

Male pedipalp morphology and copulatory mechanism in *Pholcus phalangioides* (Fuesslin, 1775) (Araneae, Pholcidae)

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Summary

Male pedipalps of *Pholcus phalangioides* are morphologically investigated, mating behaviour in this species is described and results on the copulatory mechanism are presented. With the aid of cryofixation and subsequent freeze substitution, pairs were fixed *in copula* and serially sectioned or investigated with SEM methods. Previous views of the coupling mechanism are corrected: during initial coupling the male locks the sclerotised hook of the female epigyne between two apophyses that are situated on the male chelicerae, and during genital coupling (insertion) the embolus, the appendix, the tip of the uncus and the massive procurus are intromitted into the female. Pedipalp movement during genital coupling results in an extrusion from the female genitalia of material comprising female secretion, spermatozoa and male secretions. Possible correlations between genital morphology and female choice as well as sperm competition are briefly discussed.

Introduction

Male pedipalps in Pholcidae are highly derived and easily distinguishable from any other spider pedipalp. The sclerites of the genital bulb are considered to be fused (Kraus, 1984a), and the presence of a tarsal structure named the procurus is unique among spiders. As a basis for later phylogenetic interpretations we will present a detailed morphological account of the features of the male pedipalp. Also, the complicated torsion of the palps before copulation is not understandable without a description of their morphological characteristics. Morphology and movement of pholcid spider palps were investigated by Gerhardt (1921, 1923, 1924, 1927), who stated that the uncus, embolus and appendix are inserted into the female whereas the massive procurus is kept outside the genital cavity. Since Gerhardt, no further work has been done on copulatory mechanics in haplogyne spiders, whereas a number of detailed studies have been published on entelegyne spiders (Gering, 1953; Grasshoff, 1968; Van Helsdingen, 1969; Blest & Pomeroy, 1978; Loerbroks, 1984; Huber, 1993). In the course of investigations on sperm transfer and storage in female *Pholcus phalangioides* and on copulatory mechanics we reconsidered Gerhardt's findings using modern methods: Scanning Electron Microscopy and cryofixation of copulating couples.

Material

Different stages of *Pholcus phalangioides* were collected from the Zoological Institutes in Hamburg and Freiburg and from houses in Hamburg, Tübingen, Freiburg, Denzlingen (all Germany) and Vienna (Austria). They were kept separately in plastic boxes (10 × 10 × 6 cm).

Methods

Morphological investigation

Male pedipalps were isolated, embedded in Hoyer's medium (Kraus, 1984b) and investigated light-microscopically using a Leitz Stereomicroscope and a Leitz Orthoplan with interference contrast and a drawing device.

For Scanning Electron Microscopy the male parts were either fixed in 70% ethanol, dehydrated in acetone, critical-point dried, sputter-coated with gold and investigated in a Camscan DV4, or fixed in Bouin (Gregory, 1980), dehydrated in graded series of ethanol, critical-point dried, sputter-coated with gold and examined in a Zeiss Semco Nanolab 7.

For histological investigation of the procurus, male pedipalps were fixed in Bouin (Gregory, 1980), embedded in LR-White (London Resin Co. Ltd) and cut with glass knives on a Reichert Autocut. The semithin sections (1 μm) were stained with toluidine blue.

Copulatory behaviour, palpal torsion and movements were observed under a dissecting microscope and partly video-recorded, using inexperienced spiders that were reared in the lab. Eight virgin females were used to investigate sperm extrusion from the female genital cavity during their first copulation. Six of these allowed a second mating with an inexperienced male. They were also checked for sperm extrusion.

Fixation in copula

For SEM studies, an inexperienced female was placed in a wooden frame (16 × 16 cm) on stilts (16 cm) situated in a large glass vessel. The stilts stood on petri dishes at the bottom of the glass vessel which was filled with water up to the upper rim of the petri dishes. Therefore, the spiders were forced to build their webs within the given frame. After the female had constructed sufficient threads, a male was added. Usually courtship began immediately after the spiders had calmed down. After genital coupling, the "copulation frame" with the copulating spiders was taken out of the vessel and the spiders were fixed with liquid nitrogen (−196°C) that was poured over them. For freeze substitution, the frozen spiders were transferred into 100% acetone at −70°C and kept at constant temperature in the freezer. After about 10 days the specimens were warmed up slowly and after a change of acetone they were critical-point dried, sputter-coated and examined in a Zeiss Semco Nanolab 7. For semithin sections of copulating couples, they were brought into 80% ethanol after fixation with liquid nitrogen, kept at −25°C for about three weeks, dehydrated in an ethanol series and embedded in epoxy

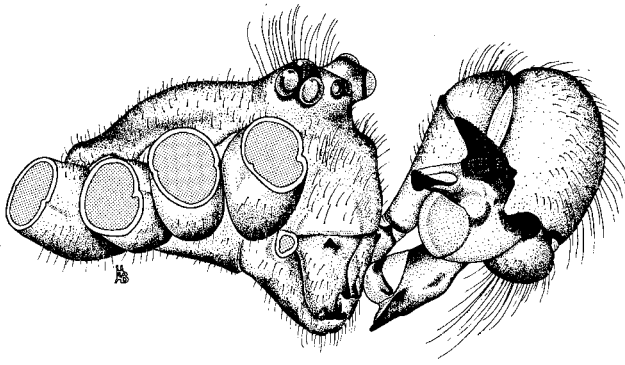


Fig. 1: Male *Pholcus phalangioides*. Prosoma with appendages removed, except for left pedipalp.

resin (Erl-4206) under vacuum impregnation. The objects were serially sectioned ($1\mu\text{m}$) on a Reichert Om U3 with diamond knives. A mixture of azure 2 (1%) and methylene blue (1%) in an aqueous borax solution (1%) was applied for staining (80°C , 10 s).

Figure orientation

Figures concerning the morphological description of the male pedipalp mostly present the morphological dorsal side upwards, despite the fact that the spiders are always found in an upside-down position within their web. In the section on copulation and copulatory posture, however, the spiders are presented as observed in the natural situation wherever possible, i.e. the morphological dorsal side of the spider is shown in a downward position.

Abbreviations used in text and figures: al=lateral trochanter process, a2=medial trochanter process, aa=apical apophysis on procurcus, ap=appendix, b=genital bulb, bp=basal prominence on genital bulb, c=callosity on procurcus, ca=apophyses on male chelicerae for initial coupling, ct=proximal teeth on male chelicerae, d=circular depression on procurcus, e=embolus, ep=epigynum, f=cheliceral fang, fe=femur, g=gland opening into female genital cavity, h=hook-like prominence on epigynum, he=haematodocha, i=inflatable area on procurcus, ll=apical lamellar process on procurcus, l2=lateral lamellar process on procurcus, p=procurcus, pa=patella, pu=protrusion on uncus, r=dark coloured ribbon around genital bulb, ta=tarsus, ti=tibia, tb=trichobothrium, tr=trochanter, u=uncus.

Results

Morphological description of male pedipalp

The male pedipalp in *Pholcus phalangioides* is a massive structure that extends far from the prosoma. In the resting posture it is U-shaped, with trochanter, femur and patella forming one axis, tarsus with procurcus and genital bulb forming the other axis, and tibia intermediate between the two (Fig. 1). The tip of the distal part of the male pedipalp is close to the chelicerae. The genital bulb lies medially.

The male pedipalp consists of various structures, some of which are highly complex (Fig. 2). The small trochanter (tr), connected with the coxa by means of

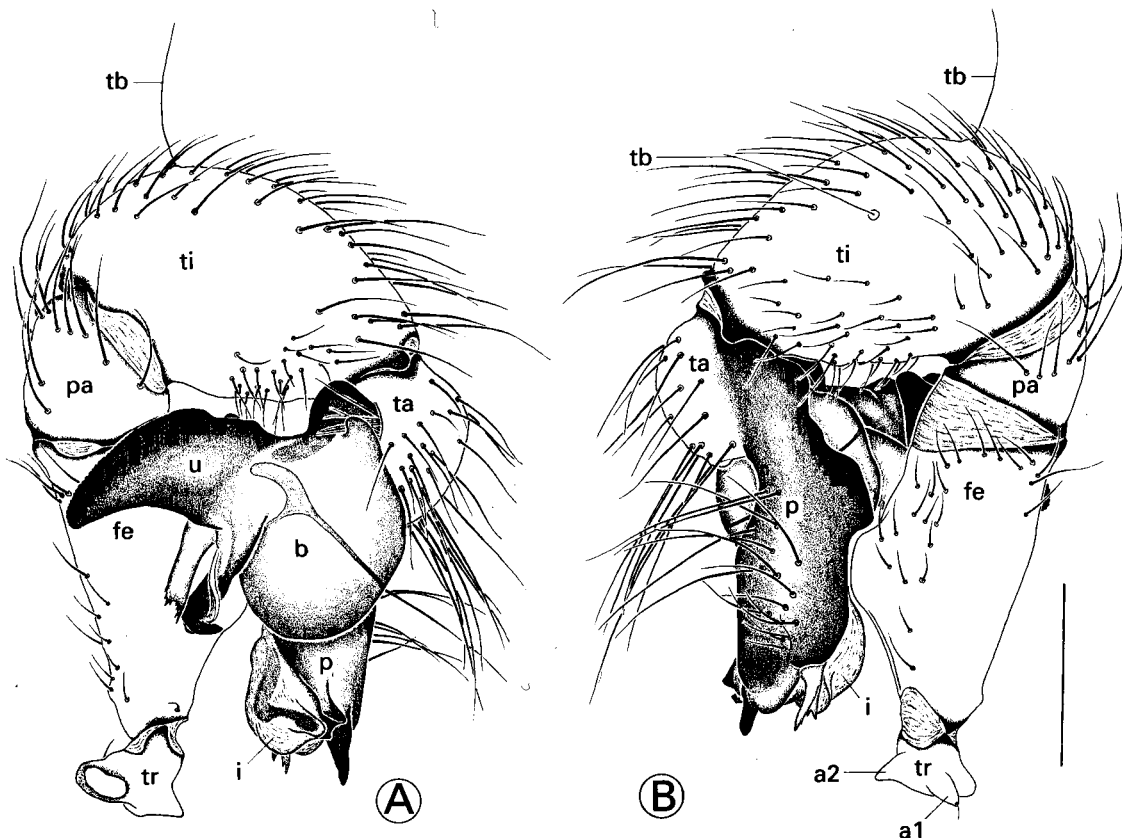


Fig. 2: Left male pedipalp. **A** Medial view; **B** Lateral view. Scale line=0.5 mm.

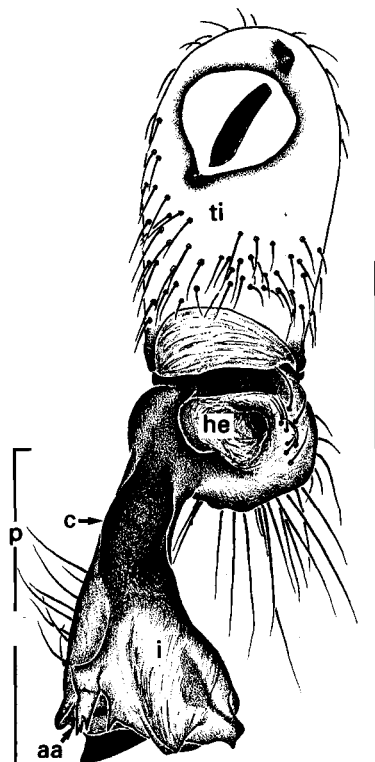


Fig. 3: Tibia and tarsus of left male pedipalp (morphological ventral side), genital bulb removed. Scale line=0.5 mm.

membranes only, exhibits two processes (a1, laterally and a2, ventrally). The process a1 plays a role during copulation which will be described in the corresponding section. A dicondylous joint connects the trochanter with the femur. Ventrally, the femur carries a bulge which corresponds to a depression on the procurus (Fig. 2B). The patella possesses dicondylous joints on each side. The tibia is bent in shape, and bears two trichobothria (tb), one laterally and one dorsally (Fig. 2). The tibia contains muscle M29, whose tendon extends into the genital bulb, and two other muscles that move the tarsus. A dicondylous joint connects the tibia with the tarsus which carries the genital bulb.

Tarsus with procurus

In the tarsus a proximal and a distal part can be distinguished (Fig. 3). The proximal part carries several bristles and a tarsal organ, and contains muscle M30 whose tendon extends into the genital bulb. In Fig. 3 the genital bulb has been removed, showing the connecting haematodocha (he). The distal part of the tarsus is called the procurus (p), a massive and partially heavily sclerotised structure. Its relatively slim base carries a callosity (c) on its ventral side (Figs. 3, 4A). In its distal region the procurus is broad in shape and flattened dorso-ventrally. Apically, the procurus is very complex in structure: on its ventral side there is a membranous, inflatable area (i) (Figs. 2A, 3, 4A) and laterally there is an apophysis with fringed ends (aa). A membranous slit runs across the apex of the procurus and terminates in a soft lamellar process (l1) (Fig. 4E), which partially surrounds a circular depression (d) (Fig. 4E). The

circular depression always contained a secretory substance (Fig. 4D) in palps that had not been treated with pepsin. This substance was present in experienced males and in males that had never mated, indicating that it is produced by the male itself. Epithelial cells close to the pores on the bottom of the depression might be responsible for producing the secretion (Fig. 4G). Further medially, there is a slightly twisted, sharp-edged lamellar process (l2) (Fig. 4E). On the dorsal side of the procurus (Fig. 4B) there is an area showing denticles in high density (Fig. 4C). The most distal region forms a sharp edge and terminates in a tooth that points laterad.

The lumen of the procurus is filled with haemolymph (Fig. 4F) and communicates with the proximal part of the procurus by means of a slit-like opening.

Bulbus genitalis

The genital bulb inserts on the ventral side of the proximal region of the tarsus. It is of compact shape and is provided with several protrusions (Figs. 5, 6A). Proximally, close to the basal haematodocha there is a prominence (bp) which is highly sclerotised. The tendons of the muscles M29 and M30 insert on the inner surface of this structure. Around the bulb runs a dark coloured ribbon (r) that ends, slightly broadened, close to the most dominant protrusion of the genital bulb, the uncus (u). The uncus is heavily sclerotised, dark coloured and roughly blade-shaped. In the resting position of the male palp the edge of the uncus points towards the prosoma. On its medial side it bears small, sclerotised denticles that are oriented towards its base. On its lateral side the uncus carries a heavily sclerotised protrusion (pu) (Fig. 5B). Between the uncus and the spherical part of the genital bulb, another protrusion called the appendix (ap) is situated (Fig. 5). It is shaped like a long, slightly twisted lamella and its apex is bent over at a right angle. Between the uncus and appendix lies the sperm transferring structure, the embolus (e). Its base consists of a soft, membranous zone that implies a certain flexibility (Fig. 6D). In the distal region, the embolus is smaller in diameter. The ductus ejaculatorius, leading from the inner sperm-storing structure to the tip of the embolus, ends at a slit-shaped opening between two rows of teeth (Fig. 6E). The apex of the embolus can vary considerably in shape (Fig. 6C, E).

Courtship

After calming down, the males approached the females which, if the males approached from the side or from behind, turned round to face the male. Males tapped lines in the female web with their legs I. Mostly only one leg tapped alternately with the other leg. Males performed bursts of quick dorso-ventral vibrations with their opisthosoma when moving towards the female. Females that later allowed copulation responded with tapping movements and moved a short distance towards an approaching male. Receptive females inflated the membranous area posterior to the epigynum. They assumed a specific posture: they moved their

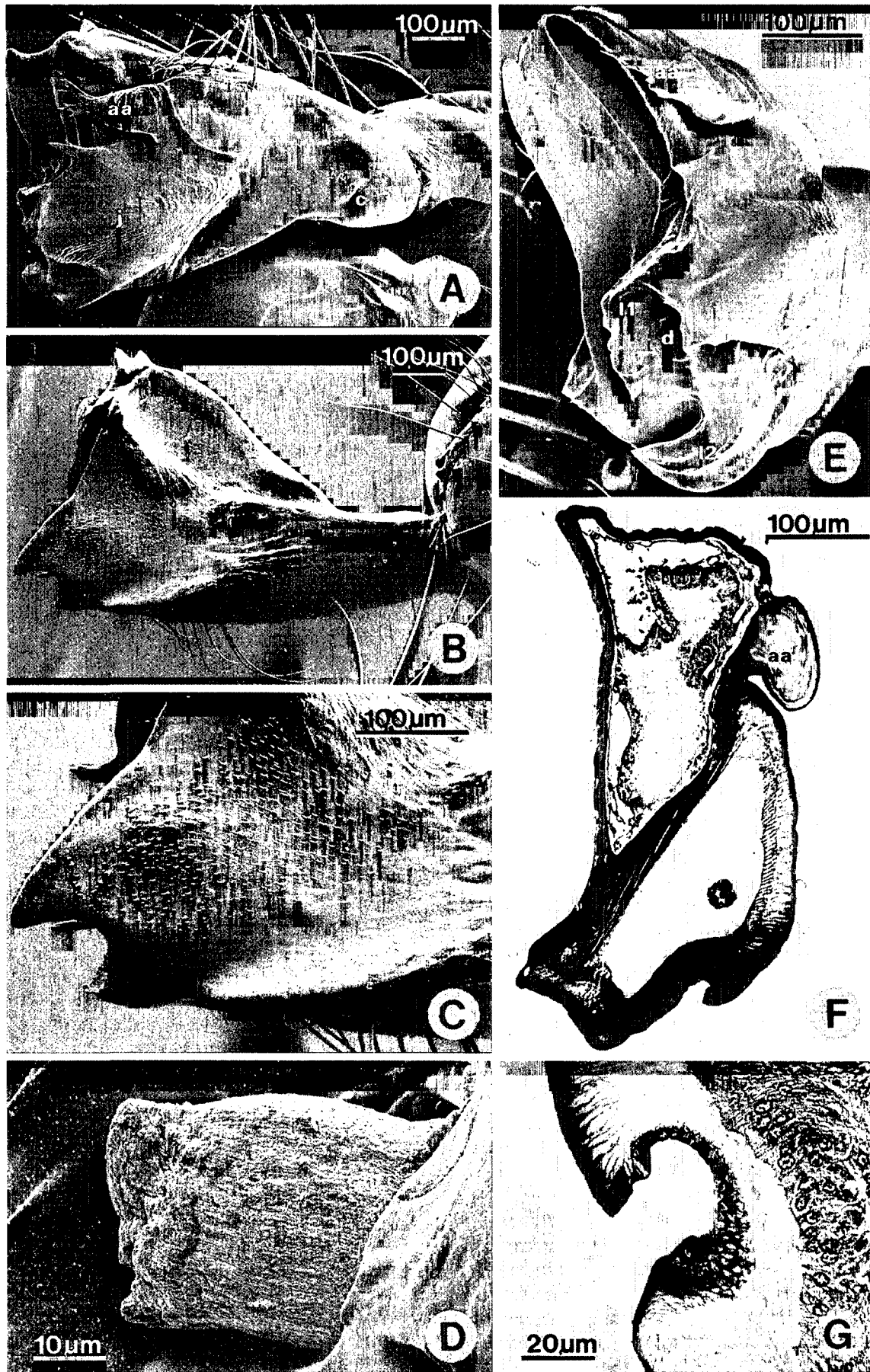


Fig. 4: Procursus of left pedipalp. **A** Ventral view; **B** Dorsal view; **C** Detail of dorsal bristles; **D** Secretory plug in apical depression; **E** Procursus, apical view (A-E, SEM); **F** Histological section; **G** Histological section of epithelial cells round apical depression.

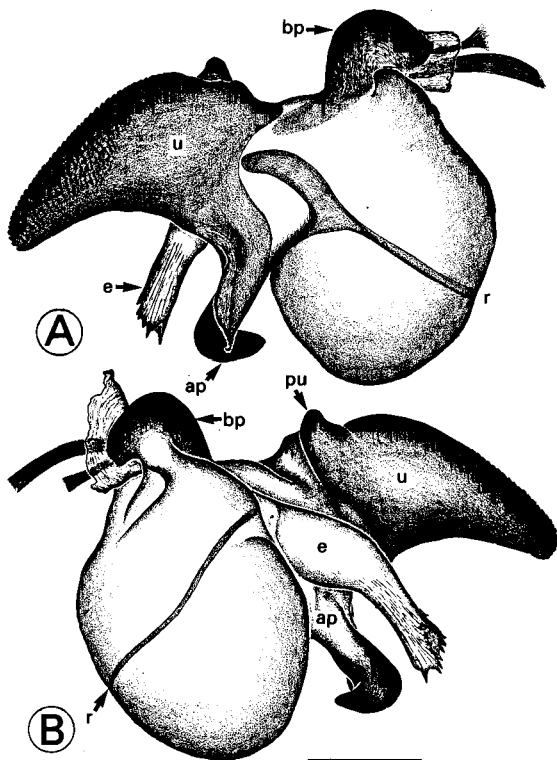


Fig. 5: Left genital bulb, removed from tarsus. **A** Medial view; **B** Lateral view. Scale line=0.25 mm.

opisthosoma into a horizontal position, extended their legs sideways and stayed motionless. Having approached close to a female, males tapped lines with their legs I and II in frequent succession. They raised their pedipalps and twisted them at the coxa-trochanter joint through 90° (Fig. 7A–C). Often, males cut some threads in the web close to a female before initial coupling.

Initial coupling

With fast movements of the whole body, holding their palps in position C (Fig. 7), males moved back and forth along the ventral body surface of the females with their chelicerae, apparently trying to seize hold of the female's body surface before insertion (for corresponding female genital morphology see Uhl, 1994a). Some of the males succeeded in seizing hold of the female after a single movement, but others required about 100 movements before coupling. During initial coupling the sclerotised hook on the female epigyne is locked between two cheliceral apophyses (ca) that are situated about one-third of the length of the chelicerae from the fangs (Fig. 8). These apophyses are partially surrounded by robust bristles and carry sensilla at their apices. After locking the epigynal hook between the apophyses, males pulled females towards themselves, changing the female position from horizontal to vertical, and insertion followed.

Genital coupling

For insertion, the pedipalps were twisted again through a further 90°, resulting in a total torsion of 180° (Fig. 7D). The proximal teeth on the chelicerae (ct) and the lateral trochanter processes (al) met, which

prevented further rotation of the palp (Figs. 8, 12). Then the bulbus genitalis moved away from the tarsus, probably by means of haemolymph pressure. The subsequent movements we deduced from the final position of the palpal parts: at first the appendix and embolus were inserted laterally and the tip of the uncus medially into the female genital opening. Then followed a twisting movement of the genital bulb which resulted in pressure of the uncus against the anterior side and of the appendix against the posterior side of the female genital cavity, which widened the narrow orifice and allowed insertion of the procurus.

In all copulating pairs the male was more or less in a horizontal position whereas the female was mostly in a vertical position (Fig. 9). Both pedipalps were kept inserted symmetrically in the female genital cavity during copulation (Figs 10A, C; 11). The procursi were inserted medially up to their prominent callosity (Fig. 10C) and the appendices and emboli were inserted laterally (Fig. 10B). The basal protrusion of the uncus (pu) was kept pressed against the distal area of the callosity on the procurus (c) (Fig. 10A, D, E), whereas the basal prominence (bp) of the bulbus genitalis was locked against the proximal part of the callosity (Fig. 10E).

From sections of cryofixed couples the internal position of the various inserted male parts can be studied (Fig. 11) and schematically reconstructed (Fig. 12). The procurus was inserted deeply into the female genital cavity, reaching up to the genital valve that separates the genital cavity from the oviducts. The circular depression on the apical tip of the procurus that contained a secretory product (Fig. 4D, E) pointed in the direction of the valve. The membranous zone of the procurus appeared to be inflated during copulation. The embolus was situated close to and pointed towards the female dorsal pore plates. The appendix was locked in a small pouch posterior to the pore plate. The tip of the uncus was inserted medially in the genital cavity.

In cryofixed spiders, the epigynal hook was found close to the apophyses on the anterior side of the male chelicerae (ca, Fig. 8), but the cheliceral fangs were never found in contact with the female body surface. Very likely, the epigynal hook is kept locked between the male apophyses during genital coupling. Observation under a dissecting microscope did not help to answer this question definitely, as the pedipalps block a direct view.

Palpal movements

The male pedipalps performed rhythmic twisting movements during the entire copulation. Outward and inward movements of both palps were sometimes slightly, sometimes notably out of phase. One palp started to move first and then the other followed, but the succession changed unpredictably. The membranous base of the genital bulb seemed to be slightly stretched and inflated just before each outward movement and to collapse during each inward movement. The genital bulb did not change position perceptibly during palpal movement, indicating that its protuberances (embolus,

appendix and uncus) also did not move. The procursi, however, were partially drawn out of the genital cavity during each outward twisting movement, and with each inward movement the procursi were inserted again deeply into the female.

Palpal movements slowed down during the course of copulation, averaging 40 outward-inward movements per five minutes at the beginning and around three outward-inward movements per five minutes at the final stage of copulation.

During each of seven copulations observed under a dissecting microscope a whitish material emerged from the female genital cavity between the procursi (Figs. 9, 10A). The material contained female secretion, encysted spermatozoa and secretory globules. Its extrusion seemed to be correlated with the palpal movements. Experiments with females of different reproductive history showed that this material was released no matter whether the females had mated for the first time or had previously mated with another male.

Discussion

Coupling mechanism

Coupling mechanisms in haplogyne spiders have so far only been studied by Gerhardt (1921, 1923, 1924), who focussed on *Pholcus opilionoides* (Schrank, 1781). In a later paper (1927) he presented results on *P. phalangioides*, stressing the strong similarities between the two species. He already knew of the 180° torsion of the pedipalp which is necessary for genital coupling that had not been noticed by Montgomery (1903). However, Gerhardt's descriptions from 1923 and 1927 of the position of the palpal parts during copulation differ significantly from what we have found. He stated that the parts inserted into the female genital cavity are embolus, appendix and uncus, whereas the massive procursus stays outside the female, providing mechanical support during mating and acting as some kind of sensory organ. According to him, after torsion the procursi are situated medially, the unci laterally and

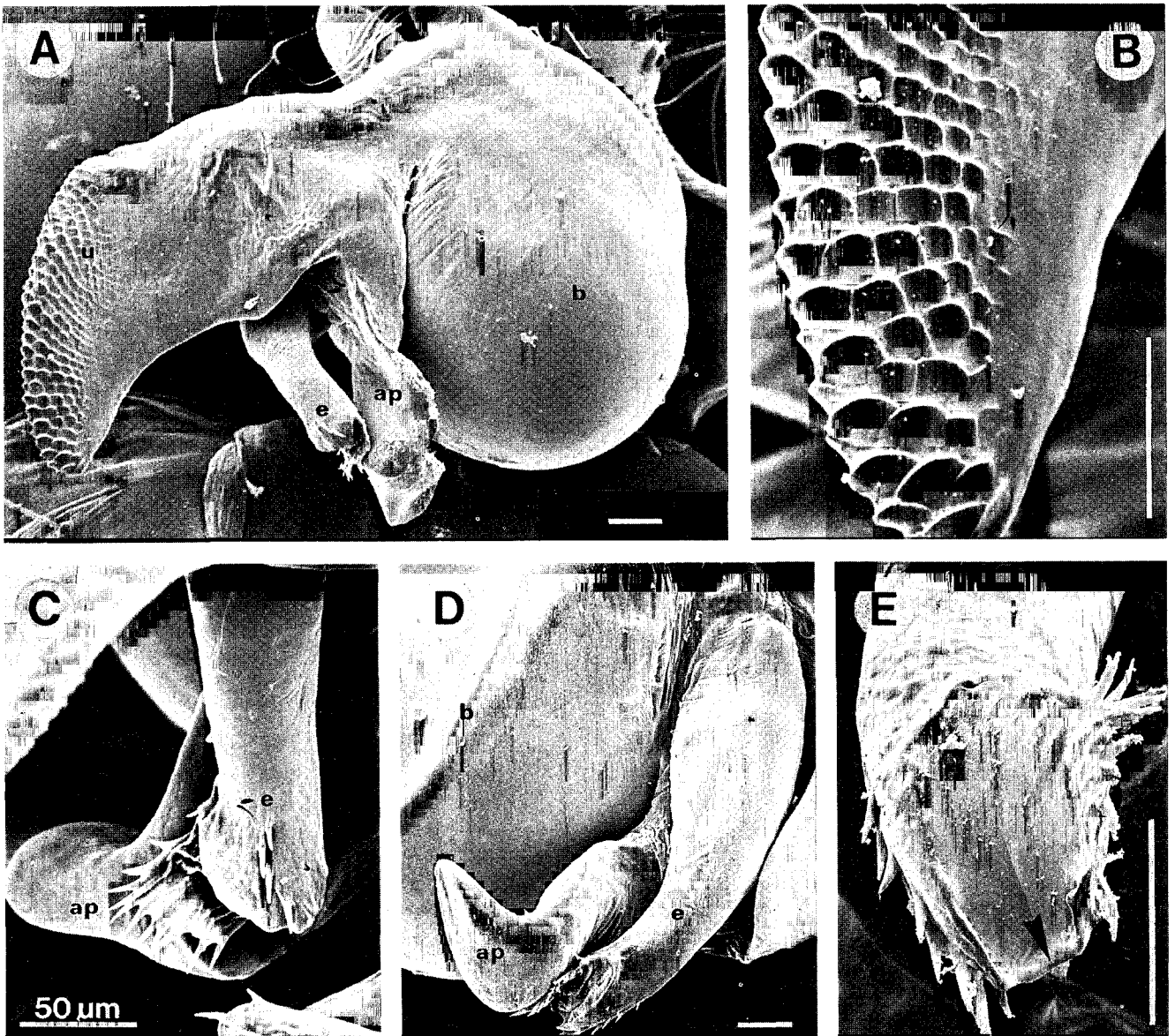


Fig. 6: **A** Left genital bulb, medial view; **B** Apical part of uncus; **C**, **D** Embolus and appendix, lateral views; **E** Tip of embolus; the arrow indicates the slit-like opening (A–E, SEM). Scale lines = 50 μ m.

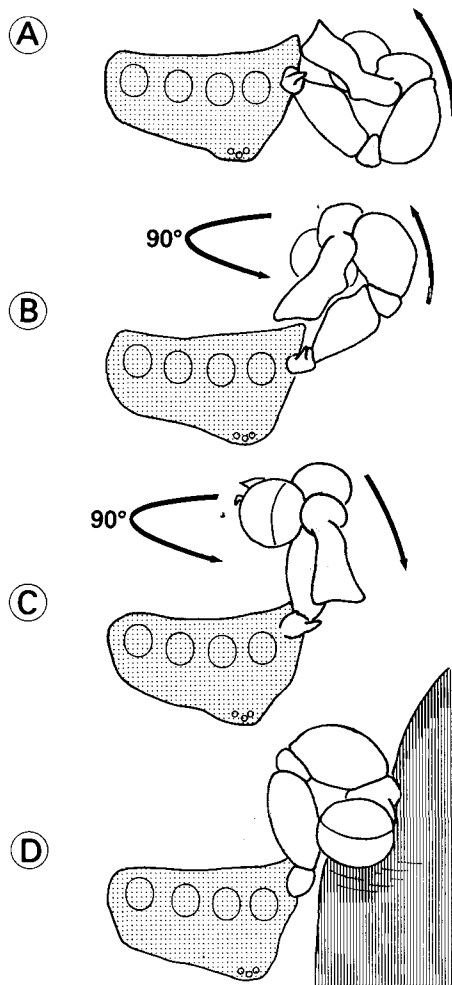


Fig. 7: Genital coupling in *P. phalangioides*. **A–D** Movement of male pedipalp from resting position (A) to insertion into female (D).

embolus plus appendix are between uncus and procurus. In *P. phalangioides*, as well as in *P. opilionoides* (Huber, unpubl. data) this is not the case. Appendices and emboli are always inserted laterally (Fig. 10B), procursi and the tips of the unci medially (Figs. 10A, C, 11). Palpal movement in *P. phalangioides* was also



Fig. 8: Male chelicerae, showing apophyses for initial coupling (ca) and proximal teeth (ct), after cryofixation (SEM). One palp (right hand side) still in copulatory position, i.e. rotated through 180°. Scale line = 250 μ m.

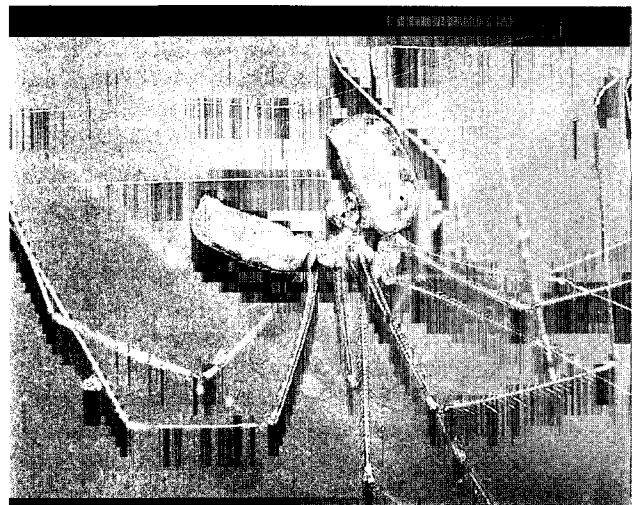


Fig. 9: Copulatory posture in *P. phalangioides*. Female on right, male on left.

observed by Montgomery (1903) and Gerhardt (1927). The latter even mentioned that the movement slowed down during the course of copulation.

Gerhardt's assumption (1927) that the cheliceral fangs grasp the hook or simply the female body surface before genital coupling has to be corrected as the male cheliceral apophyses lock the hook-like prominence on the female epigyne during initial coupling. Sensilla on the tips of these apophyses may help to find the right position on the female body surface. After genital coupling, the epigynal hook was found in the close vicinity of the cheliceral apophyses in cryofixed couples and very likely the epigynal hook remains locked between the male apophyses during genital coupling.

Sexual selection

The intromitted male palpal parts might function as internal courtship devices whose morphological characteristics and specific movements serve to increase the likelihood that females will use a given male's sperm to fertilise her eggs rather than those of another male (Eberhard, 1985). The procurus with its various apophyses, lamellar processes and the conspicuous zone that becomes inflated during intromission might play the most important part in stimulating the female. The appendix, on the other hand, does not move during palpal movement and functions as the main locking device (confirmed by A. Senglet, pers. comm.). Gerhardt (1924, 1927), who probably observed incomplete matings as the procursi were found outside the females, reported that the membranous area on the procurus was rhythmically inflated in phase with the palpal movement. So, in addition to the morphological properties and the movement of the palpal parts during insertion, rhythmic inflation of the membranous area on the procurus might be responsible for female stimulation.

If we accept the possibility of female stimulation, assumptions about female discrimination between males on the basis of differential stimulation are entailed. Females could, for example, use contact zones provided with sensilla for discrimination. However, such sensory

structures were found neither in the female genital cavity of *P. phalangoides* nor in various other spider species, e.g. *Nesticus cellulanus* (Clerck) (Huber, 1993). Other,

more cryptic means of discrimination via sensory structures such as simple stretch receptors in female membranes are conceivable.

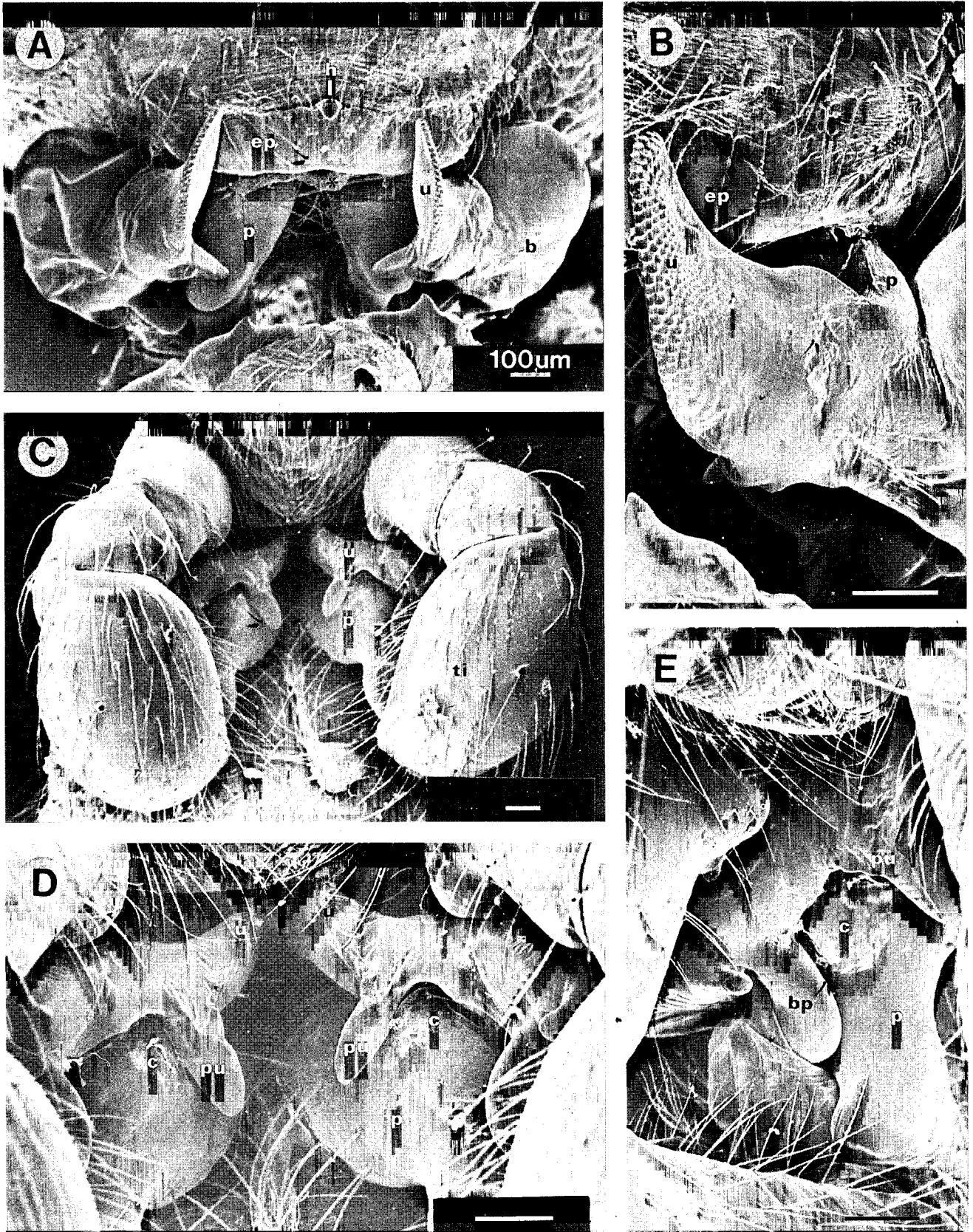


Fig. 10: Cryofixed pairs *in copula* (SEM). **A** Ventral view. Male prosoma removed, resulting in an artefact: intromitted parts are slightly pulled out of genital cavity. The asterisk marks the extruded secretion. **B** Lateral view, embolus and appendix intromitted; **C** Ventral view, male prosoma and femora conceal the epigynum; **D** Detail. Tips of unci inserted into female genital cavity. Basal protrusions (pu) of unci locked against callosity (c) on procursi. **E** Callosity (c) of procursi locked between basal protrusion of unci (pu) and basal prominence of genital bulb (bp).

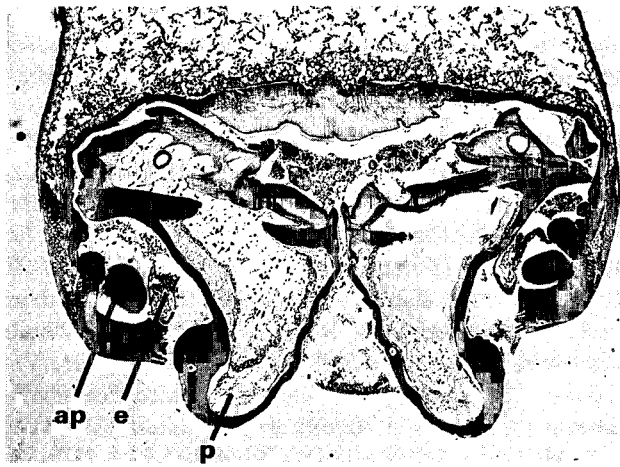


Fig. 11: Histological section of cryofixed copulating pair of *P. phalangioides*. Section plane shown in Fig. 12.

Sperm competition

Spermatozoa together with male secretion are transferred into the female genital cavity for storage. Female *P. phalangioides* do not store spermatozoa in storage structures away from the genital cavity (Uhl, 1994a). They are kept embedded in female glandular secretion that is discharged from glandular tissue in the posterior wall of the female genital cavity (Uhl, 1994b). During genital coupling the emboli lie close to the pore plates which are the orifices of the female glands and the sperm mass is pressed directly into the female glandular secretion.

The palpal movements result in extrusion of spermatozoa and secretion from the female genital cavity. Sperm displacement could be suspected if the extrusion occurred exclusively in previously mated females. But even in couples with inexperienced females the sperm mass is extruded from the genital cavity. Obviously, first males press their own spermatozoa out of the female storage structure. Copulation duration varies depending on the reproductive history of the female. Second males—if at all—are not allowed to copulate for longer than a few minutes, whereas females copulate with first

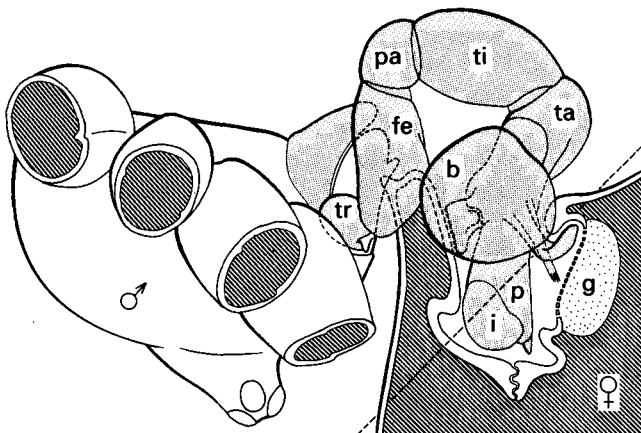


Fig. 12: Schematic reconstruction of *P. phalangioides* in copula. Section plane refers to Fig. 11.

males for 16–122 minutes (Uhl, 1993). Therefore, if displacement of a rival's sperm takes place, and the amount of sperm transferred into the female or extruded from the female genital tract is correlated with copulation duration, second males cannot be expected significantly to outnumber or displace the first males' spermatozoa.

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