

# Dwarf spiders (Erigoninae, Linyphiidae, Araneae) : good candidates for evolutionary research

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**ABSTRACT.** Males of numerous erigonine dwarf spider species, including those in the genera *Oedothorax* and *Diplocephalus*, are characterised by elaborate structures on the head region. Three evolutionary hypotheses for these head structures are : lock-and-key (reproductive isolation) hypothesis, "conflict of interest hypothesis" and diverse sexual selection hypotheses.

*Oedothorax gibbosus* (Blackwall, 1841) is a dwarf spider characterised by male dimorphism; the *gibbosus* morph has a hunch on the last third of the carapace, anterior to which is a hairy groove; the *tuberosus* morph does not have these features. During the so-called gustatorial courtship the female inserts her chelicerae into the hairy groove of *gibbosus*. Species recognition experiments reveal the occurrence of interspecific homo- and heterosexual "gustatorial courtships" of the female as well as the male of the closely related species *Oedothorax fuscus* (Blackwall, 1834) towards the *gibbosus* male. These interspecific courtships can be interpreted as robbery of the nuptial gift located in the groove and the hunch of the *gibbosus* males. *Gibbosus* males can also rob the nuptial gift of each other, but this occurs only rarely. We have never observed a 'gustatorial robbery' between a *tuberosus* male and a *gibbosus* male. There are also interspecific interactions between a *tuberosus* male and an *O. fuscus* female suggesting poorly developed reproductive isolation between these sister species.

These interspecific courtships are in disagreement with the lock-and-key hypothesis. Indeed, according to this hypothesis the head structures of erigonine males should function as an early prevention of hybridisation. Female chelicerae and male head structures thus do not operate as key and lock. Therefore, the head structures might have evolved under the influence of sexual selection.

**KEY WORDS :** Araneae, Erigoninae, speciation hypotheses, head structures, interspecific courtships, nuptial feeding.

## INTRODUCTION

Many publications have addressed the evolution of genitalia. Spiders (EBERHARD, 1997; HUBER, 1996, 1999), water striders (ARNQVIST et al., 1997; ARNQVIST & THORNHILL, 1998) and other insects (ARNQVIST, 1997, 1998; EBERHARD, 1997; ELGAR, 1998; ARNQVIST et al., 2000) have recently become preferred model organisms for such research. Spectacular morphological diversification of genitalia is widespread among animals with internal fertilisation. Even in closely related taxa, genitalic morphology typically differs greatly between species (EBERHARD, 1985). There are three main general hypotheses for the evolution of animal genitalia (EBERHARD, 1985, 1990, 1993, 1996; ARNQVIST, 1997) : the lock-and-key hypothesis (selection for pre-insemination reproductive isolation : specific and unique male intromittent genitalia -the key- fit in female genitalia -the lock), the sexual selection hypothesis (relationship between genitalic morphology and relative post-copulatory fertilisation success) and the pleiotropy hypothesis (genitalic evolution is an indirect result of evolution of genetically-correlated characters, via pleiotropic effects of genes that code for both genitalic traits and evolving general morphology (MAYR, 1963; ARNQVIST et al., 1997)).

ARNQVIST (1997) reviews the different suggestions of how genitalia might evolve through sexual selection : (1) cryptic female choice (EBERHARD, 1985), (2) sexual conflicts (THORNHILL, 1984) and (3) sperm competition (SMITH, 1984).

The evolution of non-genitalic contact structures is also very interesting. HUBER (1999) reviews the evolutionary hypotheses useful for such non-genitalic contact structures; he applied the hypotheses to the artful chelicerae of male pholcid spiders (Araneae, Pholcidae). In that publication the author considered again the lock-and-key hypothesis (reproductive isolation hypothesis) and different sexual selection hypotheses (male-male competition (EBERHARD & BRICENO, 1985) and sexual selection by female choice (EBERHARD, 1985)), but also the "conflict of interest hypothesis" ("genitalic arms race" between the sexes relating to physical coercive mating) (ALEXANDER et al., 1997) and the "sperm holder hypothesis" (pholcid chelicerae may function to hold the sperm during sperm uptake) (BRIGNOLI, 1973). By elimination, HUBER (1999) determined that cryptic female choice is the hypothesis that best fits his data. The theory of sexual conflict is the subject of several other empirical (ARNQVIST, 1998; ARNQVIST et al., 2000; ARNQVIST & ROWE, 2002) and theoretical studies (GAVRILETS, 2000).

Several publications confirm that sexual selection is more and more regarded as having the potential to play a major role in speciation (ARNQVIST & NILSSON, 2000; PANHUIS et al. 2001). According to ARNQVIST (1998), genitalic evolution is more than twice as divergent in groups in which females mate several times than in groups in which females mate only once. MASTA & MADDISON (2002) provide genetic, behavioural and simulation data that illustrate that the striking and possibly recent divergence in traits of male behaviour and morphology among populations of the jumping spider *Habronattus pugillis* Griswold, 1987 can be attributed to sexual selection.

Males of erigonine spiders and other spider species are characterised by the occurrence of elaborate structures on the head. These have been analysed morphologically in several species (LOPEZ, 1976, 1987; MEIJER, 1976; BLEST & TAYLOR, 1977; VOLLRATH, 1977; LOPEZ & EMERIT, 1981; HUBER, 1997; HEINEMANN & UHL, 2000; HORMIGA, 2000; SCHAIBLE et al., 1986; SCHAIBLE & GACK, 1987; SCHLEGELMILCH, unpubl. data). SCHAIBLE et al. (1986) suggested that the primary function of the male head structures in these erigonine spiders is to fix the position of the female during copulation. These authors assume that the exocrine glands associated with these head structures produce secretions, which females ingest during courtship and/or copulation. SCHAIBLE et al. (1986) were the first to suggest that the cephalic structures probably secrete a fluid that is important for the so-called gustatorial courtship, being the uptake of secretions by the female from a body part of the male during courtship. These cephalic structures can be seen as non-genitalic contact structures. HUBER (1997) mentions a similar case of a non-genitalic contact structure, namely the frontal lobe in male *Modisimus culicinus* (Simon, 1893).

*Oedothorax gibbosus* (Blackwall, 1841), an erigonine spider, is special because males are dimorphic. One morph, the *gibbosus* male, has cephalic structures, namely a hunch on the last third of its carapace anterior to which is a hairy groove (Fig. 1); the *tuberosus* morph on the other hand does not have these cephalic features. The large number of different gland cells in the hunch of *gibbosus*, in comparison with the few gland cells in the cephalic region of *tuberosus* (VANACKER, unpubl. data), is certainly an indication that *gibbosus* males not only secrete pheromones, but also a nuptial gift. During the gustatorial courtship, which evidently can only be performed by *gibbosus* males, the female puts its chelicerae into the hairy groove of *gibbosus* and exhibits a feeding behaviour. Because of this nuptial gift it can be assumed that *gibbosus* is sexually more attractive to females (VANACKER et al., in press).

After the courtship copulation follows. Starting from a face-to-face position, the male shifts its cephalothorax underneath that of the female. In this way the two palps can easily reach the epigyne. During a palp insertion, sperm is pumped into the epigyne by means of swelling and shrinking of the haematodoch. This last structure is a bladder and is a part of the male palp. The transition of gustatorial courtship to copulation can happen smoothly or there can be a break between courtship and copulation. During copulation most females remove their chelicerae from the hairy groove of *gibbosus*. Fixation of the position (SCHAIBLE et al., 1986) is thus not the most important



Fig. 1. – Scanning electron micrograph of a *gibbosus* male, showing the hunch and the hairy groove on the carapax function of the male head structures of the *gibbosus* morph male.

What is now the function of the different cephalic structures of the erigonine spiders? Are they used as a pre-copulatory species-recognition mechanism or as a signal in a context of sexual selection (sexual conflict) important for e.g. partner choice by the female? In order to answer these questions we did some species-recognition experiments with *Oedothorax gibbosus* and *Oedothorax fuscus* (Blackwall, 1834) and made some unexpected observations. On the basis of these experiments we also try to determine whether *gibbosus* males are sexually more attractive than *tuberosus* males.

## MATERIAL AND METHODS

*Oedothorax gibbosus* spiders were caught in an oligo- to mesotrophic alder marsh, the typical habitat of this dwarf spider species, in the public nature reserve “Het Walenbos” at Tielt-Winge, 30 km north-east of Brussels, Belgium; *O. fuscus* spiders were collected in the military domain at Nieuwpoort, Belgium. The *O. gibbosus* dwarf spiders were caught by hand on August 4 2001, October 13 2001, October 27 2001 and July 5 2002; the *O. fuscus* spiders on October 31 2001 and January 22 2003. The spiders used in the experiments were descendants of female spiders inseminated in the field or were obtained by laboratory crossing of a female with a *tuberosus* or a *gibbosus* male. All spiders were kept separately in small plastic vials (5 cm diameter and 2.5 cm height) with a thin bottom of plaster, in a climatic chamber at a photoperiod L:D 16:8 and a temperature of 20°C. Before the second moult they were fed with four *Sinella curviseta* springtails each day; after the second moult they received three fruit flies per day. The vials were moistened regularly to maintain a relative humidity near 100%.

In a first series of experiments we examined the different interactions between a *gibbosus* male, an *O. gibbosus* female and a male or female *O. fuscus* spider. In the fifth of that series of experiments we used seven *O. fuscus* males. In the sixth experiment we used another *gibbosus* male instead of *O. fuscus* spiders, to study whether there would be an interaction between the two *gibbosus* males. We also did analogous experiments with a *tuberosus* male, an *O. gibbosus* female and one *O. fuscus* spider. The *gibbosus/tuberosus* male and the *O. fuscus* spider(s) were put in the vial of the *O. gibbosus* female. This female had inhabited the vial since the first juvenile instar and had already produced a web, which is necessary for the gustatorial courtship and for the copulation. An experiment was terminated after thirty minutes without any interaction. Observation sessions were done in parallel.

In a second series of experiments we investigated the extent of occurrence of the different interspecific interactions observed in the first series. First we examined the number of interspecific interactions between a *gibbosus* male and an *O. fuscus* male in the presence of an *O. gibbosus* female. We also did this in the absence of an *O. gibbosus* female. Next we investigated the number of interactions between a *gibbosus* male and an *O. fuscus* female in the absence of an *O. gibbosus* female. Each time we also did analogous experiments with *tuberosus* males. Finally we observed the number of interactions between two *gibbosus* males (in either the absence or presence of an *O. gibbosus* female), between two *tuberosus* males and two *O. fuscus* males (in the absence of an *O. gibbosus* female). For each experiment we observed 10 repeats in

parallel during five hours. The *gibbosus/tuberosus* male as well as *Oedothorax fuscus* spider(s) were again put in the vial of the *O. gibbosus* female; in the absence of the last we put *O. fuscus* spiders in the vial of the *gibbosus/tuberosus* spider.

In a third series of experiments we investigated whether there are interactions between *gibbosus* and *tuberosus*. Each time we put one *gibbosus* male and one *tuberosus* male at the same time in the vial of an *O. gibbosus* female. With this experimental design we should be able to test whether *gibbosus* is sexually more attractive than *tuberosus*. Does the female choose more often to copulate with *gibbosus* than *tuberosus*? Is the copulation of *gibbosus* longer than this of *tuberosus*? In a first experiment with 59 repeats we stopped observations if nothing happened after 30 minutes; in a second set-up (9 repeats) we observed during a whole day.

The following statistical tests were used: one-way-ANOVA, Fisher-test and Chi-square test.

## RESULTS

### Interspecific homo- and heterosexual interactions between *O. gibbosus* and *O. fuscus*

In the first experiment a *gibbosus* morph male and an *O. fuscus* female were placed in the vial of an *O. gibbosus* female. The *O. fuscus* female grasped the *O. gibbosus* male, appearing to feed from the cephalic groove for 7 minutes. During this time the *O. gibbosus* male tried to copulate but did not succeed.

TABLE 1

First experiment of interspecific homo- and heterosexual interactions between the *gibbosus* male morph (*O. gibbosus*) and spider(s) of *O. fuscus*, in the cup of the *O. gibbosus* female. The duration of these interactions are included in the table. In the 5<sup>th</sup> part of the experiment we added one *gibbosus* male and seven *O. fuscus* males; in the 6<sup>th</sup> part of the experiment we added two *gibbosus* males.

nr	female	added morph of <i>O. gibbosus</i>	added spiders of <i>O. fuscus</i>	gustatorial courtship between	duration
1	<i>O. gibbosus</i> female	<i>gibbosus</i> male	1 <i>O. fuscus</i> female	<i>gibbosus</i> male & <i>O. fuscus</i> female	7 min
2	<i>O. gibbosus</i> female	<i>gibbosus</i> male	1 <i>O. fuscus</i> male	<i>gibbosus</i> male & <i>O. gibbosus</i> female	10 min
				<i>gibbosus</i> male & <i>O. fuscus</i> male	2 min
				<i>gibbosus</i> male & <i>O. fuscus</i> male	3 sec
				<i>gibbosus</i> male & <i>O. fuscus</i> male	2 sec
3	<i>O. gibbosus</i> female	<i>gibbosus</i> male	1 <i>O. fuscus</i> male	<i>gibbosus</i> male & <i>O. fuscus</i> male	5 min
				<i>gibbosus</i> male & <i>O. fuscus</i> male	2 min
				<i>gibbosus</i> male & <i>O. fuscus</i> male	6 sec
4	<i>O. gibbosus</i> female	<i>gibbosus</i> male	1 <i>O. fuscus</i> male	<i>gibbosus</i> male & <i>O. fuscus</i> male	6 min
				<i>gibbosus</i> male & <i>O. fuscus</i> male	4 min
5	<i>O. gibbosus</i> female	<i>gibbosus</i> male	7 <i>O. fuscus</i> males	<i>gibbosus</i> male & <i>O. fuscus</i> male	5 min
				<i>gibbosus</i> male & <i>O. fuscus</i> male	1 min
				<i>gibbosus</i> male & <i>O. fuscus</i> male	5 sec
				<i>gibbosus</i> male & <i>O. fuscus</i> male	30 sec
				<i>gibbosus</i> male & <i>O. fuscus</i> male	5 min
				<i>gibbosus</i> male & <i>O. fuscus</i> male	1 min
				<i>gibbosus</i> male & <i>O. fuscus</i> male	6 min
				<i>gibbosus</i> male & <i>O. fuscus</i> male	1 min
nr	female	added morph of <i>O. gibbosus</i>	added spiders of <i>O. gibbosus</i>	gustatorial courtship between	duration
6	<i>O. gibbosus</i> female	<i>gibbosus</i> male	1 <i>gibbosus</i> male	<i>gibbosus</i> male & <i>gibbosus</i> male	12 min

TABLE 2

Second experiment of interspecific homo- and heterosexual interactions between the *tuberosus* male morph (*O. gibbosus*) and spider(s) of *O. fuscus*, in the cup of the *O. gibbosus* female. The duration of the observed intraspecific copulations are included in the table and there were not any interspecific interactions in this experiment.

nr	female	added morph of <i>O. gibbosus</i>	added spiders of <i>O. fuscus</i>	courtship and copulation between	copulation time
1	<i>O. gibbosus</i> female	<i>tuberosus</i> male	1 <i>O. fuscus</i> female	<i>tuberosus</i> male & <i>O. gibbosus</i> female	70 min
2	<i>O. gibbosus</i> female	<i>tuberosus</i> male	1 <i>O. fuscus</i> male	<i>tuberosus</i> male & <i>O. gibbosus</i> female	67 min
				<i>tuberosus</i> male & <i>O. gibbosus</i> female	64 min
3	<i>O. gibbosus</i> female	<i>tuberosus</i> male	1 <i>O. fuscus</i> male	<i>tuberosus</i> male & <i>O. gibbosus</i> female	67 min
4	<i>O. gibbosus</i> female	<i>tuberosus</i> male	1 <i>O. fuscus</i> male	<i>tuberosus</i> male & <i>O. gibbosus</i> female	66 min
5	<i>O. gibbosus</i> female	<i>tuberosus</i> male	1 <i>O. fuscus</i> male	<i>tuberosus</i> male & <i>O. gibbosus</i> female	68 min
6	<i>O. gibbosus</i> female	<i>tuberosus</i> male	1 <i>O. fuscus</i> male	<i>tuberosus</i> male & <i>O. gibbosus</i> female	70 min

Is such contact also possible between an *O. fuscus* male and a *gibbosus* male morph? In a second experiment a *gibbosus* morph male and an *O. fuscus* male were therefore brought together with an *O. gibbosus* female. Initially, the *gibbosus* male and *O. gibbosus* female engaged in a copulation posture for 10 minutes, but without palp insertion. Shortly after the copulatory posture ended the *O. fuscus* male grasped the *gibbosus* male at its cephalic groove for 2 minutes (Fig. 2). The *O. fuscus* male showed

feeding behaviour during the whole time interval, while the *O. gibbosus* male drummed its palps on the ventral side of the *O. fuscus* male. The same interspecific behaviour was repeated briefly two times. A third and a fourth experiment were analogous to the second experiment and resulted in respectively three (5 min, 2 min and 6 sec) and two interspecific interactions (6 min and 4 min) between an *O. fuscus* male and a *gibbosus* male morph.



Fig. 2. – Homosexual interaction between a *Oedothorax fuscus* male (top) and a *gibbosus* male morph. The *O. fuscus* male has grasped the *gibbosus* male at its cephalic groove and shows feeding behaviour.

In a fifth experiment seven *O. fuscus* males were combined with one *O. gibbosus* female and one *gibbosus* morph male. We used seven males to make it more difficult for the *O. gibbosus* female to choose. Several *O. fuscus* males displayed gustatorial courtship postures; altogether there were eight interspecific homosexual courtships. During most interactions the haemotodoch of the male palp was already visible.

In a sixth experiment two *gibbosus* males were brought together with an *O. gibbosus* female to observe if a gustatorial courtship is also possible between two *gibbosus* morph males. There was no contest between the two *gibbosus* morph males for the *O. gibbosus* female; instead of this, a gustatorial interaction happened between the two *gibbosus* male morphs during 12 minutes.

We also did analogous experiments with *tuberosus* males; but there was no resultant contact between the *tuberosus* morph male and the *O. fuscus* males or females. In the experiment with a *tuberosus* male, an *O. gibbosus* female and an *O. fuscus* female there occurred one intraspecific copulation (70 min). In one of the five experiments with a *tuberosus* male, an *O. gibbosus* female and an *O. fuscus* male there occurred two intraspecific copulations (67 min and 64 min respectively) and in each of the others there was only one intraspecific copulation (67, 66, 68 and 70 min respectively).

Because of the aforementioned interactions between the *gibbosus* morph male and the both sexes of *O. fuscus*, it was impossible to compare the number of copulations respectively achieved by *gibbosus* and *tuberosus*.

### The extent of interspecific interactions between *O. gibbosus* and *O. fuscus*

In the experimental series with a *gibbosus* male and an *O. fuscus* male in presence of an *O. gibbosus* female, interspecific courtships between a *gibbosus* male and an *O. fuscus* male occurred in seven of the ten cases (in one case twice, in another three times and in the others once). *Tuberosus* did, however, also perform in five of the ten repeats an intraspecific copulation; *gibbosus* only did so in three cases. In the absence of an *O. gibbosus* female it only occurred in three of the ten repeats (each time twice). In the analogous experiments with the *tuberosus* male there occurred no interspecific courtship between *tuberosus* and an *O. fuscus* male, either in the presence or absence of an *O. gibbosus* female.

In the experiment with a *gibbosus* male and an *O. fuscus* female, interspecific courtship occurred in only two of the ten repeats (in one case once, in the other twice). In the combination of a *tuberosus* male and an *O. fuscus* female, in contrast with the first experiment, in five of the ten repeats interspecific courtships occurred (in one case twice, in another three times and in the others one).

Finally, in the ten repeats of two *gibbosus* males no gustatorial interactions were observed, in contrast with the first experiment, in either the presence or the absence of an *O. gibbosus* female; the same was seen in the ten repeats of two *tuberosus* males and two *O. fuscus* males.

### Is there a gustatorial interaction between *gibbosus* and *tuberosus* males?

In the 68 (59+9) cases of an *O. gibbosus* female to which a *gibbosus* and a *tuberosus* male were added we never observed a gustatorial courtship between *gibbosus* and *tuberosus* males. The only kinds of interactions between both male morphs that occurred were aggressive contacts or disturbance of copulation. *Tuberosus* sometimes also disturbed the gustatorial courtship between *gibbosus* and the female. This disturbance of the other male morph only exceptionally led to an interruption of the copulation or gustatorial courtship.

In the first experiment there was no significant difference in the number of allowed copulations between the two male morphs according to a Fisher test ( $p = 0,1861$ ); the female chose nine times (on 50 refusals) for *gibbosus* and 15 times (on 44 refusals) for *tuberosus*. If the observation time was prolonged to a whole day, the number of allowed copulations between both male morphs was also not significantly different. The female chose only three times (on six refusals) for *gibbosus* and four times (on five refusals) for *tuberosus*.

Does *tuberosus* copulate longer than *gibbosus*? According to different ANOVA tests on the data of the first part of the experiment, there was no significant difference in duration of the first palp insertion between both male morphs (ANOVA: df Effect = 1, df Error = 6,  $F = 0,0938$ ;  $p = 0,770$ ;  $\bar{x}_{gib} = 35 \pm 4,58$  min;  $n = 9$ ;  $\bar{x}_{tub} = 33,87 \pm 4,31$  min;  $n = 15$ ), either in duration of the second palp insertion (ANOVA: df Effect = 1, df Error = 6,  $F = 0,662$ ;  $p = 0,447$ ;  $\bar{x}_{gib} = 34,83 \pm 6,55$  min;  $n = 6$ ;  $\bar{x}_{tub} = 30,5 \pm 6,36$  min;  $n = 2$ ), or in the duration of the complete copulation (both palps) (ANOVA: df Effect = 1, df Error = 6,  $F = 0,0611$ ;  $p = 0,464$ ;  $\bar{x}_{gib} = 41,78 \pm 13,20$  min;  $n = 9$ ;  $\bar{x}_{tub} = 47,83 \pm 18,87$  min;  $n = 15$ ). In the experiment with the long observation period there were only enough results to examine the difference in duration of the first palp insertion. No significant difference for the first palp insertion between both male morphs was found (ANOVA: df Effect = 1, df Error = 5,  $F = 0,973$ ;  $p = 0,369$ ;  $\bar{x}_{gib} = 36,33 \pm 9,86$  min;  $n = 3$ ;  $\bar{x}_{tub} = 27,5 \pm 12,82$  min;  $n = 4$ ).

## DISCUSSION

According to the lock-and-key hypothesis genitalia and non-genitalic contact structures evolve by pre-insemination hybridisation avoidance (ARNQVIST, 1998). According to several publications the lock-and-key hypothesis has fared poorly in many attempts to test it (SHAPIRO & PORTER, 1989; ARNQVIST et al., 1997; ARNQVIST & THORNHILL, 1998).

SCHAIBLE et al. (1986) suggested that the most important function of the male head structures of the *gibbosus* morph male is the fixation of the position for copulation. This could be in agreement with the lock-and-key hypothesis. This is, however, quite improbable because the contact between the female chelicerae and male head structures in most cases does not last during the copulation. Also the observed homo- and heterosexual interspecific contacts between males or females of *O. fuscus* and

the *gibbosus* male are in disagreement with the lock-and-key hypothesis. These interspecific gustatorial courtships are useless sexual interactions and the carapace structure of the *gibbosus* male cannot, therefore, be considered to have evolved in order to avoid interspecific sexual interactions. We also observed interspecific gustatorial courtships between an *O. retusus* (Westring, 1851) male and a *gibbosus* male (VANACKER, unpubl. data). *Gibbosus* even tried to copulate with *O. fuscus* males, which is evidently also a waste of energy. Not being occupied with such kinds of interspecific gustatorial courtships, *tuberosus* has more opportunity to copulate with an *O. gibbosus* female. In the first series of experiments *gibbosus* was indeed only able to perform one intraspecific gustatorial courtship not leading to a copulation. We never observed *tuberosus* males making use of the hairy groove of *gibbosus*, but two *gibbosus* males on the other hand can perform a gustatorial courtship. Presumably, this last interaction occurs only rarely; in the second experiment we did not observe it at all.

Besides pheromones, the hunch of *gibbosus* probably also secretes a nuptial gift because this hunch is completely filled with gland cells of different kinds (VANACKER, unpubl. data). Nuptial feeding is already known to occur in some spiders, such as the red back spider (FORSTER, 1992; ANDRADE, 1996) and *Pisaura mirabilis* (Clerck, 1757) (LANG, 1996; NITZSCHE, 1999; STALHANDSKE, 2001). If we assume that *gibbosus* indeed produces a nuptial gift, *O. fuscus* males and females could be attracted by the smell of the nutritional fluid itself, by male pheromones or by a combination of both. These interspecific "gustatorial courtships" can probably be interpreted as "robbery" of the nuptial gift at the cost of the *gibbosus* males; this could also explain the "gustatorial courtship" between the two *gibbosus* males. It is surprising, however, that *tuberosus* does not rob the nuptial gift of its "competitor" *gibbosus*. In the field these interspecific interactions might not be a real problem because of the aggregated distribution of *O. gibbosus* spiders in the moss. The only interspecific interaction that *tuberosus* males perform is with an *O. fuscus* female, suggesting poorly developed reproductive isolation between both species. It is striking that more interspecific interactions occur in the presence of an *O. gibbosus* female; the chance that *gibbosus* males make a wrong choice seems to be greater if they are excited by female pheromones.

Also the "sperm holder hypothesis" (see above) cannot hold for the cephalic structures of *Oedothorax gibbosus*; this hypothesis is specific for pholcid spiders. Sexual selection by female choice or sexual conflict is thus probably the force for the evolution of the cephalic structures of male erigonines.

Is *gibbosus* now sexually more attractive than *tuberosus*? We cannot answer this question yet on the basis of the third experiment. The presence of both male morphs in the vial of the female probably provokes too much disturbance; comparing *gibbosus* male – *Oedothorax gibbosus* female and *tuberosus* male – *Oedothorax gibbosus* female couples separately could solve this problem.

The results we obtained thus far, however, show that dwarf spiders probably are excellent candidates for speci-

ation research. Besides further species-recognition experiments between different *Oedothorax* species, we will study the interactions between different *Diplocephalus* Bertkau, 1883 species in the near future. Also more genetic and histological research is necessary.

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