

GENITAL MORPHOLOGY, COPULATORY MECHANISM AND
REPRODUCTIVE BIOLOGY IN *PSILOCHORUS SIMONI*
(BERLAND, 1911) (PHOLCIDAE; ARANEAE)

by

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ABSTRACT

The functional morphology of the genitalia of the pholcid spider *Psilochorus simoni* (BERLAND, 1911) is analyzed using the method of freeze-fixation of copulating pairs and the preparation of histological serial sections of the copulatory organs in functional contact. Courtship and copulation behaviour are described and preliminary notes on egg-sac production and life history are given. A median pouch in the vulva of *P. simoni* is interpreted as seminal receptacle and a convergent origin of receptacles in Pholcidae is discussed. The male cheliceral apophyses, found in most pholcids, are considered to have evolved in the context of copulation and mate choice, rather than male-male combat.

KEY WORDS: *Psilochorus simoni*, genital morphology, copulatory mechanism, cheliceral apophyses, sperm storage.

INTRODUCTION

Psilochorus simoni is a rarely found synanthropic pholcid spider that has dispersed over most parts of Europe since the beginning of this century (FÜRST & BLANDENIER, 1993). It was presumably introduced from America (GERTSCH in LOCKET *et al.*, 1974) and was discovered for the first time in Paris in 1911. Apart from sporadic ecological notes (summarized in FÜRST & BLANDENIER, 1993) and a few behavioural observations in BRISTOWE (1958) nothing is known about the ecology and reproductive biology of this species.

On the other hand, much information is available on the frequent cosmopolitan *Pholcus phalangioides*, including detailed descriptions of reproductive biology and copulatory mechanism (UHL, 1993, 1994; UHL *et al.*, 1994). Considering the provisional division of Pholcidae by BRIGNOLI (1981) into one largely "Old World-group" (including *Pholcus*) and one largely "American-group" (including *Psilochorus*), a comparative investigation promises to provide important information on the range of numerous behavioural and functional characters within the family Pholcidae.

MATERIALS AND METHODS

Penultimate-stage and adult specimens of *Psilochorus simoni* (BERLAND, 1911) were collected in a bathroom in the second district in Vienna, Austria. They were reared individually in small plastic boxes at room temperature (about 18-24°C) and fed with *Drosophila* (one fly every week).

Copulatory behaviour was observed under red light with a stereomicroscope at about 22°C. Five pairs were shock-fixed with liquid nitrogen during copulation, transferred into 80% ethanol at -25°C and either serially sectioned or studied with the SEM. For serial sectioning, three pairs were dehydrated, embedded in Spurr medium (ERL 4206 epoxy resin) under vacuum impregnation and sectioned with a Reichert OM U3 ultramicrotome with diamond knives (section thickness 1 µm). The sections were stained with a mixture of azure 2 (1%) and methylene blue (1%) in an aqueous borax solution (1%) at 80°C for about 10 s.

Both the individual genitalia and the genitalia in functional contact were studied with a Jeol JSM-35 CF scanning electron microscope.

Abbreviations

- b genital bulb
- ba... bulbal apophysis
- bp .. bulbal pouch
- c chelicera
- f femur
- fca.. frontal cheliceral apophysis
- g..... vulval glands
- lp ... lateral pouch in the uterus externus
- p procursus
- pa... patella
- s spur on procursus
- t tarsus
- tí tibia
- tr.... trochanter

RESULTS

Genital morphology

The male copulatory organ, the genital bulb, is situated at the pro-lateral side of the pedipalpal tarsus (fig. 1). It is a globulous structure with a strong curved (bulbal) apophysis situated apically (figs. 2B, 3A). Dorsally there are two further prominences, one knob-like, the other one provided with numerous cuticular denticles (fig. 3B). Denticles are also found on the membrane at the basis of the bulbal apophysis (figs. 3C, 3E). Ventrally, the genital bulb is provided with a sclerotized pouch (bp in fig. 2A). The sperm duct that fills the genital bulb together with glandular tissue, opens distally between the bulbal apophysis and the knob-like prominence without an embolus.

The genital bulb is flanked by a long narrow branch of the tarsus, the procursus (figs. 2A, 3A). This structure is distally provided with a strong spur and membraneous fringes that encircle a concavity. Other

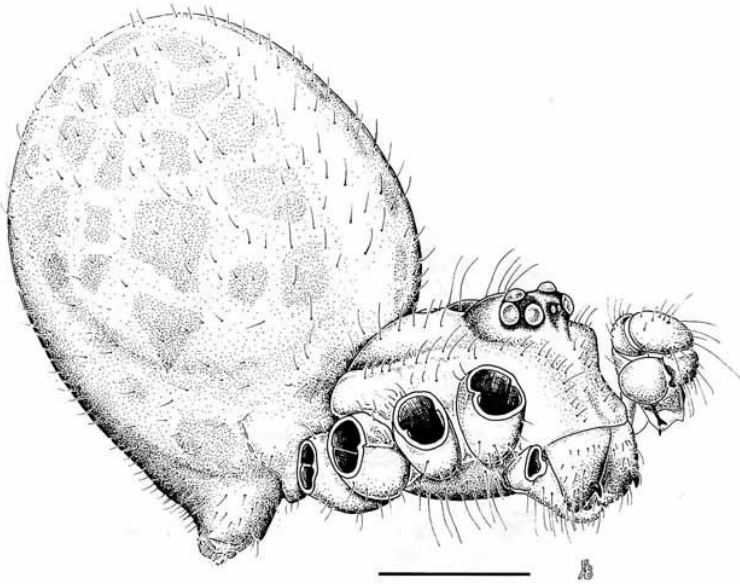


Fig. 1. Male *Psilochorus simoni*. All extremities removed except left pedipalp. Scale bar: 0.5 mm.

male structures which are modified in the context of copulatory mechanics, are the pedipalpal femora and the chelicerae. The femora are provided with two apophyses each (fig. 2A), one basally with two long setae and one distally that is more sclerotized. The chelicerae bear a pair of simple apophyses at their anterior faces (figs. 1, 3D, E).

The female copulatory organ lies ventrally on the opisthosoma. It is externally characterized by a simple transversal slit that is bordered by lightly sclerotized epigyneal plates, and two pouches anterior to these plates (figs. 4A, B). In figure 4B (situation during copulation), the plates are drawn asunder, showing the entrance into the uterus externus. The dorsal wall of the uterus externus is provided with a pair of pore plates (partially visible in fig. 4B) through which the dorsal vulval glands discharge their products. Anteriorly, paired lateral membraneous pouches (fig. 6E) and a median sclerotized pouch (fig. 6B) extend from the uterus externus. After copulation, sperm is primarily found in the anterior median pouch (fig. 6B), that is also surrounded by glandular tissue. A rather simple valve separates the uterus externus from the uterus internus (fig. 6C).

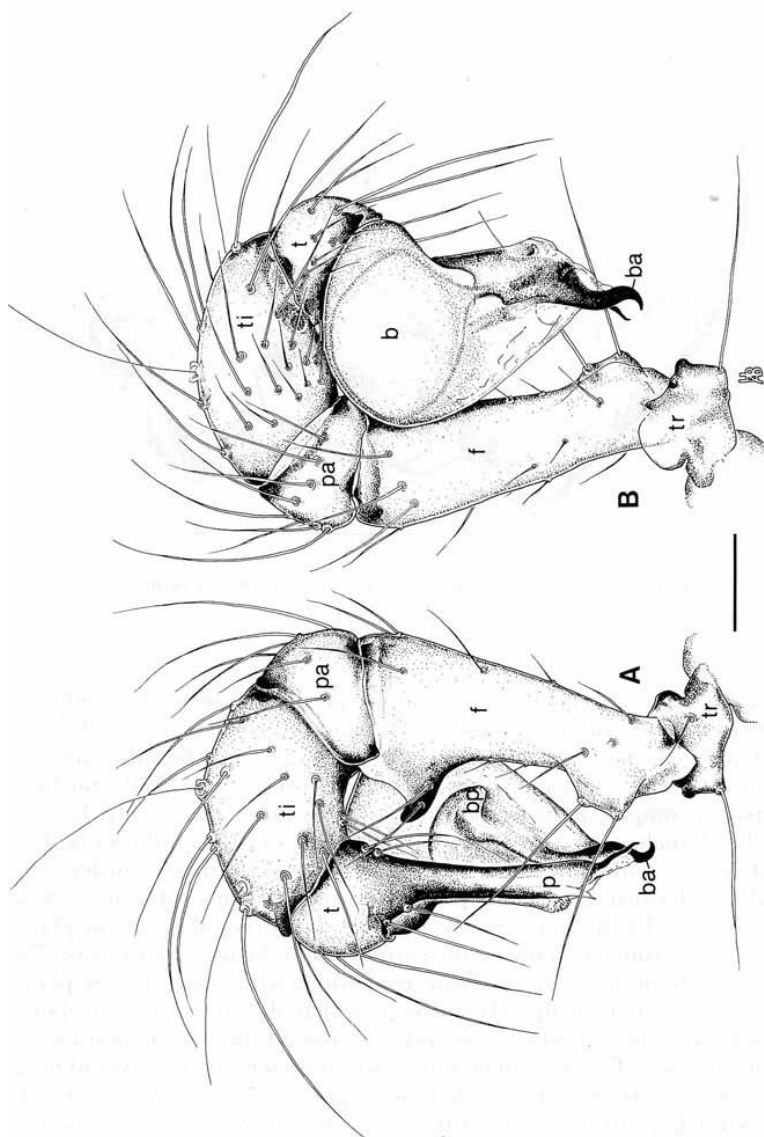


Fig. 2. Left male pedipalp, retrolateral (A) and prolateral (B) view. Scale bar: 100 μ m.

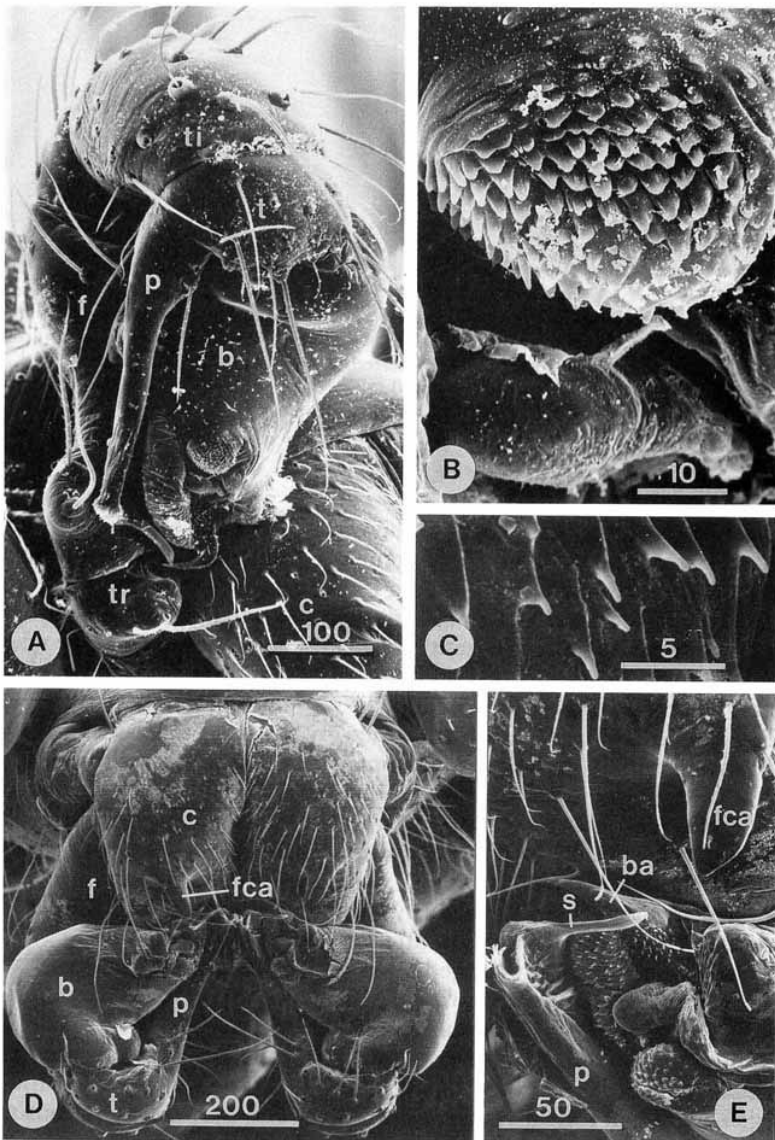


Fig. 3. Male copulatory apparatus (SEM). — A. Right pedipalp, frontal view. — B. Dorsal prominences on genital bulb. — C. Cuticular denticles on membrane at the basis of bulbal apophysis. — D. Male pedipalp in copulatory position, *i.e.* rotated for 180° (*cf.* fig. 1). — E. detail of fig. D, showing distal parts of procursus and genital bulb. Scale bars in μm .

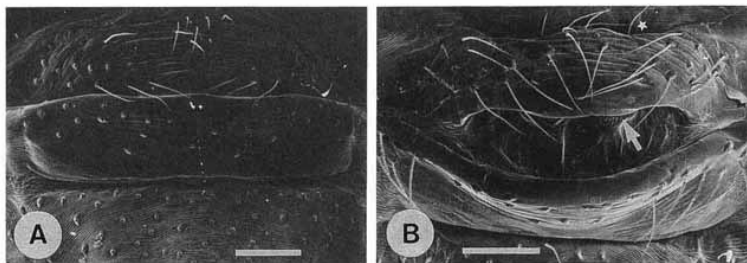


Fig. 4. Female epigyne (SEM). — A. Situation at rest. — B. Situation during copulation (male parts removed): epigynal plates are drawn asunder. Asterisk marks anterior groove into which male cheliceral apophysis is inserted. Arrow points at pore plate. Scale bars: 100 μ m.

Courtship and copulation

In seven cases, the whole copulation was observed. Courtship duration ranged from 7 to 53 min and generally accorded to the following pattern: After hanging motionless in the female's web for some seconds, the male slowly walks around, then starts to jerk the web with the anterior legs and performs gentle seesawing movements with the whole body. This behaviour is repeatedly interrupted by periods in which the male cuts some threads in the female's web and spins own ones. At this time the female begins to turn around to face the male and in some cases performs slow waving movements with the extended anterior legs. Courtship intensity increases just before copulation. Alternately, the male vigorously jerks the web with the anterior legs and vibrates his entire body. Finally, with a vibrating opisthosoma, the male hastily approaches the female, rotates the pedipalps (see below) and inserts the copulatory organs simultaneously, usually without any problems (*i.e.* without unsuccessful insertion attempts or "flubs").

Copulation duration ranged from 14 to 19 min in six pairs with virgin females. In the seventh case, in which the female had already produced four egg-sacs, copulation duration was only 9 min. The first minutes of copulation are characterized by intensive leg movements, in which the male seems to stroke back the fidgeting female legs with his legs I-III. Then the movements slow down and during the last minutes one can only observe the male gently vibrating his opisthosoma and occasionally moving his pedipalps sideways, either simultaneously or alternately. Figure 5 shows a pair in this phase of copulation.

The pairs separate after a sudden unrest and calm down after a short period of renewed male courtship. In some cases the females rushed

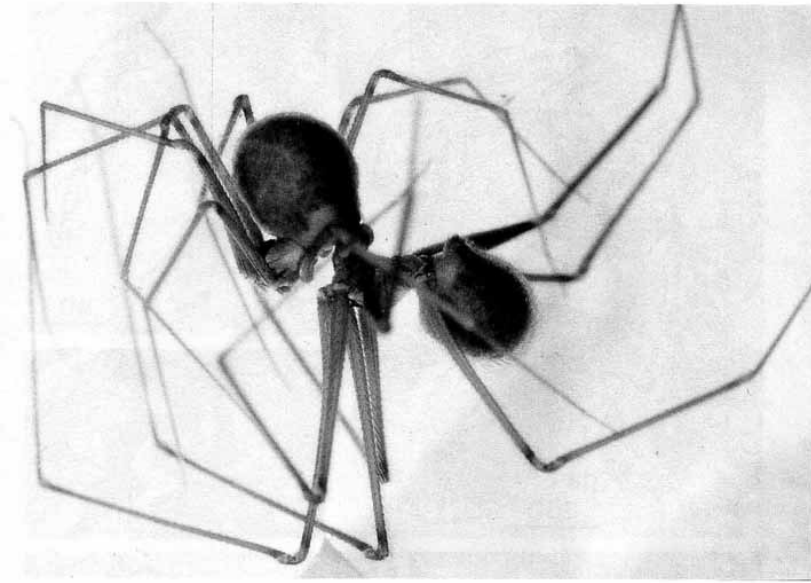


Fig. 5. *Psilochorus simoni* pair in copulatory position. Male on right side.

aggressively against the males during this period, but I could never see one feeding upon the male.

Genitalia coupling (fig. 7)

As indicated, the pedipalps are rotated (180° in the coxa-trochanter joint) before copulation. They become arrested in this position by jamming in the trochanter and the proximal femoral apophysis between the chelicera and the pedipalpal coxa (figs. 6A, D). Correct positioning of the male relative to the female is guaranteed by the insertion of the cheliceral apophyses into the female pouches anterior to the epigyne (fig. 6E). The distal parts of the genital bulb and the procursus are inserted together into the uterus externus. The bulbal apophyses are hooked into the lateral pouches in the uterus externus and together with the cheliceral apophyses provide a fast locking mechanism, whereas the dorsal bulbal prominences simply are pressed against the dorsal wall of the uterus externus. The spurs on the procursi point to the valve, and medially the apical concavities of the procursi open immediately at the entrance into the anterior median

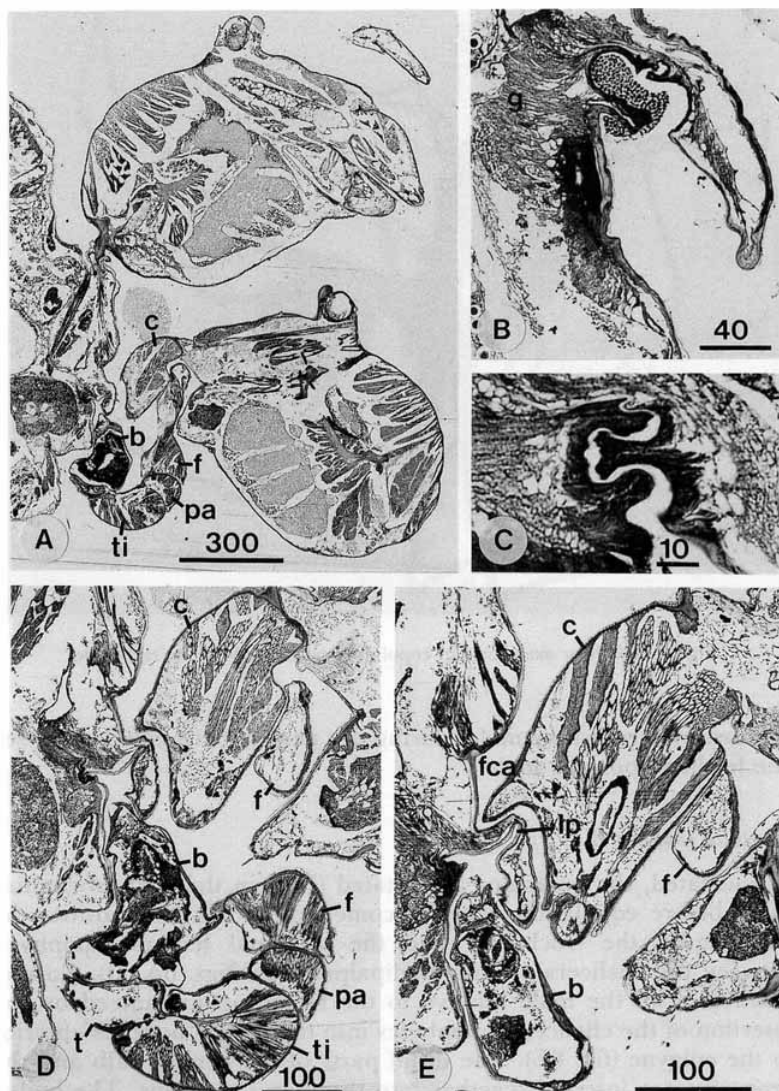


Fig. 6. Semithin sections through the copulatory organs in functional contact and of the female vulva respectively. Orientation is always as in A. — A. Overview, male below, with pedipalps in inverted position. — B. Median section through female vulva with unpaired receptacle, packed with sperm. — C. Sclerotized valve, separating uterus externus and u. internus. — D. Distal femoral apophysis hooked into bulbal pouch. — E. Male cheliceral apophysis inserted into anterior epigyneal groove. Scale bars in μm .

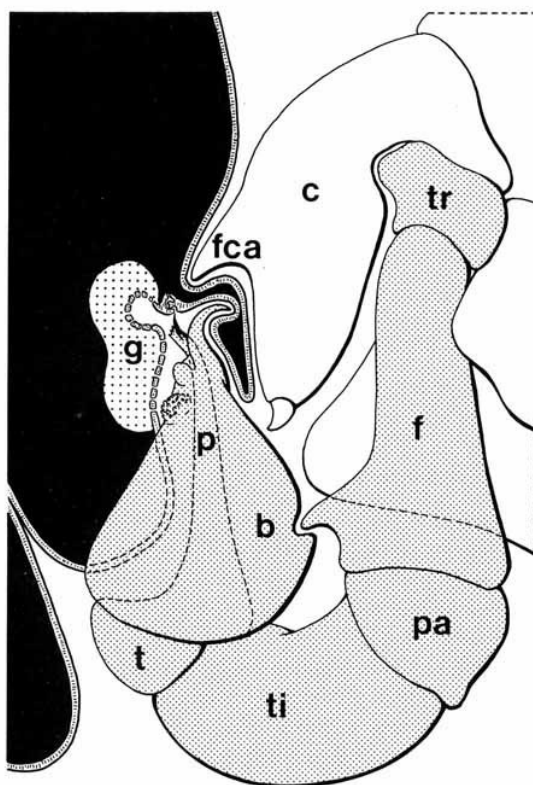


Fig. 7. Schematic reconstruction of the copulatory organs in functional contact as derived from the serial sections.

pouch. The distal femoral apophysis is hooked into the ventral pouch of the genital bulb (fig. 6D), thus stabilizing the copulatory apparatus internally.

Preliminary notes on egg-sac production and life history

P. simoni females can produce at least four egg-sacs after one insemination. This was observed in four cases, but these females were already fertilized when captured and may have made one or more egg-sacs before. The period between copulation and production of the first egg-sac was determined in three cases, and ranged from 15 to 22 days. Each batch contained about 20 to 30 eggs. Egg-sacs are enveloped by a

fine but dense layer of silk and are carried by the female with her chelicerae (as in *Ph. phalangioides*). Spiderlings hatched after 25 to 50 days ($N = 15$). The intervals between the production of two egg-sacs ranged from 30 to 70 days ($N = 13$). Both periods increased in length with the number of egg-sacs produced by one female.

The number of spiderlings that hatched from a fourth (? see above) egg-sac was only 0, 10, 12 and 17. The other eggs had shrunk and had been removed from the egg-sac by the female.

In all cases the spiderlings were released in the original habitat in order to maintain the population and because of the difficulty to feed the spiderlings. Thus, only the period between the last two moults before maturity could be ascertained. It ranged between 36 and 42 days ($N = 3$).

DISCUSSION

Ecology, life history and behaviour

FÜRST & BLANDENIER (1993) have summarized the ecological notes on *P. simoni* given by previous authors. According to them, the species prefers dark places with temperatures between 15 and 18°C and is hardly influenced by the degree of humidity. This is largely confirmed by the present study. Males did not react to females in daylight but soon began to court when observed under red light. Humidity in the original habitat (bathroom) varied strongly. However, *P. simoni* does not seem to be bound to low temperatures. During summer, the spiders were kept at 22-24°C and showed normal activity.

Equally, *P. simoni* does not seem to prefer a special diet. BRISTOWE (1933) fed it with a pseudoscorpion (*Chthonius*), "cellar flies" and moths. DZIABASZEWSKI (1967) found rests of anobiid beetles in the webs and experimentally fed in with flies and gnats, and I have reared some individuals for more than one year with *Drosophila* flies only.

Considering the apparent ecological plasticity of *P. simoni*, the question arises about why it is so rarely found. In Austria, for instance, the finding of one single male has been documented by KRITSCHER (1969). The simplest explanation seems to be that it is small and lives in dark corners, preferably close to the floor (KLAUSEN, 1972; personal observation). BRISTOWE (1958) admits that *P. simoni* had been living freely but undiscovered for some years in the British Museum of Natural History. Quite probably, *P. simoni* is much more common than suggested by the few findings documented in the literature.

Life history has been shortly described by BRISTOWE (1958). According to BONNET (in BRISTOWE, 1958), *P. simoni* moults 5 times in 6-7 months until reaching maturity. Some differences with the present

results in respect to time periods may be due to the dependence of these from temperature and food supply. BRISTOWE specifies the period from copulation to first egg laying as 1-2 months, which is much longer than that found in this study (15-20 days). The interval between the production of two egg-sacs was given as about 10 weeks, but can be much shorter (4 weeks; see above). BONNET (in BRISTOWE, 1958) observed that *P. simoni* females copulate only once. They do, however, accept a second male after the production of an egg-sac (own observations). Such a correlation between female life history and receptivity was also found in *Ph. phalangioides* (UHL, 1993). The number of eggs and egg-sacs is significantly higher in *Ph. phalangioides* (up to 6 batches and 170 eggs, UHL, 1993) which may be correlated to the different mode of sperm storage (see below).

Behaviour is considered to be very uniform among pholcids (SIMON, 1893; MELLO-LEITAO, 1918; GERHARDT, 1933). Most elements of courtship and copulation observed in *P. simoni* have also been reported for other pholcid genera. Similar descriptions of courtship exist for *Pholcus* spp. (e.g., GERHARDT, 1921; UHL *et al.*, 1994), *Holocnemus* spp. (GERHARDT, 1927, 1933), *Hoplopholcus forscali* (GERHARDT, 1924), *Modisimus* spp. and *Blechnoscelis* sp. (EBERHARD & BRICEÑO, 1985). Rotation of the pedipalps for 180° before intromission seems to be as usual as pedipalp movements and opisthosoma-vibrations during copulation (MONTGOMERY, 1903; GERHARDT, 1921, 1923, 1924, 1927; UHL *et al.*, 1994). One difference between *P. simoni* and the hitherto observed species is the peculiar leg movements during the first minutes of copulation. So far, it is not possible to ascribe a clear function to this behaviour, but it appears as if the mechanical fit of the genitalia is tested during this phase. A correlation of this behaviour with the thickening of the male femora III (fig. 8) could not be found. Such thickenings are also present in male *Blechnoscelis* (femora III) and male *Coryssocnemis* (femora II) (SIMON, 1893; MELLO-LEITAO, 1918) but have not been interpreted functionally in either genus.

In accordance with BERLAND (1911), *P. simoni* was never observed to oscillate its body in the "typical" pholcid manner.

Sperm storage

P. simoni produces several egg batches until more than 6 months after copulation. How is the sperm stored? Some authors did not find seminal receptacles and proposed the absence of such structures to be a general character in Pholcidae (DEELEMEN-REINHOLD & DEELEMEN, 1983; UHL, 1994). As a consequence, the whole uterus externus is assumed to be used for sperm storage (BRIGNOLI, 1981; UHL, 1993,

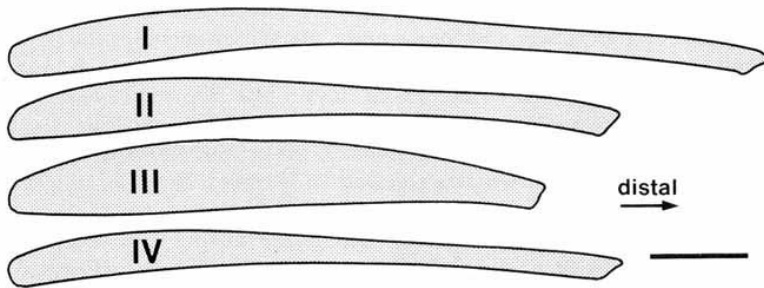


Fig. 8. Femora I-IV of a *Psilochorus simoni* male in lateral view. Note the thickening of the third femur. Scale bar: 0.5 mm.

1994). In *Ph. phalangioides*, the sperm is thought to be stored in a secretory substance that is discharged by dorsal glands through the vulval pore plates into the uterus externus (UHL, 1994). However, there are some references that mention the existence of receptacles in American pholcids, e.g., for *Metagonia* (GERTSCH, 1977) and *Anopsicus* (GERTSCH, 1979). In *P. simoni*, the fact that the supposed receptacle is packed with sperm after copulation and is in connection with glands, indicates its function as a sperm storing organ.

Most probably, such receptacles have evolved several times convergently, in pholcids as well as generally in haplogyne spiders (c.f. FORSTER, 1980). It is interesting to note in this connection that in the sister taxon of Pholcidae (according to the phylogenetic tree of CODDINGTON & LEVI, 1991) different kinds of receptacles occur: the Diguettidae have unpaired receptacles (GERTSCH, 1958a) like *P. simoni*, the Plectreuridae probably have paired ones (GERTSCH, 1958b) like *Metagonia* and *Anopsicus* (for references see above). Convergent evolution is apparently the best explanation for this pattern.

The cheliceral apophyses — used for fighting or for copulation?

In almost all pholcid species, the male chelicerae are provided with special apophyses in addition to the usual armature found in both sexes. They can provisionally be classified into two categories: (1) the frontal cheliceral apophysis (fca) that is in most cases situated on the anterior face of the chelicera. Only a few pholcids lack this apophysis, e.g., *Psilochorus acanthus* CHAMBERLIN & IVIE, 1942, and certain *Panjange* species (DEELMAN-REINHOLD & DEELEMAN, 1983). Instead of a real

apophysis, there may be groups of special bristles in certain species; (2) the lateral cheliceral apophysis that is usually situated basally on the fronto-lateral side of the chelicera and is often accompanied by a smaller frontal prominence. This apophysis is present only in some genera (e.g. *Pholcus*, *Panjange*, *Micromerys*, *Calapnita*; see e.g. DEELEMEN-REINHOLD, 1986; DEELEMEN-REINHOLD & PLATNICK, 1986) and is apparently correlated functionally with the trochanter-apophysis (UHL *et al.*, 1994; Huber, pers. obs.). It is not present in *Psilochorus* and will not be further discussed in this paper.

The fca is highly species-specific and often represents the best character for species discrimination (see e.g., BANKS, 1921; GERTSCH, 1935; GERTSCH & IRBY-DAVIS, 1937). As to the function, two different hypotheses have been proposed: KRAUS (1984) has speculated that the male fca (in particular that of *Smeringopus*) might be inserted into paired grooves of the female epigyne in order to safeguard sperm transfer. On the other hand, EBERHARD & BRICEÑO (1985) interpreted the fca of *Blechnroscelis* and *Modisimus* in the context of male-male combat. The present study has confirmed the hypothesis of KRAUS for *P. simoni* and I will postulate this to be the general function of the fca in pholcids for the following reasons: (1) In all four species that have been investigated by freeze-fixation of copulating pairs, the fca contacts the female during copulation: *Pholcus phalangioides* (UHL *et al.*, 1994), *Holocnemus pluchei* and *Pholcus opilionoides* (Huber, pers. obs.) and *P. simoni*. (2) Morphological data and illustrations given by previous authors strongly suggest that this may be generalized for whole genera. In the illustrations of e.g. SENGLET (1971, 1974) and MILLOT (1941), all *Pholcus* species show the epigyneal hook as well as the medially directed fca like *Ph. phalangioides* and *Ph. opilionoides*. According to KRAUS (1957) the genera *Smeringopus* and *Smeringopina* are characterized by the fca in the male and paired grooves (several times misinterpreted as vulval openings) in the female. (3) In many cases the fca is minute and appears highly unsuitable for battles. Additionally, the interpretation of EBERHARD & BRICEÑO (1985) is founded on a few, technically unaided observations of male-male combat and copulation. Also in *Ph. phalangioides*, the function of the fca was not realized by a number of careful observers until freeze-fixation and subsequent preparation of serial sections revealed it (UHL *et al.*, 1994). EBERHARD & BRICEÑO (1985) further admit that combat movements were too quick to ascertain whether or not the males contacted each other with their chelicerae. (4) The general uniformity of the family Pholcidae is an additional, although weak argument for a uniform function of the fca. A detailed investigation of further genera will certainly show whether or not this generalization is justified.

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