lea (SAM). *Queensland:* 1 ♂, 1 ♀, Molangool W. [24°45'S, 151°32'E], H.H.B. Bradley (AMS, asigned as types of *Dysdera australiensis*). *South Australia:* 1 ♂, 1 ♀, Adelaide, Marino [35°02'S, 138°30'E], 10 August 1970, R.V. Southcott (SAM); 1 ♂, Adelaide [34°55'S, 138°35'E], 18 September 1911, G. Hilbig (SAM); 1 ♀, same location, 31 March 1976, R.V. Southcott (SAM); 1 ♀, same location, 26 August 1980, Cooter (SAM); 3 ♂, 2 ♀, 3 juveniles, Adelaide, Medindee [34°55'S, 138°35'E], 24 April 1989, Huilde (SAM); 1 ♀, Adelaide, Trinity Gardens [34°55'S, 138°35'E], 28 February 1987, D. Hirst (SAM); 1 ♀, Adelaide, Payneham [34°53'S, 138°37'E], 14 August 1967, R. Briggs (SAM); 1 juvenile, Adelaide, Windsor Gardens [34°55'S, 138°35'E], 14 September 1991, D. Hirst (SAM); 1 ♀, Adelaide, Highgate [34°55'S, 138°35'E], October 1958, H.R. Lindsay (SAM). *Tasmania:* 3 ♂, 4 ♀, 3 juveniles, New Town [42°51'S, 147°17'E], 25 March 1939, March 1953, 16 March 1961, 27 October 1963, March 1965, V.V. Hickman AMS); 1 ♂, Risdon Rise [42°48'S, 147°21'E], 27 May 1929, V.V. Hickman (AMS); 2 ♀, Launceston [41°26'S, 147°08'E], 3 September 1929, V.V. Hickman (AMS); 2 ♂, Ulverstone [41°09'S, 146°10'E], 11 March 1992, A.F. Longbottom (WAM); 1 ♀, Davenport, the Forth river [41°10'S, 146°20'E], January 2003, M. Strnadová (MR). *Victoria:* 1 ♀, 3 juveniles, Balwyn [37°48'S, 145°05'E], 6 January 1982, 1 January 1983, M.S. Harvey (WAM); 1 ♂, 1 juvenile, Geelong [38°08'S, 144°20'E], 23 May 1978, R. Easton (WAM); 1 ♀, Melbourne, Ashburton [37°52'S, 145°04'E], 5 January 1988, P.K. Lillywhite (WAM); 2 juveniles, Wonthaggi [38°36'S, 145°35'E], 15 December 2002, M.S. Harvey (WAM); 1 ♀, Donvale [37°47'S, 145°11'E], 16 January 1983, M.B. Darby (WAM); 1 ♂, 1 juvenile, Surrey Hills [37°49'S, 145°05'E], 9 January 1982, M.S. Harvey (WAM); 1 ♀, Clayton [37°56'S, 145°08'E], 23 September 1982, B.E. Roberts (WAM). AUSTRIA: 1 ♀, Tyrol [47°15'N, 11°20'E] (BMNH). BELGIUM: 1 ♂, Nieuwpoort [51°07'N, 2°45'E], 30 April 2004, P. Saska (MR). CROATIA: 1 ♀, Senj (=Zeng) [44°59'N, 14°54'E], C. Chyzer (HNHM). CZECH REPUBLIC: 1 ♀, Prague [50°04'N, 14°26'E], 13 May 2001, Václavková (NMPC); 1 ♀, Mikulov [48°47'N, 16°37'E], 6 October 2002, J. Chytil (MR); 3 ♂, Brno, reserve Kavky [49°11'N, 16°36'E], 4 July 2005, 17 August 2005, S. Vinkler (VB). FRANCE: 1 ♂, Corsica [42°09'N, 9°04'E] (MNHN); 1 ♂, Banyuls [42°29'N, 3°07'E], 25 September 1962, L. Berland (MNHN); 1 ♂, Cerbère, Provence [42°26'N, 3°09'E] (BMNH). GREECE: 1 ♂, Leptokaria [40°03'N, 22°33'E], 4–13 June 1996, J. Dolanský (MR); 1 ♀, Chios island [38°23'N, 26°02'E], C.L. Koch (BMNH). IRELAND: 2 ♀, Dublin [53°20'N, 6°15'W], A.K.J. de Montmorency (BMNH). ITALY: 1 ♂, Naples [40°51'N, 14°16'E], Olf (ZMHB). PORTUGAL: 1 ♂, Algarve, Santa Bárbara de Nexe [37°06'N, 7°57'W], April 1963 (MNHN); 1 ♀, Mitra near Evora [38°33'N, 7°52'W], 1 November 2001, S. Pekár (MR). ROMANIA: 1 ♂, 1 ♀, Orşova [44°42'N, 22°23'E], Böckh

(HNHM); 1 ♂, Costineşti [43°57'N, 28°37'E], 7–8 August, Dobnlu (NMPC). ?RUSSIA: 1 ♂, Caucasus (MNHN, *sub D. hungarica*). SLOVENIA: 1 ♀, Pridvor, Sv. Anton, Dekani, Koper [45°31'N, 13°50'E], August 1995, S. Toth (UL). SOUTH AFRICA: 1 ♂, 1 ♀, Bloemfontein [29°06'S, 26°13'E], 5 February 2005, M. Řezáč (MR). SPAIN: 1 ♀, unspecified location (ZMHB). *Minorca:* many ♂, ♀, unspecified location, D. Braun (BMNH); 2 ♂, 2 ♀, Mahon [39°53'N, 4°15'E], 28 December 1958, H. Coiffait (MNHN). *Tenerife:* 1 ♂, 1 ♀, Los Cristianos [28°03'N, 16°43'W], July 1972, I. Zunino (MNHN); 1 ♂, Anaga mountains, Taborno [28°32'N, 16°14'W], 2 March 2006, M. Řezáč (MR); 1 ♂, Orotava valley, Aquamansa, La Caldera [28°20'N, 16°29'W], 7 March 2006, M. Řezáč (MR); 1 ♂, La Esperanza, Las rosas, Las Raices [28°26'N, 16°21'W], 8 March 2006, M. Řezáč (MR); 1 ♂, Labrada cave [28°27'N, 16°25'W], 17 March 2006, M. Řezáč (MR); 1 ♂, Icod de los Vinos, San Marcos [28°22'N, 16°42'W], 19 March 2006, M. Řezáč (MR). TUNISIA: 2 ♂, 2 ♀, unspecified location (NHRS); 2 ♀, Hammamet [36°24'N, 10°36'E], 7–20 May 1997, J. Dolanský (MR); 1 ♀, 1 juvenile, Zughonan [36°24'N, 10°08'E], 12 May 1997, J. Dolanský (MR); 1 ♂, 1 ♀, Kairanan [35°40'N, 10°05'E], April 1914 (MNHN). UKRAINE: *Crimea:* 2 ♂, 1 ♀, Cherson Taurica, Sevastopol [44°36'N, 33°31'E] (NHRS); 1 ♂, Yalta, Massandra Park [44°30'N, 34°11'E], 20 May–19 June 2001, N. Kovblyuk (MR); 1 ♂, Karadag, Beregovoy mountains [44°54'N, 33°36'E], 26 April 2003, N. Kovblyuk (MR). UNITED KINGDOM: 1 ♀, Box Hill, Surrey [51°23'N, 2°14'W], August 1989, M.R. Gray (AMS); 1 ♀, Worcestershire [52°17'N, 2°16'W] (AMS), 1 ♀, Brighton, Sussex [50°49'N, 0°08'W], 5 November 1933, A.F. Brazenor (BMNH); 1 ♀, Lewes, Sussex [50°52'N, 0°00'W], 3 May 1925, J.C. Campbell-Layor (BMNH); 1 ♀, London, Chiswick [51°29'N, 0°14'W], N.H. Benett (BMNH); 1 ♀, Weybridge [51°22'N, 0°27'W], D.Y. Burry (BMNH); 1 ♀, London, Acton [51°30'N, 0°16'W], 8 February 1944, W.E. Woodward (BMNH). U.S.A.: 1 ♀, Michigan, Ann Arbor [42°16'N, 83°43'W], April 1992, A. Richards (WAM). UZBEKISTAN: 1 ♀, Buchara [39°46'N, 64°25'E] (ZMHB).

Diagnosis.—This species is very similar to some species of the *crocata* group, which are restricted to the southern part of Mediterranean region, mainly northern Africa, and require further taxonomic study. Among central European species it belongs to the largest ones; it is characteristic by femur IV with one or more dorsal spines and by remarkably parallel lateral margins of cephalic part of carapace; the males are characteristic by inflexed distal division of the bulbus; the females are characteristic by proximally situated, wide, equally incurved spermatheca and by endogynal ventral arch with remarkable shoulders.

Description.—*Carapace* (Fig. 1): carapace 4.2–4.9 mm long, slightly wrinkled, ferruginous to orange, dorsoventrally flat. Lateral margins of cephalic part parallel. *Chelicerae* (Fig. 1): basal segment elongated (basal segment length/carapace length = 0.53), dorsally convex, slightly wrinkled, covered with piligerous granulations. Groove elongated (length of groove/basal segment length = 0.61), equipped with three small teeth in basal half. Basal cheliceral tooth > median cheliceral tooth > distal cheliceral tooth. Median cheliceral tooth close to basal cheliceral tooth. Fang elongated (fang length/carapace length = 0.51), thorn-shaped. *Legs:* femora I–III spineless, femora IV usually with 1–3 dorsal spines. Tibiae III–IV dorsally spineless, ventrally with a pair of apical spines and usually with 1–2 additional spines. *Bulbus* (Figs. 2, 3): distal division narrower than tegulum, incurved, with pronounced posterior apophysis on flexion. Posterior apophysis not fused to tegulum. Arch-like ridge on apical part of bulbus without any apophysis. *Vulva* (Fig. 4): spermatheca proximally situated, wide, equally incurved. Dorsal arch rectangular. Neck connecting spermatheca with ventral wall of copulatory bursa with prominent frill in retroventral view. For detailed description see Deeleman-Reinhold & Deeleman (1988).

Remarks.—This species has been described several times under different names from various parts of the world. Cooke (1967) suggested that *Dysdera magna* Keyserling 1877,

described from Brazil and reported also from Uruguay (Díaz & Sáez 1966) and *D. australiensis* Rainbow 1900 from Australia, are both junior synonyms of *D. crocata*. However, this synonymy was not definitive and not accepted [see Platnick (2007)]. We checked the genital morphology of the type specimens of these two species and found them to be morphologically identical with *D. crocata*. Furthermore, after examination of the relevant collections from Australian museums, we were unable to locate any species other than *D. crocata*. Díaz & Sáez (1966) reported a different chromosome number (2n ♂ = 9) from a population from Uruguay identified as *D. magna*. This population might represent a cryptic species introduced to South America together with *D. crocata*. The synonymies of *D. balearica* Thorell 1873 and *D. coerulescens* Koch 1874 with *D. crocata* are based on the conjectures published by Simon (1914). Even though they have never been accurately argued they are currently accepted (Platnick 2007). Both species were described after comparison with true *D. crocata* (Thorell 1873; Koch 1874). Unfortunately the deposition of the type material of these two species, necessary for conclusive confirmation or rejection of synonymy, is unknown. A female identified as *D. crocata* illustrated in Planet (1905) resembles *D. longirostris* due to the remarkably elongate chelicerae.

Karyotype.—Analysis of male meiotic division indicated the sex chromosome system X0 in all specimens. Remarkable variation was found in the number of autosomal pairs. Males from Bulgaria and South Africa exhibited four, those from Turkey five, and those from the Canary Islands and Portugal six autosomal pairs (Fig. 17).

Habitat.—In central Europe *D. crocata* occurs only in relatively dry, synanthropic, or semisynanthropic and adjacent habitats.

Distribution.—This species has been found on all continents except for Antarctica. In central Europe, its distribution is usually limited to urban areas. This species is new for the Czech Republic. Maps of occurence in other European countries can be found in Deltshev *et al.* (2003: map 15) (Serbia), Ribera *et al.* (1989: fig. 1) (Spain), Romano & Ferrández (1983: map 4) (Spain, province Navarra), Gajdoš *et al.* (1999: map 150) (Slovakia, partly based on misidentifications).

Dysdera maurusia Thorell 1873 status revised

Figs. 5–8

Dysdera maurusia Thorell 1873: 467.
Dysdera crocota var. *hamulata* Kulczyński, in Chyzer & Kulczyński 1897: 268, plate 10, fig. 41. **New synonymy.**
Dysdera hamulata: Simon 1914: 112.
Dysdera crocata: Drensky 1938: 92, fig. 8a.
? *Dysdera hamulata*: Deeleman-Reinhold & Deeleman 1988: 160, fig. 23a, 24a. (misidentification).

Type specimens.—*Dysdera maurusia*: ALGERIA: syntypes: 1 male, 2 females, Alger, El Harrach (=Maison Carrée) (36°42'N, 3°07'E), H.A. Eurén (NHRS, examined).

Dysdera hamulata: SLOVAKIA: male holotype, Vranov nad Topľou (48°53'N, 21°41'E) (locality possibly in error, see below) (repository unknown, not examined).

Other material examined.—ALGERIA: 3 ♂, M'sila area, Bou Saada [35°12'N, 4°10'E] (MNHN); 1 ♂, unspecified location (MNHN); 1 ♂, Alger area, Kouba, Ravin de la Femme Sauvage [36°43'N, 3°04'E], December 1892, P. Lesne (MNHN); 1 ♂, Tlemcen [34°53'N, 1°18'W] (MNHN). U.S.A.: *New York*: 1 ♂, Poughkeepsie [41°42'N, 73°54'W], N. Banks (MNHN) (probably mislabeled, see below).

Diagnosis.—In contrast to the otherwise similar *D. crocata*, this species is smaller and the lateral margins of the cephalic part of carapace are not distinctly parallel; in males the arch-like ridge on the apical part of bulbus is elongated to a hook-shaped apophysis; in females the neck connecting the spermatheca with the ventral wall of the copulatory bursa is without a frill.

Description.—*Carapace* (Fig. 5): carapace 2.3–4.0 mm long, slightly wrinkled, ferruginous to orange, dorsoventrally flat. Lateral margins of cephalic part are slightly convergent. *Chelicerae* (Fig. 5): basal segment elongated (basal segment length/carapace length = 0.55), dorsally convex, slightly wrinkled, covered with piligerous granulations. Groove elongated (length of groove/basal segment length = 0.61), equipped with three small teeth in basal half. Basal cheliceral tooth > median cheliceral tooth > distal cheliceral tooth. Median cheliceral tooth close to basal cheliceral tooth. Fangs elongated (fang length/carapace length = 0.50), thorn-shaped. *Legs:* femora I–II spineless, femora III sometimes with 1, femora IV usually with 2–5 dorsal spines. Tibiae III–IV dorsally spineless, ventrally with a pair of apical spines and usually with 1–2 additional spines. *Bulbus* (Figs. 6, 7): distal division narrower than tegulum, incurved, with pronounced posterior apophysis on its flexion. Posterior apophysis not fused to tegulum. Arch-like ridge in apical part of bulbus elongated to hook-shaped apophysis. *Vulva* (Fig. 8): spermatheca proximally situated, wide, equally incurved. Dorsal arch rectangular. Neck connecting spermatheca with ventral wall of copulatory bursa basally robust, without frill. For detailed description see Thorell (1873).

Remarks.—The original description of *D. maurusia* is insufficient, as it lacks any drawings (Thorell 1873). Simon (1914) synonymized it with *D. crocata* without examining the type material, and this synonymy is still accepted [see Platnick (2006)]. Thorell's syntypes comprise a single male and two females. Both females belong to the same species. Since the species diversity of *Dysdera crocata* group in northern Algeria is enormous, the pairing of these females with the male is not definite. The male corresponds with the description of *D. hamulata* Kulczyński 1897. Moreover the apical portion of the bulbus is identical in every detail with the detailed drawing of *D. hamulata* in Chyzer & Kulczyński (1897). Therefore, we propose to remove *D. maurusia* from the synonymy with *D. crocata* and consider *D. hamulata* a junior synonym of *D. maurusia*.

The record of *D. hamulata* from Turkey (Deeleman-Reinhold & Deeleman 1988) is erroneous as the bulbus depicted suggests it belongs to *D. flagellata* Grasshoff 1959.

A drawing of *D. crocata* in Drensky (1938) is remarkably similar to *D. maurusia*; however, neither *D. maurusia* nor *D. crocata* was found in Drensky's collection (Ch. Deltshev, pers. comm.). His drawing is probably a compilation of fig. 41a (general shape of *D. crocata* bulbus) and 41d (detail of apical part of *D. crocata* var. *hamulata* bulbus) from Chyzer & Kulczyński (1897).

Distribution.—This species is known from northern Algeria. The record from Slovakia (Gajdoš *et al.* 1999) is based on the reference in Chyzer & Kulczyński (1897); we consider this record referring to a single male doubtful. This species has never been found again despite an intensive search all over Slovakia (*cf.* Gajdoš *et al.* 1999). Furthermore, we failed to find this species at the only locality mentioned in Chyzer & Kulczyński (1897), Vranov nad Topľou. It appears that the type material of *D. hamulata* was mislabeled. The drawing of this species in Drensky (1938) does not seem to be based on material from Bulgaria (see Remarks). The material labeled with an American locality (see Material examined) is probably also from north Africa because it contains not only *D. maurusia* but also another species belonging to the *crocata* group, the species-group which is exclusively restricted to northern Africa and closely adjacent regions.

Dysdera ninnii species-group

Remarks.—This species-group was first recognized by Deeleman-Reinhold (1988). Two closely related representatives of this group have been found to occur in central Europe, *D. ninnii* Canestrini 1868 and *D. dubrovninnii* Deeleman-Reinhold 1988.

Dysdera ninnii Canestrini 1868

Figs. 9–12, 18, 24, 26

Aranea hombergi Scopoli 1763: 403 (nomen dubium).

Dysdera ninnii Canestrini 1868: 190; Canestrini & Pavesi 1868: 845; Canestrini & Pavesi 1870: 25, plate 3, fig. 2; Herman 1879: 204–205; Chyzer & Kulczyński 1897: 268, plate 10, fig. 44; Roewer 1928a: 49, plate 7, fig. 561; Drensky 1938: 93, fig. 8d (possibly compilation of figures from Chyzer & Kulczyński (1897) and Simon (1914)); Loksa 1969: 74, figs. 49B, D, 50, 51A-B; Deeleman-Reinhold & Deeleman 1988: 180, figs. 14, 16, 111–118; Heimer & Nentwig 1991: 44, fig. 92; Thaler & Knoflach 2002: 418, figs. 6–7; Pesarini 2001: figs. 7, 9, 11; Schult 1983: 71, fig. 6 (misidentification); Simon 1914: 95, 112, fig. 159 (doubtful).

Dysdera pavesii Thorell 1873: 564 (doubtful).

Type specimens.—*Dysdera hombergi:* syntypes: SLOVENIA: unknown number of specimens, Carniola (repository unknown, not examined).

Dysdera ninnii: syntypes: ITALY: unknown number of males and females, regions Trentino, Veneto and Modenese (repository unknown, not examined).

Dysdera pavesii: syntypes: ITALY: males and females, G. Canestrini (repository unknown, not examined).

Material examined.—AUSTRIA: 1 ♀, unspecified location (NHRS). BOSNIA & HERCEGOVINA: 1 ♀, Visovica [43°59'N, 18°27'E], 22 June 1893, L. Gíró (HNHM). CROATIA: 1 ♂, 21 ♀, Velebit, Paklenica [44°19'N, 15°28'E], 18–21 June 2005, M. Řezáč (MR); 3 ♀, Šibenik, Solaris [43°44'N, 15°53'E], 16–17 June 2005, M. Řezáč (MR); 4 ♀, Plitvička jezera, Korana [44°54'N, 15°36'E], 22 June 2005, M. Řezáč (MR). CZECH REPUBLIC: *Tišnovsko area:* 1 ♀, Horní Čepí near Nedvědice [49°28'N, 16°20'E], 10 May, F. Miller (NMPC); 2 ♀, Doubravník [49°26'N, 16°22'E], 10 June 1983, F. Miller (NMPC). *Pálava biospheric reserve:* 1 ♀, Pouzdřany, reserve Pouzdřanská step-Kolby [48°56'N, 16°38'E], 1983, F. Miller (NMPC); 1 ♀, same location, 24 April–22 May 2005, S. Vinkler (VB). *Moravský kras area:* 1 ♂, 2 ♀, 1 juvenile, Blansko, Těchov, reserve Vývěry Punkvy, Skalní mlýn [49°23'N, 16°47'E], 21 May 1993, 31 May 1997–27 May 1998, V. Růžička (VR); 1 ♂, 2 ♀, Brno, reserve Kavky [49°11'N, 16°36'E], 18 May 2005, 18 October 2005, S. Vinkler (VB). *Jihlavské vrchy mountains:* 1 ♂, Brtnice, Přímělkov [49°21'N, 15°43'E], 8 June–11 July 1995, A. Jelínek (AJ); 1 ♀, Brtnice, Rokštejn ruin [49°19'N, 15°43'E], 26 May 1994, E. Svatoňová (JS). *Znojemská pahorkatina (hilly country):* 1 ♂, Mohelno, reserve Hadcová step [49°06'N, 16°10'E], 1 June 1983, F. Miller (NMPC); 3 ♂, 4 ♀, Vranov nad Dyjí, Braitava [48°53'N, 15°48'E], 9–24 May 1995, 15 May–5 June 1996, 28 August–18 September 1996, 18 September–9 October 1996, 9–30 October 1996, A. Reiter (VB); 1 ♀, 1 juvenile, Vranov nad Dyjí [48°53'N, 15°48'E] (NMPC). HUNGARY: 4 ♀, 1 juvenile, Misina hill above Pécs [46°05'N, 18°13'E], 30 September 2006, M. Řezáč (MR). ITALY: 1 ♂, 1 ♀, Gorizia, Monfalcone [45°48'N, 13°31'E], 14 April 1991, F. Gasparo (MR); 1 ♂, 1 ♀, Trieste, Muggia, S. Floriano [45°36'N, 13°46'E], 19 April–15 May 2000, G. Colombetta (MR). ROMANIA: 1 ♀, Banat area, Carasova, Anina, Sopotu Nou [44°48'N, 21°51'E], 5–10 August 1998, V. Lemberk (MR). SLOVAKIA: 1 ♀, unspecified location, E. Žitňanská (JS). SLOVENIA: 1 ♀, Bepše pri Logatcu [45°55'N, 14°13'E], September 1934 (NMPC); 1 ♀,

Kamniška Bistrica [46°20'N, 14°35'E], 8–15 August 1921, J. Hadži (NMPC); 1 ♀, Maaswald, Soča, Kranj, Unt [46°14'N, 14°16'E] (ZMHB). YUGOSLAVIA: 1 ♀, Belgrade [44°47'N, 20°28'E] (NMPC).

Diagnosis.—*Dysdera ninnii* is very similar to number of species, which are restricted to the Balkan and Apennine Peninsula. For diagnosis see Deeleman-Reinhold & Deeleman (1988). From other central European species, except for *D. dubrovninnii*, it differs by smooth carapace with rounded pits.

Description.—*Carapace* (Fig. 9): carapace 3.2–3.9 mm long, smooth, with rounded pits, darkly ferruginous, gibbous. Margins indented. Lateral margins of cephalic region convergent. *Chelicerae* (Fig. 9, 24): basal segment length/carapace length = 0.37. Dorsal sides of basal segments straight, smooth, covered with piligerous pits. Groove slightly elongated (length of groove/basal segment length = 0.52), equipped with three small close teeth in basal third. Basal cheliceral tooth > median cheliceral tooth > distal cheliceral tooth. Fangs elongated (fang length/carapace length = 0.35), thorn-shaped. *Legs:* femora spineless. Tibiae III–IV dorsally spineless, ventrally usually with only a single apical spine. *Bulbus* (Figs. 10, 11): distal division with simply incurved lateral sheet projection and with flagellum. Apex with short subapical tooth. *Vulva* (Fig. 12): spermatheca almost as wide as dorsal arch. Dorsal arch wider than long. For detailed description see Deeleman-Reinhold & Deeleman (1988).

Remarks.—The oldest name related probably to this species is *D. hombergi*. Scopoli (1763) described this species as a spider with a shiny punctate carapace and shiny yellow legs. This is in contradiction with the appearance of any species of the genus *Harpactea* Bristowe 1939 for which this name is erroneously used [see also Thaler & Knoflach (2002)]. From all dysderid species occuring in the type locality "Carniola" (an ancient province in Slovenia), the type description fits two species, *D. ninnii* and *D. dubrovninnii*. The latter species is very rare in this region, and it is likely that Scopoli described *D. ninnii*. However, his type material is probably lost, thus a definitive resolution of its identity is not possible. Therefore, we hereby designate *Aranea hombergi* as a nomen dubium.

We consider the synonymy of *D. pavesii* with *D. ninnii* (Platnick 2007) to be doubtful. In Italy, at the type locality of *D. pavesii*, several closely related species of the *ninnii* group occur. Thorell (1873) described this species based on material provided by G. Canestrini five years after Canestrini had described *D. ninnii*. Thus, Thorell was presumably aware of the existence of *D. ninnii*.

A drawing of the bulbus in Schult (1983) and perhaps also in Simon (1914), both attributed to *D. ninnii*, probably represents an undescribed species from Corsica.

Karyotype.—The male karyotype is composed of seven pairs of autosomes and a single X chromosome (Fig. 18). The sex chromosome system is thus X0.

Habitat.—In the Czech Republic and Hungary this species occurs in xerothermic forests on slopes (e.g., plant communities *Carpinion* and *Quercion pubescenti-petraeae*), in bushes (e.g., *Berberidion*) and in the shaded parts of rocky steppes (e.g., *Festucion valesiacae*). It is also common in semi-ruderal habitats, especially in the surroundings of ruins (particularly castle ruins) overgrown by bushes. In Croatia and Slovenia it occurs in lowland *Carpinus* and planted *Pinus* forests as well as in mountain *Picea*, *Fagus sylvatica*, and *Pinus nigra* forests.

Phenology.—Mating takes place from April to June, eggs are laid in June and July. Spiderlings disperse from maternal silk retreats from August to September. The spiders mature in autumn of the following year, overwinter as adults, and mate the next spring. Thus this species has a biennial life-cycle.

Distribution.—*Dysdera ninnii* is also known from the northwestern part of the Balkan Peninsula and northeastern Italy. In Slovenia and Croatia it occurs sympatrically with *D. dubrovninnii* (syntopical localities: Bač, Bepše pri Logatcu, Postojna, Planina, Paklenica,

Plitvička jezera, Šibenik). The record from southern France (Simon 1914) remains to be confirmed. The northern border of its distribution runs through the Czech Republic and Slovakia, where it occurs only in the Pannonian region (Fig. 26).

The distribution maps were published by Deeleman-Reinhold & Deeleman (1988: 260, map 7; for the whole area), Drensky (1938: 14, map 2; for the entire area, partly based on misidentifications), Deltshev *et al.* (2003: 251, map 19, for Serbia), Gajdoš *et al.* (1999: map 200, for Slovakia, together with undistinguished *D. dubrovninnii*), and Buchar & Růžička (2002: 205, for the Czech Republic). The map of *D. punctata* in Gajdoš *et al.* (1999: map 210) probably also refers to this species.

Dysdera dubrovninnii Deeleman-Reinhold 1988

Figs. 13–16, 19, 25, 26

Dysdera dubrovninnii Deeleman-Reinhold in Deeleman-Reinhold & Deeleman 1988: 184, figs. 125–128.

Type specimens.—*Dysdera dubrovninnii:* CROATIA: holotype male, Babin kuk, Dubrovnik (42°39'N, 18°05'E), 10 April 1976, J. & F. Murphy (BMNH, not examined). Paratypes: 1 female, collected with holotype (BMNH, not examined); 1 male, 2 females, Dubrovnik, 19 & 22 April 1976, J. & F. Murphy (coll. J. & F. Murphy, Hampton, UK, not examined); 3 males, 1 female, Dalmatia, Croatia (MHNG, not examined).

Material examined.—CROATIA: 1 ♂, Korčula town [42°56'N, 16°54'E], 26 August 1997, F. Gasparo (FG); 1 ♀, Lanaka [45°53'N, 17°35'E], July 1935 (NMPC); 1 ♂, 12 ♀, Velebit, national park Paklenica, surroundings of Vaganski vrh and Ivine Vodice [44°19'N, 15°28'E], 20 June 2005, M. Řezáč (MR); 1 ♀, Šibenik, Solaris [43°42'N, 15°51'E], 16–17 June 2005, M. Řezáč (MR); 1 ♀, Plitvička jezera, Korana [44°54'N, 15°35'E], 22 June 2005, M. Řezáč (MR). ROMANIA: 1 ♂, 2 ♀, Hideselu de Jos, Bihor mountains [46°57'N, 22°03'E], May–September 2004, I. Sas (MR). SLOVAKIA: *Beskydské predhorie mountains:* 1 ♂, 4 ♀, Humenné, reserve Podskalka [48°54'N, 21°55'E], 30 July–25 August 1987, 7 July 1994, 21 May–22 June 1994, 5 September 2002, V. Thomka (VMH); 1 ♀, same location, 14 August 2003, M. Řezáč (MR); 2 ♂, Kamenica nad Cirochou [48°55'N, 21°59'E], 13 August–2 November 1998, 11 May–16 July 1999, V. Thomka (VMH); 5 ♂, 1 juvenile, Kamenica nad Cirochou, Hôrka [48°55'N, 21°59'E], 13 August 1998, 20 October 1999–2 May 2000, 2 May–6 July 2000, V. Thomka (VMH); 8 ♂, 1 ♀, Kamenica nad Cirochou, Žbír [48°55'N, 21°59'E], 18 May–30 July 2001, 18 May–30 July 2001, 30 July–26 September 2001, 29 October 2001–3 May 2002, V. Thomka (VMH); 2 ♂, Dlhé nad Cirochou [48°57'N, 22°03'E], 10 September 1998–2 June 1999, 8 September–23 October 2000, V. Thomka (VMH); 1 ♂, 1 ♀, 2 juveniles, Ptíčie, reserve Humenský Sokol [48°53'N, 21°57'E], 20 May–3 August 1993, 30 June 1994, 3 October 1994, V. Thomka (VMH); 6 ♂, 3 ♀, 1 juvenile, Brekov castle [48°53'N, 21°49'E], 28 April–3 July 1998, 5 October 1998, 3 July–5 October 1998, 24 August 1999, 2 November 1999, 4 May–30 June 1999, 5 October 1998–4 May 1999, 2 November 1999–27 April 2000, V. Thomka (VMH); 1 ♀, 1 juvenile, Kamienka, Spálené mosty [48°54'N, 22°00'E], 1 October 1996–13 June 1997, V. Thomka (VMH); 21 ♂, 8 ♀, 9 juveniles, Lackovce, pod Velikou [48°56'N, 21°56'E], 4 May–2 July 2001, 2 July–31 August 2001, 23 May–9 July 2002, 12 April–23 May 2002, 5 November 2001–12 April 2002, 23 May–9 July 2002, 4 September–17 October 2002, 12 April–23 May 2002, 9 July–4 September 2002, V. Thomka (VMH). *Bukovské vrchy mountains:* 1 juvenile, Kalná Roztoka, reserve Havešová [48°58'N, 22°19'E], 27 May–30 July 1999, V. Thomka (VMH); 1 ♀, same location, 21 September 1998, J. Svatoň (JS); 1 ♂, 1 ♀, Nová Sedlica [49°02'N, 22°31'E], 15 June 1980, V. Thomka (VMH); 1 ♂, Kolbasov, reserve Bzana [49°00'N, 22°22'E], 17 May–

26 July 2000, V. Thomka (VMH); 1 ♂, 2 ♀, 1 juvenile, Ošadné, reserve Hlboké [49°09'N, 22°10'E], 3 August–15 October 1999, 1 June–3 August 1999, 26 May–3 August 2000, V. Thomka (VMH); 1 ♂, Ruské, reserve Pod Ruským [49°07'N, 22°20'E], 27 October 2000–21 May 2001, V. Thomka (VMH); 1 ♂, Zboj, reserve Riaba skala [49°01'N, 22°29'E], 12 October 1994–1 June 1995, V. Thomka (VMH). *Košická kotlina basin:* 1 ♂, 1 juvenile, Prešov, castle [48°59'N, 21°14'E], 8 July 1934, F. Miller (NMPC). *Laborecká vrchovina mountains:* 1 ♂, Stakčín, reserve Hrúnok [49°00'N, 22°13'E], 11 May–26 July 2000, V. Thomka (VMH); 4 ♂, 1 ♀, 1 juvenile, Stakčín, dolina Chotínka valley [49°00'N, 22°13'E], 15 June 1995, 21 October 1999–11 May 2000, 25 July–9 October 2000, 11 May–25 July 2000, V. Thomka (VMH); 1 ♂, Snina [48°58'N, 22°09'E], 9 May–11 August 2000, V. Thomka (VMH); 2 ♂, 1 ♀, 1 juvenile, Roškovce, reserve Jarčiská [49°14'N, 21°50'E], 4 September 2001–15 March 2002, 15 March–27 May 2002, 27 May–16 July 2002, V. Thomka (VMH); 5 ♂, 3 ♀, 1 juvenile, Starina, reserve Starina [49°03'N, 22°15'E], 30 July–3 September 1999, 25 July–9 October 2000, 19 October 1999–11 May 2000, 11 May–25 July 2000, V. Thomka (VMH). *Ondavská vrchovina mountains:* 1 ♂, Humenné, Holá hora hill [48°56'N, 21°53'E], 14 November 1996, V. Thomka (VMH); 2 juveniles, Myslina [48°56'N, 21°50'E], 10 July 1995, V. Thomka (VMH); 20 ♂, 4 ♀, 1 juvenile, Humenné [48°55'N, 21°54'E], 14 October 1996, 4 October 1999, 12 June–17 August 2000, 28 April–12 June 2000, 17 August–20 October 2000, 30 April–25 June 2001, 25 June–9 August 2001, V. Thomka (VMH); 1 ♂, same location, 18–19 July 2004, F. Šťáhlavský (MR). *Spišsko-šarišské medzihorie mountains:* 2 juveniles, Kapušany, reserve Kapušianský hradný vrch [49°02'N, 21°19'E], 6 July 1934, F. Miller (NMPC); 5 ♂, 1 ♀, 1 juvenile, same location, 23 April–20 June 1996, 20 June–30 August 1996, 1 July 1997, 30 August 1996–20 May 1997, V. Thomka (VMH). *Vihorlatské vrchy mountains:* 1 ♀, Brekov, Krivošťany [48°53'N, 21°50'E], 11 September 2002, V. Thomka (VMH); 1 juvenile, Ptičie, reserve Humenské [48°53'N, 21°57'E], 12 August–21 October 2002, V. Thomka (VMH); 2 ♀, Remetské Hámre [48°51'N, 22°11'E], 27 October, F. Miller (NMPC); 7 ♂, 6 ♀, 2 juveniles, Chľmec, reserve Chľmecká skalka [48°53'N, 21°56'E], 21 September–13 November 2001, 17 June–7 August 2002, 16 April–17 June 2002, 7 August–29 October 2002, V. Thomka (VMH); 1 ♀, 4 juveniles, Jasenov pri Humennom, castle [48°54'N, 21°53'E], 26 August 1994, 28 June 1999, V. Thomka (VMH); 2 ♂, 1 juvenile, Jasenov-Hôrka [48°54'N, 21°53'E], 30 July–27 August 1987, 2–29 June 1987, 13 May–15 June 1994, V. Thomka (VMH); 1 ♀, Vinné, Vinnianské jazero lake [48°48'N, 21°58'E], 16 August 2003, M. Řezáč (MR); 7 ♀, Vinné town [48°48'N, 21°58'E], 13 July 1967, J. Vachold (PG); 7 ♂, 4 ♀, 2 juveniles, Vinné, reserve Vinnianský hradný vrch [48°48'N, 21°58'E], 3 June–31 July 1992, 9 March–3 June 1992, 13 July–19 August 1993, 19 August 1993, 22 April 1994, 22 April–24 June 1994, 8 August–26 September 1994, V. Thomka (VMH; 1 ♀, same location, 17 August 2003, M. Řezáč (MR). *Východoslovenská pahorkatina (hilly country):* 3 ♂, 2 ♀, Klokočov pri Zemplínskej Šírave [48°49'N, 22°01'E], 12 September, F. Miller (NMPC). SLOVENIA: 1 ♂, Postojna [45°46'N, 14°12'E], 25 October 1994, S. Polak (UL); 1 ♀, Bač [45°37'N, 14°16'E], 8–24 May 1994, S. Polak (UL); 1 ♀, 1 juvenile, Planina, Unška koliševka chasm [45°50'N, 14°15'E], 2000, M. Řezáč (MR); 1 ♀, Bepše pri Logatcu [45°55'N, 14°13'E], September 1934 (NMPC).

Diagnosis.—This is the only central European species of *Dysdera* that possesses dorsoventrally flattened cheliceral fangs. It is further distinguished from *D. ninnii* by the smaller body, lighter coloration, less gibbous carapace with no indented margins, and by the shape of the bulbus (e.g., lateral sheet apophysis missing, doubly incurved lateral sheet), and endogyne (narrower spermatheca).

Description.—*Carapace* (Fig. 13): carapace 2.6–4.4 mm long, smooth, with rounded pits, ferruginous, slightly gibbous. Margins not indented. Lateral margins of cephalic part convergent. *Chelicerae* (Fig. 13, 25): basal segment length/carapace length = 0.35. Basal

segments dorsally convex, smooth, covered with piligerous pits. Groove slightly elongated (length of groove/basal segment length = 0.56), with three small teeth in basal half. Basal cheliceral tooth > median cheliceral tooth > distal cheliceral tooth. Teeth equally distant. Fangs short (fang length/carapace length = 0.28), dorsoventrally flattened. *Legs:* femora spineless. Tibiae III–IV dorsally spineless, ventrally usually with only a single apical spine. *Bulbus* (Figs. 14, 15): distal division with hook-shaped, twice incurved lateral sheet projection and flagellum. Subapical tooth absent. *Vulva* (Fig. 16): spermatheca narrower than dorsal arch. Dorsal arch wider than long. For detailed description see Deeleman-Reinhold & Deeleman (1988).

Remarks.— *Dysdera dubrovninnii* was based on material from the countries of the former Yugoslavia and from northern Albania. Therefore, the discovery of this species in central Europe was unexpected.

Karyotype.—The male karyotype is composed of eight pairs of autosomes and a single sex chromosome (Fig. 19). Details of the male meiotic division indicated the sex chromosome system X0.

Habitat.—In central Europe, the habitats of D. *dubrovninnii* are similar to that of *D. ninnii*. It occurs on bed-rocks rich in minerals within xerothermic natural (*Quercus* spp., *Carpinus betulus*, rarely *Fagus sylvatica*) or planted forests (e.g., *Pinus* sp.). In the Balkan Peninsula it occurs in a wide range of elevations (from planted pine forests on the seashore to mountain beech forests). In southwestern Balkan (Slovenia and Croatia), where this species co-occurs with *D. ninnii*, it prefers marginal habitats such as villages, stony debris in cold chasms, steppes, alpine grasslands and mountain *Pinus mugo* bush. In comparison with *D. hungarica* it occurs on relatively more humid and more shaded habitats as evident from syntopic occurrence in Vinnianský hradný vrch hill in Slovakia.

Phenology.—Similar to that of *D. ninnii* in central Europe.

Distribution.—This species has been previously known only from the countries of the former Yugoslavia (Croatia, Slovenia, southern Montenegro) and from northern Albania (Deeleman-Reinhold & Deeleman 1988). Recently, it has been discovered in Romania and the eastern part of Slovakia, but erroneously identified as *D. ninnii* (e.g., Thomka 1997). The distribution of *D. dubrovninnii* and *D. ninnii* do not overlap in the northern part of central Europe (Fig. 26). In contrast, they occur sympatrically but rarely in the same localities in the northwest part of the Balkan Peninsula (syntopic localities in Slovenia: Bač, Bepše pri Logatcu, Postojna, Planina; Croatia: Paklenica, Plitvička jezera, Šibenik). Since *D. dubrovninnii* presumably dispersed to central Europe from northwestern Balkans, it is likely to also occur in Hungary. It probably also occurs in southeastern Poland and westernmost Ukraine, since the known localitions in eastern Slovakia are close to the Polish and Ukrainian borders. A distribution map was published by Deeleman-Reinhold & Deeleman (1988: 261, map 9). The map of *D. ninnii* in Gajdoš *et al.* (1999: map 200) partially refers to this species.

Dysdera longirostris species-group

Remarks.—Deeleman-Reinhold (1988) first established this species-group. Three species of the group are known from central Europe. Although they can be relatively easily distinguished, much confusion exists in the literature.

Dysdera hungarica **Kulczyński 1897**

Figs. 20, 27–30

Dysdera hungarica Kulczyński, in Chyzer & Kulczyński 1897: 268, plate 10, fig. 42; Roewer 1928a: 49, plate 7, fig. 563 (probably redrawn after Chyzer & Kulczyński 1897);

Charitonov 1956: 26, fig. 17; Loksa 1969: 78, figs. 53A–C; Polenec 1985: 103, fig. 8; Deeleman-Reinhold & Deeleman 1988: 168, figs. 60–65; Heimer & Nentwig 1991: 44, fig. 96; Dunin 1992: 64, fig. 9; Řezáč & Bryja 2002: 75, figs. 1–2; Thaler & Knoflach 2002: 428, fig. 8.

Dysdera longirostris Doblika: Miller 1971: 74, plate 5, fig. 6.

Type specimens.—*Dysdera hungarica:* syntypes: SLOVAKIA: 1 male, 7 females, Hrušov (=Körtvélyes) (48°35'N, 20°37'E), C. Chyzer (HNHM, examined). HUNGARY: unknown number of adult specimens: Satorvaralja Ujhely (48°23'N, 21°39'E), Kám (47°05'N, 16°52'E), Budapest (Kelenföld, Gellérthegy) (47°28'N, 19°02'E), Kalocsa (46°31'N, 18°59'E), Marillavölgy (47°25'N, 18°38'E) (repository unknown, not examined). ROMANIA: unknown number of adult specimens: Zalău – Meseş mountains (=Zilah – Meszeshegy) (47°10'N, 23°03'E), Cluj (=Kolozsvár) (46°46'N, 23°36'E), Gherla (=Szamosujvár) (47°01'N, 23°53'E), Alba Iulia (=Gyulafehérvár) (46°04'N, 23°34'E), Sibiu (=Nagy-Szeben) (45°47'N, 24°08'E), Haţeg (=Hátszeg) (45°36'N, 22°57'E) (repository unknown, not examined).

Material examined.—AUSTRIA: *Burgenland:* 2 ♀, Seewinkel, western Stundlacke [47°50'N, 16°40'E], 6 August–30 October 1960, J. Gruber (NMW); 3 ♀, Parndorfer Platte [47°59'N, 16°51'E], 1988–1989, K.H. Steinberger (NMW); 1 ♀, north Leithagebirge, Bruckneudorf [48°00'N, 16°46'E], 23 April 1963, J. Gruber (NMW); 1 ♀, Leithagebirge, Eisenstadt [47°50'N, 16°32'E], 8 May 1963, J. Gruber (NMW). *Nordtirol:* 5 ♀, Ahrnkopf near Innsbruck [47°12'N, 11°25'E], 1983–1984, K.H. Steinberger (NMW); 3 ♀, 1 juvenile, same location, 26 September 2005, M. Řezáč (MR). *Wachau:* 1 ♀, Dunkelsteiner Wald, Unterloiben [48°22'N, 15°31'E], 21 May 1998, J. Gruber (NMW). *Wien:* 1 ♀, [48°11'N, 16°25'E], 2 July 2006, W. Nentwig (MR); 3 ♀, Wien II, Unterer Prater [48°11'N, 16°25'E], 29 March 1981, 7 June 1980, 14 December 1980, J. Gruber (NMW); 1 ♀, Wien III, Alter St. Marxer Friedhof [48°12'N, 16°21'E], 26 May–17 June 1973, J. Gruber (NMW); 4 ♀, Wien X, Laaer Wald [48°12'N, 16°21'E], 12 April 1980, 15 August 1980, J. Gruber (NMW); 1 ♀, 1 juvenile, Wien XI, Zentralfriedhof [48°12'N, 16°21'E], 2–21 June 1973, J. Gruber (NMW); 66 ♀, 3 juveniles, Wien XIX, Grinzing [48°16'N, 16°20'E], 22–26 April 1986, 26 April–18 May 1986, 1 June 1980, 12 May 1983, 17 April 1983, 3–4 April 1983, 22 May 1982, 3 September 1978, 26 July 1981, 19 June 1986, 19–23 April 1983, 13 May 1978, 10 April 1983, 29 July 1977, 27 March 1983, 20 April 1980, 15 May 1982, 27 April 1983, 19 May 1977, 2 July 1983, 2 June 1983, 30 April 1978, 11 May 1980, J. Gruber (NMW); 3 ♀, Wien XIX, Kaasgraben [48°16'N, 16°20'E], 29 September 1960, 31 May 1956, 16 May 1964, J. Gruber (NMW); 1 ♀, Bisamberg near Wien, Ortschaft [48°19'N, 16°21'E], 15 July 1989, J. Gruber (NMW). *Wiener Becken:* 1 ♀, 1 juvenile, southern Haslau [48°06'N, 16°42'E], 8 August–1 September 1960, J. Gruber (NMW); 2 ♀, southwestern Tattendorf [47°57'N, 16°17'E], 21 October 1989, J. Gruber (NMW). *Wiener Wald:* 2 ♀, Königstetten [48°18'N, 16°08'E], 24 May–22 June 1975, J. Gruber (NMW); 2 ♀, Unter-Purkersdorf [48°12'N, 16°10'E], 27 September 1980, J. Gruber (NMW). BULGARIA: 4 ♀, Kranevo near Zlatni piasaci, Varna area [43°20'N, 28°02'E], 10 August 2005, M. Řezáč (MR). CZECH REPUBLIC: *Brno:* 2 ♀, reserve Kavky [49°11'N, 16°36'E], 8 May 2004, 29 June 2005, S. Vinkler (VB); 3 ♀, reserve Obřanská stráň [49°11'N, 16°36'E], 8 May 2005, S. Vinkler (VB); 4 ♀, Kopanina [49°15'N, 16°35'E], 15 June 2005, 17 August 2005, 5 October 2005, S. Vinkler (VB). *Pálava biospheric reserve:* 1 ♀, reserve Svatý kopeček [48°47'N, 16°38'E], 14 September–22 October 2001, M. Hluchý (VB); 1 ♀, Milovický les wood [48°50'N, 16°43'E], 14 May 2003, J. Chytil (VB); 1 ♀, Mikulov, reserve Kočičí skála [48°48'N, 16°37'E], 6–11 June 1996, J. Chytil (VB); 1 ♀, Dolnodunajovický potok stream [48°51'N, 16°36'E], 21 March 2004, V. Bryja (MR); 5 ♀, Dolní Dunajovice, reserve Dolnodunajovické kopce

[48°50'N, 16°33'E], 16 May–28 May 2004, 7 June–6 August 2004, 6 August–27 September 2004, S. Vinkler (VB); 2 ♀, Kinberk [48°47'N, 16°49'E], 30 September–28 November 2003, 20 March–20 May 2004, J. Chytil (VB); 3 ♀, Mikulov, reserve Slanisko u Nesytu [48°46'N, 16°41'E], 15 October 1993, J. Chytil (JS); 25 ♀, 2 juveniles, Pouzdřany, reserve Pouzdřanská step-Kolby [48°56'N, 16°37'E], 16 May–12 June 2004, 12 June–25 August 2004, 4 July–7 August 2004, 7 August–19 September 2004, 19 September–17 October 2004, 17 October–10 November 2004, 10 November 2004–4 January 2005, 12 June–12 July 2005, 12 July–6 August 2005, 30 September 2005, 28 October 2005, S. Vinkler (VB); 4 ♀, Pouzdřany, Kolby [48°57'N, 16°38'E], 30 July 1968, 25 May 1969, 20 November, 20 May, F. Miller (NMPC); 25 ♀, same location, 16 May–12 June 2004, 7 August–19 September 2004, 19 September–17 October 2004, 17 October–10 November 2004, 24 April–22 May 2005, 22 May–12 June 2005, 28 October 2005, S. Vinkler (VB). *Podyjí area:* 1 ♀, Havraníky, reserve Údolí Dyje, Šobes [48°48'N, 15°58'E], 13–17 June 1999, M. Řezáč (MR). *Prague:* 10 ♀, Ruzyně [50°05'N, 14°17'E], 22 June 1994, 30 June 1994, 15 September 1994, 23 May 1996, 10 June 1997, S. Pekár (MR). HUNGARY: 1 ♀, Velence [47°14'N, 18°39'E], 18 May 1951, L. Balogh & E. Somfai (HNHM); 1 ♀, same location, 16 June 1951, L. Vas-Borosy (HNHM); 3 ♀, 2 juveniles, Nadap, Meleghegy [47°15'N, 18°37'E], 9 June 1951, K. Zoltán (HNHM); 2 ♀, Nadap [47°15'N, 18°37'E], 24 October 1951, K. Zoltán (HNHM); 7 ♀, Pákozd, Bella völgy valley [47°13'N, 18°32'E], 9 October 1951, K. Zoltán (HNHM); 1 ♀, Alsópetény [47°53'N, 19°14'E], July 1944, I. Loksa (HNHM); 1 ♀, Györ [47°40'N, 17°38'E], July 1949, I. Andrássy (HNHM); 1 ♀, Balatonfüred, Tihany peninsula [46°55'N, 17°52'E], June 1928 (HNHM); 4 ♀, 1 juvenile, same location, 28 September 2006, M. Řezáč (MR); 1 ♀, Pécs, foot of the Misina hill [46°05'N, 18°13'E], 30 September 2006, M. Řezáč (MR); 1 ♀, Mohácsi sziget island, Kölkedi erdö forest [45°56'N, 18°42'E], 23 April 1923, E. Bokor (HNHM); 4 ♀, 2 juveniles, Szombathely, near the main railway station [47°13'N, 16°37'E], 1 October 2006, M. Řezáč (MR). ROMANIA: 2 ♀, Bucharest [44°26'N, 26°06'E], 1909, A.S. Montandon (NMPC); 1 ♂, 1 ♀, Transsylvania, 1914 (NMPC); 2 ♂, 3 ♀, Hideselu de Jos, Bihor mountains [46°57'N, 22°03'E], May–September 2004, I. Sas (MR); 2 ♀, Cluj [46°45'N, 23°57'E], 20 May 2006, W. Nentwig (MR); 1 ♂, Cluj, Suatu reserve [46°45'N, 23°57'E], 1998, I. Urák (MR); 1 ♂, mont Csik, Kászon, Salutaris [46°13'N, 26°08'E], 10–31 July 1943, Székessy (HNHM); 1 ♂, Tordai salty lake [46°33'N, 23°47'E], 10 May 1904, L. Gíró (HNHM). SLOVAKIA: *Burda mountains:* 1 juvenile, Chľaba, Kováčov [47°50'N, 18°47'E], 22 June 1960, J. Žďárek (MR); 6 ♀5 juveniles, Chľaba [47°49'N, 18°49'E], 14 August–26 October 1978, 12 September–1 November 1977, 1 June 1977–18 July 1978, 22 August–12 September 1977, V. Petřvalský (PG). *Hornonitrianska kotlina basin:* 1 ♀, Bojnice [48°46'N, 18°34'E], 11 August 1961, J. Vachold (PG). *Hronská pahorkatina (hilly country):* 2 ♀, Gbelce, reserve Parížske močiare [47°50'N, 18°30'E], 15 March–2 May 2001, 4 July–13 September 2001, P. Gajdoš (PG); 2 ♀, Paríž, reserve Gbelce [47°51'N, 18°32'E], 9 May 1999, 9 May–20 May 1999, O. Majzlan (PG); 1 ♀, Mužla, Čenkov [47°47'N, 18°35'E], 20 May–27 June 1998, O. Majzlan (PG). *Košická kotlina basin:* 1 juvenile, Svinica, Bidovce [48°44'N, 21°26'E], 25 July 1995, P. Gajdoš (PG). *Kremnické vrchy mountains:* 1 ♀, Budča, reserve Boky [48°34'N, 19°04'E], 1976, V. Thomka (VMH). *Krupinská planina plain:* 1 juvenile, Krupina town [48°21'N, 19°04'E], August 1963, J. Vachold (PG); 1 ♀, Litava [48°17'N, 19°10'E], 30 September 1963, J. Vachold (PG). *Malá Fatra mountains:* 1 ♀, Terchová, Rozsutec [49°17'N, 19°00'E], F. Miller (NMPC). *Malé Karpaty mountains:* 1 juvenile, Bratislava, reserve Devínská Kobyla [48°10'N, 17°00'E], 7 April–9 May 1978, P. Gajdoš (PG); 1 ♀, Pezinok, near Chrastina [48°17'N, 17°16'E], 27 May–24 June 1994, P. Gajdoš (PG); 1 juvenile, Pezinok, Stará hora hill, Wimperegly [48°18'N, 17°16'E], 17 July–15 December 1994, P. Gajdoš (PG); 1 ♀, Stupava, Vrchná hora hill [48°17'N, 17°02'E], 23 May–19 June 1999, O. Majzlan (PG); 1 ♀, Čachtice [48°43'N, 17°47'E], 25 July 1974, J.

Vachold (PG). *Ondavská vrchovina mountains:* 2 ♀, Humenné [48°56'N, 21°54'E], 22 October 1990, 20 May 1996, V. Thomka (VMH). *Podunajská rovina lowland:* 30 ♀, 10 juveniles, Bohelov [47°56'N, 17°43'E], 2 April–7 May 1992, 6 May–3 June 1992, 3 June–2 July 1992, P. Gajdoš (PG); 1 ♀, Rusovce [48°03'N, 17°08'E], P. Gajdoš (PG); 1 ♀, Bratislava-Vinohrady, Vlčie hrdlo [48°10'N, 17°08'E], 10 April 1991, O. Majzlan (PG); 2 ♀, Čilizský potok stream [47°52'N, 17°37'E], 6 May–2 June 1992, 2 June–1 July 1992, P. Gajdoš (PG); 11 ♀, Jurová [47°56'N, 17°30'E], 2 June–1 July 1992, P. Gajdoš (PG). *Považské podolie:* 1 juvenile, Trenčín [48°53'N, 18°02'E], 19 June–24 July 1998, P. Gajdoš (PG). *Slovenský kras area– Plešivecká planina plateau:* 1 ♀, Kunova Teplica, Veľký vrch hill [48°36'N, 20°22'E], 16 October 1984, J. Svatoň (JS); 2 ♀, Kružná, Veľký vrch hill II [48°37'N, 20°26'E], 23 July 1984, J. Svatoň (JS); 1 ♂, Veľká stráň [48°38'N, 20°23'E], 15 September 1983, J. Svatoň (JS); 1 ♂, Plešivec, Koniar, Hôrka [48°34'N, 20°24'E], 26 June 1984, J. Svatoň (JS). *Slovenský kras area– Silická planina plateau:* 1 ♂, Kečovo, reserve Kečovské škrapy [48°30'N, 20°28'E], 22 September 1982, J. Svatoň (JS); 1 ♂, 1 ♀, Kečovo, reserve Domické škrapy [48°28'N, 20°28'E], 25 May, F. Miller (NMPC); 1 ♀, same location, 22 September 1982, J. Svatoň (JS); 3 ♂, 2 ♀, same location, 22 August–8 October 2003, 8 October–26 November 2003, P. Gajdoš (PG); 1 ♀, Hrušov nad Turňou, reserve Hrušovská lesostep [48°35'N, 20°36'E], 23 August 1984, J. Svatoň (JS); 1 ♀, Jablonov, Hradište hill [48°36'N, 20°40'E], 16 October 1984, J. Svatoň (JS); 1 ♂, 1 ♀, Hrušov nad Turňou, Hradisko hill [48°36'N, 20°40'E], 19 August 2003, M. Řezáč (MR). *Spišsko-šarišské medzihorie mountains:* 1 ♂, Kapušany, reserve Kapušianský hradný vrch [49°02'N, 21°19'E], 31 July–9 October 1997, V. Thomka (VMH). *Tríbeč mountains:* 2 ♀, Nitra, reserve Zoborská lesostep [48°20'N, 18°06'E], 1 May 1978, 1 May 1980, P. Gajdoš (PG); 1 ♀, Velčice, reserve Velčické cery [48°24'N, 18°18'E], 22 April–22 June 1985, P. Gajdoš (PG). *Vihorlatské vrchy mountains:* 3 ♀, Vinné, reserve Vinnianský hradný vrch [48°48'N, 21°58'E], 19 August 1993, V. Thomka (VMH); 1 ♂, 1 ♀, same location, 17 August 2003, M. Řezáč (MR). *Východoslovenská pahorkatina (hilly country):* 1 ♂, 1 ♀, Velaty [48°28'N, 21°40'E], 18 August 2003, M. Řezáč (MR); 1 ♂, Vranov nad Topľou [48°53'N, 21°41'E] (MNHN); 1 ♂, 1 ♀, same location, 15 August 2003, M. Řezáč (MR). *Zemplínske vrchy mountains:* 1 ♂, 1 ♀, Veľká Tŕňa, Rozhľadňa [48°27'N, 21°41'E], 18 August 2003, M. Řezáč (MR). *Žitavská pahorkatina (hilly country):* 1 ♀, Velké Janíkovce [48°17'N, 18°08'E], 24 September 1987, V. Petřvalský (PG); 3 ♀, Nitrianské Hrnčiarovce, Malanta, way to Pohranice [48°19'N, 18°07'E], 26 June 1991, 5 May 1992, 12 November 1992, P. Gajdoš (PG). UKRAINE: *Crimea:* 1 ♀, Cherson Taurica, Simferopol [44°57'N, 34°06'E] (NHRS); 5 ♂, 8 ♀, Kordon Bukovskogo, 35 km S of Simferopol [44°42'N, 34°07'E], 18 July 2001, N. Kovblyuk (MR); 1 ♀, Yalta, Massandra Park [44°30'N, 34°11'E], 20 May–19 June 2001, N. Kovblyuk (MR).

Diagnosis.—*Dysdera hungarica* is closely related to *D. pristiphora* Pesarini 2001 described from northern Italy and *D. hungarica atra* Mcheidze 1979 and *D. hungarica subalpina* Dunin 1992 from the Caucasus. Amongst central European species it is characterised by the convergent lateral anterior margins of the carapace, the bulbus is characterised by a robust tegulum and the presence of a finger-like lateral sheet apophysis, and the vulva is characterised by two parallel chitinized bands on the ventral wall of the copulatory bursa.

Description.—*Carapace* (Fig. 27): carapace 2.5–3.4 mm long, slightly wrinkled, shiny, dark brown to ferruginous, dorsoventrally flat. Lateral margins of cephalic part convergent. *Chelicerae* (Fig. 27): basal segment elongate (basal segment length/carapace length = 0.53). Inner margin straight, dorsal side convex, smooth with sparse small hairy pits. Groove elongated (length of groove/basal segment length = 0.73), equipped with three small teeth in basal half. Median cheliceral tooth > basal cheliceral tooth > distal cheliceral tooth. Median cheliceral tooth close to basal tooth. Fangs elongated (fang length/carapace length = 0.52),

thorn-shaped. *Legs:* femora spineless. Tibiae III–IV dorsally spineless, ventrally with a pair of apical spines and usually with a single additional spine. *Bulbus* (Figs. 28, 29): tegulum wider than distal division. Apical part of distal division with relatively large, parallel finger-like lateral sheet apophysis. *Vulva* (Fig. 30): spermatheca straight, lateral parts almost as thick as medial part. Dorsal arch slightly wider than long. Ventral wall of copulatory bursa with paired, large, parallel chitinized bands. For detailed description see Deeleman-Reinhold & Deeleman (1988).

Remarks.—Miller (1971) erroneously attributed this species to *D. longirostris*. Amongst his papers, we found unpublished drawings of the same specimen in different views that enabled us to determine these specimens unambiguously as *D. hungarica*.

Karyotype.—The male karyotype is composed of eight pairs of autosomes and a single sex chromosome (Fig. 20). Analysis of male meiotic division confirmed a X0 sex chromosome system.

Habitat.—Sexual populations occur in xerothermic forests (*Quercus* spp., *Carpinus betulus*, monocultures) on bed-rocks rich in minerals. It also occurs on semirural habitats around old ruins of buildings, such as castle ruins, overgrown by bushes. We noted considerable ecological plasticity of parthenogenetic clones. They occur in the same habitats as sexual populations, especially semirural woods and bushes, often with liana *Hedera helix* on the ground, and often within cities. Moreover they can occur on aforested habitats, such as wetlands with *Phragmites australis*, salt marshes, wet meadows, agroecosystems (orchards, vineyards). Low abundances are characteristic for the clones in such habitats.

Phenology.—Similar to *D. ninnii*.

Distribution.—Distribution of the nominate subspecies stretches from the Caucasus and Crimea to the Balkan Peninsula (Romania, Bulgaria) and central Europe (Hungary, Czech Republic, Slovakia, Austria). It reaches as far south as Bulgaria and Yugoslavia, and as far north as the Czech Republic and Slovakia. The subspecies *D. hungarica subalpina* is known from north Caucasus (North Osetia); *D. hungarica atra* from Georgia and Azerbaijan (Dunin 1992). Moreover, geographic parthenogenesis is present in this species (Deeleman-Reinhold 1986; Gruber 1990). In the eastern part of the distribution only sexual populations are found, while in the western part only thelytokous clones occur. The western "populations" are characterized by isolated localities (e.g., Prague-Ruzyně). The transient zone between sexual and thelytokous forms runs through Slovakia and Hungary, specifically through Rimavská Sobota and Eger. Due to the fact that determination of members of the genus *Dysdera* is usually based on the morphology of the male copulatory organ, *D. hungarica* is largely overlooked in the western part of its distribution.

Distribution maps were published by Deeleman-Reinhold & Deeleman (1988: map 4), Deeleman-Reinhold (1986: 27, only for the central part of the distribution area, with distinguished sexual populations and parthenogenetic clones), Řezáč & Bryja (2002: fig. 3, for the Czech Republic), Buchar & Růžička (2002: 205, for the Czech Republic), Deltshev *et al.* (2003: map 17, for Serbia), and Gajdoš et al. (1999: map 180, for Slovakia).

Dysdera adriatica Kulczyński 1897

Figs. 21, 31–34

Dysdera hungarica var. *adriatica* Kulczyński, in Chyzer & Kulczyński 1897: 270.
Dysdera adriatica: Deeleman-Reinhold & Deeleman 1988: 170, figs. 66–72; Thaler & Knoflach 2002: 417, figs. 1–2, 4.

Type specimens.—*Dysdera adriatica*: syntypes: CROATIA: 1 male, 1 female, 2 juveniles, Orehovica (45°19'N, 14°28'E), north Dalmatia, C. Chyzer (HNHM, examined);

unknown number of adult specimens, Bakarac (45°17'N, 14°34'E), Martinšcina (=Martinscizza) (46°08'N, 16°03'E), Vrata (45°18'N, 14°43'E), Risnjak (45°25'N, 14°37'E) (repository unknown, not examined).

Material examined.—BULGARIA: 4 ♀, Bajkal near Izvor, Kiustendil area [42°26'N, 22°52'E], 8 August 2005, M. Řezáč (MR). CROATIA: 1 ♂, 12 ♀, Plitvička jezera lakes, Korana [44°54'N, 15°36'E], 22 June 2005, M. Řezáč (MR). SLOVENIA: 1 ♀, Ig. Kremenški gozd [45°56'N, 14°33'E], 7 June 1997, S. Brelih (UL); 7 ♂8 ♀, Slavnik, V. Gobovica [45°33'N, 13°58'E], 7–8 September 1996, M. Kuntner (UL); 2 ♀, Podgorje, Slavnik hill [45°31'N, 13°57'E], 26 July 1996, M. Kuntner (UL); 1 ♂, 1 ♀, Dolina Kolpe, Slavski Laz [45°29'N, 14°54'E], 29 April 2001, S. Brelih (UL); 1 ♀, Grahovo [45°46'N, 14°26'E], 6 November 1992, S. Brelih (UL). *Novo Mesto area:* 1 juvenile, Čatež near Trebnje [45°57'N, 14°57'E], 28 June 1997, M. Kuntner (UL); 1 ♀, Pleš hill near Semič [45°39'N, 15°10'E], 27 July 2001 (UL). *Lipica area:* 5 ♀, 1 juvenile, Glavica, 2km S of Kozina [45°36'N, 13°56'E], 26 July 1996, 7 September 1996, M. Kuntner (UL). *Ljubljana area:* 1 juvenile, Ljubljana, Rašila [46°03'N, 14°30'E], July 1994, M. Jernejc (UL); 1 ♂, Rašica [45°51'N, 14°37'E], 7 April 1995, M. Kuntner (UL); 1 juvenile, Brkini, Javorje [46°13'N, 14°28'E], 25 July 1996, M. Kuntner (UL); 1 ♀, Borovnica, Pekel [45°55'N, 14°21'E], September 1996, J. Mazi (UL); 13 ♂5 ♀, 2 juveniles, Ljubljana, Ljubljanski vrh hill, 3km S of Vrhnik [45°56'N, 14°17'E], 2–23 May 1996, 23 May–13 June 1996, 13 June–4 July 1996, 23 July–21 August 1996, 21 August–15 September 1996, M. Kuntner (UL). *Maribor area:* 1 juvenile, Maribor, Zgornji Duplek [46°30'N, 15°43'E], June–July 1991 (UL). *Postojna area:* 6 ♀, 1 juvenile, Planinsko polje plain [45°50'N, 14°14'E], May 1982, June 1983, 8 June 1984 (UL); 2 ♂, 3 ♀, 1 juvenile, Laze near Planinsko polje plain [45°51'N, 14°15'E], 17 July–21 August 1994, 21 September–16 October 1994, 16 October–21 November 1994, March–1 May 1995, M. Kuntner (UL; 1 ♂, June 1997, A. Gregorčič (UL); 2 ♂, 4 ♀, Razdrto [45°45'N, 14°03'E], 14 June 1957 (NMPC); 2 ♀, Planina, Unška koliševka chasm [45°50'N, 14°14'E], 2000, M. Řezáč (MR). *Kočevje area:* 1 ♂, Mahovnik near Kočevje [45°39'N, 14°50'E], 23 June 1930 (NMPC). *Ilirska Bistrica area:* 1 juvenile, Koritnice, Milanja [45°37'N, 14°16'E], 23 May 2003, S. Polak (UL); 10 ♂, 1 ♀, Koritnice, Cerje [45°37'N, 14°16'E], 1 ♂, 14 May 1994, 28 June 1994, S. Polak (UL); 4 ♂, 4 ♀, 1 juvenile, Koritnice [45°37'N, 14°16'E], 7 May 1995, 14 June 1995, 12 July 1995, 26 July 1995, 14 August 1995, S. Polak (UL); 1 ♂, Bač, Tuščak [45°38'N, 14°16'E], 4 April 1994, S. Polak (UL). *Krško area:* 1 ♀, 2 juveniles, Kozje [46°04'N, 15°33'E], 31 July, 1 August, 12 August 1999, G. Bergthaler (UL); 1 ♂, same location, 13 August 1999, M. Šuštar (UL); 1 juvenile, Krško, Pečice [46°01'N, 15°34'E], 15 May 1992, S. Brelih (UL). *Celje area:* 1 ♀, 1 juvenile, Logaška planota, near Laška Kukava, Senca [46°09'N, 15°14'E], 1–14 May 1995, 27 July–13 August 1995, M. Kuntner (UL). *Nova Gorica area:* 1 ♂, 1 ♀, Nova Gorica, Panovec [45°56'N, 13°39'E], 16 March 2001, S. Brelih (UL). *Portorož area*: 2 juveniles, Koštabona, Supot [45°29'N, 13°43'E], 24 May 1992, S. Brelih (UL). *Julijske Alpe mountains:* 1 juvenile, Zatolmin, Tolminska korita [46°11'N, 13°43'E], 10 June 1997, S. Brelih (UL); 1 ♀, Kranjska Gora, Vršič [46°28'N, 13°46'E], June 1981 (UL); 1 ♂, 2 juveniles, Čepovan– Most na Soči [46°09'N, 13°43'E], 10 June 1997, S. Brelih (UL); 1 ♂, Jesenice [46°26'N, 14°02'E], 20 September (ZMHB). *Kranj area:* 1 ♀, Kranj, Šmarjetna gora hill [46°14'N, 14°21'E], 30 June–8 July 1991, K. Prosenc (UL); 1 ♀, Udin Boršt, Spodnje Duplje, near Arnševa jama cave [46°17'N, 14°17'E], 1 August 1995, J. Kristanc (UL). YUGOSLAVIA: 1 juvenile, Vojvodina, Ruma [45°00'N, 19°49'E], 1 August 1976 (UL).

Diagnosis.—This species is very similar to *D. hungarica*, from which it differs by the smaller body, less smooth and more hairy carapace and dorsal side of basal cheliceral segment; males differ by the smaller and more protruding finger-like lateral sheet apophysis; females differ by the dorsal arch being remarkably wider than long and by the paired

chitinised bands on the ventral wall of the copulatory bursa being narrow and anteriorly convergent.

Description.—*Carapace* (Fig. 31): carapace 2.3–3.4 mm long, slightly wrinkled, ferruginous, dorsoventrally flat. Lateral margins of cephalic part convergent. *Chelicerae* (Fig. 31): basal segment elongated (basal segment length/carapace length = 0.58). Inner margin of basal segment straight, dorsal side convex, with relatively dense small hairy pits. Groove elongated (length of groove/basal segment length = 0.72), with three small teeth in basal half. Median cheliceral tooth > distal cheliceral tooth > basal cheliceral tooth. Median cheliceral tooth close to basal cheliceral tooth. Fangs elongated (fang length/carapace length = 0.50), thorn-shaped. *Legs:* femora spineless. Tibiae III–IV dorsally spineless, ventrally with a pair of apical spines and usually with 1–3 additional spines. *Bulbus* (Figs. 32, 33): tegulum wider than distal division. Apical part of distal division with protruding finger-like lateral sheet apophysis. *Vulva* (Fig. 34): Medial part of spermatheca thicker than lateral parts. Dorsal arch wider than long. Ventral wall of copulatory bursa with paired, narrow, anteriorly convergent chitinized bands. For detailed description see Deeleman-Reinhold & Deeleman (1988).

Karyotype.—The karyotype of the sole male examined consists of 20 chromosomes (Fig. 21). Analysis of male meiotic division revealed a sex chromosome system of X0. Moreover, one large and two small autosomes form a trivalent during meiosis (Fig. 43).

Habitat.—*Dysdera adriatica* occurs in various xerothermic forests and shrubland, mainly with dominant *Carpinus betulus, Fagus sylvatica, Quercus cerris* or *Pinus nigra.*

Phenology.—Similar to that of *D. ninnii.*

Distribution.—This species occurs in the northwestern regions of the Balkan Peninsula (together with *D. ninnii* it is the most common species in Slovenia and north-western Croatia) and in the Austrian southern Alps. Since *D. adriatica* occurs in westernmost Slovenia and southernmost Austria, it is expected to also occur in northeastern Italy. Distribution maps have been published by Deeleman-Reinhold & Deeleman (1988: map 5), and Deltshev *et al.* (2003: map 14, only for Serbia).

Dysdera longirostris Doblika 1853

Figs. 22, 35–38

Dysdera longirostris Doblika 1853: 122; Chyzer & Kulczyński 1897: 218, plate 10, fig. 43; Charitonov 1956: 25, fig. 11; Oltean 1962: 578, fig. 2; Loksa 1969: 77, figs. 53D–E, 54C; Deeleman-Reinhold & Deeleman 1988: 167, figs. 51–56; Heimer & Nentwig 1991: 46, fig. 97; Thaler & Knoflach 2002: 418, figs. 3, 5.

Dysdera longitarsis [sic]: Herman 1879: 206–207.

Type specimens.—*Dysdera longirostris:* syntypes: UKRAINE: unknown number of males and females, Crimea (perhaps NMW, not examined).

Material examined.—BULGARIA: 2 juveniles, Rilski manastir monastery [42°07'N, 23°20'E], 4 August 2005, M. Řezáč (MR); 2 ♀, Kranevo near Zlatni piasaci, Varna area [43°20'N, 28°03'E], 10 August 2005, M. Řezáč (MR); 1 ♀, Albena, Varna area [43°14'N, 28°01'E], 9 August 2005, M. Řezáč (MR); 1 ♂, Vračanski Balkan, Vratsa, Čelopeč [43°09'N, 23°27'E], 8 June 1957 (NMPC). GREECE: 1 ♂, 1 ♀, Leptokaria [40°03'N, 22°33'E], 4 June–13 June 1996, J. Dolanský (MR). HUNGARY: 1 ♀, Buda, Viranyi utca [47°30'N, 19°01'E], G. Kolosváry (HNHM); 1 ♀, Misina hill above Pécs [46°07'N, 18°12'E], 11 July 1951, Somfai (HNHM); 1 ♂, 1 ♀, same location, 30 September 2006, M. Řezáč (MR); 1 juvenile, Kölked near Mohács [45°56'N, 18°42'E], 29 September 2006, M. Řezáč (MR). MACEDONIA: 1 ♀, Šar planina [41°48'N, 20°41'E], 12 June 1974, Hladík (NMPC). TURKEY: 1 ♂, Bolu province, Düzce, Üç Köprü [40°47'N, 31°14'E], 2 May 2004, M.

Horsák (MR). UKRAINE: *Crimea:* 1 ♂, 2 ♀, Cherson Taurica [44°42'N, 34°01'E] (NHRS); 3 ♂, 1 ♀, Yalta area, 1 km N of Nikitskaja School [44°29'N, 34°09'E], 3–11 June 2000, N. Kovblyuk (MR); 2 ♂, Simferopol district, 3 km NW of Skvortsovo [45°04'N, 33°48'E], 30 June–10 July 2002, N. Kovblyuk (MR). YUGOSLAVIA: 1 ♂, Belgrade [44°47'N, 20°28'E] (NMPC).

Diagnosis.—*Dysdera longirostris* is very similar to *D. hattusas* Deeleman-Reinhold 1988, a species endemic to northern Turkey. Among central European species it is characterised by the extremely elongated chelicerae. From *D. hungarica* and *D. adriatica*, the males can be further distinguished by the slender tegulum, and the medially curved finger-like lateral sheet apophysis; the females by the high, distally situated spermatheca, and by the distinct arcuate dorsal arch with the posterior extremities remarkably curved laterally.

Description.—*Carapace* (Fig. 35): carapace 3.0–3.8 mm long, wrinkled, shiny, dark brown to ferruginous, remarkably dorsoventrally flat. Lateral margins of cephalic part convergent. *Chelicerae* (Fig. 35): basal segment very elongated (basal segment length/carapace length = 0.67). Inner margin straight, dorsal side convex, slightly wrinkled, shiny, with sparse, small hairy pits. Groove very elongated (length of groove/basal segment length = 0.87), with three small teeth in basal quarter. Median cheliceral tooth > distal cheliceral tooth > basal cheliceral tooth. Teeth equally distant. Fangs very elongated (fang length/carapace length = 0.77), thorn-shaped. *Abdomen:* in males, book lung opercula and margins of spiracles heavily sclerotized. *Legs:* femora spineless. Tibiae III–IV dorsally spineless, ventrally with a pair of apical spines and usually with 1–2 additional spines. *Bulbus* (Figs. 36, 37): tegulum slightly wider than distal division. Apical part of distal division with relatively long, medially curved finger-like lateral sheet apophysis. *Vulva* (Fig. 38): spermatheca high, in respect to dorsal arch distally situated. Dorsal arch distinctly arcuate, with posterior extremities curved laterally. For detailed description see Deeleman-Reinhold & Deeleman (1988).

Karyotype.—The male karyotype is composed of 40 chromosomes (Fig. 22). The sex chromosome system is uncertain.

Habitat.— *Dysdera longirostris* occurs in various xerothermic forests and shrublands, often semirural ones, mainly with dominant *Carpinus betulus, Fagus sylvatica, Quercus* sp., or *Pinus* sp.

Phenology.—Similar to that of *D. ninnii*.

Distribution.—This species occurs in the Balkan Peninsula, northwestern Turkey, and Crimea. The northern border of its distribution runs through north Hungary and Romania. All records from Slovakia (Gajdoš *et al.* 1999: map 190) are erroneous. However, its occurence in the warmest parts of southern Slovakia, especially in the surroundings of Slovenské Nové Mesto, is possible. Distribution maps have been published by Deeleman-Reinhold & Deeleman (1988: 258, map 2), and Deltshev *et al.* (2003: 250, map 18, for Serbia).

Dysdera lata species-group

Remarks.—This species-group was first recognized by Deeleman-Reinhold (1988). In central Europe, the *lata* group is represented by a single species, *D. taurica*.

Dysdera taurica **Charitonov 1956**

Figs. 23, 39–42

Dysdera taurica Charitonov 1956: 36, fig. 10; Tyschenko 1971: 71, fig. 103; Deeleman-Reinhold & Deeleman 1988: 208, figs. 208, 215; Heimer & Nentwig 1991: 44, fig. 93.

Dysdera westringi Pickard-Cambridge: Herman 1879: 205–206; Chyzer & Kulczyński 1897: 267, plate 10, fig. 39; Loksa 1969: 75, figs. 52A–B; Drensky 1938: 92, fig. 8b (doubtful identification).

Type specimens.—*Dysdera taurica:* syntypes: UKRAINE: 1 male, 1 female, Kekeneiz (44°24'N, 33°55'E), Crimea, 1927 (repository unknown, not examined); 1 male, 1 female, Crimea, 1947, D.M. Fedotov (repository unknown, not examined).

Material examined.—BULGARIA: 3 juveniles, Kranevo near Zlatni piasaci, Varna area [43°19'N, 28°02'E], 10 August 2005, M. Řezáč (MR). HUNGARY: 2 ♂, 1 ♀, Buda, Virányi u. [47°30'N, 19°01'E], G. Kolosváry (HNHM). ROMANIA: 1 ♂, Transylvania, Zickeli (BMNH). TURKEY: 1 ♀, Konya province, Akţehir district, Ortaköy [38°27'N, 31°31'E], 13 May 2005, T. Türket (MR); 1 ♀, Niđde province, Gümüţler town [37°59'N, 34°46'E], 4 June 2002, H. Demir (MR); 1 ♂, 1 ♀, Niđde province, Alihoca [37°29'N, 34°41'E], 18 June 2002, H. Demir (MR).

Diagnosis.— *Dysdera taurica* is the only central European *Dysdera* species possessing dorsal spines on tibiae III and IV and one of two species (with *D. lantosguensis*) possessing a concave mediodorsal margin of the basal cheliceral segment. It is very similar to other members of the *lata* group, especially *D. westringi* Pickard-Cambridge 1872, *D. lata* Wider 1834 and *D. spinicrus* Simon 1882, which are restricted to the Mediterranean region, mainly the Near East. From these species the males of *D. taurica* are recognised by presence of three teeth on the apical lobe (crest) of the bulbus, and the females by the shape of the dorsal arch of the anterior diverticulum.

Description.—*Carapace* (Fig. 39): carapace 3.4–5.9 mm long, strongly wrinkled/foveated, dark brown-red to ferruginous, gibbous. Lateral margins of cephalic part parallel. *Chelicerae* (Fig. 39): basal segment slightly elongated (basal segment length/carapace length = 0.40). Dorsal side and inner margin concave, smooth, covered with dense, short hairs and several long hairs. Groove elongated (length of groove/basal segment length = 0.52), with three small teeth in basal half. Basal cheliceral tooth > median cheliceral tooth > distal cheliceral tooth. Teeth equally distant. Fangs elongated (fang length/carapace length = 0.34), thorn-shaped. *Legs:* femora I–II spineless, femora III usually with 1, femora IV are usually with 5–6 dorsal spines. Tibiae III–IV dorsally with 1 or more spines, ventrally with a pair of apical spines and usually with 2–4 additional spines. *Bulbus* (Figs. 40, 41): tegulum long, distal part contracted. Distal division apically with a lateral lobe and a spine. Lateral lobe with three ridge-like teeth. *Vulva* (Fig. 42): spermatheca thin, the extremities dilated. Dorsal arch wider than high. For detailed description see Deeleman-Reinhold & Deeleman (1988).

Remarks.— *Dysdera taurica* has, for a long time, been identified as *D. westringi* in central Europe, but Deeleman-Reinhold & Deeleman (1988) demonstrated that *D. westringi* is in fact restricted to the eastern Mediterranean region. Central European populations belong to *D. taurica*, which was originally described from Crimea. A drawing labeled *D. westringi* in Drensky (1938) is perhaps a compilation of a figure of *D. taurica* from Chyzer & Kulczyński (1897) and a figure of *D. lata* from Simon (1914).

Karyotype.—The male karyotype is composed of 11 pairs of autosomes and a single sex chromosome (Fig. 23). Study of male meiotic plates confirmed that the sex chromosome system is X0.

Habitat.— *Dysdera taurica* occurs in xerothermic *Quercus* and *Caprinus* forests and its fringes.

Phenology.—Similar to that of *D. ninnii*.

Distribution.—This species occurs in the Balkan Peninsula, Turkey, Crimea, and on islands in the Aegean Sea. The northern border of its distribution runs through Romania, north

Hungary and south Slovakia, where it occurs only in the warm limestone area of Slovak Karst. A distribution map has been published by Deeleman-Reinhold & Deeleman (1988: 264, map 14). The maps of *D. westringi* in Gajdoš *et al.* (1999: map 220) and in Deltshev *et al.* (2003: 252, map 20) actually refer to this species.

Dysdera erythrina species-group

Remarks.—This species-group was first recognized by Deeleman-Reinhold (1988). Two closely related species of this group, *D. erythrina* and *D. lantosquensis*, occur in central Europe. A more detailed study on this group is presented by Řezáč *et al.* (submitted). In this contribution, we provide a list of material examined and a diagnosis.

Dysdera erythrina (Walckenaer 1802)

Material examined.—CZECH REPUBLIC: *Doupovské hory mountains:* 1 juvenile, Kadaň, reserve Úhošť [50°21'N, 13°11'E], 20 August 2004, M. Řezáč (MR). *Prague:* 3 ♂, 3 ♀, reserve Lochkovský profil [49°58'N, 14°20'E], 25 May–16 June 1960, 26 May–10 June 1961, 6–19 August 1961, 2–21 September 1961, 14 October–4 November 1961, 9 April–4 May 1960, E. Žďárková (MR); 1 ♀, reserve Cikánka [49°59'N, 14°20'E], 25 April 2004, M. Řezáč (MR); 1 ♂, 1 juvenile, reserve Slavičí údolí [49°58'N, 14°20'E], 14 October 2002, J. Strejček (MR); 2 ♀, reserve Radotínské údolí [49°58'N, 14°19'E], 20 May 2004, 3 May 2005, M. Řezáč (MR); 2 ♀, reserve Prokopské údolí [50°02'N, 14°21'E], 1995, 10 June 2003, M. Řezáč (MR); 1 ♂, 4 ♀, same location, 23 October 1976, 8 September 1979, 2 October 1976, M. Antuš (MA); 1 ♀, Dalejské údolí valley [50°02'N, 14°20'E], 2003, M. Řezáč (MR); 2 ♀, reserve Šance [49°58'N, 14°24'E], 2 April 1999, 3 May 2004, M. Řezáč (MR); 1 ♀, reserve Kalvárie [50°04'N, 14°20'E], 2004, M. Řezáč (MR); 1 ♀, Karlov [50°04'N, 14°25'E], 2004, M. Řezáč (MR); 1 ♂, Žižkov, Vítkov hill [50°05'N, 14°27'E], 18 May 1976, M. Antuš (MA); 1 ♀, Klánovice [50°04'N, 14°39'E], 28 April–10 June 2001, Š. Táborská (MR); 1 ♀, reserve Opukový lom [50°07'N, 14°17'E], 21 April 1982, J. Buchar (NMPC); 2 ♂, 4 ♀, reserve Baba [50°07'N, 14°23'E], 1 November 1978, 15 May 1979, 6 May 1979, 24 October 1979, A. Kůrka (NMPC); 2 ♂, reserve Sedlecké skály [50°08'N, 14°23'E], 23 May 1986, 18 July 1986, A. Kůrka (NMPC); 1 ♀, reserve Obora Hvězda [50°04'N, 14°19'E], 2003, M. Řezáč (MR); 3 ♂, reserve Královská obora [50°06'N, 14°25'E], 4 April 2001, J. Strejček (MR); 1 ♂, Ruzyně [50°05'N, 14°17'E], 2 July 1993, Zavoralová (NMPC); 1 ♂, 1 ♀, 1 juvenile, same location, autumn 2002, M. Řezáč (MR); 2 ♂, 1 ♀, reserve Tiché údolí, Sluneční stráň [50°09'N, 14°23'E], 16 July 1980, 4 June 1981, 2 October 1981, A. Kůrka (NMPC); 1 ♀, reserve Tiché údolí, Holý vrch hill [50°09'N, 14°22'E], 20 September 1980, A. Kůrka (NMPC); 1 juvenile, reserve Tiché údolí, Roztocký háj [50°08'N, 14°23'E], 30 August 2003, M. Řezáč (MR). *Český kras area:* 1 ♂, Choteč, Škrábek hill [49°58'N, 14°16'E], 6 May 1959, J. Buchar (NMPC); 1 ♀, Srbsko, reserve Koda [49°55'N, 14°07'E], 6 May 1959, J. Buchar (NMPC); 1 juvenile, same location, 3 September 2003, M. Řezáč (MR); 1 ♀, 1 juvenile, Suchomasty, reserve Lom na Kobyle [49°54'N, 14°02'E], 16 June 1995, A. Kůrka (NMPC); 1 ♀, Svatý Jan pod Skalou, reserve Karlštejn [49°57'N, 14°08'E], 2003, M. Řezáč (MR); 1 ♀, Mořina, Velká Amerika quarry [49°57'N, 14°14'E], 2003, M. Řezáč (MR); 2 juveniles, Koněprusy, Čertovy schody quarry [49°55'N, 14°03'E], 8 September 1994, A. Kůrka (NMPC); 1 ♀, Koněprusy, reserve Kotýz [49°55'N, 14°03'E], 15 April 2000, M. Řezáč (MR); 1 ♂, 1 ♀, Beroun, Merhantova skála rock [49°58'N, 14°04'E], 17 June 2004, P. Špryňar (MR); 1 ♂, Suchomasty, reserve Na Voskopě [49°54'N, 14°02'E], 2 June 1999, A. Kůrka (NMPC); 1 ♂, same location, 3 August 2000, V. Pfleger (NMPC); 1 ♀, 1 juvenile, Suchomasty, Újezdce hill [49°54'N, 14°02'E], 30 July 2001, M. Řezáč (MR); 2 ♂, same

location, 23 September 2001, J. Strejček (MR); 1 ♀, Karlštejn [49°56'N, 14°10'E], 6 November 1998, M. Řezáč (MR); 2 ♂, 1 ♀, 1 juvenile, Srbsko, reserve Karlštejn, Komárkova lesostep [49°56'N, 14°09'E], 3 May–30 June 1965, J. Buchar (NMPC); 1 ♂, 1 ♀, same location, 12 May 2000, 9 June 2001, M. Řezáč (MR); 4 ♀, same location, 1 August 2000, 3 October 2001, 28 October 2001, L. Kubcová (LK). *České středohoří mountains:* 1 ♂, Ústí nad Labem, Koštov [50°38'N, 13°59'E], 27 September–23 October 1995, J. Hajer (VR); 1 ♂, Ústí nad Labem, Opárenské údolí valley [50°37'N, 14°05'E], 18 June 1978, M. Antuš (MA); 1 ♂, Ústí nad Labem, Klíše, Střížovický vrch hill [50°39'N, 10°00'E], 18 April–8 May 2002, V. Hula (VH); 1 ♂, Měrunice [50°29'N, 13°48'E], 19 May 1977, A. Kůrka (NMPC); Chraberce, reserve Oblík [50°25'N, 13°49'E], 4 August 1999, M. Řezáč (MR). *Rakovnicko area:* 2 ♀, 2 juveniles, Rakovník [50°06'N, 13°43'E], 1941, F. Miller (NMPC); 1 ♀, Křivoklát [50°02'N, 13°51'E], 1941, F. Miller (NMPC); 1 ♀, Lišany [50°08'N, 13°43'E], 1941, F. Miller (NMPC). *Střední Povltaví area:* 1 ♀, Nalžovické Podhájí, reserve Drbákov-Albertovy skály [49°44'N, 14°22'E], 28 June 1991, V. Růžička (VR); 1 ♂, 2 ♀, 1 juvenile, Rabyně, Vltava valley [49°49'N, 14°25'E], 6 October 1996, 29 July 1999, M. Řezáč (MR). GERMANY: 1 ♂, 2 ♀, Hamburg [53°36'N, 10°02'E] (ZMHB); 1 ♀, 1 juvenile, Muggendorf am Nordhange [49°48'N, 11°15'E], 2 August 1908, F. Dahl (ZMHB); 1 ♂, 1 ♀, Pommelsbrunn near Nürnberg, [49°30'N, 11°30'E], 16 April 1905, F. Dahl (ZMHB); 1 ♀, Geroldsgrün [50°20'N, 11°35'E], 11 May 1905, F. Dahl (ZMHB); 2 ♂, 3 juveniles, Münster, Rothenfels an der Nahe [51°57'N, 7°38'E], 25 October 1916, F. Dahl (ZMHB); 1 ♀, 1 juvenile, Staffelstein [50°05'N, 10°58'E], 7 October 1920, F. Dahl (ZMHB); 1 ♀, Schlangenbad, Georgenborner Wand [50°05'N, 8°06'E], 27 October 1916, F. Dahl (ZMHB); 1 ♀, Doulen, Dona, 24 September, K. Verhoeff (ZMHB); 1 ♀, Wadewitzgrund, 15 June, K. Verhoeff (ZMHB); 4 ♀, Landstuhl [49°24'N, 7°34'E], C. L. Koch (BMNH); 4 ♀, Grütz [52°40'N, 12°16'E], C.L. Koch (BMNH); many ♂ ♀, Fränkischer Jura, C.L. Koch (BMNH); 3 ♂, 1 ♀, same location, L. Koch (NMW); many ♂ ♀, Würzburg [49°47'N, 9°56'E], C.L. Koch (BMNH); 1 ♀, Freiburg im Breisgau [47°59'N, 7°50'E], C.L. Koch (BMNH); 1 ♂, 1 ♀, Hartmanshof [49°28'N, 11°34'E], C.L. Koch (BMNH); 1 ♀, unspecified location (BMNH). HUNGARY: 2 ♀, unspecified location, C. Chyzer (HNHM). SLOVAKIA: 1 ♂, Belanské Tatry [49°13'N, 20°09'E], 25 July 1957, J. Žďárek (MR).

Diagnosis.—*Dysdera erythrina* is very similar to several sibling species, so far considered subspecies of *D. erythrina* [see Platnick (2007)], which are, however, restricted to northeastern Spain and southern France. It differs from the second central European member of the *erythrina* group, *D. lantosquensis*, by the convex mediodorsal margin of the basal cheliceral segment and the less wrinkled and less gibbous carapace.

Dysdera lantosquensis Simon 1882

Material examined.—AUSTRIA: *Wachau area:* 1 ♀, Spitz an der Donau, north of Roten Tor, 15 June 1996, J. Gruber (NMW); *Hainburger Berge mountains:* 1 ♀, Holfsthal [48°07'N, 16°57'E], 24 May 1959, J. Gruber (NMW). *Burgenland area:* 1 ♀, southern Leithagebirge, 14km ENE from Wimpassing, Gaibunhal [47°56'N, 16°35'E], 11 May–29 June 1969, J. Gruber (NMW); 1 ♀, Leithagebirge, Grenzweg, Kaisereiche [47°53'N, 16°31'E], 28 June 1959, J. Gruber (NMW); 3 ♀, southern Leithagebirge, SE from Wimpassing, Lebzelter Bg. [47°53'N, 16°28'E], 4 July 1959, J. Gruber (NMW); 1 ♀, Leithagebirge, Zeilerberg [47°55'N, 16°36'E], 17 May 1959, J. Gruber (NMW); 1 ♂, 1 ♀, Wulkaniederung, Osliper Meierhof [47°49'N, 16°36'E], 29 April 1964, J. Gruber (NMW); 1 ♀, southern Leithagebirge, Müllendorf [47°50'N, 16°27'E], 29 September 1958, J. Gruber (NMW). CZECH REPUBLIC: *Bohemia:* 2 ♂, Hradčany, reserve Báň [50°09'N, 15°16'E], 2 May–3 June 2002, J. Dolanský (JD); 1 ♀, Žehuň, reserve Žehuňský rybník [50°09'N,

15°18'E], 26 May 1961, J. Buchar (JS); 2 ♂, 1 ♀, Pardubice, Kunětická hora hill [50°04'N, 15°48'E], 4 May–18 June 1997, J. Dolanský (JD); 2 ♂, Žumberk [49°53'N, 15°52'E], 7 May 1996–10 July 1996, J. Dolanský (JD). *Moravia:* 1 ♀, Střelice near Brno, reserve Střelický les [49°08'N, 16°30'E], 28 April 1999, V. Bryja (VB); 1 ♀, Brno, Hádky [49°12'N, 16°39'E], 5 June, F. Miller (NMPC); 1 ♂, Dambořice [49°02'N, 16°56'E], 30 June 1967, F. Miller (NMPC); 1 ♂, 1 ♀, Blansko [49°20'N, 16°45'E], 15 May 1979, F. Miller (NMPC); 1 ♀, Vilémovice [49°22'N, 16°45'E], 28 September 2006, J. Vašátko (MR); 4 ♂, 2 ♀, 1 juvenile, Drslavice, reserve Terasy [49°03'N, 17°35'E], 2 June 2005, 8 August 2005, 15 September 2005, Z. Majkus (ZM); 1 ♀, Teplice nad Bečvou, near Zbrašovské aragonitové jeskyně caves [49°31'N, 17°36'E], 21 April–31 May 2004, K. Tajovský (MR); 1 ♀, Hradčovice, reserve Rovná hora [49°03'N, 17°35'E], 15 September 2005 (ZM); 1 ♀, Bruntál, reserve Ptačí hora [49°59'N, 17°27'E], 19 May 1998, Z. Majkus (JS); 2 ♂, 1 ♀, Bučovice, reserve Malhotky [49°09'N, 17°00'E], 26 June 2004, 5 September 2004, V. Hula (MR); 1 ♂, Mohelno, reserve Hadcová step [48°56'N, 16°38'E], 1983, F. Miller (NMPC); 1 ♂, same location, 10 May 1995, J. Buchar (NMPC); 1 ♀, Pouzdřany, reserve Pouzdřanská step-Kolby [48°56'N, 16°38'E], 25 October 1967, F. Miller (NMPC); 2 ♂, 2 ♀, same location, 16 May–12 June 2004, 22 May–12 June 2005, S. Vinkler (VB); 1 ♀, Horní Věstonice, reserve Děvín-Kotel-Soutěska [48°52'N, 16°38'E], 15 June 1956, F. Miller (NMPC); 1 ♂, same location, 26 October 1992–14 May 1994, V. Růžička (VR); 1 ♂, 1 ♀, same location, 2 August 2003, V. Bryja (MR). HUNGARY: 1 ♂, Miskolcz, Also-Hámor [48°05'N, 20°40'E], July 1873, O. Herman (HNHM); 2 ♂, 11 ♀, Balatonfüred, northern part of Tihany peninsula [46°55'N, 17°52'E], 28 September 2006, M. Řezáč (MR); 1 ♀, Misina hill above Pécs [46°06'N, 18°13'E], 30 September 2006, M. Řezáč (MR). SLOVAKIA: *Beskydské predhorie mountains:* 1 juvenile, Brekov [48°53'N, 21°49'E], 14 June–15 August 2000, V. Thomka (VMH). *Biele Karpaty mountains:* 3 ♂, 1 ♀, Dolná Súča, reserve Krasín [48°57'N, 18°01'E], 6 April–11 October 1989, May–11 October 1989, P. Devan (PG). *Burda mountains:* 2 ♂, 1 ♀, Chľaba, Kováčov [47°50'N, 18°46'E], 8 August 1986, 9 August 1986, P. Gajdoš (PG); 21 ♂, 16 ♀7 juveniles, Chľaba [47°49'N, 18°49'E], 14 August–26 October 1978, 6 May–20 June 1977, 12 September–1 November 1977, 1 June 1977–18 July 1978, 12 April–23 May 1977, 20 June–18 July 1977, 6 May–1 June 1977, March–12 April 1977, 12 April–6 May 1977, 12 September–2 October 1977, 22 August–12 September 1977, V. Petřvalský (PG). *Čergov mountains:* 1 ♂, 2 ♀, Hradisko [49°08'N, 21°13'E], 26 May 1936, F. Miller (NMPC). *Hornonitrianska kotlina basin:* 1 ♀, Zemianske Kostolany [48°41'N, 18°32'E], 14 May 1975 (PG). *Hronská pahorkatina (hilly country):* 1 ♀, Štúrovo [47°47'N, 18°43'E], 18 June 1964, J. Buchar (NMPC). *Kremnické vrchy mountains:* 1 ♂, 2 ♀, Budča, reserve Boky [48°34'N, 19°04'E], 1975, 1976, V. Thomka (VMH). *Malá Fatra mountains:* 1 ♂, Nezbudská Lúčka, reserve Starhrad [49°10'N, 18°51'E], F. Miller (NMPC); 1 ♀, same location, 6 May 1973, J. Svatoň (JS); 1 ♀, Strečno [49°10'N, 18°51'E], 11 May 1936, F. Miller (NMPC). *Malé Karpaty mountains:* 2 ♂, 1 juvenile, Stupava, Vrchná hora hill [48°16'N, 17°01'E], 30 April–23 May 1999, 23 May–19 June 1999, 19 June–17 July 1999, O. Majzlan (PG); 1 ♂, 2 ♀, Bratislava, reserve Devínska Kobyla [48°10'N, 17°00'E], 21 May, 21 June, F. Miller (NMPC); 1 ♂, 2 ♀, same location, 7 May 1975, 10 November 1978, O. Žitňanská (JS); 2 ♀, 2 juveniles, same location, 10 May–8 June 1979, 5 July–26 September 1979, 5 September 1980, P. Gajdoš (PG). *Myjavská pahorkatina (hilly country):* 1 ♀, Brezová pod Bradlom [48°39'N, 17°32'E], 9 June 1973, J. Vachold (PG). *Nitrianska pahorkatina (hilly country):* 2 ♂, 2 ♀, Veľký Báb, reserve Veľký Báb [48°19'N, 17°52'E], 10 May 1973, O. Žitňanská (JS). *Považské podolie:* 1 ♂, Trenčianské Bohuslavice, reserve Turecký vrch [48°47'N, 17°52'E], May–16 July 1985, P. Devan (PG). *Považský Inovec mountains:* 1 juvenile, Lúka, ruins of the castle Tematín [48°39'N, 17°52'E], 1 July 1985, P. Gajdoš (PG); 1 ♀, Beckov, Beckovské Skalice, Dubový vŕšok hill [48°47'N, 17°53'E], May–16 July 1985, P. Devan (PG). *Revúcka*

vrchovina mountains: 1 ♂, Sirk, Valašská dolina valley [48°37'N, 20°05'E], 23 September–17 October 1987, I. Mihál (JS); 1 ♂, 1 ♀, Sirk, Pod Ladislavou [48°37'N, 20°05'E], 3 June–10 July 1987, I. Mihál (JS); 1 juvenile, Sirk, Čierna dolina [48°37'N, 20°05'E], 27 August–23 September 1987, I. Mihál (JS). *Slovenský kras area– Plešivecká planina plateau:* 1 ♂, Gočaltovo, Pod Železnými vrátami [48°37'N, 20°20'E], 13 June 1983, J. Svatoň (JS); 1 ♂, Vidová, Teplá stráň [48°34'N, 20°25'E], 12 June 1983, J. Svatoň (JS); 1 ♀, Plešivec, Veľký vrch hill [48°34'N, 20°24'E], 25 June 1984, J. Svatoň (JS). *Slovenský kras area– Silická planina plateau:* 1 ♂, 1 ♀, Kečovo, Domica [48°30'N, 20°27'E], 15 May, F. Miller (NMPC); 2 ♀, 2 juveniles, same location, 22 August–8 October 2003, P. Gajdoš (PG); 1 ♀, Hrušov nad Turňou, Hradisko hill [48°35'N, 20°36'E], 19 August 2003, M. Řezáč (MR); 1 ♂, Hrušov nad Turňou, reserve Hrušovská lesostep [48°35'N, 20°36'E], 28 June 1984, J. Svatoň (JS); 1 ♂, 2 ♀, Jablonov, Hradište hill [48°36'N, 20°39'E], 16 October 1984, 24 July 1984, 16 October 1984, J. Svatoň (JS). *Spišsko-šarišské medzihorie mountains:* 1 ♀, 1 juvenile, Kapušany, reserve Kapušianský hradný vrch [49°02'N, 21°20'E], 20 June–30 August 1996, 31 July–9 October 1997, V. Thomka (VMH). *Štiavnické vrchy mountains:* 1 ♂, Počúvadlo, reserve Holík [48°21'N, 18°50'E], 13 May–17 July 1985, P. Gajdoš (PG); 1 juvenile, Tlmače, Krivín [48°16'N, 18°31'E], 4 July 1990, P. Gajdoš (PG). *Strážovské vrchy mountains:* 1 ♂, 1 ♀, Malé Krštеňany, reserve Veľký vrch [48°38'N, 18°25'E], 6 May–4 July 1984, 4 July–8 September 1984, P. Gajdoš (PG); 1 juvenile, Súľov-Hradná, reserve Súľovské skaly [49°09'N, 18°35'E], 3 July 1963, J. Vachold (PG); 1 juvenile, Bojnice, Kalvária hill [48°46'N, 18°34'E], 12 June 1991, S. Pekár (MR). *Tríbeč mountains:* 1 ♀, 2 juveniles, Nitrianska Streda, reserve Hrdovická [48°31'N, 18°10'E], 31 July–9 October 1986, 30 April–6 June 1986, 6 June–31 July 1986, P. Gajdoš (PG); 1 ♂, 1 ♀, Solčany, Úkropová [48°32'N, 18°12'E], 30 April–6 June 1986, P. Gajdoš (PG); 1 ♂, 2 ♀, Solčany, reserve Solčiansky háj [48°32'N, 18°12'E], 26 August–24 November 1987, 6 June–21 July 1987, P. Gajdoš (PG); 1 juvenile, Nitra, reserve Zoborská lesostep [48°20'N, 18°05'E], 10 May–12 June 1978, P. Gajdoš (PG). *Turčianska kotlina basin:* 3 ♂, 1 ♀, Vrútky, Chrapovský potok stream valley [49°06'N, 18°54'E], 23 July 1987, 23 July 1987, J. Svatoň (JS). *Vtáčnik mountains:* 1 ♀, Bystričany, Bystričianska dolina valley [48°39'N, 18°30'E], 3 April 1998, O. Majzlan (PG). *Zemplínske vrchy mountains:* 3 ♀, Viničky [48°23'N, 21°44'E], 12 April 1983, P. Gajdoš (PG). *Žilinská kotlina basin:* 1 ♂, 2 ♀, Žilina [49°13'N, 18°44'E], 2 May 1936, 25 May 1936, F. Miller (NMPC). *Žitavská pahorkatina (hilly country):* 9 ♂, 9 ♀, 1 juvenile, Nitrianské Hrnčiarovce, Malanta, way to Pohranice [48°19'N, 18°07'E], 5 May 1992, 11 June 1992, 11 June–15 July 1992, 25 August 1992, 25 August–29 September 1992, 12 November 1992, P. Gajdoš (PG).

Diagnosis.— *Dysdera lantosquensis* and *D. taurica* are the only central European *Dysdera* species possessing a concave mediodorsal margin of the basal cheliceral segment. In contrast to *D. taurica*, *D. lantosquensis* does not possess dorsal spines on tibiae III and IV.

DISCUSSION

Nomenclature.—The name *Aranea hombergi* Scopoli 1763 was regarded as a senior synonym of *D. ninnii* or *D. dubrovninnii*. However without access to the type material it is not possible to ascertain its exact identity. Therefore we suggest to regard the name *Aranea hombergi* as a nomen dubium (*sensu* International Commission on Zoological Nomenclature 2007). As the name *A. hombergi* was so far erroneously used for the common species of the genus *Harpactea*, the oldest synomym of this *Harpactea* species, *Harpactea latreillii* (Blackwall, 1832), should be used henceforward.

Distribution.—Nearly all species of *Dysdera* are restricted to the Palearctic region. Of the 241 species of *Dysdera* described so far, only *D. crocata* occurs outside the Palearctic

region. The remaining four species (Platnick 2007) are either synonyms of *D. crocata* (the Australian *D. australiensis* and the American *D. magna*) or are misplaced in the family Dysderidae. *Dysdera solers* Walckenaer 1837, described from Colombia, possesses apically rounded gnathocoxae (Walckenaer 1837) which are never present in members of *Dysdera*. Other features mentioned by Walckenaer (1837) (e.g., the body length and orange coloration) possibly correspond to a member of the family Caponiidae. The type material was not found in either the BMNH or MNHN. *Dysdera bicolor* Tatzanovski 1874, described from French Guyana, is only 2.5 mm long and possesses abdominal scuta (Tatzanovski 1874), which are never present in species of *Dysdera*, suggesting that it is a representative of the family Oonopidae, subfamily Gamasomorphinae. The type material was not found in either the Museum and Institute of Zoology in Warszawa or in the Museum of Natural History in Krakow. We can conclude that the genus, like all other members of the family, is originally endemic to the Palearctic region.

Patterns of distribution of *Dysdera* species in central Europe suggest limited migration abilities of these spiders. For example, *D. ninnii* is absent in the apparently climatically suitable but, by mountain range, isolated area of central Bohemia, Czech Republic. Representatives of the genus *Dysdera* are characterised by a long life and relatively low fecundity (*cf.* Cooke 1965). Thus they belong to K-selected species which do not undergo high-risk dispersal behaviors such as ballooning. Balloon dispersal has never been reported in *Dysdera* spiders, and they have never been recorded in aerial samples. For example, not a single specimen was captured among 10,000 spider specimens collected in Switzerland (Blandenier & Fürst 1998). A single ballooning dysderid recorded in Blandenier & Fürst (1998) turned out to be juvenile of *Harpactea* (Řezáč, unpublished). Nevertheless, *Dysdera* species are prone to passive accidental transport with human material due to their tendency to attach silken retreats to large objects lying on the ground. Chance dispersal by such transport is frequent among species with affinities for synanthropic habitats. The most extensive expansion of this type has been performed by *D. crocata*. Based on the distribution of its sister species, the autochthonous area of *D. crocata* is probably in the southern part of the Mediterranean, perhaps in northern Africa. Due to its adaptations to arid environments, it is able to survive a transport in dry conditions and to colonize relatively arid synanthropic habitats. Similar, yet less extensive, expansions to synanthropic habitats have also been recorded for several other species, namely *D. aculeata, D. lata, D. spinicrus, D. westringi* (Deeleman-Reinhold & Deeleman 1988), *D. kollari* (Gasparo 2004), and *D. erythrina* (a single occurrence in Slovakia). Further expansions of these species can be expected in the future.

A special preadaptation for migration is parthenogenesis within *D. hungarica*. As each adult specimen can produce eggs, thelytokous reproduction is twice as fast as bisexual reproduction where half of the population is males. Moreover, new localities can be colonized more quickly as a single individual can give rise to a new clone (Suomalainen *et al.* 1987). Recent expansion of parthenogenetic clones is documented in isolated localitions with anthropic habitats on the western edge of the distribution of *D. hungarica* (e.g., a commercial orchard in Prague).

Habitat requirements.—In central Europe, *Dysdera* species are characteristic of warm areas, where they occur mainly in xerothermic forests on bedrocks rich in minerals. This type of biotope seems to be common for the majority of *Dysdera* species even in the Mediterranean area, i.e., the speciation center of the genus (see Deeleman-Reinhold & Deeleman 1988). In contrast to the majority of species of other central European dysderid genera, *Harpactea* and *Dasumia* Thorell 1875, *Dysdera* species usually avoid distinctly dry microhabitats in forests. Central European *Dysdera* species also occur in semi-synanthropic habitats, e.g., in the vicinity of ruins overgrown by woody plants. We suggest that an affinity

for human buildings and their surrounds may be the result of rich calcium in the building materials, allowing the proliferation of woodlice, the principal prey of *Dysdera* (Cooke 1965).

In areas frequented by *D. ninnii*, the closely related species *D. dubrovninnii* is concentrated in non-forest habitats which is unusual for *Dysdera* species. Although this hypothesis is untested, we suggest that this could be a consequence of competition between these two species. A similar phenomenon was recorded from the sympatric area of *D. erythrina* and *D. crocata* in England (Cooke 1967).

Unusual ecological plasticity was observed in parthenogenetic clones of *D. hungarica*. These clones were found even in anomalous non-forest habitats such as wetlands with *Phragmites australis*, salt marshes, wet meadows, or vineyards. Thelytoky may enable the clones to survive even in suboptimal habitats, which are, however, not suitable to harbour the high abundance necessary for sexual reproduction.

Karyotype evolution.—The genus *Dysdera* exhibits the highest variation in chromosome number of all spider genera thus far studied (Král, unpublished data). Male diploid number ranges from 9 (*D. crocata*; Díaz & Sáez 1966; this study) to 40 (*D. longirostris*, this study). Such enormous variation, as well as an absence of karyotype data from other genera of the family, render it difficult to determine the ancestral karyotype of the genus *Dysdera*. However, due to the fact that even closely related species differ in chromosome number (*D. ninnii-D. dubrovninnii, D. hungarica-D. adriatica-D. longirostris*, this study; *D. erythrina-D. lantosquensis*, Řezáč *et al.* submitted), karyotype appears to be a useful character for the taxonomy of the genus. The high variation in chromosome numbers may be related to the holocentric structure of the chromosomes. Holocentric chromosomes exhibit kinetochore along the major part of their length. Therefore, products of chromosome fissions (fragments) or fusions (fused chromosomes) often segregate regularly to the poles during division and are then more easily tolerated than in organisms with more common monocentric chromosomes (Jacobs 2004). The structure of meiotic trivalent found in *D. adriatica* suggests that the specimen studied was heterozygous for chromosome fusion or fission. This finding supports our hypothesis about the frequent occurrence of these rearrangements in karyotype evolution in the genus *Dysdera*. Concerning sex chromosomes, we confirmed a sex chromosome system of X0 in *D. crocata* previously found by Díaz & Sáez (1966), Benavente & Wettstein (1980), Benavente (1982) and Rodríguez Gil *et al.* (2002). In contrast to the considerable variability in chromosome numbers, most *Dysdera* species exhibit an X0 sex chromosome system with the X chromosome being the largest chromosome. However, even number of chromosomes in male mitoses of *D. longirostris* indicates other sex chromosome systems than X0. The absence of meiotic plates made impossible determination of sex chromosome system in this species.

In *D. crocata*, we also detected interpopulation polymorphism in chromosome number. Males from various populations possessed four (2n = 9), five (2n = 11) or even six (2n = 13) pairs of autosomes. A similar range of variation in chromosome numbers also has been described in South American populations of *D. crocata*. Nine chromosomes were recorded in the population called *D. magna* from Uruguay (Díaz & Sáez 1966) and 11 chromosomes in the population from Argentina (Rodríguez Gil *et al.* 2002). We suggest the ancestral male karyotype of *D. crocata* probably contained 13 chromosomes as this chromosome number was also found in the related species *D. gammarae* from the Iberian Peninsula (Král, unpublished). The considerable chromosome polymorphism found in *D. crocata* indicates differentiation of this species into chromosomal races or even the existence of cryptic species.

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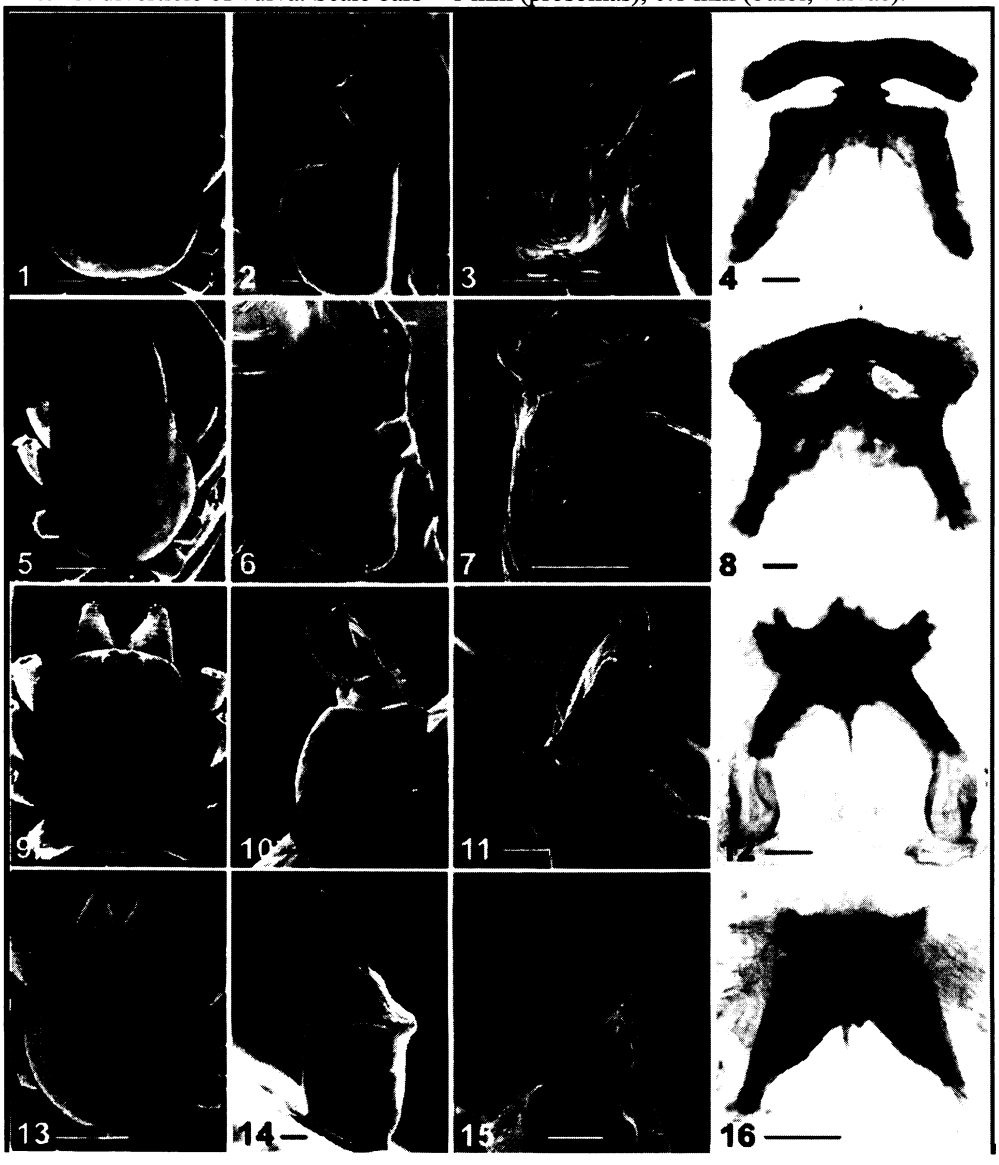
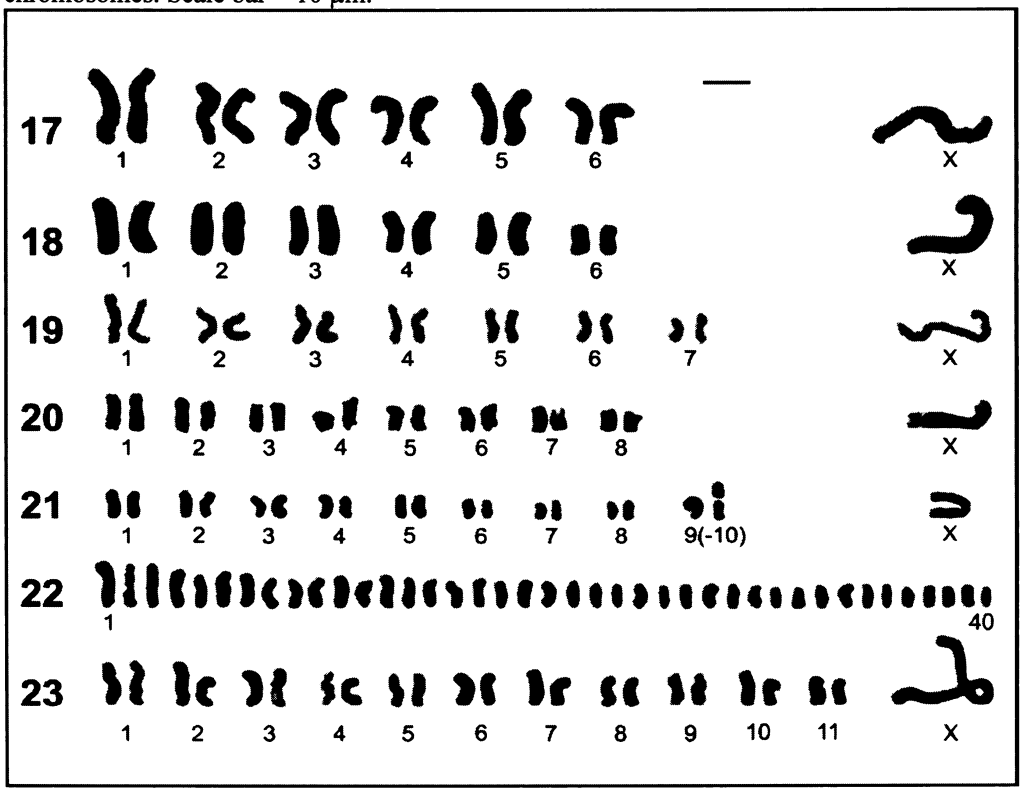
FIGURE LEGENDS

Figures 1–16.—Characters of central European *Dysdera* species, *Dysdera crocata* and *D. ninnii* groups. 1–4. *Dysdera crocata*, male, from Mikulov, Czech Republic; female from Nieuwpoort, Netherlands; 5–8. *D. maurusia*, male from Beni Sauda, Algeria; female from Maison Carrée, Algeria; 9–12. *D. ninnii*, male and female from Brtnice, Czech Republic; 13–16. *D. dubrovninnii*, male and female from Michalovce, Slovakia: 1, 5, 9, 13. Male prosoma, dorsal view; 2, 6, 10, 14. Bulbus; 3, 7, 11, 15. Detail of distal division of bulbus; 4, 8, 12, 16. Anterior diverticle of vulva. Scale bars = 1 mm (prosomas), 0.1 mm (bulbi, vulvae).



Figures 17–23.—Male karyotypes: 17. *Dysdera crocata*; 18. *D. ninnii*; 19. *D. dubrovninnii*; 20. *D. hungarica*; 21. *D. adriatica*; 22. *D. longirostris*; 23. *D. taurica*. Karyotypes are based on spermatogonial metaphases. The numbers indicate autosome pairs except for the unresolved karyotype of *D. longirostris*, where they indicate particular chromosomes. Scale bar = 10 μm.



Figures 24–25.—Chelicerae, ventral view. 24. *Dysdera ninnii*; 25. *D. dubrovninnii*. Scale bars = 1 mm.

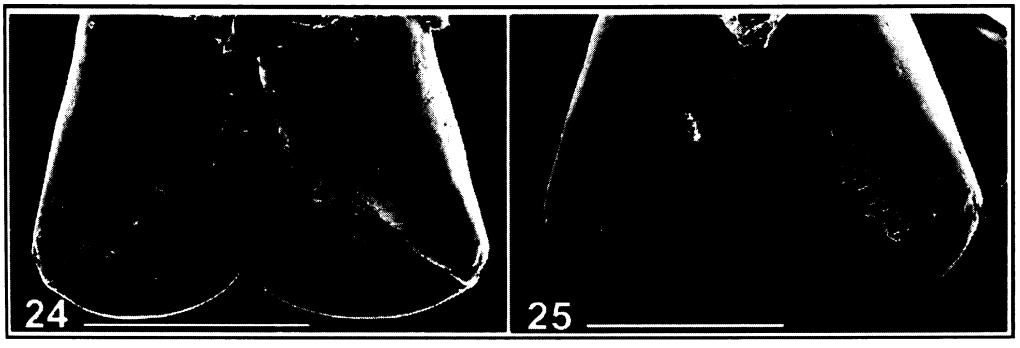
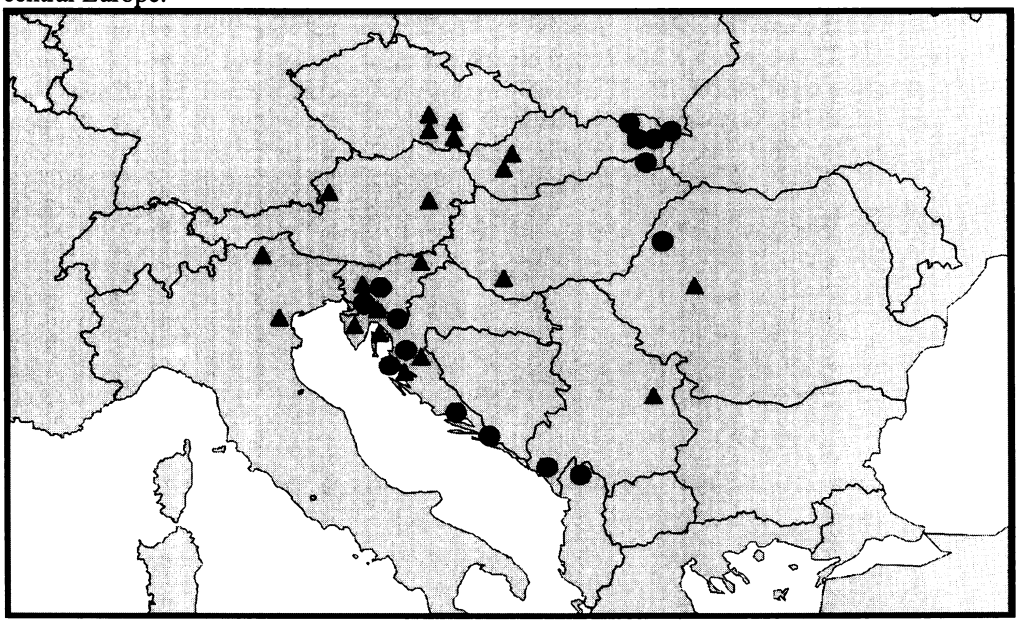


Figure 26.—Distribution of *Dysdera ninnii* (▲) and *Dysdera dubrovninnii* (●) in central Europe.



Figures 27–42.—Characters of central European *Dysdera* species, *Dysdera longirostris* and *D. lata* groups. 27–30. *D. hungarica*, male from Michalovce, Slovakia; female from Prague, Czech Republic; 31–34. *D. adriatica*, male and female from Postojna, Slovenia; 35–38. *D. longirostris*, male and female from Yalta, Crimea; 39–42. *D. taurica*, male from Niđde, Turkey; female from Konya, Turkey. 27, 31, 35, 39. Male prosoma, dorsal view; 28, 32, 36, 40. Bulbus; 29, 33, 37, 41. Detail of distal division of bulbus; 30, 34, 37, 41. Anterior diverticle of vulva. Scale bars = 1 mm (prosomas), 0.1 mm (bulbi, vulvae).

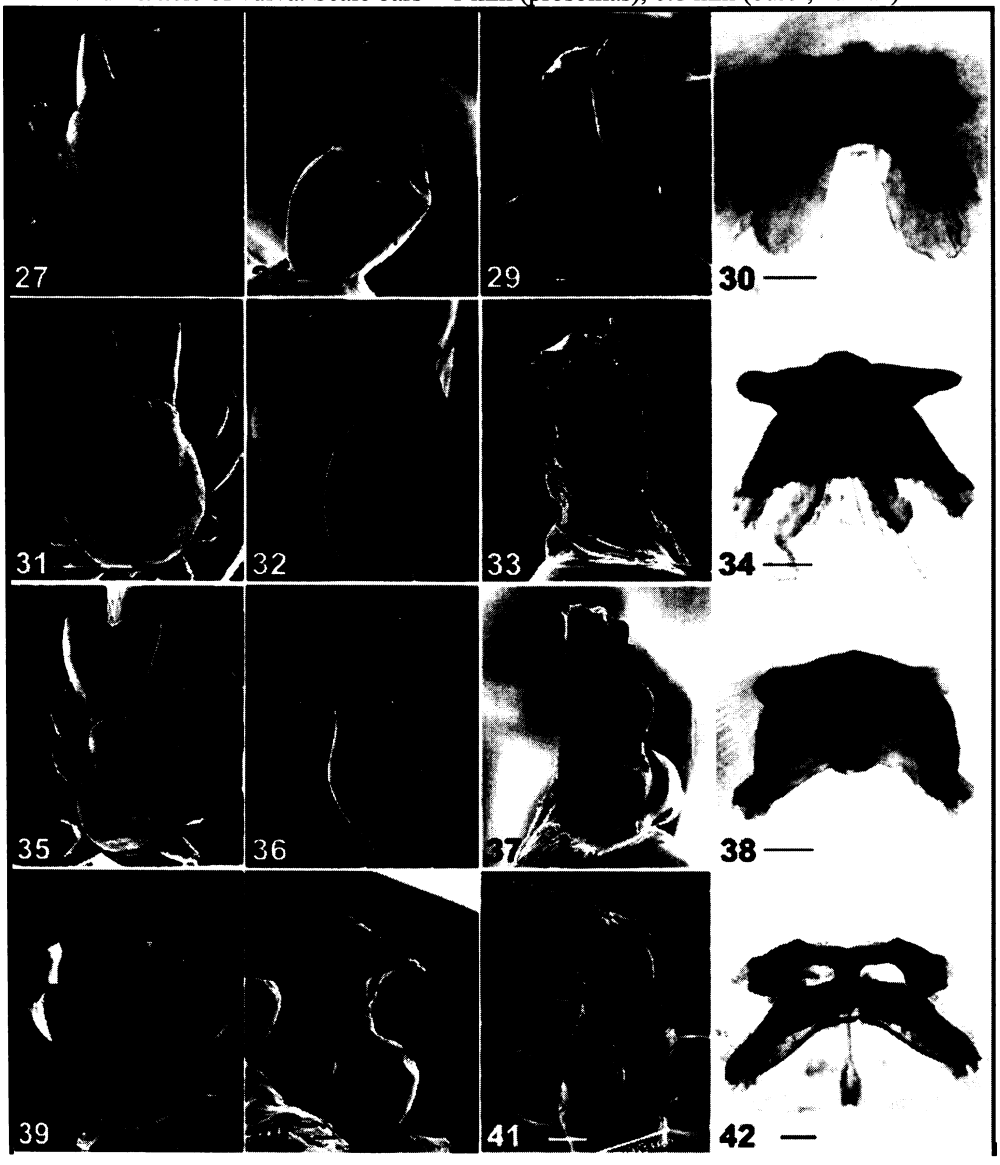
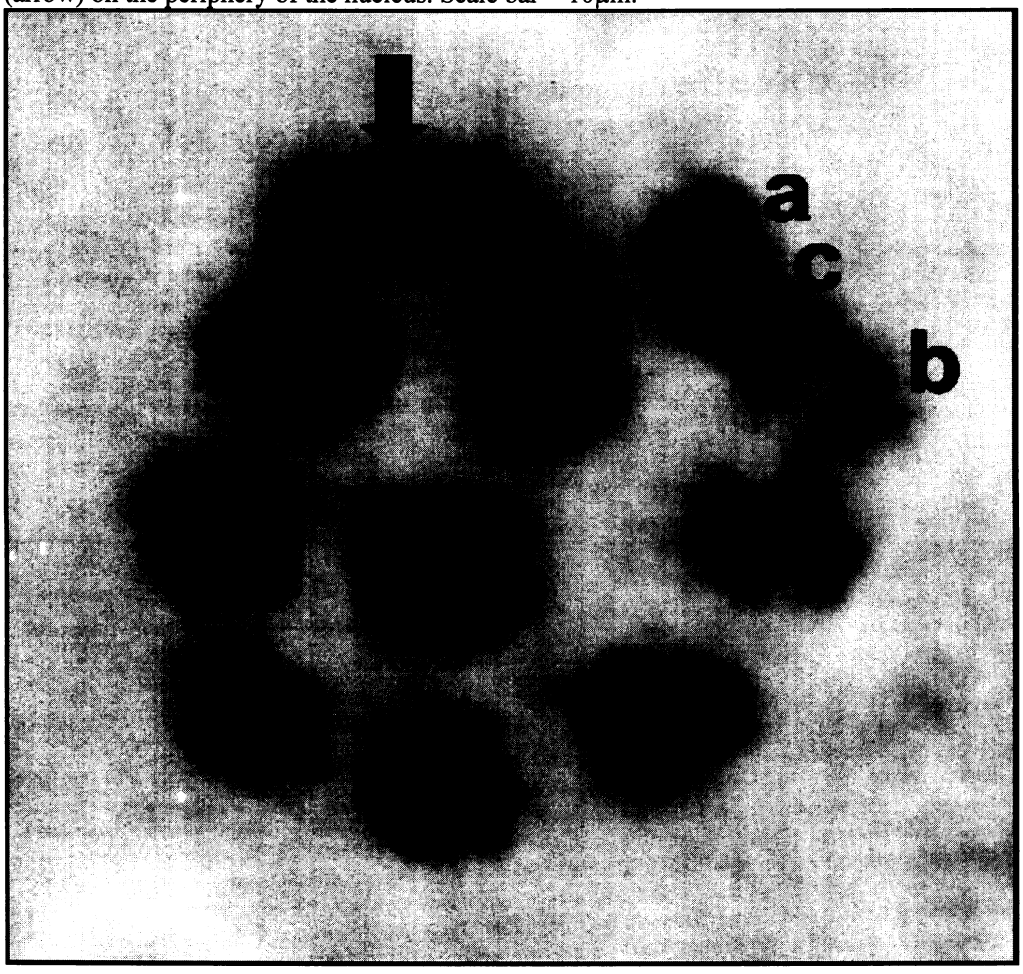


Figure 43.—*Dysdera adriatica,* male metaphase I. Note autosome trivalent (a, b – short chromosomes, c – long chromosome) and positively heteropycnotic X chromosome (arrow) on the periphery of the nucleus. Scale bar = 10μm.



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Evolution of the karyotype and sex chromosome systems in basal clades of araneomorph spiders (Araneae: Araneomorphae)

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Abstract

Concepts of spider karyotype evolution are based mostly on advanced and most diversified clade, the entelegyne lineage of araneomorph spiders. Hence the typical spider karyotype is supposed to consist exclusively of acrocentric chromosomes including the multiple X chromosomes. However, our data show considerable diversity of chromosome morphology and sex chromosome systems in basal clades of araneomorphs. Karyotypes of basal araneomorphs consist of holocentric (superfamily Dysderoidea) or normal chromosomes with localized centromere. In males of basal araneomorphs the prophase of first meiotic division includes a long diffuse stage. Multiple X chromosomes are less common in basal clades. The sex chromosome system of many families includes a Y chromosome or nucleolus organizer region that occurs rarely in the entelegyne spiders. A derived X_1X_2Y system with an achiasmatic sex-chromosome pairing during meiosis was found in the families Drymusidae, Hypochilidae, Filistatidae, Sicariidae, and Pholcidae. This suggests a monophyletic origin of the families. In some lineages the X_1X_2Y system converted into an X0 system, as found in some pholcids, or into an XY system, which is typical for the family Diguetidae. The remarkable karyotype and sex chromosome system diversity allows us to distinguish four evolutionary lineages of basal araneomorphs and hypothesize about the ancestral karyotype of araneomorphs.

Introduction

With regard to global diversity, spiders rank among the largest orders in the animal kingdom (Coddington & Levi 1991). Till now, roughly 39 500 species, classified into 111 families, have been described. From the evolutionary point of view, spiders form three basic monophyletic lineages, namely Mesothelae, Mygalomorphae, and Araneomorphae. However, the bulk of spider diversity is confined to the most derived spider group, the entelegyne lineage of the infraorder Araneomorphae (roughly 33 600 species) (Platnick 2006).

In keeping with the exceptional species diversity, spiders exhibit a great diversity in diploid chromosome numbers that ranges from 7 to 94 (Suzuki 1954). In contrast to this, the typical spider karyotype is uniform, consisting exclusively of acrocentric chromosomes (Rowell 1990). A unique feature of spider karyotypes is predominance of the multiple sex chromosome system $♂X_1X_2/♀X_1X_1X_2X_2$ (Maddison 1982). This system, often assigned as X_1X_20 (where 0 denotes the absence of the Y chromosome) was found in 77% of spider species studied so far (Araújo *et al.* 2005a). In contrast to other animals the X_1X_20 system seems to be an ancestral trait in spiders, resulting from its presence in the most primitive recent spider taxon, suborder Mesothelae (Suzuki 1954). The origin of the X_1X_20 sex chromosome system in spiders is unresolved. Published hypotheses stress its origin from an X0 system, usually by nondisjunction (Brum-Zorrilla & Postiglioni 1981) or fission (Suzuki 1954). In male prophase I the X chromosomes show higher superspiralization and, therefore, are stained more intensively than autosomes (i.e. exhibit the so-called positive heteropycnosis). They pair at the periphery of the nucleus without chiasma formation and segregate precociously to one of the spindle poles at anaphase I (Hackman 1948).

Despite evolutionary stability the X_1X_20 system was replaced by secondary systems in some spiders. In some genera $X_1X_2X_30$, or exceptionally $X_1X_2X_3X_40$, sex chromosome systems had evolved from the X_1X_20 mode by nondisjunction (Brum-Zorrilla & Postiglioni 1981). Some spider lineages are characterized by a X0 system that originated by centric fusion (Hackman 1948) or tandem fusion (Bole-Gowda 1950) between the X_1 and X_2 chromosomes.

Till now, karyotypes of more than 600 spider species belonging to 51 families have been described (J. Král, unpublished checklist). However, taking into account the enormous diversity of the spiders, our knowledge concerning their cytogenetics is still unsatisfactory. Moreover, the vast majority of studied species belong to the entelegyne araneomorphs. Analysis of the other groups, including phylogenetically basal clades of araneomorph spiders (sensu e.g. Coddington & Levi 1991, further basal araneomorphs), is highly underestimated. The basal araneomorph clades include more than 3200 species classified into 20 families (Platnick 2006). The most diversified basal araneomorphs are haplogyne spiders (17 families) that are considered to be a sister group of the entelegyne spiders. Beside haplogyne spiders, basal araneomorphs comprise two relict superfamilies, Hypochiloidea and Austrochilioidea (Coddington 2005).

Karyotypes of only 28 species of haplogynous spiders belonging to six families have been described so far (see Hetzler 1979, Rodríguez Gil *et al.* 2002, Silva *et al.* 2002, Araújo *et al.* 2005b,c). Karyotypes of the superfamilies Hypochiloidea and Austrochilioidea remain unknown. In spite of this, available data indicate remarkable karyotype differences between the entelegyne lineage and basal araneomorphs (Rodríguez Gil *et al.* 2002). Representatives of the families Dysderidae and Segestriidae possess holocentric chromosomes (Díaz & Sáez 1966, Benavente & Wettstein 1980, Rodríguez Gil *et al.* 2002). In contrast to this, monocentric chromosomes (i.e. chromosomes with localized centromere) compose karyotypes of other studied families, namely Filistatidae (Rodríguez Gil *et al.* 2002), Pholcidae (Araújo *et al.* 2005b), Scytodidae (Araújo *et al.* 2005c), and Sicariidae (Silva *et al.* 2002).

The present study aims to determine fundamental trends in karyotype evolution of basal araneomorphs. Species examined belong to 14 families, representing a cross-section through all clades of basal araneomorphs. Karyotypes of eight families are analysed for the first time. Our data conflict with a widely accepted assumption that karyotypes of almost all spiders are formed exclusively by acrocentric chromosomes and do not have the Y chromosome. Considerable differences found in basal araneomorphs indicate that the evolution of spider karyotypes was complicated and cannot be clarified by analysis of entelegyne groups only.

Material and methods

Specimens

Spiders were either collected individually or sifted from forest leaf litter. If necessary they were reared up to a stage suitable for karyotype analysis. Penultimate and/or adult males were found to be most suitable for the study. Their testes contained spermatogonial mitoses and numerous meiotic spermatocytes. Except *Segestria* and *Filistata*, penultimate males are already distinguishable from preceding instars by the inflated bulb. Subadult males were not optimal for the analysis in *Austrochilus* sp.; their testes contained mitoses only. On the other hand,

Table 1. List of species including karyotype, localities, instar and sex of examined specimens, and date(s) of chromosome preparation

Species	2n	Sex chrom.	Locality	Instar and sex (month of experiment)
Austrochilus sp.	38	XY	Chile: Villarica	1 mn, 2 sm, 2 fn (March 2004)
Diguetia albolineata	20	XY	USA: Arizona, Yarnell	6 f (Oct. 2004); 8 m, 3 f (Aug. 2005)
Diguetia canities	16	XY	USA: Arizona, Yarnell	4 f (Oct. 2004); 2 fn (Oct. 2004); 2 m, 2 f (Aug. 2005)
Drymusa capensis	37	X_1X_2Y	South Africa: Cape Town	1 fn, 2 f (May 2005); 2 m (Jul. 2005)
Dysdera crocata	13	X0	Portugal: Mitra near Evora	1 mn (Nov. 2004); 1 m (Dec. 2004); 2 f (April 2005); 2 sm, 3 m (Nov. 2005)
Filistata insidiatrix	33	X_1X_2Y	Greece: Thessaloniki	4 fn, 2 f (Jul. 1994); 1 mn, 1 m (May 2003); 3 fn (Jul. 2003)
			Greece: Epiros, Chani Terovou	1 sm (Sep. 2003); 1 m (Oct. 2004)
			Portugal: Mitra near Evora	1 mn (Nov. 2002); 1 sm (March 2003); 1 sm (March 2004); 1 m (May 2004)
Holocnemus caudatus	23	X0	Portugal: Mitra near Evora	2 sm, 1 m (Nov. 2001); 2 m (Jan. 2002)
Hypochilus pococki	29	X_1X_2Y	USA: Appalachian Mts., Cullowhee, NC	3 sm, 1 sf, 2 f (Jul. 2003)
Leptoneta infuscata	14	XY	Spain: Barcelona	3 mn, 1 sm, 2 sf, 7 f (Jun. 2003)
Loxosceles spinulosa	19	X_1X_2Y	South Africa: Ndumo Game Reserve	1 mn, 2 sm, 2 m, 3 f (Aug. 2003)
Loxosceles rufescens	21	X_1X_2Y	Portugal: Mitra near Evora	1 m, 2 f (Oct. 2003)
			Portugal: Mesquita	1 sm, 1 m (Oct. 2003)
Monoblemma muchmorei	23	X0	USA: Puerto Rico, Luquillo	12 m, 16 f (Oct. 2004); 7 m, 10 f (Feb.2005)
Ochyrocera sp.	13	X0	USA: Puerto Rico, Luquillo	1 m (Oct. 2004)
Plectreurys tristis	18	X_1X_20	USA: Arizona, Yarnell	2 mn, 3 fn, 2 f (Oct. 2004)
Pholcus phalangioides	25	X_1X_2Y	Czech Republic: Ústí nad Labem	5 sm (Jun. 1995)
			Czech Republic: Prague	14 m, 13 f (Dec. 1995); 2 m, 1 f (April 2000)
			Czech Republic: Pardubice	4 m, 3 f (Jul. 2000)
			Czech Republic: České Budějovice	11 sm, 12 m, 3 f (Oct. 2000)
			Czech Republic: Nový Jičín	3 m, 1 f (Jun. 2004); 2 m (Sep. 2004)
Scytodes thoracica	19	X0	Czech Republic: Mikulov	5 m, 2 f (Sep. 2003)
Segestria bavarica	14	X_1X_20	Belgium: Gent	1 sm, 2 f (Aug. 2004)
Segestria senoculata	14	X_1X_20	Czech Republic: Valašské Meziříčí	2 m (Sep. 2003)
			Czech Republic: Hostašovice	1 m (Aug. 2004); 1 fn (Oct. 2004)
			Czech Republic: Tupadly near Mělník	1 mn, 1 fn (March 2006)
Spermophora senoculata	25	X_1X_2Y	Portugal: Mitra near Evora	4 m, 2 f (Dec. 2001); 6 m, 5 f (Jan. 2002)
			Portugal: Evora	1 sm (Oct. 2003); 2 f (Nov. 2003)

m = male, f = female, sm = subadult male, sf = subadult female, mn = male nymph, fn = female nymph.

adult testes of some species contained only rare cells (*Filistata insidiatrix*) or no dividing cells (*Plectreurys tristis*). The male karyotype of *Plectreurys* was determined using mitotic cells from the intestine. Female mitotic metaphases were obtained from the ovaries, intestine or whole content of the abdomen, respectively. Dissected specimens are deposited in the collection of J.K. Detailed data concerning specimens used are presented at Table 1.

Chromosome preparations

Chromosomes were prepared by a spreading technique described by Traut (1976), with some modifications. The gonads were hypotonized in 0.075 M KCl for 10–15 min and fixed in two changes of freshly prepared methanol:acetic acid (3:1) (10 and 20 min). Cell suspension was prepared from a piece of tissue in a drop of 60% acetic acid on a microscope slide. The preparation was displaced on a histological plate (temperature 40°C). The drop of suspension was moved on the slide by a tungsten needle until the drop had evaporated. Preparations were stained with 5% Giemsa solution in Sörensen buffer (pH 6.8) for 25–30 min or left unstained for C-banding. In some spiders the staining time was prolonged due to a low affinity of chromatin to the Giemsa dye, namely in pholcids (40 min) and drymusids (50 min). For application of the following techniques the temperature of the plate was reduced to 30°C for better preservation of chromatin structure. C-

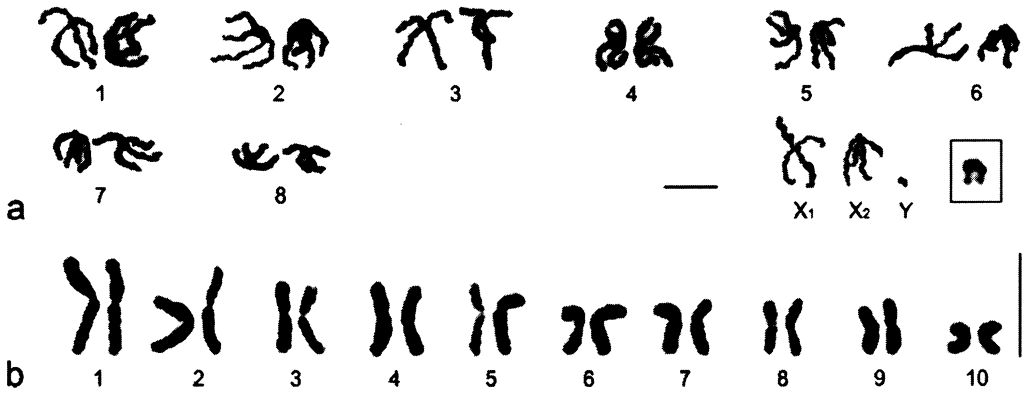


Figure 1. Karyotype of *Loxosceles spinulosa* (Sicariidae): (**a**) male (metaphase II). Inset: magnified Y chromosome from another metaphase II. Note metacentric morphology of Y chromosome. (**b**) Female (mitotic metaphase). Bars = 10 μm.

banding was carried out according to Sumner (1972). Staining of nucleolar organizer regions (NOR) by $AgNO_3$ was performed according to Howell & Black (1980).

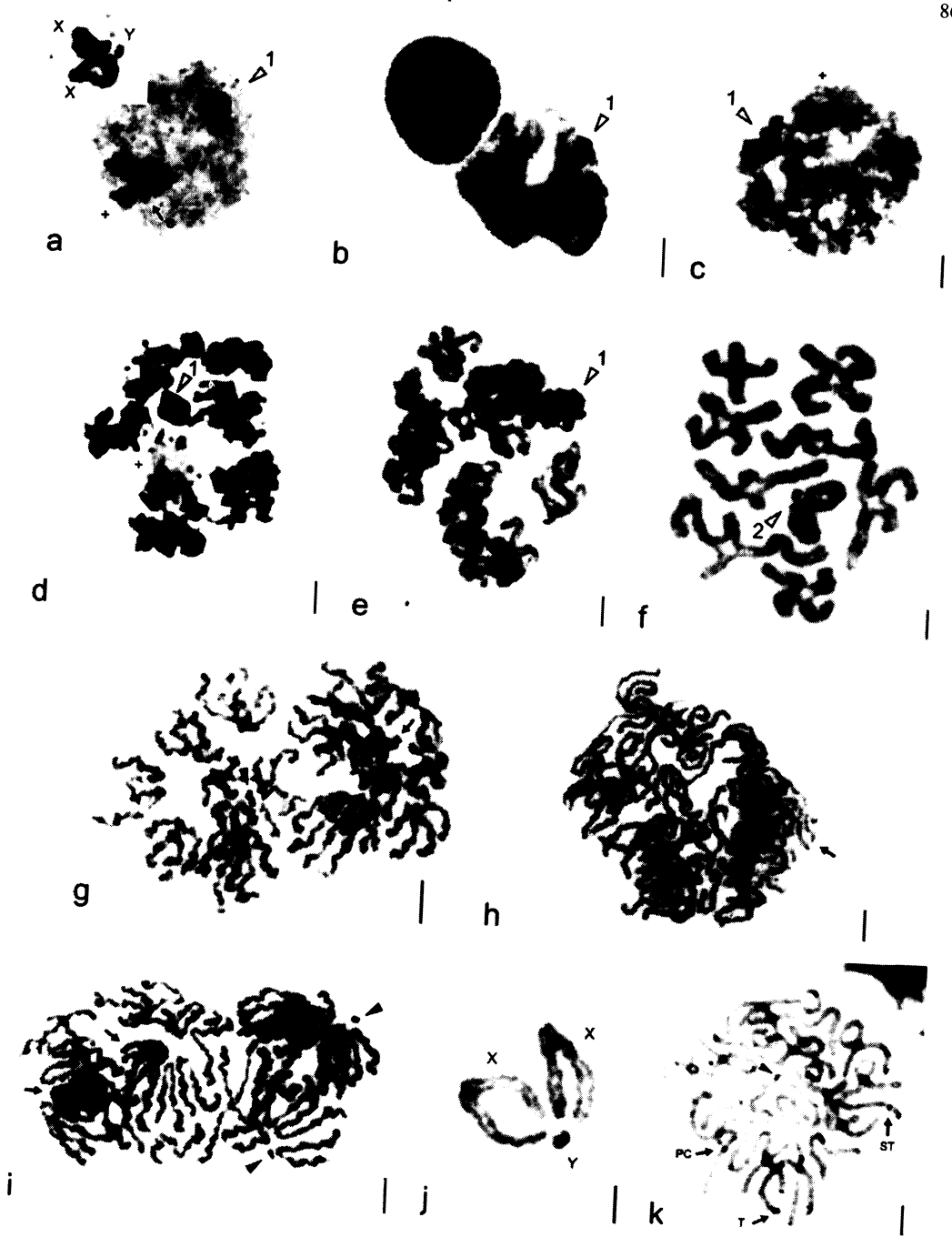
The majority of species was studied for the first time. Karyotype data were revised in three species, namely *Pholcus phalangioides* (Rodríguez Gil *et al.* 2002), *Spermophora senoculata* (Painter 1914), and *Segestria senoculata* (Suzuki 1954). Chromosome preparations were inspected in a Jenaval microscope and selected figures were photographed on Kodak Technical Pan film. Ten mitotic metaphases or metaphase II of each species were evaluated to construct the karyotype. In the latter case the plates containing both sister metaphase II were used for evaluation. Relative chromosome lengths were calculated as a percentage of the total chromosome length of the diploid set, including the sex chromosome(s) (% TCL). Chromosome morphology was classified according to Levan *et al.* (1964). In holocentric chromosomes only the chromosome length was evaluated, due to absence of the centromere.

Results

Basal araneomorphs with X_1X_2Y system

Owing to large chromosomes the genus *Loxosceles* (Sicariidae) has been found to be a suitable model of basal araneomorphs with the peculiar X_1X_2Y system. The male karyotype of *L. spinulosa* comprises eight autosome pairs and three sex chromosomes, X_1, X_2, and Y (Figure 1a), whereas females have $2n = 20$ (Figure 1b). In contrast to the considerable sizes of autosomes and X chromosomes the Y chromosome is tiny (0.6% of TCL). Except for two submetacentric autosome pairs (Nos 3 and 5), chromosomes are metacentric (Figure 1a). The male karyotype of *L. rufescens* ($2n♂ = 21$) contains eight metacentric and one submetacentric autosome pairs. After C-banding the autosomes and X chromosomes of both species show the same pattern, all carrying a pericentromeric block of heterochromatin of a variable size. Moreover, some chromosomes contain telomeric and subtelomeric block(s) of heterochromatin. The Y chromosome

Figure 2. Behaviour and structure of sex chromosomes in males of the family Sicariidae. Open arrowhead = chromosomes X_1, X_2, and Y forming body (1) or trivalent (2); arrowhead = Y chromosome; arrow = X_1X_2 pseudobivalent; crosslet = pair of metacentric chromosomes associated lengthwise. *Loxosceles spinulosa*: (**a**) premeiotic interphase. Sex chromosomes form heteropycnotic body (1), centromeres of heteropycnotic chromosome pair are marked by knob (c). Top left = X_1X_2Y trivalent, interphase; (**b**) pachytene nucleus, peripheral body formed by sex chromosomes is not heteropycnotic; (**c**) early diffuse stage; (**d**) late diffuse stage; (**e**) early diplotene, note unusual coiling of bivalents; (**f**) diakinesis; (**g**) anaphase I; (**h**) prophase II; (**i**) anaphase II. *L. rufescens*; (**j**) diakinesis, X_1X_2Y trivalent; (**k**) mitotic metaphase, C banding. Note pericentromeric (PC), subtelomeric (ST), and telomeric (T) blocks of constitutive heterochromatin. Arrowhead = Y chromosome with prominent block of pericentromeric heterochromatin. Bars = 5 μm.


X
Y
X
1
a
1
b
1
+
c
1
+
d
1
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i
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X
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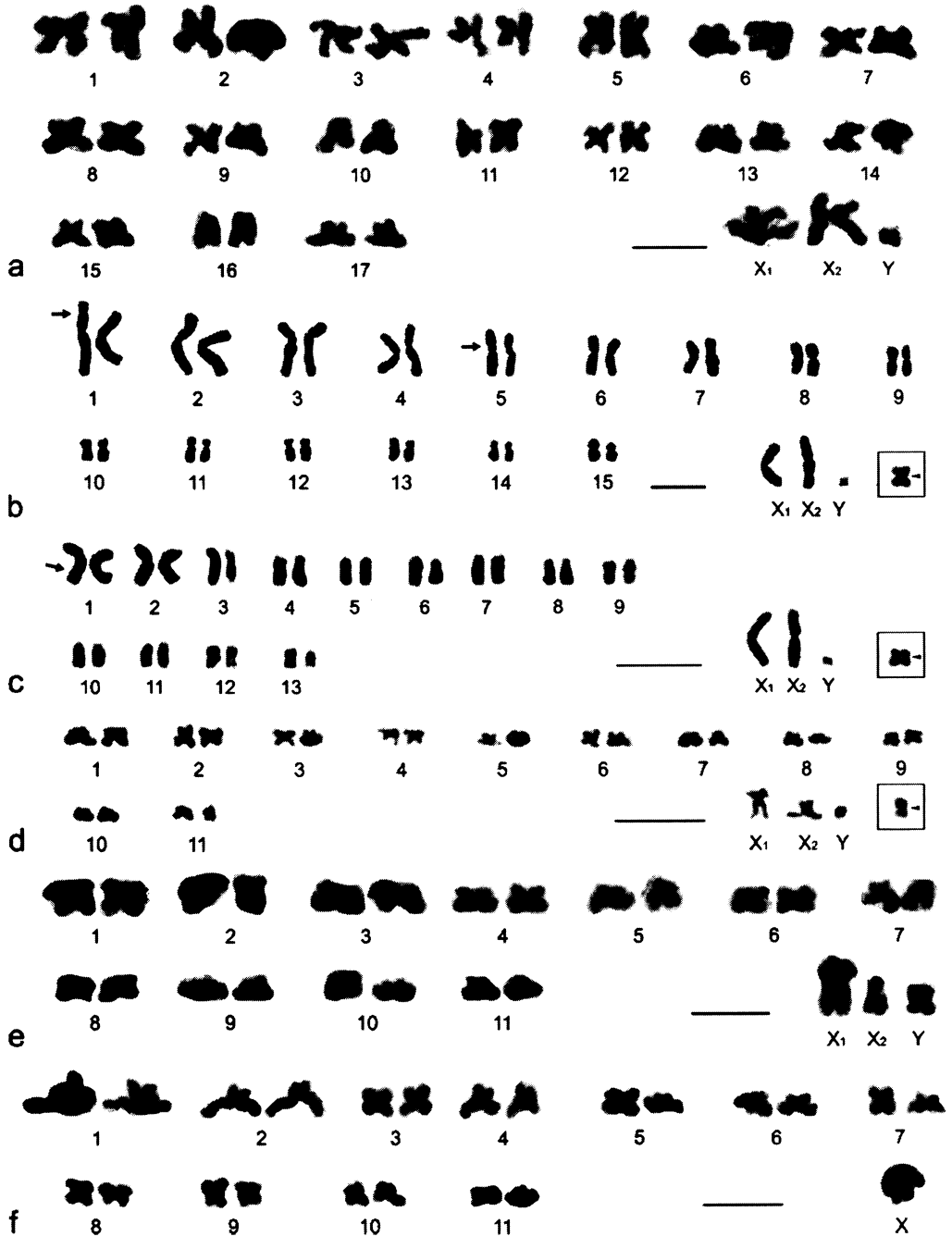
j
PC
ST
T
k


1 2 3 4 5 6 7
8 9 10 11 12 13 14
a 15 16 17 X1 X2 Y
1 2 3 4 5 6 7 8 9
b 10 11 12 13 14 15 X1 X2 Y
1 2 3 4 5 6 7 8 9
c 10 11 12 13 X1 X2 Y
1 2 3 4 5 6 7 8 9
d 10 11 X1 X2 Y
1 2 3 4 5 6 7
e 8 9 10 11 X1 X2 Y
1 2 3 4 5 6 7
f 8 9 10 11 X

carries a distinct centromeric block of heterochromatin (Figure 2k).

During the premeiotic interphase of *L. spinulosa*, the sex chromosomes exhibit distinctive heteropycnosis forming a trivalent on the periphery of the nucleus (Figure 2a). The same behaviour was also observed in other spiders with an X_1X_2Y system. Interestingly, two other chromosomes exhibit similar behaviour in interphase nuclei of *Loxosceles*. They display positive heteropycnosis and are associated lengthwise on the periphery of the nucleus. This association seems to be most stable at telomeric regions. Both chromosomes are metacentric and of a similar size, and their centromere regions are marked by knobs (Figure 2a). From their clear morphological similarity we infer that they belong to the same pair. The curious autosome pair is often associated with the sex chromosome trivalent. Both chromosome groups lose heteropycnosis at the onset of meiosis (Figure 2b). Following pachytene the spermatocytes enter the diffuse stage. In contrast to considerable despiralization of autosome bivalents the X_1X_2Y trivalent and curious autosome pair form heteropycnotic bodies on the periphery of the nucleus (Figure 2c). The two chromosome groups are often associated with each other (Figure 2c,d). During the late diffuse stage the curious bivalent becomes partially negatively heteropycnotic and coupled with a nucleolar mass. On the other hand, the remaining bivalents spiralize (Figure 2d). A similar diffuse stage was also found in the other basal araneomorphs under study. In *Loxosceles* the diffuse stage is followed by a short diplotene: autosomes display sudden changes of morphology that are manifested by unusual coiling of bivalents (Figure 2e). These changes give rise to standard morphology of the bivalents with chiasmata. Subsequently the sex chromosomes lose heteropycnosis due to extensive despiralization. At diakinesis and metaphase I, the arms of the metacentric X chromosomes exhibit distal end-to-end pairing with arms of the tiny metacentric Y chromosome (Figure 2f,j, Figure 11a). The arms of the Y chromosome are usually closely aligned during pairing. The same arrangement of sex chromosomes was found during premeiotic interphase (Figure 2a). The anaphase I shows segregation of heteropycnotic X chromosomes (associated by centromeres) to one pole, and the heteropycnotic Y chromosome to the other pole being in the centre of figure (Figure 2g). By prophase II the despiralized X chromosomes form a curious lump on the periphery of the plate (Figure 2h). During the following condensation the X chromosomes lie close to each other. During anaphase II the sex chromosomes exhibit a similar behaviour as at anaphase I (Figure 2i).

Our study also revealed the presence of the X_1X_2Y system in other families of basal araneomorphs (Table 1). Sex chromosomes of *Drymusa capensis* ($2n♂ = 37$, Drymusidae), *Filistata insidiatrix* ($2n♂ = 33$, Filistatidae), and *Hypochilus pococki* ($2n♂ = 29$, Hypochilidae) exhibit a similar morphology (Figure 3a–c), mode of meiotic pairing (Figure 4a–c), and anaphase segregation as the genus *Loxosceles*. On the other hand, autosome complements of these spiders are diversified. Autosomes of *Drymusa* are metacentric except for one submetacentric pair (No. 16) (Figure 3a). The mitotic metaphase of the *Filistata* male shows 11 metacentric and five submetacentric (Nos 3 and 11–14) autosome pairs. The first three pairs are formed by large biarmed chromosomes (from 6% to 4.6% of TCL). The first pair contains subterminal, and the fifth pair pericentromeric, secondary constrictions (Figure 3b). Autosomes of *Hypochilus* can be divided into two size groups: (a) three large pairs of metacentric autosomes, and (b) smaller autosome pairs with metacentric (Nos. 9 and 12), submetacentric (No. 4), and acrocentric (remaining pairs) morphology (Figure 3c). Ag-staining corroborates one NOR at the intercalar secondary constriction of the largest autosome pair and another NOR at the end of one arm in one short metacentric pair. Male meiosis of *Hypochilus* shows an extremely long diffuse stage; bivalents with chiasmata appear during prometaphase I only.

In the family Pholcidae we found remarkable diversity in sex chromosome systems. All autosomes and both X chromosomes of *Spermophora senoculata* ($2n♂ = 25$, X_1X_2Y) are metacentric. The tiny Y

Figure 3. Male karyotypes of the families Drymusidae, Filistatidae, Hypochilidae, and Pholcidae. Unless otherwise indicated, based on metaphase II. (**a**) *Drymusa capensis*; (**b**) *Filistata insidiatrix* (mitotic metaphase); (**c**) *Hypochilus pococki* (mitotic metaphase); (**d**) *Spemophora senoculata*; (**e**) *Pholcus phalangioides*; (**f**) *Holocnemus caudatus*. Arrow = secondary constriction. Insets: magnified Y chromosome from another mitotic metaphase (**b,c**) or metaphase II (**d**). Note metacentric morphology of Y chromosome (arrowhead = primary constriction). Bars = 10 μm.

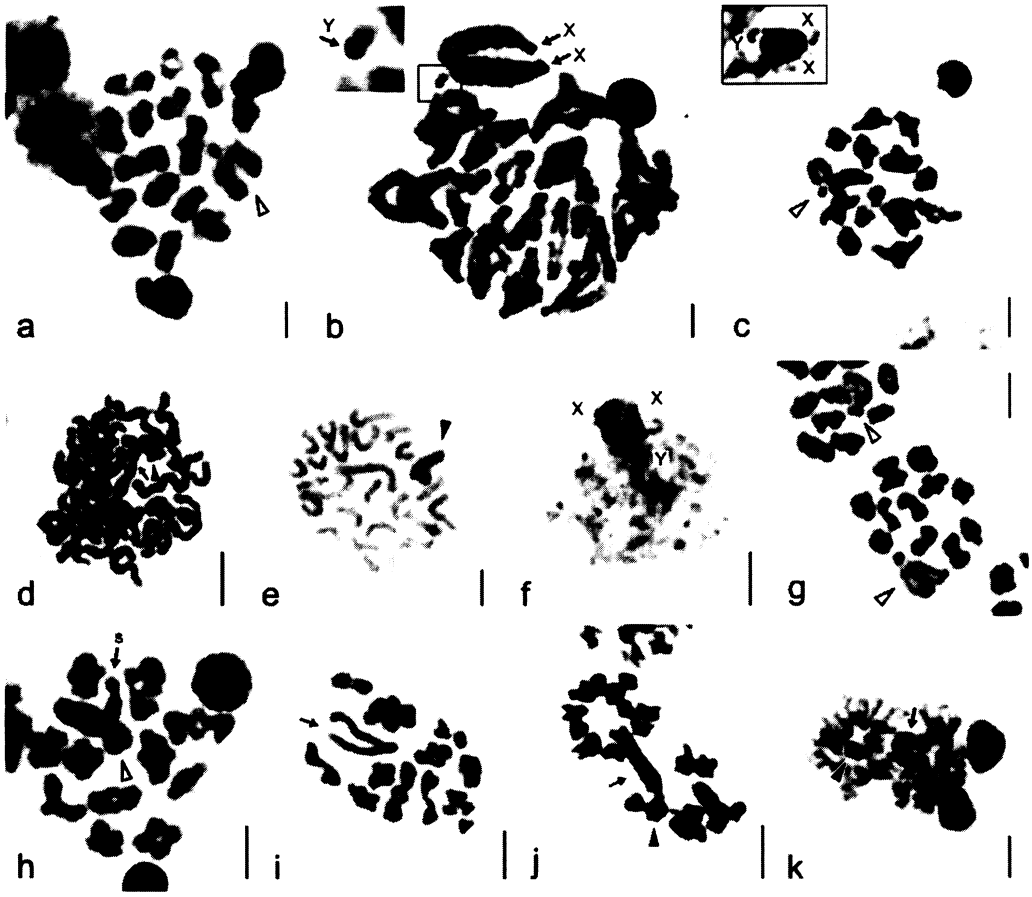


Figure 4. Behaviour and structure of sex chromosomes in males of the families Drymusidae, Filistatidae, Hypochilidae, and Pholcidae. Open arrowhead = trivalent X_1X_2Y; arrowhead = Y chromosome; arrow = X chromosome(s). *Drymusa capensis*: (**a**) metaphase I. *Filistata insidiatrix*: (**b**) metaphase I, note X_1X_2Y trivalent (top left = detail of Y chromosome pairing). Centromeric knobs (X = knobs of X chromosomes, Y = knob of Y chromosome) do not take part in pairing. Pairing is ensured by distal ends of arms; *Hypochilus pococki*: (**c**) metaphase I. Top left = X_1X_2Y trivalent, pachytene nucleus. Note ends of Y chromosome take part in pairing. *Pholcus phalangioides*: (**d**) late spermatogonial prophase, note association of sex chromosomes; (**e**) spermatogonial metaphase, C banding. Heterochromatinic Y chromosome is placed on the periphery of the plate. The other chromosomes show tiny blocks of pericentromeric heterochromatin; (**f**) premeiotic interphase, note heterochromatinic trivalent on the periphery of the nucleus. *Spermophora senoculata*: (**g**) metaphase I. *P. phalangioides*: (**h**) metaphase I, s = short arm of X_2 chromosome. *Holocnemus caudatus*: (**i**) metaphase I. *P. phalangioides*: (**j**) anaphase I, sex chromosomes form bridge between sister plates; (**k**) telophase I, sex chromosomes exhibit heteropycnosis. Associated X chromosomes move to one pole (right), and Y chromosome to the other pole (left). Bars = 5 μm.

chromosome (1.6% of TCL) is probably also a metacentric chromosome; its primary constriction was seen only in some plates (Figure 3d). Sex chromosomes exhibit the same type of meiotic pairing as the previous families (Figure 4g). The autosome complement of *Pholcus phalangioides* ($2n♂ = 25, X_1X_2Y$) is similar to *Spermophora*. Except for two submetacentric pairs (Nos 7 and 10), all autosomes are metacentric. Relative lengths of autosomes range from 5.3% to 2.7% of TCL. The metacentric X_1 is the lon-

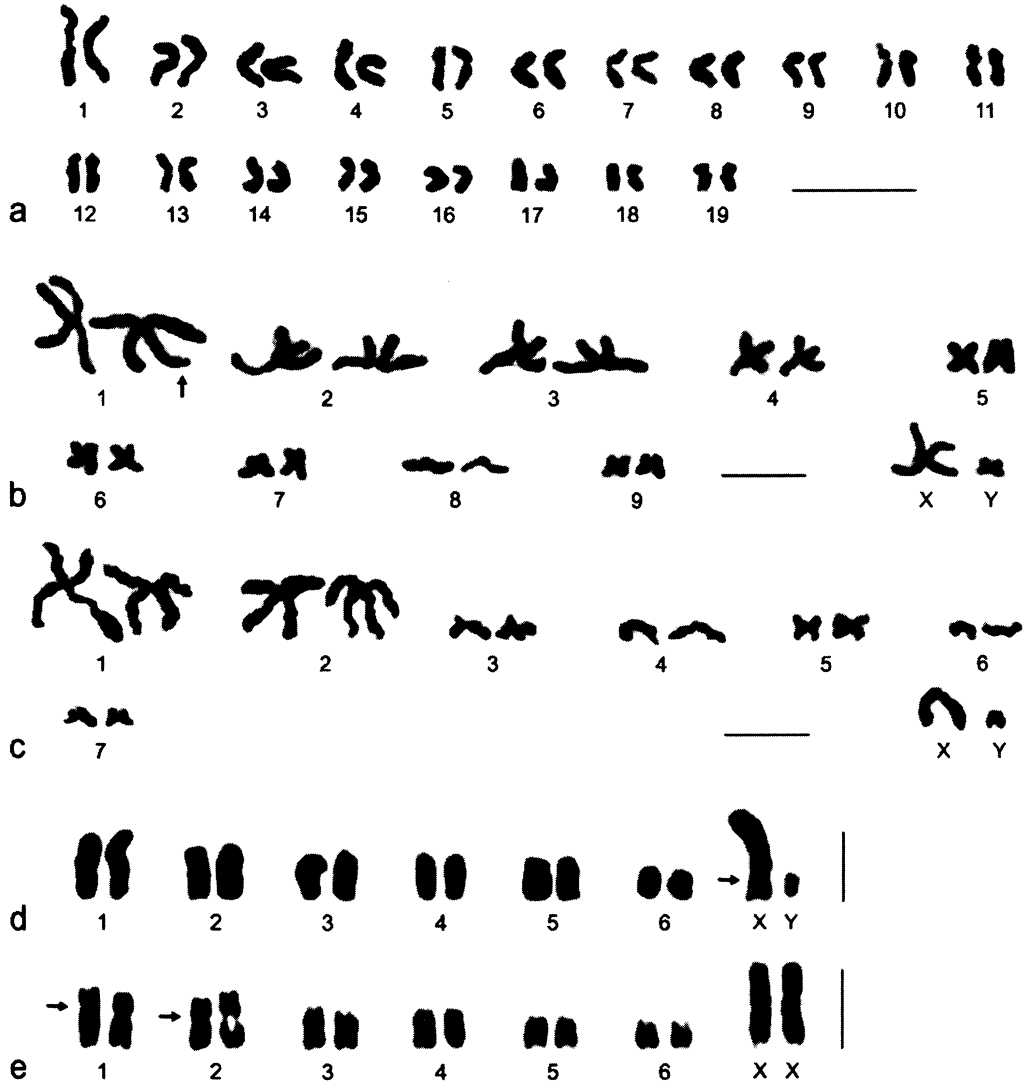


Figure 5. Karyotypes of basal araneomorphs with XY system. (**a**) *Austrochilus* sp., female (mitotic metaphase); (**b**) *Diguetia albolineata*, male (metaphase II); (**c**) *D. canities*, male (metaphase II); *Leptoneta infuscata*, male (**d**) and female (**e**) (mitotic metaphase). Arrow = secondary constriction. Bars = 10 μm (**a–c**) and 5 μm (**d–e**).

gest chromosome, submetacentric X_2 medium-sized, and metacentric Y small (6.8%, 4.2% and 2.9% of TCL, respectively) (Figure 3e). In contrast to the other species with an X_1X_2Y system, the short arm of the X_2 chromosome does not take part in meiotic pairing with the Y chromosome (Figure 4h). Moreover, the Y chromosome is formed entirely by constitutive heterochromatin (Figure 4e). The male karyotype of *Holocnemus caudatus* is most derived, composed of 11 autosome pairs and an X chromosome (Figure 4i).

Except for three submetacentric pairs (Nos 2, 4, and 9), all autosomes are metacentric (Figure 3f). The size of autosomes of the first pair (8.1% of TCL) approximates nearly the metacentric X chromosome, which is the longest element in the karyotype (9.7%), while autosomes of the remaining pairs are shorter, ranging from 5.2% to 2.6% of TCL.

The behaviour of sex chromosomes in pholcids is somewhat different from that in other spiders with an X_1X_2Y system. The sex chromosomes of pholcids are already heteropycnotic at the spermatogonial prophase and prometaphase. In *P. phalangioides* the sex chromosomes are associated with each other during early prophase (Figure 4d). By late prophase the association is abandoned first by the Y chromosome and then by X chromosomes. In spite of this, sex chromosomes remain close to each other during the entire process of mitosis. Furthermore, the sex chromosome trivalent formed at interphase nuclei (Figure 4f) does not lose heteropycnosis at early prophase I. Segregation of pholcid sex chromosomes is lagged during anaphase I so that the X_1X_2Y trivalent becomes stretched between sister plates (Figure 4j). Sex chromosomes segregate during telophase I only (Figure 4k).

Basal araneomorphs with an XY system

The XY system was found in *Austrochilus* sp. (Austrochilidae), the genus *Diguetia* (Diguetidae), and *Leptoneta infuscata* (Leptonetidae) (Table 1). Considering karyological data, basal araneomorphs with an XY system constitute a quite heterogeneous group.

In *Austrochilus* sp., we obtained only mitotic plates. Both sexes regularly show 38 small chromosomes (Figure 5a). This implies the presence of an XY sex chromosome system. The sex chromosomes are, however, indistinguishable from autosomes. Except for one submetacentric pair (No. 19), all chromosomes are metacentric (Figure 5a).

The karyotype of the genus *Diguetia* contains two size groups of autosomes. Three large pairs of *D. albolineata* ($2n♂ = 20$) are metacentrics (from 11.1% to 8.1% of TCL). Six small pairs (from 4.3% to 2.7% of TCL) also show metacentric morphology except for the acrocentric pair No. 8 (Figure 5b). The acrocentric pair and one large metacentric pair each possess a subterminal NOR. Moreover, distinct pericentromeric NOR is located in one small metacentric pair. X and Y chromosomes differ considerably in size, the X chromosome being nearly the size of large metacentric autosomes (7.9% of TCL) while the Y is the smallest chromosome (2.2% of TCL) (Figure 5b). The karyotype of *D. canities* ($2n♂ = 16$) contains two pairs of large metacentrics (15.1% and 12.8% of TCL) and five small pairs (from 4.3% to 2.9% of TCL) that exhibit metacentric (Nos 3, 5 and 7), subtelocentric (No. 6), and acrocentric morphology (No. 4) (Figure 5c). The acrocentric X chromosome is medium-sized (5.5% of TCL) whereas the metacentric Y is the smallest chromosome (2.1% of TCL) (Figure 5c).

During the premeiotic interphase of *Diguetia* the X chromosome pairs by one end with the Y chromosome that is usually placed beneath the nuclear envelope. Besides sex chromosomes, another heteropycnotic chromosome pair is situated on the periphery of the nucleus. This pair is often associated by one end with the XY pair via Y chromosome (Figure 6a). Ag staining revealed a frequent association of the pair with the nucleolus in interphase nuclei. Association of the sex chromosomes and the curious bivalent is often also seen during the diffuse stage. Despiralization of sex chromosomes following the diffuse stage allows us to determine the mode of their pairing. Long arm of the X chromosome shows distal end-to-end pairing with both arms of the metacentric Y chromosome (Figure 6c–e). In *D. albolineata* heteropycnosis of two curious autosomes appears once again, namely at the beginning of the second meiotic division. Prometaphase II revealed that these autosomes are large metacentric chromosomes (Figure 6f); they do not differ significantly by size or morphology.

The karyotype of *Leptoneta infuscata* ($2n♂ = 14$) is formed by acrocentric chromosomes exclusively, and the longest and shortest chromosomes are odd in the male (Figure 5d). A comparison of male and female karyotypes revealed that the odd elements are X and Y chromosomes (Figure 5d,e). The two longest autosome pairs each bear an intercalar secondary constriction (Figure 5e). The X chromosome of *Leptoneta* carries a subterminal secondary constriction (Figure 5d). In onset of prophase I the X chromosome differentiates into a proximal heteropycnotic rod and a distal filament (Figure 6g), which is much longer than the proximal part (Figure 6h). The distal filament runs to the opposite side of the nucleus, where it is associated by its end with both the large nucleolus (Figure 6i) and the tiny Y chromosome (Figure 6h). In contrast to *Diguetia* the morphology

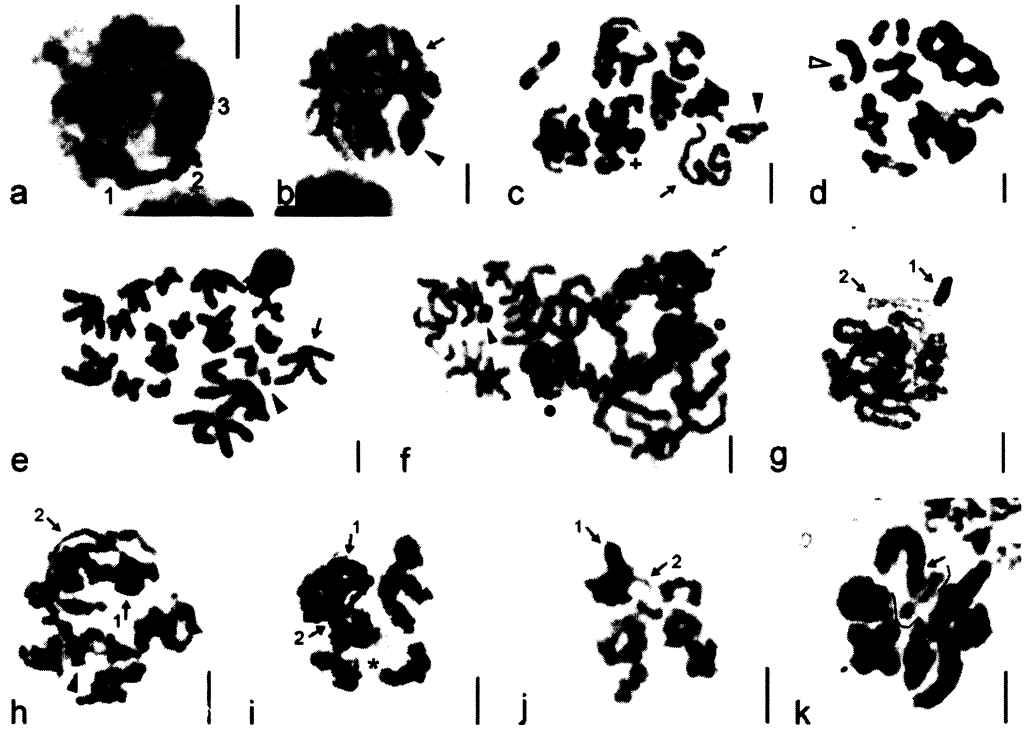


Figure 6. Behaviour of sex chromosomes in males of basal araneomorphs with XY system. Open arrowhead = heterobivalent XY, arrowhead = Y chromosome, arrow = X chromosome, + = curious bivalent. *Diguetia albolineata*: (**a**) premeiotic interphase. Note association among X chromosome (1), Y chromosome (2), and heteropycnotic pair (3) on the periphery of the nucleus; (**b**) pachytene; (**c**) diplotene, note coiling of bivalents including curious heteropycnotic bivalent (+). One X chromosome arm shows distal end-to-end pairing with both Y chromosome arms. *D. canities*: (**d**) diakinesis, note heterobivalent XY. *D. albolineata*: (**e**) early anaphase I, chromosomes X and Y start to separate; (**f**) prometaphase II, encircled asterisks = chromosomes of curious pair. *Leptoneta infuscata*: proximal (1) and distal (2) part of X chromosome differ by pattern of condensation during early meiosis I. (**g**) pachytene; (**h**) late diffuse stage; (**i**) diakinesis, asterisk = nucleolus; (**j**) prometaphase I; (**k**) metaphase I, note razor-like heterobivalent XY. Arrow points to X chromosome constriction. Encircled = chiasma between distal part of X chromosome and minute Y chromosome. Bars = 5 μm.

of autosome bivalents becomes clearly discernible already at the late diffuse stage. However, bivalents still remain considerably despiralized (Figure 6h). In contrast, the filamentous part of the X chromosome exhibits considerable condensation (Figure 6i) becoming shorter than the proximal part by prometaphase I (Figure 6j). During metaphase I heteropycnosis of the X chromosome disappears, accompanied by considerable changes in the morphology of XY pair, which mostly adopts a strange razor-like appearance (Figure 6k). The two X-chromosome parts do not differ by their morphology; however, they are separated by a distinct constriction. 'Head of razor' is formed by a Y chromosome and the distal part of X chromosome that are connected by a chiasma (Figure 6k).

Basal araneomorphs with monocentric chromosomes and X0 system

Representatives of the families Ochyroceratidae (*Ochyrocera* sp., $2n♂' = 13$), Scytodidae (*Scytodes thoracica*, $2n♂' = 19$), and Tetrablemmidae (*Monoblemma muchmorei*, $2n♂' = 23$) are remarkable for an X0 system including NOR. The male karyotype of *S. thoracica*

Figure 7. Male karyotypes of families with monocentric chromosomes and X0 system. (**a**) *Scytodes thoracica* (metaphase II); (**b**) *Ochyrocera* sp. (mitotic metaphase); (**c**) *Monoblemma muchmorei* (mitotic metaphase). Arrow = secondary constriction. Bars = 5 μm.

shows metacentric (Nos 2 and 4), submetacentric (No. 3), subtelocentric (Nos 5 and 6), and acrocentric (Nos 1, 7–9) pairs of autosomes. The metacentric X chromosome is the longest chromosome of the complement (Figure 7a) with one arm displaying a distinct intercalar constriction. Although we failed to visualize this constriction as NOR in mitosis, Ag staining revealed a frequent association of the X chromosome and one interphase nucleolus. Analysis of meiotic division confirmed the presence of an X0 system (Figure 8a).

The karyotype of *Ochyrocera* and *Monoblemma* comprises metacentric chromosomes only. One autosome pair and the X chromosome of *Ochyrocera* carry a subterminal secondary constriction (Figure 7b). The X chromosome of *Monoblemma* is more than twice as long as the longest autosome pair (Figure 7c). Ag staining revealed two NOR on the X chromosome of this spider: one in a subterminal position of one arm and one at the end of the other arm.

Moreover, the longest autosome pair exhibits a pericentromeric NOR. In contrast to *Scytodes*, X-linked NOR of *Ochyrocera* and *Monoblemma* is active during prophase I. During pachytene the X chromosome of these spiders shortens substantially, forming a heteropycnotic body associated with the nucleolus. In *Monoblemma* the arms of the X chromosome usually pair with each other, forming a loop surrounding the nucleolus (Figure 8b). In both genera chiasmata already appear to be discernible during the late diffuse stage (Figure 8f). In spite of this, the course of the diffuse stage is very complicated in *Monoblemma*. At the end of pachytene the X chromosome shows transient decondensation (Figure 8c). At the early diffuse stage bivalents show almost complete despiralization. The condensed X chromosome is associated with an expanded nucleolus (Figure 8d). Subsequent condensation of bivalents is accompanied by transient but very intensive despiralization of the X chromosome that follows the same pattern as at the end of pachytene (Figure 8e). During the late diffuse stage the X chromosome again becomes heteropycnotic (Figure 8f), but this feature disappears together with degrading nucleoli. In metaphase and anaphase I the two X arms remain associated with each other (Figure 8g,h). The lagging X chromosome forms a bridge between sister plates at anaphase I (Figure 8h).

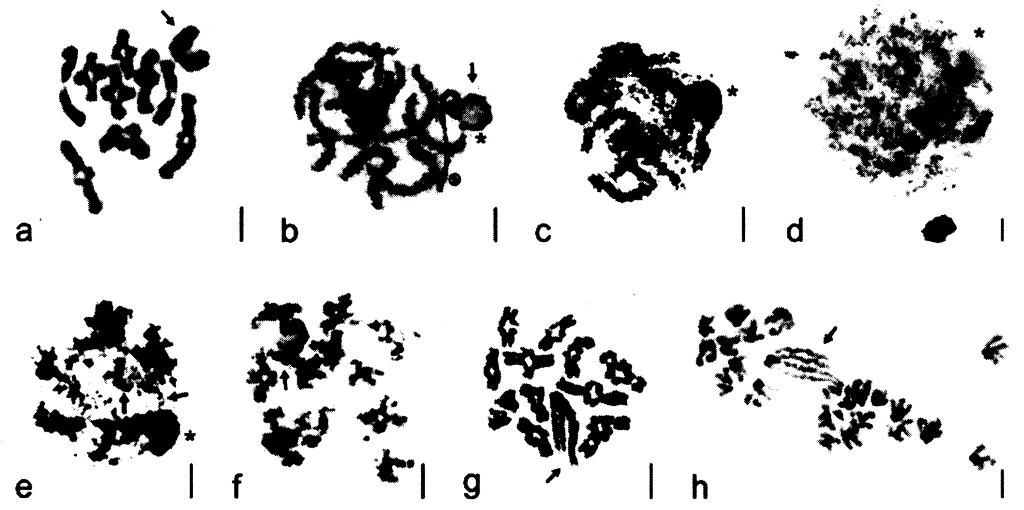


Figure 8. Behaviour of sex chromosomes in males of the families with monocentric chromosomes and X0 system. Arrow = X chromosome, asterisk = nucleolus. *Scytodes maculata*: (**a**) metaphase I. *Monoblemma muchmorei*: (**b**) pachytene, one arm of X chromosome is associated with nucleolus. Second arm bearing terminal knob (encircled asterisk) was released from nucleolus during preparation; (**c**) shift to diffuse stage, Ag staining. X chromosome is despiralized and not visible; (**d**) early diffuse stage, prominent nucleolus is associated with heteropycnotic X chromosome; (**e**) middle diffuse stage, Ag staining. Sex chromosome is largely despiralised; (**f**) late diffuse stage, X chromosome is associated with nucleolus; (**g**) metaphase I; (**h**) anaphase I, X chromosome forms bridge. Centromeres of all chromosomes are marked by distinct knob. Bars = 5 μm.

Basal araneomorphs with monocentric chromosomes and an X_1X_20 system

The male karyotype of *Plectreurys tristis* (Plectreuridae) consists of 18 chromosomes (Figure 9a) and a female karyotype of 20 chromosomes (Figure 9b). A comparison of both sexes implies an X_1X_20 sex chromosome system. We obtained only mitotic plates. The chromosome complement is dominated by metacentric chromosomes. The X_1 chromosome is metacentric and X_2 is subtelocentric (Figure 9a).

Basal araneomorphs with holocentric chromosomes

Representatives of the families Dysderidae and Segestriidae show holocentric chromosomes. Males of *Dysdera crocata* exhibit six autosome pairs and an X chromosome (Figure 9c). One autosome pair carries a terminal NOR. Moreover, the X chromosome is associated with one or two nucleoli during the diffuse stage (Figure 10b). Males of *Segestria senoculata* and *S. bavarica* show six autosome pairs and two sex chromosomes of similar lengths (Figure 9d), whereas females have 2n = 16. The mode of sex chromosome segregation at male meiosis suggests that they represent two X chromosomes (Figure 10j,k).

Following standard pachytene (Figure 10a), nuclei enter a diffuse stage (Figure 10b,c); chiasmata are formed during diakinesis (*Segestria*, Figure 10h) or metaphase I (*Dysdera*, Figure 10d) only. Autosomes are characterized by telokinetic activity at anaphase of first and second meiotic division (10 e,g,i,k). The two genera differ considerably by behaviour of sex chromosomes during segregation. In metaphase I the X chromosome of *Dysdera* lies in parallel to the equator with both ends of each chromatid slightly upturned to the same pole (Figure 10d). This orientation precedes inverted meiosis of X chromosome, i.e. the X chromatids separate at anaphase I moving in parallel to the equator (Figure 10e). This orientation of sex chromosome is retained during metaphase II (Figure 10f). Sex chromosomes of *Segestria* exhibit extreme decondensation from anaphase I (Figure 10i) until the end of prometaphase II,

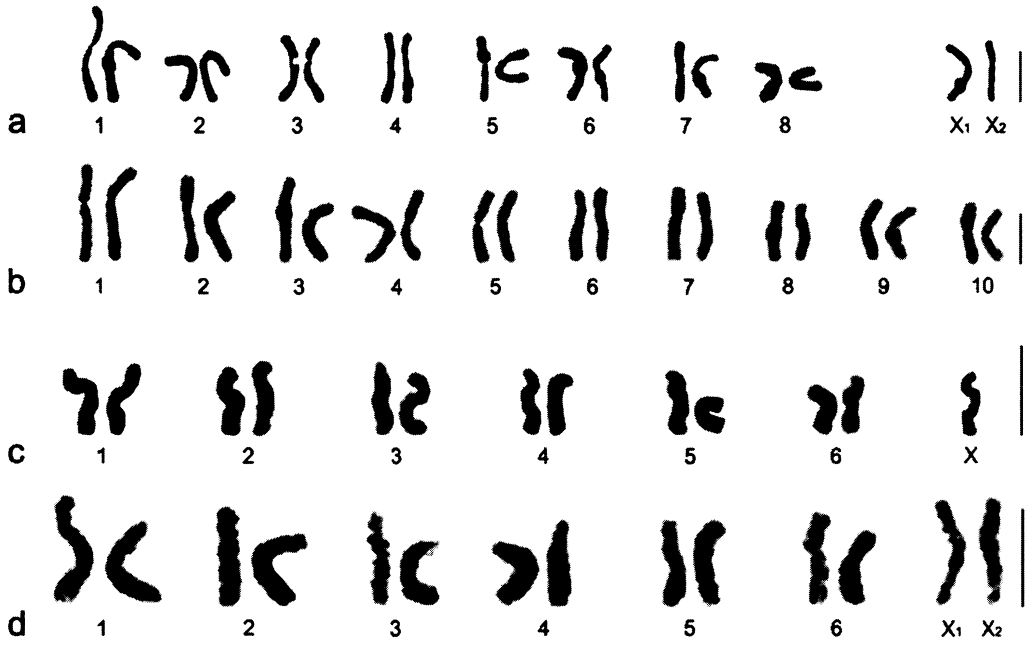


Figure 9. Karyotypes of the families Plectreuridae, Dysderidae and Segestriidae; based on mitotic metaphases. *Plectreurys tristis*, male (**a**) and female (**b**); (**c**) *Dysdera crocata*, male; (**d**) *Segestria bavarica*, male. Bars = 10 μm.

which complicated analysis of their segregation. However, analysis of the following meiotic stages shows that sister chromatids of the X chromosomes separate during anaphase II only (Figure 10j,k).

Discussion

Karyotypes of basal araneomorphs

Based on high chromosome numbers in primitive spiders of the suborder Mesothelae, Suzuki (1954) assumed that the karyotype evolution in spiders has been realized via reduction of chromosome numbers. This author classified spiders into three types according to their chromosome numbers. Spiders with a high chromosome numbers ($2n > 46$ for males), which was regarded as the primitive type, those with $2n = 34–46$ (the so-called intermediate type), and with low chromosome numbers ($2n < 34$). From this standpoint, karyotypes of most araneomorph spiders are derived, having relatively low chromosome numbers. In males of basal araneomorphs, 2n ranges from 7 (*Ariadna lateralis*, Segestriidae; Suzuki 1954) to 38 (*Austrochilus* sp., Austrochilidae; this study). In addition, $2n = 7$ in *A. lateralis* is the lowest diploid chromosome number known in spiders. Males of entelegyne araneomorphs show a similar range of chromosome numbers from $2n = 10$ (*Uloborus danolius*, Uloboridae; Parida & Sharma 1987) to $2n = 49$ (*Araneus ventricosus*, Araneidae; Wang *et al.* 1993). Basal araneomorphs much like entelegyne spiders exhibit a considerable variability in chromosome sizes. Some groups possess large chromosomes (Plectreuridae, Segestriidae, Sicariidae) whereas others have minute chromosomes (Austrochilidae, Hypochilidae, Leptonetidae, Ochyroceratidae, some Pholcidae, Tetrablemmidae).

A distinctive feature of most entelegyne karyotypes is the predominance of acrocentric chromosomes and constancy of the sex chromosome system X_1X_20. In contrast, basal lineages of araneomorphs are characterized by considerable variability of chromosome structure (Rodríguez Gil *et al.* 2002) and sex chromosome systems (Král *et al.* 2004, this

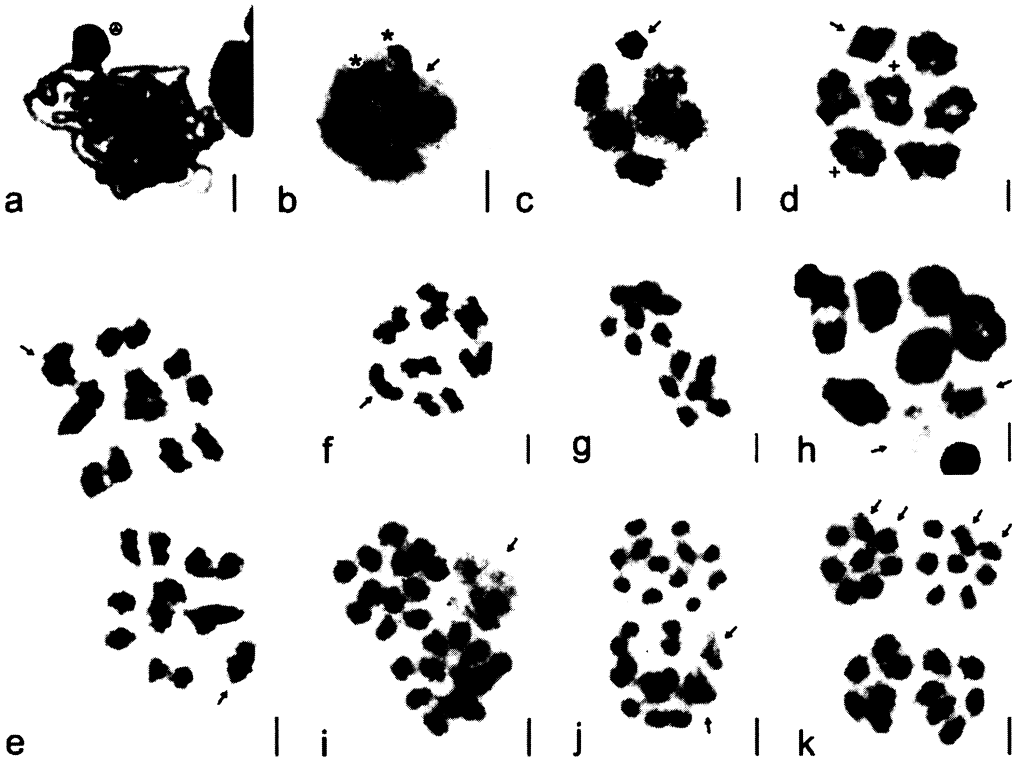


Figure 10. Behaviour of sex chromosomes in males of the families Dysderidae and Segestriidae. Arrow = X chromosome(s), asterisk = nucleolus. *Dysdera crocata*: (**a**) pachytene, encircled triangle = sperm nucleus; (**b**) early diffuse stage, Ag staining. Note two nucleoli associated with X chromosome; (**c**) late diffuse stage; (**d**) metaphase I, crosslet = bivalent with visible chiasmata; (**e**) anaphase I; (**f**) metaphase II; (**g**) anaphase II. *Segestria senoculata*: (**h**) diakinesis; (**i**) anaphase I; (**j**) metaphase II; (**k**) anaphase II, distal parts of X chromosomes are underspiralized. Bars = 5 μm.

study). According to the structure of chromosomes, basal araneomorphs can be divided into two groups. Representatives of the families Dysderidae and Segestriidae possess holocentric chromosomes (Díaz & Sáez 1966, Benavente & Wettstein 1980, Rodríguez Gil *et al.* 2002). Our study shows that holocentric chromosomes are characteristic also for the remaining families of the superfamily Dysderoidea, Oonopidae and Orsolobidae, and thus probably ancestral for this group (Král *et al.* 2004). In general, holocentric chromosomes are of polyphyletic origin, since there is no coherent pattern in their occurrence throughout the animal and plant kingdoms (Král 1994a, Rodríguez Gil *et al.* 2002, Maddox *et al.* 2004). Most probably the holocentric chromosomes originated from the normal (monocentric) chromosomes by expansion of kinetic activity over the large area of the chromosome surface (Král 1994a, Nagaki *et al.* 2005). Amongst arachnids, holocentric chromosomes also occur in buthid scorpions (Shanahan 1989) and acariform mites (Oliver 1977). Karyotypes of the other groups of basal araneomorphs are composed of monocentric chromosomes. In contrast to entelegyne spiders, biarmed chromosomes (i.e. metacentric and submetacentric) predominate in karyotypes of these clades except for the family Leptonetidae (this study) and some species of the family Scytodidae (Araújo *et al.* 2005c, this study). Biarmed chromosomes also prevail in the sister group of araneomorph spiders, the infraorder Mygalomorphae (Řezáč *et al.* 2006). This evolutionary pattern indicates

that predominance of biarmed chromosomes is probably an ancestral trait of spider karyotypes. We suggest that acrocentric chromosomes of leptonetids and scytodids were derived from original biarmed chromosomes by pericentric inversions.

Structure and evolution of sex chromosome systems

From the evolutionary point of view an X_1X_20 sex chromosome system appears to be ancestral in spiders (Suzuki 1954). However, in contrast to entelegyne spiders, where this system predominates, it has been found in only two genera of basal araneomorphs. Concerning spiders with holocentric chromosomes the X_1X_20 system was confirmed in the genus *Segestria* (Suzuki 1954, Díaz & Sáez 1966, Benavente & Wettstein 1980). Other representatives of the superfamily Dysderoidea (*Dysdera*, Benavente & Wettstein 1980; *Ariadna*, Suzuki 1954, Rodríguez Gil *et al.* 2002) show an X0 system that probably arose by fusion of the sex chromosomes X_1 and X_2. In basal clades with monocentric chromosomes the X_1X_20 system was found only in a representative of the family Plectreuridae (this study). In many other families with monocentric chromosomes our study revealed the presence of the Y chromosome, which is very rare in entelegyne spiders (Maddison 1982, Rowell 1985).

A highly derived X_1X_2Y system with a peculiar type of chromosome pairing during meiosis was found in the families Drymusidae, Filistatidae, Hypochilidae, Pholcidae and Sicariidae. This system differs from the X_1X_20 system both in structure and meiotic pairing. In spite of this, the X_1X_2Y mode was usually misinterpreted as an X_1X_20 system, probably due to the tiny size of the Y chromosome and the poor availability of published data. The Y chromosome in spiders was first discovered by Hetzler (1979) in *Kukulcania hibernalis* (Filistatidae) and *Loxosceles reclusa* (Sicariidae), both belonging to the haplogyne lineage. However, his finding was published only as an abstract. Thus, the X_1X_2Y system was properly described for the first time by D. Silva (1988) in *L. laeta*. In the present study we found the X_1X_2Y system in European pholcids and also in other basal araneomorphs. In the majority of studied species the X_1 and X_2 chromosomes are large metacentric chromosomes. The Y chromosome probably exhibits a metacentric morphology in all species studied, though its primary constriction was not seen in all plates due to the tiny size of this chromosome. In species with metacentric morphology of X chromosomes we have found the same type of meiotic pairing as proposed by Silva *et al.* (2002) in *Loxosceles*. During prophase and metaphase I, arms of the X_1 and X_2 chromosomes exhibit distal end-to-end pairing with both arms of Y chromosome (Figure 11a). In comparison with autosome bivalents the X_1X_2Y trivalent exhibits frequent disintegration in preparations, which indicates an achiasmatic mode of sex chromosome pairing. Besides this, achiasmatic pairing is also indicated by an abnormal ratio (2:1) of X and Y chromatids involved in pairing. However, structural details of the pairing are unknown. The X_1X_2Y system also shows specialized behaviour during anaphase segregation, where the X chromosomes are associated forming a pseudobivalent. In the family Pholcidae the anaphase segregation of sex chromosomes is lagged, with the trivalent being stretched between sister plates.

Surprisingly, the X_1, X_2 and Y chromosomes pair during premeiotic interphase, being ordered in the same manner as during subsequent prophase I. Inter-

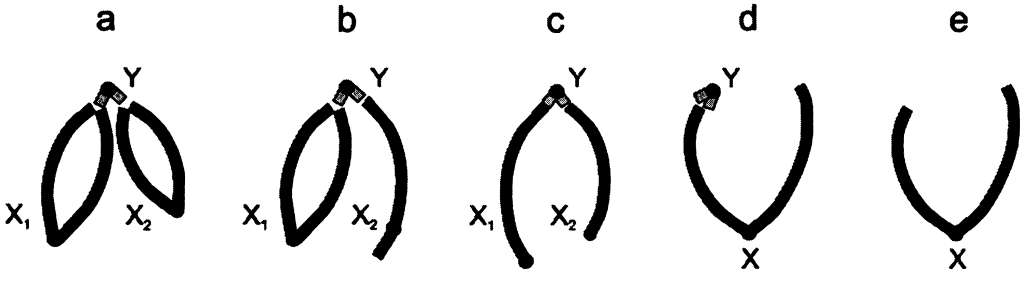


Figure 11. Conversion of X_1X_2Y system into X0 system. (**a**) *Spermophora senoculata* (X_1X_2Y); (**b**) *Pholcus phalangioides* (X_1X_2Y); (**c**) hypothetical X_1X_2Y system with acrocentric X chromosomes; (**d**) *Diguetia albolineata* (XY); (**e**) *Holocnemus caudatus* (X0).

phase pairing was also observed between X and Y chromosomes in the genus *Diguetia*. A similar phenomenon is known in entelegyne spiders, in which multiple X chromosomes are associated on the periphery of the premeiotic interphase nuclei (Hackman 1948). In *Pholcus phalangioides* the sex chromosomes are already associated at spermatogonial prophase. This observation implies that pairing of X_1, X_2 and Y chromosomes at premeiotic interphase is preceded by their association at spermatogonial interphase and mitosis. The relative position of sex chromosomes at mitotic prophase of other X_1X_2Y species remains unresolved due to an unsufficient intensity or absence of sex chromosome heteropycnosis. In the premeiotic interphase and diffuse stage of the genera *Loxosceles* and *Diguetia*, chromosomes of one NOR-bearing pair were heteropycnotic and associated with each other like sex chromosomes. Heterochromatinization during two metabolically active periods, interphase and diffuse stage, suggests transcriptional inactivation of the curious chromosome pair. Frequent association of these chromosomes with the sex chromosomes indicates their possible integration into the sex chromosome system.

Chromosomes of the X_1X_2Y system retain the conservative metacentric morphology and pairing mode in all groups studied except the most diversified family of basal araneomorphs, Pholcidae. From a karyological point of view the pholcids are the best-explored group of basal clades with 11 species belonging to seven genera examined (Araújo *et al.* 2005b). In spite of this, the evolution of pholcid sex chromosomes is still poorly known. Our results show that the X_1X_2Y system has been interpreted erroneously as an X_1X_20 system in *Pholcus phalangioides* (Painter 1914, Rodríguez Gil *et al.* 2002) and *Spermophora senoculata* (Painter 1914). The X_1X_20 system was also reported in *P. crypticolens* (Suzuki 1954) and *Artema atlanta* (Parida & Sharma 1987). We suppose that the X_1X_2Y system also occurs with all probability in these species. The remaining pholcids examined have an X0 system (Araújo *et al.* 2005b).

Diversity in the structure of pholcid sex chromosome systems allowed us to follow the gradual conversion of the X_1X_2Y system into the X0 system found in some pholcid lineages. The original type of X_1X_2Y system is still retained in *S. senoculata* (Figure 11a). We suggest that transformation of the X_1X_2Y system was initiated by a conversion of one metacentric X chromosome into a subtelocentric or acrocentric one by pericentric inversion as found in *P. phalangioides* (Figure 11b). A similar morphology of one X chromosome was also found in *Loxosceles intermedia* (Silva *et al.* 2002). The following evolution of the X_1X_2Y system was characterized by a pericentric inversion in the second X chromosome (Figure 11c). Then a Robertsonian translocation of both X chromosomes produced an XY system; this stage is found in the pholcid *Smeringopus pallidus* (J. Král, unpublished). Similar conversion of the X_1X_2Y mode is supposed to be responsible for the origin of the XY system of *Diguetia*. Accretion of Y chromosome size found in *Smeringopus* and *Diguetia* indicates that this stage of X_1X_2Y conversion could be even more complex. Despite the presence of a single X chromosome the Y chromosome of *Diguetia* retained a metacentric morphology. In contrast to the X_1X_2Y system, both arms of the Y chromosome pair with one arm of X chromosome only (Figure 11d). We suppose that the acrocentric X chromosome of *D. canities* originated from a metacentric X, such as found in *D. albolineata*, by a pericentric inversion. Finally, the loss of Y chromosome led to the X0 system occurring in some pholcids (Figure 11e). A substantial amount of constitutive heterochromatin in the Y chromosome of *P. phalangioides* indicates that the Y chromosome has been enriched by heterochromatin during final degeneration. Conversion of the X_1X_2Y mode is also supposed to result in the X0 system of the genus *Scytodes* (Rodríguez Gil *et al.* 2002, Araújo *et al.* 2005c, this study).

The evolutionary stability and broad taxonomic distribution of the X_1X_2Y system indicate its antiquity. Filistatid spiders were found in the Jurassic (Eskov 1989). The most stable chromosome structure of the X_1X_2Y system appears to be the Y chromosome that probably exhibits metacentric morphology in all species studied. Metacentric morphology of the Y chromosome is also retained at the derived XY system of diguetids. The evolutionary constraints that conserved the structure of X_1X_2Y system, namely metacentric morphology of sex chromosomes and pairing mode, remain unknown. However, restrictions imposed by the peculiar mode of pairing might cause strong selection against changes of sex chromosome morphology. Interestingly, the structure of the spider X_1X_2Y system appears to be similar to an XnY system (n varies from 2 to 4) of tiger beetles (Cicindelidae), namely by chromosome morphology and pairing mode by ends of

chromosome arms. Moreover, sex chromosomes of tiger beetles also show evolutionary stability of the metacentric structure (Galián *et al.* 2002). The derived state of the spider X_1X_2Y system does not allow us to reconstruct its origin from the X_1X_20 system. While virtually nothing is known about genetic determination of the spider sex, the antiquity of the X_1X_2Y system points to considerable differences between the systems. In this respect it would be especially interesting to analyse the role of minute Y chromosome.

In contrast to entelegyne spiders, sex chromosome systems of basal araneomorphs often include NOR. In animals, NOR is frequently located on sex chromosomes, as found for example in various groups of insects, fishes, and mammals (Artoni & Bertollo 2002). Concerning spiders, NOR was earlier found only on sex chromosome of *Dysdera crocata* (Dysderidae). This NOR is active during prophase I forming a nucleolus (Benavente & Wettstein 1980, this study). We found NOR also on the X chromosome of some haplogyne spiders with monocentric chromosomes. In these spiders the meiotic activity of X-linked NOR affects the behaviour of the X chromosome. In *Monoblemma* (Tetrablemmidae) and *Ochyrocera* (Ochyroceratidae), the X chromosome undergoes intensive condensation during prophase I, being associated with the periphery of the nucleolus. In *Leptoneta* (Leptonetidae), the proximal and distal parts of the X chromosome differ remarkably by morphology during prophase I. We suggest that the complicated pattern of X chromosome condensation in *Leptoneta* is probably caused by addition of an autosome material. We assume that the XY system of this spider is derived from an X0 system. The distal part of the X chromosome, which exhibits a different pattern of condensation, probably corresponds to the traslocated autosome. The homologue of the autosome was transformed to the Y chromosome. Despite its minute size the Y chromosome preserved chiasmatic pairing with the X chromosome. In contrast to previous species, NOR on the X chromosome of *Scytodes thoracica* is silent during meiosis. Neither NOR nor secondary constriction was reported on the X chromosome of other *Scytodes* species (Rodríguez Gil *et al.* 2002, Araújo *et al.* 2005c).

Modifications of meiotic division

In accordance with karyotype diversity, basal araneomorphs show remarkable modifications of meiotic division. Particularly, the late prophase I in basal araneomorph males differs from most entelegyne spiders. Following pachytene, autosome bivalents exhibit extensive despiralization. On the contrary, sex chromosome(s) form a compact heteropycnotic element on the periphery of the nucleus. We interpret this phase as a diffuse stage. To date the diffuse stage was observed in various animals and plants (e.g. Klášterská 1977, Šťáhlavský *et al.* 2006). It is usually considered as a separate period of prophase I between pachytene and diplotene (Macgregor 1993). Expansion of nucleoli suggests transcriptional activity during the diffuse stage (Klášterská 1977). The diffuse stage apparently occurs more often in females due to the need to synthesize reserve substances in the developing oocytes; the occurrence in spermatocytes is not as common (Benavente & Wettstein 1980). Based on timing in meiosis and metabolic activity, Stack & Anderson (2001) consider the diffuse stage to be a probable equivalent to the late G_2 phase in the mitotic cell cycle. Among basal araneomorphs the diffuse stage was described in males of the families Dysderidae, Segestriidae (Benavente & Wettstein 1980, Rodríguez Gil *et al.* 2002), and Filistatidae (Rodríguez Gil *et al.* 2002). Our data indicate that this stage is obligatory in males of basal araneomorphs.

The diffuse stage of basal araneomorphs can be divided into two periods: early and late. The early diffuse stage is marked by expanded nucleoli and considerable despiralization of bivalents. Extreme despiralization of autosome chromatin was found in *Monoblemma*. Moreover, almost the whole X chromosome of *Monoblemma* becomes decondensed twice during the diffuse stage. The intensive despiralization of the sex chromosome may reflect its transcriptional activity. A relationship between despiralization of sex chromosomes and their transcriptional activity during early stages of spermatogenesis was demonstrated, for example, in some grasshoppers (Church 1979). The late diffuse stage of basal araneomorphs is characterized by gradual recondensation of bivalents and lowered nucleolar activity. Bivalents of *Leptoneta*, *Monoblemma* and *Ochyrocera* become gradually well defined during the late diffuse stage. The morphology of bivalents suggests that the late diffuse stage of these genera equals approximately that of diplotene. In contrast, bivalents of the other basal araneomorphs condense into irregular discrete bodies without well-defined chiasmata. The diffuse stage of these spiders is usually followed by short diplotene showing particular coiling of biva-

lents. Our data confirmed a very long duration of the diffuse stage in spiders with holocentric chromosomes (Benavente & Wettstein 1980, Rodríguez Gil *et al.* 2002) in which the typical diplotene (*Segestria*) or even diakinesis (*Dysdera*) are replaced by the late diffuse stage. In *Dysdera*, the bivalents show chiasmata at metaphase I only. A similar course of the late diffuse stage was also observed in *Hypochilus* (this study).

On the basis of an imperfect morphology of the synaptonemal complex and a very short pachytene stage, Benavente & Wettstein (1980) suggest that the male meiosis of *Dysdera* and *Segestria* evolves towards the achiasmatic mode. However, this view should not be considered as conclusive until it is complemented by detailed ultrastructural analysis of the first meiotic division. Pachytene bivalents exhibit a standard morphology in the light microscope. Furthermore, our data suggest the seeming absence of chiasmata is due to the very long diffuse stage. Chiasmata are formed but only in latest prophase I or metaphase I, respectively.

Other modifications of meiotic division are coupled with the holocentric structure of chromosomes. Within a given karyotype, the holocentric chromosomes often display variable behaviour during meiosis (Sybenga 1981). Our study confirmed the different behaviour of sex chromosomes and autosomes in meiosis of *Dysdera crocata*. The X chromosome of *Dysdera* shows an inverted meiosis (Benavente & Wettstein 1980, Rodríguez Gil *et al.* 2002). On the other hand the telocentric activity of autosomes during anaphase of both meiotic divisions indicates a normal course of their segregation (Feiertag-Koppen 1980). Our study also confirmed standard meiosis in all chromosomes of *Segestria* including X_1 and X_2 chromosomes (Benavente & Wettstein 1980).

Karyotype evolution of araneomorph spiders

Karyotype diversity presented in this study allows us to distinguish four basic evolutionary lineages of basal araneomorphs. The first lineage is represented by the family Plectreuridae, in which the only species examined (this study) shows the most plesiomorphic karyotype, namely predominance of biarmed chromosomes and the X_1X_20 sex chromosome system. The second lineage involves the whole superfamily Dysderoidea with more than 1200 species (Platnick 2006). This group is characterized by holocentric chromosomes. In spite of the derived chromosome structure, some representatives of the family Segestriidae, being considered the most basal within the superfamily (Coddington 2005), retain the ancestral spider sex chromosome system, X_1X_20. The derived position of the family Dysderidae is indicated by an extremely long diffuse stage as well as by inverted meiosis of the sex chromosome. According to the recent schemes the family Tetrablemmidae is regarded as a sister group of the superfamily Dysderoidea (Platnick *et al.* 1991). In contrast to this, karyological data place tetrablemmids into the third evolutionary lineage that also includes the families Leptonetidae and Ochyroceratidae. Besides localization of NOR on the X chromosome, these families (further X-NOR clade) share a similar behaviour of the X chromosome during male prophase I as well as a similar course of the diffuse stage.

Conserved structure of the X_1X_2Y system led us to separate the most diversified lineage of basal araneomorphs (the fourth lineage; further X_1X_2Y clade). Beside families with the X_1X_2Y system, this group also includes the family Diguetidae with an XY system that was apparently derived from the X_1X_2Y mode, and probably also the families Scytodidae and Austrochilidae. Within the X_1X_2Y lineage, families Diguetidae and Sicariidae are distinguished by formation of a strange chromosome pair during premeiotic interphase. The family Hypochilidae has been classified as the most basal of all araneomorph spiders, having an unusual combination of primitive remarks (Forster *et al.* 1987). In contrast to this hypothesis the structure of the sex chromosome system brings hypochilids into the X_1X_2Y clade (Král *et al.* 2004) whose other families belong mostly to the extensive scytodoid clade of haplogyne spiders (Coddington & Levi 1991). Within the X_1X_2Y clade the karyotype of *Hypochilus* is the closest to *Filistata*, a primitive representative of the family Filistatidae (Gray 1995). Besides the similar number of autosome pairs, the morphology of the three longest autosome pairs is nearly the same in both genera, including the intercalar secondary constriction in the longest pair. In contrast to *Hypochilus*, the remaining pairs of *Filistata* exhibit exclusively biarmed morphology. The position of the family Filistatidae represents one of the crucial problems in spider phylogeny, as it can be documented by different interpretations of Lehtinen (1967), Eskov & Zohnstein (1989), and Platnick *et al.* (1991). Derived karyotypes of scytodids deter a hypothesis about placement of this family within the X_1X_2Y clade. However, the karyological data do not support a close relationship to the family Sicariidae as

sometimes suggested (Platnick *et al.* 1991). The exact position of the family Austrochilidae is also unclear in our scheme, as data on sex chromosome behaviour during male meiosis are missing. Karyotype data indicate a possible relationship to the family Drymusidae (a member of the X_1X_2Y clade). Karyotypes of both groups display similar number, size and morphology of chromosomes.

Finally, it should be emphasized that the karyotype data obtained appear to be insufficient to solve the relative position of the four clades suggested. However, one attractive possibility that remains to be tested is that NOR on the X chromosome of the X-NOR clade and some dysderoids represents synapomorphy of these two lineages.

In conclusion our data allow us to compare the karyotype evolution of basal and entelegyne araneomorphs. In contrast to the enormous diversity of entelegynes, their chromosome morphology and sex chromosome systems appear to be conservative. A basic trend of entelegyne karyotype evolution is towards reduction of 2n (Suzuki 1954). Centric fusion in entelegynes is generally an 'all-or-nothing' phenomenon (Rowell 1990). This means that acrocentric karyotypes have been quickly saturated with Robertsonian translocations in some entelegyne groups, i.e. their karyotypes consist entirely of metacentric chromosomes. However, absolute dominance of entelegyne karyotypes formed exclusively by acrocentric chromosomes suggests that chromosome numbers of most entelegyne groups were reduced rather by tandem fusions. The presented concept of karyotype evolution implies that the ancestral karyotype of entelegynes (a) was most probably placed close to the upper boundary of their chromosome numbers, (b) consisted exclusively of acrocentric chromosomes, and (c) contained an X_1X_20 system. We suggest that the male karyotype of $2n=42$, X_1X_20 is most probably ancestral in entelegynes. Such karyotype, together with its derived variant of $2n=43$, $X_1X_2X_30$, is much more frequent than any other entelegyne karyotypes with high diploid number being found in various disparate families. Moreover, these two karyotypes concentrate in clades that are supposed to be basal within entelegynes. They have been found in the families Oecobiidae (Suzuki 1954), Sparassidae (Suzuki 1954, Díaz & Sáez 1966, Rowell 1985), Agelenidae, Amaurobiidae, Cybaeidae, Hahniidae (Král 1994b), Eresidae, and Zodariidae (J. Král, unpublished). A closely related karyotype of $2n=41$, $X_1X_2X_30$ was found in the families Sparassidae (Rowell 1985) and Deinopidae (J. Král, in preparation). Except for a tendency to reduce diploid numbers, the basic karyotype trends of basal araneomorphs and entelegynes probably differ due to the different structure of karyotypes. Male meiosis of basal clades displays two characters that are very rare in entelegynes, namely a long diffuse stage and a frequent absence of sex chromosome heteropycnosis at early prophase I. These differences can reflect monophyly of basal clades; however, their distribution in non-araneomorph spiders is unknown. Taking into account the similar upper limit in diploid numbers in basal araneomorphs and entelegynes, one can speculate that the male complement of ancestral araneomorphs was formed approximately by 40 chromosomes. Karyotype of these spiders was most likely dominated by biarmed chromosomes that seem to be a plesiomorphic trait in spiders.

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3. CONCLUSIONS

3.1. Dietary specialisation

Results on cheliceral morphology and prey preference suggest that there are three groups of prey-specificity in *Dysdera*: (1) prey generalists represented by the species with unmodified chelicerae, (2) facultative woodlice-specialists represented by species with moderate cheliceral modifications, and (3) obligatory woodlice-specialists represented by species with extreme cheliceral modifications. The species with unmodified chelicerae used standard capture behaviour similar to other spiders. It refused woodlice but readily captured some other arthropods. In contrast to this, all the studied species with modified chelicerae readily captured woodlice. Facultative woodlice-specialists readily capture woodlice but are able to feed also on other prey. The obligatory woodlouse-specialists almost do not capture anything else beside woodlice. However, particular adaptation experiments showed that woodlice are an essential component of diet also for "facultative" woodlice-specialists. *Dysdera hungarica* spiderlings, which captured significantly more often flies than woodlice in my prey choice experiments, developed significantly faster and grew more on the woodlice-containing diets, than those reared on fly diet. This study provides the first evidence of metabolic specialisation on woodlice. The contradictional results from my prey preference experiment were rather a result of unnatural conditions. Nutritonal adaptation experiments appear to provide more accurate information on dietary specialisation than prey choice experiments.
Observations of capturing behaviour revealed that the *Dysdera* species possessing different cheliceral modifications use different grasping tactics to capture woodlice. Species with elongated chelicerae grasp the prey by inserting one chelicera to the soft ventral side of woodlouse and holding the dorsal side of woodlouse by the other one. Thus the spider gripped the woodlouse in a grasp similar to that of pincers. Species with dorsally concave chelicerae tuck them quickly under woodlouse in order to bite woodlice into ventral side of body. The concave shape of the dorsal side of chelicerae helped to get beneath the ventral side of woodlouse in a movement similar to scooping up a bite with a fork. Species with flattened chelicerae insert a chelicera between sclerites of the armoured woodlouse. Flattening of cheliceral fang allows to insert the fang between the sclerites. I called this a 'key tactic' as it reminded me of skilful opening a closed safe using a key. In summ, presented study reveals that the various cheliceral modifications and capture tactics allowed *Dysdera* spiders to overcome defence tactics of woodlice, namely heavy armour protecting most of their body and behavioural defences protecting their soft ventral side. As the cheliceral morphology, prey preference and the grasping tactic are obviously tightly coherent, cheliceral morphology can be used to predict the prey preference and the grasping tactic in species whose diet and grasping behaviour are unknown.
To my knowledge *Dysdera* spiders are the only specialised woodlice predators occuring outside tropical zones. With the striking variability of morphological adaptations and grasping tactics described here, these spiders form a highly diversified clade of oniscophagous feeders.

3.2. Diversification

A review of all species of *Dysdera* named from outside the Palearctic region demonstrated that the genus, like all other members of the family, is originally endemic to the Palearctic region. Only *D. crocata* was introduced by man to almost all the continents. Patterns of distribution of *Dysdera* species in central Europe suggest limited migration abilities of these spiders. In this context, parthenogenetic reproduction in *D. hungarica* appears to be a special preadaptation for migration which allows thelytokous clones to colonise isolated locations.

In central Europe, *Dysdera* spiders prefer xerothermic forests, particularly sites enriched by calcium. They often occur also in semi-synanthropic habitats, *e.g.*, in the vicinity of ruins overgrown by woody plants. Unusual ecological plasticity was observed in parthenogenetic clones of *D. hungarica*. These clones were found even in anomalous non-forest habitats such as wetlands with *Phragmites australis*, salt marshes, wet meadows, or vineyards. Thelytoky may enable the clones to survive even in suboptimal habitats, which are, however, not suitable to harbour the high abundance necessary for sexual reproduction.

I found no variability of phenology among central European *Dysdera* spiders. All species have probably biennal life-cycles.

The genus *Dysdera* exhibits the highest variation in chromosome number of all spider genera studied so far. Male diploid numbers of eleven examined species range from 9 to 40. All studied species possess holocentric chromosomes. Holokinetic structure of chromosomes, allowing facile transmission of some rearrangements, probably contributed to the high variation in chromosome numbers. The fact that closely related species differ in karyotype gives evidence for important role of karyotype rearrangements in speciation. Due to the fact that closely related species differ in chromosome number, karyotype appears to be a useful character for the taxonomy of the genus.

During analysis of the *D. erythrina* agreggate, I did not find any obvious differences in habitat preferences; they even occured together in some locations. The species exhibit differences in karyotype, sculpture of carapace, morphology of the groove accessing the spermatheca for sperm, morphology of mouth-parts, and body size. Experimental crossing showed a partial precopulatory behavioral barrier between two species. This pattern of interspecific differences found in the *D. erythrina* aggregate allowed me to hypothesize about the history of the speciation process in *Dysdera*. I hypothesize that chromosome rearrangements played a primary role in speciation of the aggregate. Rapid divergence of karyotypes might have been facilitated by inability of *Dysdera* to disperse to a long distance. Without efficient migration ability, habitat fragmentation might have led to separation of populations. In small isolated populations, chromosome rearrangements could have been easily fixed by the genetic drift. Secondary contact of new and ancestral cryptic species likely gave rise to recognition mechanisms that would have prevented them from wasting their reproduction potential (reinforcement). A consequence of the recognition might be the observed one-sided precopulatory barrier between *D. erythrina* and *D. lantosquensis*. I assume the different intraspecific recognition might be facilitated by sculpture of the carapace. I suppose that studied species of the *Dysdera erythrina* aggeragte can occur sympatrically due to dietary specialisation avoiding competition for prey. All species fed on woodlice. However, I found remarkable interspecific differences in characters determining potencial prey, particularly body size and the morphology of mouth parts, particularly chelicerae, that suggest the specialisation of these species on different species or size of woodlice.

According to the suggested mode, the initial causes of speciation in *Dysdera* aggregates were incompatible chromosome mutations that were fixed by genetic drift (speciation by genetic drift). Following sympatric coexistence of particular species was likely allowed by further ecological/morphological differentiation driven by natural selection. In contrast to the ecological hypothesis of speciation the suggested mode predicts existence of cryptic species possessing karyotypic but not morphological differences in case that they remained to be geographically isolated.