Courtship, copulation, and genital mechanics in *Physocyclus globosus* (Araneae, Pholcidae)

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Abstract: The pholcid spider *Physocyclus globosus* (Taczanowski, 1873) was observed and videotaped courting and copulating, and genital mechanics and movements were analyzed by serial sectioning of freeze-fixed pairs. Just prior to copulation, the chelicerae of the male engage an apophysis on the female's epigynum. During copulation the male vibrates his abdomen rhythmically and makes repeated, relatively stereotyped twisting and flexing movements with his pedipalps, which are inserted simultaneously but asymmetrically in the female. The palps squeeze the female in the area of her epigyneal plate. Copulation with non-virgin females results in the extrusion of a mass of sperm from the female's genitalia during copulation or up to several minutes after it ends; no such masses result from copulations with virgin females. Sperm extrusion was not associated consistently with precedence of sperm from either the first or the second male. It is argued that the palpal movements, and perhaps most rhythmic genitalic movements, in spiders may best be interpreted as a result of sexual selection by means of cryptic female choice, and probably function to provide females with additional information about the male. Pholcids in general, and some genera in particular (including *Physocyclus*), may be unusual in that the vigour of males may play a significant role during copulatory courtship, as their palps have massive muscles that are only used during copulation.

Résumé: Le comportement de cour et la copulation ont été étudiés chez l'araignée *Physocyclus globosus* (Taczanowski, 1873) (Pholcidae) par observation directe et par vidéoscopie; d'autre part, la mécanique et les mouvements de ses organes génitaux ont été analysés par examen de coupes sériées de couples fixés par congélation. Les chélicères du mâle projettent une apophyse sur l'épigyne de la femelle juste avant la copulation. Pendant l'accouplement, le mâle agite son abdomen rhythmiquement et fait des mouvements répétés relativement stéréotypés de torsion et de flexion avec ses pédipalpes qui sont insérés simultanément, quoique asymétriquement, dans la femelle. Les palpes enserrent la femelle dans la région de sa plaque épigynéenne. La copulation avec des femelles non vierges aboutit à l'expulsion d'une masse de sperme par les genitalia femelles, soit durant la copulation, soit jusqu'à plusieurs minutes aprés, un phénomène qui n'a pas été observé au cours de copulations avec des femelles vierges. L'expulsion de sperme n'est pas reliée de façon particulière au rang du mâle copulateur. Il semble que les mouvements de palpes, et peut-être aussi les mouvements les plus rythmiques des genitalia chez les araignées, soient le résultat d'une sélection sexuelle due au choix de femelles cryptiques, et servent probablement à fournir aux femelles des informations additionnelles sur les mâles. Il faut peut-être penser que les Pholcidae en général, et certains genres en particulier (dont *Physocyclus*), sont inusités en ce que la vigueur du mâle joue peut-être un rôle important au cours du comportement pré-copulatoire puisque ses palpes ont des muscles puissants qui ne servent que durant la copulation.
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Introduction

The function of male courtship behaviour is often thought to be to induce the female to allow the male to copulate with her. An additional possibility is that male courtship, both preceding and during copulation, may function in the context of "cryptic female choice" (Thornhill 1983), by inducing the female to perform further post-intromission behaviours and processes which increase the chances that the male's gametes will be used to fertilize her eggs. Since courtship behaviour that occurs during copulation (copulatory courtship) is apparently common, at least in insects (Eberhard 1991, 1994), cryptic female choice may also be a common, though generally neglected selective force. If this is true, it is in accord with the contention that the widespread tendency of male genitalia and non-genitalic sexual contact organs to evolve rapidly and divergently is due to sexual selection by means of cryptic female choice (Eberhard 1985).

Most descriptions of copulation behaviour in spiders do not mention any obvious copulatory courtship movements. However, rhythmic twisting movements and pulsations of genitalic membranes are very common. The present study of *Physocyclus globosus* describes in detail how genitalic structures of the male fit with those of the female, and how they are moved, in an attempt to evaluate the functional significance of genitalic morphology and the secondary sexual modifications of the male chelicerae in this species.

Materials and methods

Adult and penultimate-instar individuals of the anthropophilic pholcid *Physocyclus globosus* (Taczanowski, 1873) were collected on Naos Island, Panama, and in San José, Costa Rica. Spiders were observed in the field during July 1990 in Panama with the aid of a headlamp

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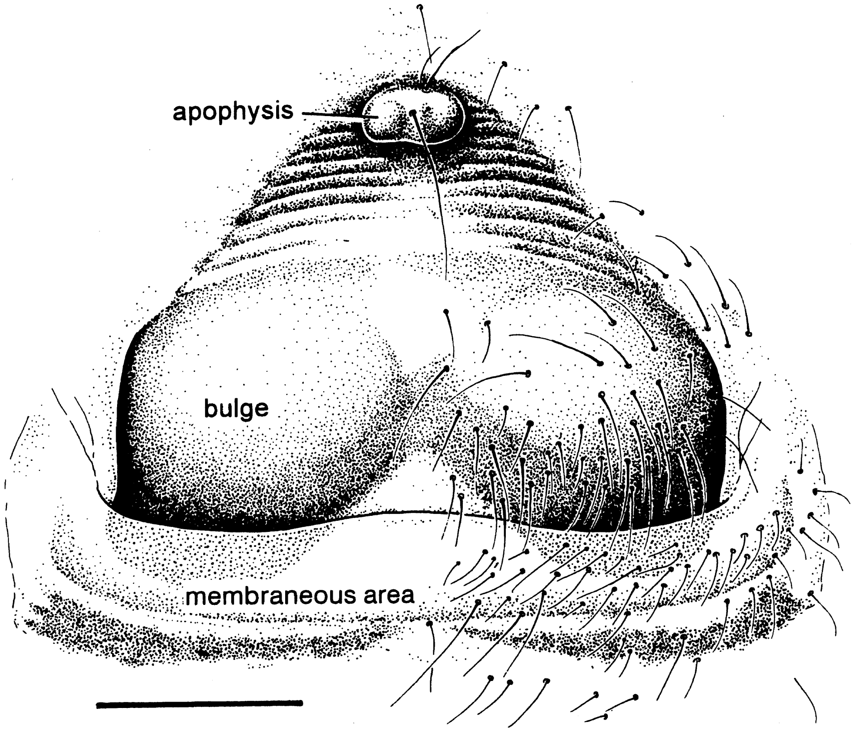
Fig. 1. Female epigynum, ventral view. Hairs on the left side are omitted. The bifurcated apophysis lodges in the paired cavities on the male chelicerae (Fig. 2). Scale bar = 0.3 mm.



(see Eberhard 1992). In addition, spiders raised from immaturity in captivity (under room conditions) and spiders captured as adults were observed as they courted and mated on webs they had spun in 8 and 20 cm diameter cylindrical containers. To check for a correlation between sperm extrusion and sperm precedence, six males were sterilized by exposure to 5 krad of radiation as adults, while six others were untreated (Eberhard et al. 1993). A total of 51 copulations were observed, involving 45 females and 33 males. Both the first and the second copulations of six females were observed, with different males each time. Males courting a female were seen in the field on six occasions. None of these courtships led to copulation, but on two occasions females moved as if to begin to accede, only to desist eventually. All second copulations occurred before the female had laid her first clutch of eggs. Since all sexual behaviour was performed with the body ventral side up, it was possible to observe fine details with magnifications of up to 80 x under a dissecting microscope. In two pairs, genitalic movements were videotaped at 30 frames/s using a National Newvicon VHS camera equipped with +6 close-up lenses, and analyzed frame by frame. Nine other pairs were freeze-fixed with liquid nitrogen during copulation; two of these were then embedded in epoxy resin (ERL 4206) and serially sectioned (1 μm) with an ultramicrotome (for details of the method see Huber 1993). Positions of copulating pairs (anterior, posterior, etc.) refer to the female's body unless specified otherwise.

Results

Courtship

Mature males in the field cohabited, at least briefly, with a variety of conspecific spiders, including females with egg sacs, females without offspring, and immature nymphs of both sexes (Eberhard 1992; Eberhard et al. 1993). Courting males typically faced females and tapped lines in the web with their legs II and, to a lesser extent, legs I. Tapping legs were held in a flexed rather than an extended position. Each leg gave a series of about three quick taps about 1–3 times/s, often but not always in alternation with another leg. At least one leg was tapping at least half the time during active courtship.

Both in the field and in captivity courting males moved their palps dorsoventrally in bursts of activity in which each palp alternated with the other. These movements probably caused a modified hair on the base of the palpal femur to rub against the striated region on the side of the male's chelicerae (see below). Courting males also occasionally performed brief vibrations of the entire body. They did not bob their abdomens dorsoventrally as did males, females, and immatures during routine movements outside the context of intraspecific interaction.

Courting males were generally at least one or two body lengths from the female, and did not move closer as they courted. It appeared that the male's courtship was an attempt to induce the female to move toward him. This probably means that a female with an egg sac had to hang up the ball of eggs before moving to the male (as in *Pholcus phalangioides*; Bristowe 1958). The female of one pair observed copulating in the field during the day was about two body lengths from a suspended egg sac, facing away from it; she returned to the eggs immediately the pair separated.

Receptive females observed under the microscope clearly inflated the membraneous area just posterior to the epigynum (Fig. 1) during courtship. This swelling deflected the epigynum so that its rear edge was more ventral than its anterior edge.

In one case the female clearly moved these swollen membranes during courtship.

Successful males usually courted for less than 10 min before approaching the female, whereas unsuccessful males courted for up to 40 min before desisting. Although the male usually then remained motionless, facing the female, in two cases he left her web and walked away. Some females responded aggressively to courting males in captivity. In several cases the female attacked the male as if he were prey as soon as he was introduced into her container, applying adhesive lines. On two occasions a female attacked and wrapped the male after copulation. These cases may be partly due to observing the spiders in small containers, where it was difficult for the male to move away from the female. Such attacks apparently also occur in nature, however, as two males were found dead and wrapped and being fed upon by a mature female. We never observed a male attacking a female.

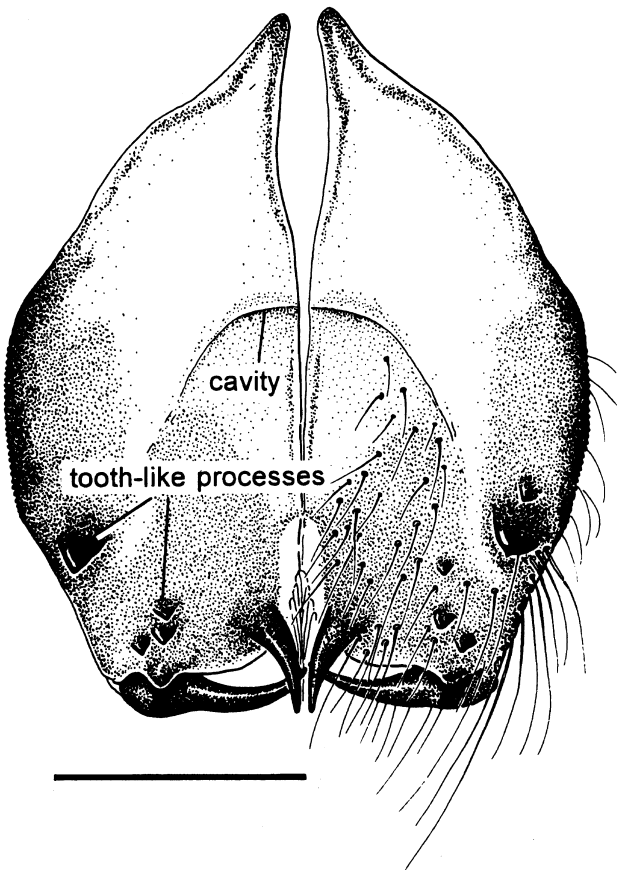
Copulation and genital mechanics

Copulations with virgin females were longer ($x = 36.8 \pm 5.6$ min, $N = 13$) than those with non-virgins ($x = 21.4 \pm 11.5$ min, $N = 14$) ($p = 0.0014$ with a two-tailed Mann–Whitney U test). All copulations but one consisted of a single long insertion of both pedipalps simultaneously. In the one exception (a copulation with a virgin female), the male made a “preliminary” insertion lasting only 37 s; 25 s after he withdrew he inserted his palps again for a 33-min copulation.

Male positioning and pedipalp rotation prior to insertion

Prior to copulation the male moved forward to bring his chelicerae into contact with the female’s epigynum, which placed him in an appropriate position to insert his genitalia. This often involved a few preliminary “flubs” in which the male scraped the anterior surface of his chelicerae over the ventral side of the female abdomen. In one such case the male was misaligned and his chelicerae were too far ventral. Eventually the male chelicerae engaged the female’s epigynum, with the bifurcated apophysis on the anterior end of the epigynum (Fig. 1) lodged in the paired cavities on the male’s chelicerae (Fig. 2). This contact between female’s apophysis and male’s cavity persisted throughout copulation. In one pair observed carefully from the side there was no noticeable movement of the male’s chelicerae against the female’s epigynum once they were locked together. The tooth-like processes on the male’s chelicerae (Fig. 2) were pressed against the heavily sclerotized bulges of the female epigynum (Fig. 1). There are no corresponding female cavities or hoods into which these processes could fit, as have been described in some other pholcids (Kraus 1984; Huber 1994*a*, 1995*a*).

Fig. 2. Male chelicerae, frontal view. Hairs on the left side are omitted. Scale bar = 0.3 mm.



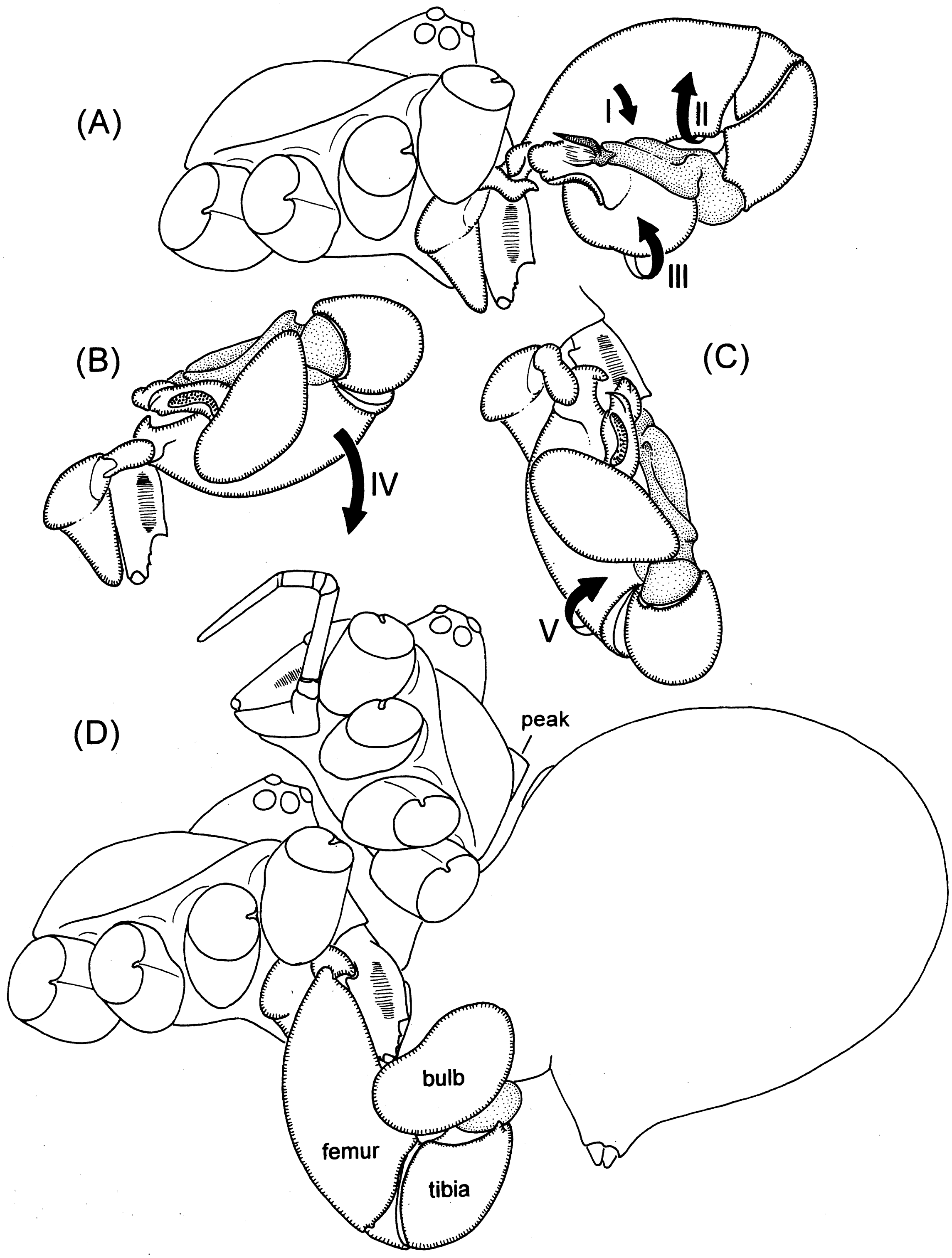
During copulation the male was ventral and anterior to the female, corresponding to von Helversen’s (1976) “copulatory position of web spiders” (Fig. 3D). Both palps (cf. Figs. 6, 7, and 9 for palpal morphology) were inserted simultaneously into the female’s genital opening. The palps were flexed ventrally, with their femora forming an angle of approximately 90° with the male’s sternum (Fig. 3D). To achieve this position the palps were first twisted dramatically. A few seconds prior to his final approach to the female, the male lowered his pedipalps a few degrees and twisted them about 90° at the coxa-trochanter joint (Fig. 3A, arrows I and II). At the same time the bulbs were rotated about 300° (right bulb clockwise when a view through the cymbium is imagined; Fig. 3A, arrow III). Then the palps were bent ventrally about 90° at the coxa-trochanter joint (Fig. 3B, arrow IV). Up to this point, movements had lasted for about 2 s in two videotaped pairs. In the resulting position (Fig. 3C) the male then moved forward and established cheliceral contact. The duration of this approach phase depended on the male’s ability to orient himself and on the female’s cooperation. Finally, within about 1 s of cheliceral contact the male twisted the palps another 90° (Fig. 3C, arrow V), inserting the emboli and procursi into the female.

Copulation behaviour and the mechanics of insertion

Male behaviour during copulation included movements of the pedipalps, vibrations of the abdomen, and occasional leg vibrations, and followed more or less predictable patterns.

Pedipalp movements: While both emboli and procursi remained inserted in the female throughout copulation, the palps were rhythmically moved, with twisting and squeezing movements. Early in copulation, squeezing movements were of higher amplitude, resulting in conspicuous movements of the procursi, which were rhythmically partially withdrawn and driven back into the female. The strength of these pushing movements varied in different copulations. Later in copulation the pushing was reduced or imperceptible. At no time were

Fig. 3. Male pedipalp movements prior to copulation (A-D) and copulatory position (D). The cymbium and procursus are stippled. For a detailed explanation see the text.



any palpal membranes seen to expand or contract, as occurs during copulation in many other spiders, especially entelegynes (e.g., Gerhardt 1921-1933).

The pattern of palpal movements gradually changed during copulation. Early in copulation, twists (which were always combined with a squeezing movement) were more frequent

(Fig. 4). Very early in copulation each inward twist lasted for only about 2 s, and was followed by an outward twist of about the same duration. Later the inward twists became longer, and lasted for many seconds before the next outward twist, which lasted only 1-2 s before the following inward twist occurred. Still later the single inward twists were replaced by short bursts of twisting, in which several inward-outward twists were followed by a long period of immobility during which the palps were held in the inward twist ("in") position. The number of twists in these bursts increased gradually from 2 to about 6 or 7 as copulation proceeded. Just before separation, twisting movements became more frequent again, though less regular than before.

The palps were always inserted asymmetrically into the female. When they twisted to the "in" position, the "central" palp was nearer the median line of the female than the "lateral" palp (Fig. 5A). When the palps twisted to the "out" position, they were about the same distance from the median line. As the next inward twist began, the central palp slipped slightly anterior to the lateral palp, and the basal projection of the central palp's procursus usually engaged on the basal hood of the lateral palp's procursus (Fig. 7A). The two palps then pressed on into the female as a single mechanical unit (Figs. 5B, 5C), Occasionally (especially later in copulation) the procursi did not engage; in such cases both palps nevertheless made the inward twisting movement.

Examination of' the muscles and their attachments in the pedipalp showed that the twisting movements were produced by muscles in the tibia (Fig. 6B), while the squeezing movements resulted from contractions of muscles in both the femur and the tibia (Fig. 6A). Most of the femur is filled with muscles that are attached to apodemes of the patella or to the ventral basal rim of the tibia, causing the flexion of the patella-tibia complex (muscles M14, M15, and M19 following Ruhland and Rathmayer 1978). The articulations for this movement are close together on the dorsal side of the pedipalp, between the femur and the patella (small arrows in Fig. 5B). The tibia is filled with two sets of muscles that cause two movements: the deflection of the cymbium against the tibia (M25 - M28; two-articulation joint) and the rotation of the genital bulb against the cymbium (M29; one-articulation joint). The latter muscle is also responsible for precopulatory bulb rotation (see above).

The pedipalp movements cause the male "clamp" (chelicerae on one side, procursi and bulbs on the other; Fig. 6) to squeeze the female epigyneal area. This squeezing pressure is produced by the huge muscles in the femur and the cymbium deflectors in the tibia (Fig. 6A). The procursus of the lateral palp strongly indented the membranes posterior to the epigyneal plate (Fig. 6B), whereas the tip of the central procursus was in contact with the "valve" apparatus that separates the uterus externus from the uterus internus (Fig. 6A). The functions of the distal structures on the procursus (Fig. 7A) are unclear. The position of the tuft of hairs in freeze-fixed pairs suggests that this structure might be moved over the openings of the vulval glands (Fig. 6B) during in-and-out movements of the procursus. The embolic sclerites pressed against the genital cavity (uterus externus) (Fig. 6B) in a ventrolateral direction. The small denticles on the embolic sclerite (Fig. 7B) seem to be designed to increase surface contact, perhaps to prevent slipping and guarantee a strong hold on the female, or to stimulate her. The ventrolateral pressure of the emboli on the genital cavity of the female is caused by the bulb rotator in the tibia (M29). The tendon of this muscle, when at rest, is wound around the basal stalk of the bulb; contraction causes unwinding and rotation of the bulb. Since the stalk is situated laterally rather than at the center of the bulb (Fig. 7B), the rotation causes the embolus to move in a wide circle rather than to rotate around its longitudinal axis. The inward twisting movements of the pedipalpal tibiae seen in ventral views of copulating pairs (Figs. 5B, 5C) are probably the by-product of this outward pressure of the emboli, and move the bases of the procursi together so that they can engage before the male "clamp" exerts its squeezing force (Fig. 5C). There is some evidence that the bulb rotators exert only a relatively weak force on the female: they are small in comparison with the squeezing muscles (about one-quarter of the volume of the other muscles in the tibia); the joint between bulb and cymbium is a weakly sclerotized one-articulation joint; and we never observed outward movements of the epigynum.

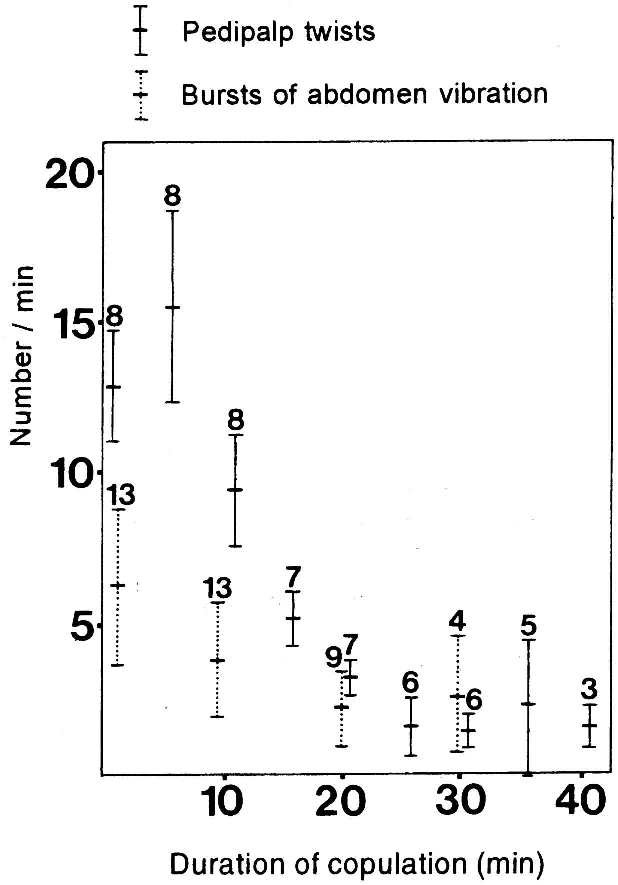
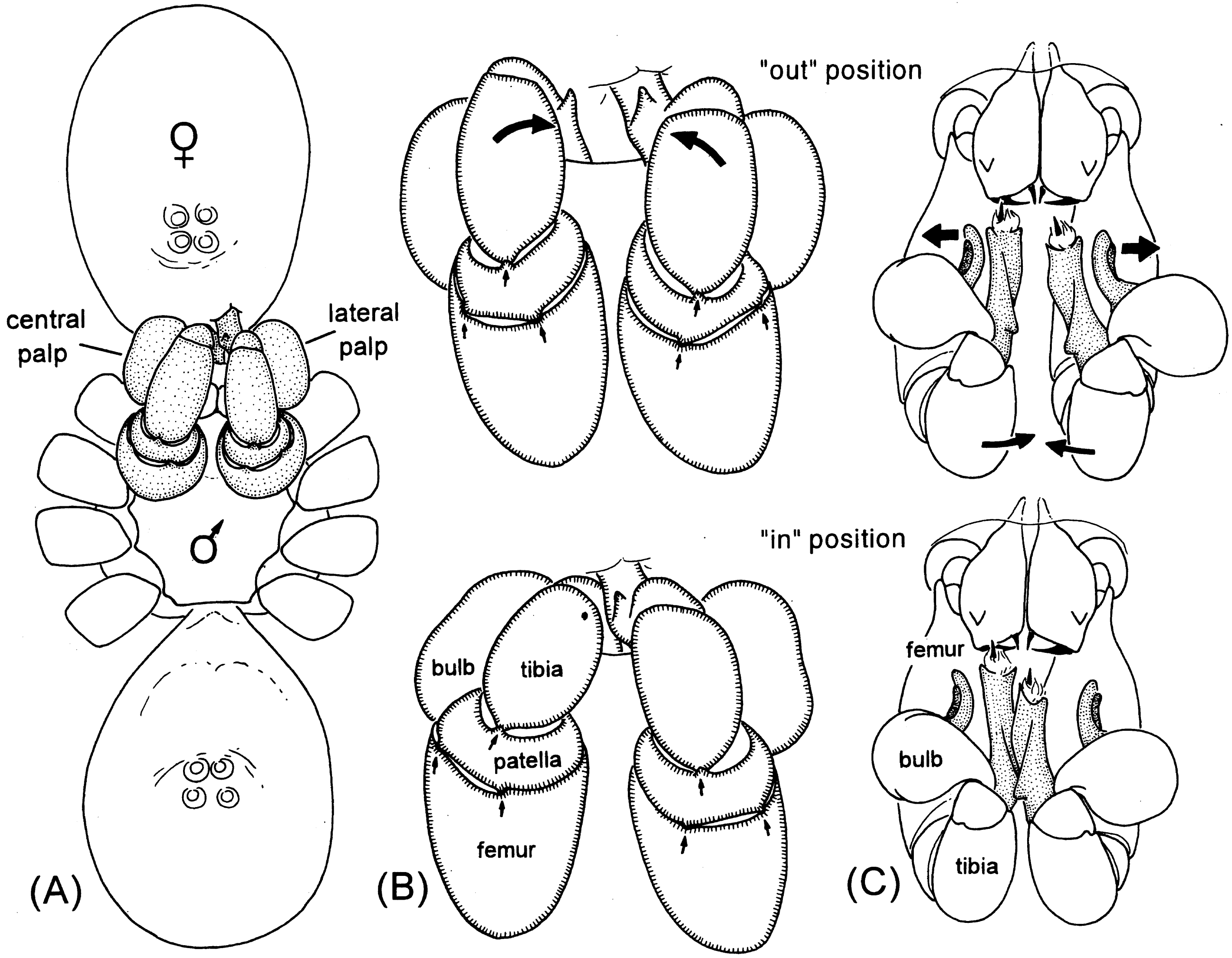


Fig. 4. Frequency of male pedipalp movements and bursts of abdomen vibration. Bars represent means ± SD; numbers above the bars indicate the number of copulations.

Although their pedipalps are morphologically symmetrical (Huber 1996), males never changed the central and lateral positions of their palps during a given copulation (this detail was checked in seven cases). However, the insertion asymmetry sometimes changes from one copulation to the next, as occurred in two of three doubly mated males in which this detail was checked.

Fig. 5. Twisting movements of the pedipalps during copulation. (A) Overview of a pair in copulation in ventral view (female above) with the palps in the "in" position (drawn from a freeze-fixed pair); the male pedipalps are stippled. (B) Pedipalps at the limits of the twisting movements (same view as in A) (drawn from a video recording). (C) Pedipalps at the limits of the twisting movements, frontal view, with the female omitted; the emboli and procursi are stippled. The thick arrows in C indicate the pressure of the emboli against the lateral cuticle of the uterus externus, the thin arrows in B and C indicate the resulting passive movement of the pedipalps that results in the engagement of the two procursi. The smallest arrows in B indicate points of articulation.



Other male movements during copulation: In all copulations the male vibrated his abdomen in short bursts of rapid dorsoventral flexions at the pedicel, with each burst lasting on the order of 0.1 s. The vibrations in a burst were too rapid to count, but usually appeared to consist of 2 – 5 cycles of down-up flexions. Abdomen vibration during copulation was much more rapid than the abdomen bobbing (on the order of 2 cycles/s) that was often performed by males, females, and immatures. The frequencies of the bursts of abdomen vibrations decreased as copulation proceeded (Fig. 4), but continued throughout. Bursts of abdomen vibrations were spaced more or less evenly during the later stages of copulation. There may have been a tendency for abdomen vibration to occur during bursts of palp twisting, but it also occurred at other times. The strongest vibrations caused the male's entire body and legs to vibrate.

Several other types of movements were performed during copulation by some males but not others. One male clearly vibrated his anterior legs (probably both I and II) in synchrony with bursts of abdomen vibration. Another male performed long series of weak quivering movements of his body (possibly only the abdomen was moved). Two different males twitched their legs weakly but more or less continually, keeping both male and female in motion; both of these males vibrated this way during each of two copulations with a different female.

Sperm extrusion: A ribbonlike, irregularly shaped white mass appeared on the ventral surface of the female's abdomen during all 13 copulations involving non-virgin females that were checked for this detail. In none of the 11 copulations with virgin females that were checked for this detail did a mass of this sort appear. Masses began to emerge as early as about 90 s into an 18-min copulation, and some continued to emerge after copulation ended. The mass emerged from the side of

Fig. 6. Positions of the genitalia in the “in” position during copulation and muscles responsible for pedipalpal movements during copulation, based on two series of sagittal sections of freeze-fixed pairs. (A) Right (“central”) palp; arrows indicate the principal directions of the squeezing force (see Fig. 5. for the twisting force). (B) Left (“lateral”) palp. The tip of the procursus of the “central” palp (A) is near the “valve” of the uterus; in the “lateral” palp (B) it is embedded in membranes behind the epigyneal plate.

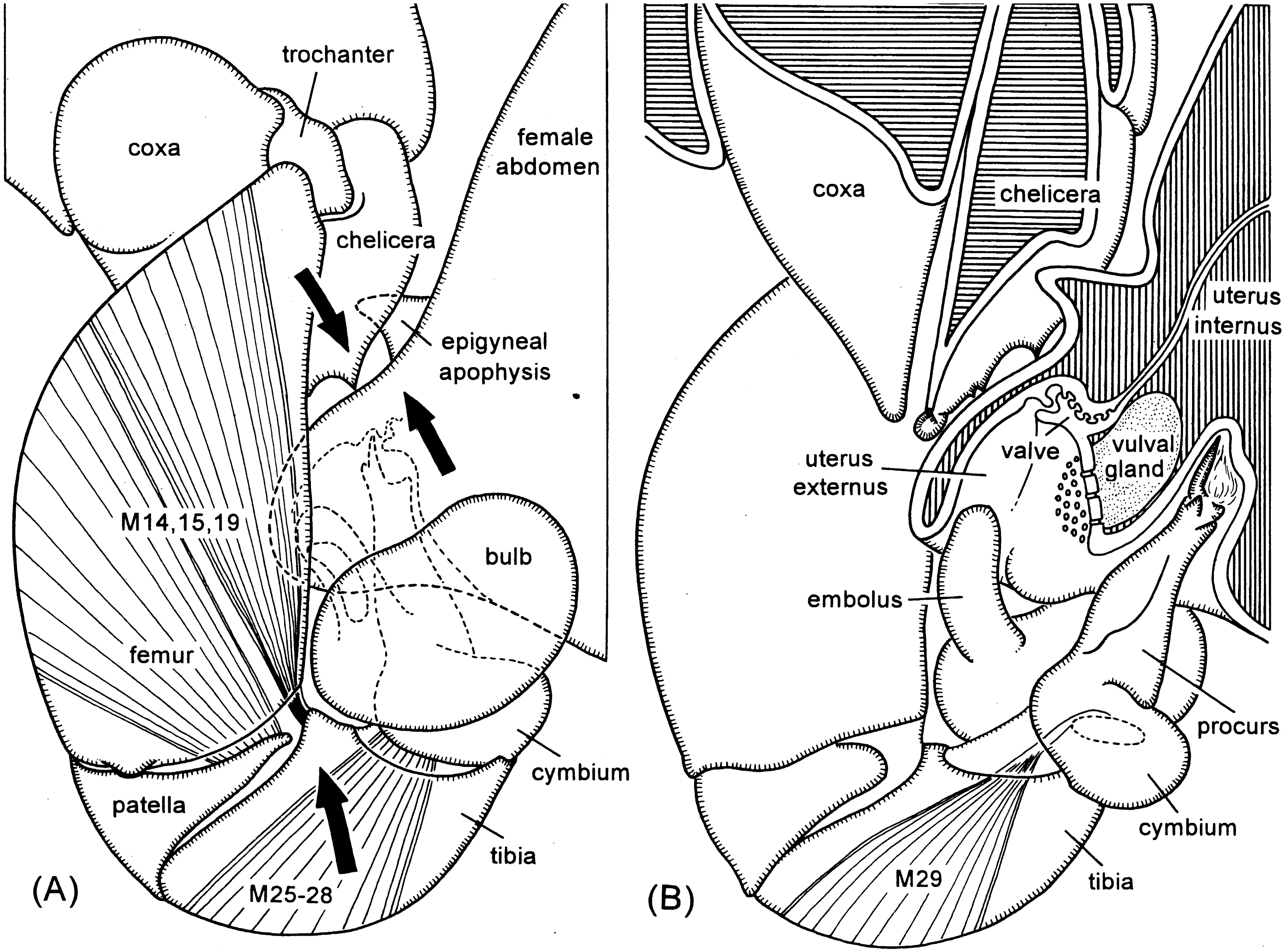
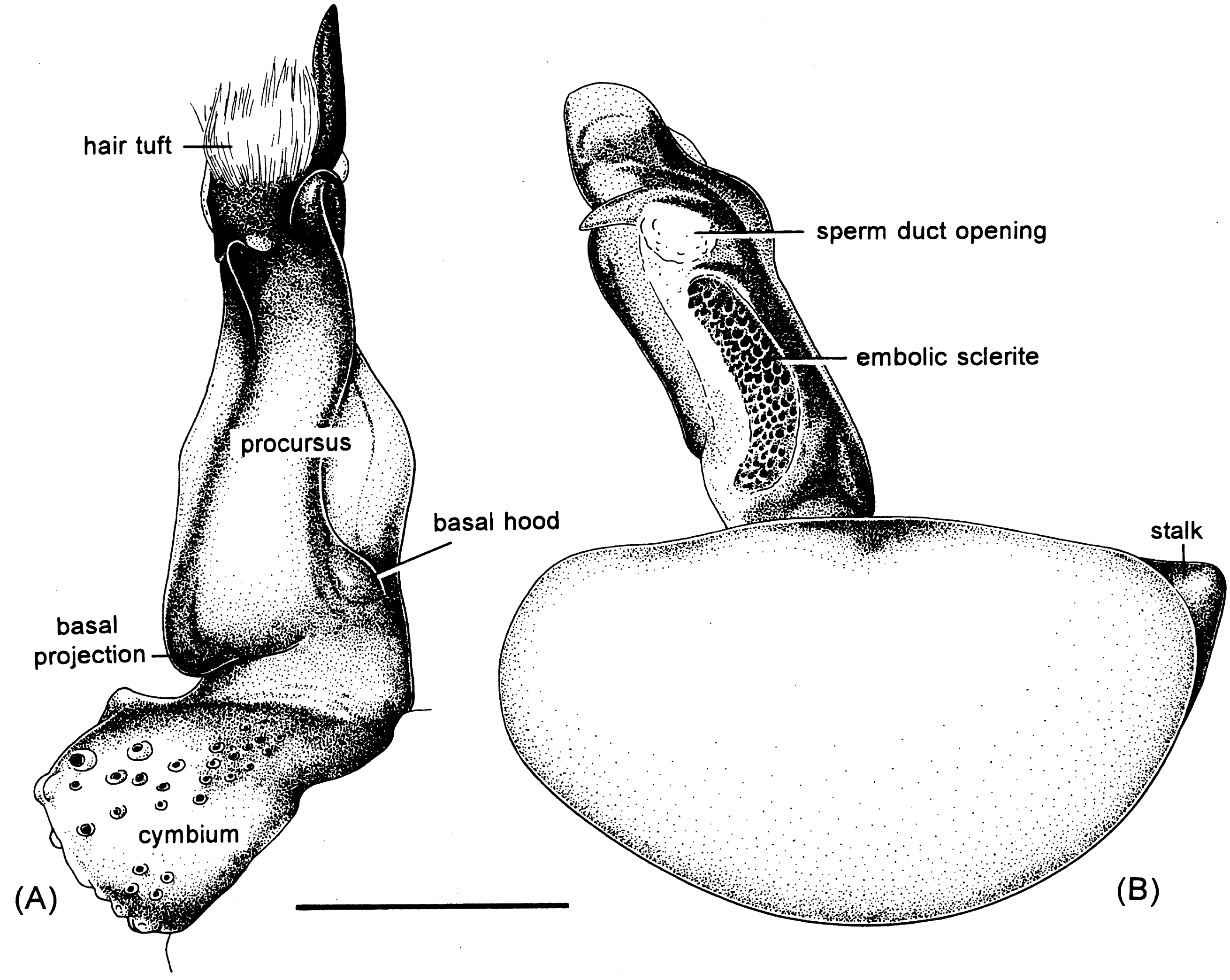


Fig. 7. The procursus with cymbium (A) and the genital bulb (B) of the right pedipalp. Hairs are omitted. For the positions of these structures on the pedipalp see Figs. 6 and 9. Scale bar = 0.3 mm.



the swollen membraneous portion of the female abdomen just posterior to the rear edge of the epigynum, where the lateral palp had been in six of the seven cases checked for this detail (it emerged near the center of the female in the other). In two cases the mass adhered to the male's palp when it was withdrawn, and the male later ingested the mass. In one recently mated female the mass gradually emerged while the membraneous area repeatedly moved like a mouth pursing its lips; at least 60% of this mass emerged after copulation had ended. When examined in saline solution under a compound microscope, seven masses all proved to be composed of encapsulated sperm embedded in a matrix. There was no correlation between sperm extrusion and male sperm precedence. Sperm emerged from the female following one copulation in which the second male achieved 100% sperm precedence in the eggs that were laid later, and in another in which the second male had 0% precedence (the average in this species is about 50%; Eberhard et al. 1993).

Female activities during copulation: Some vibrations during copulation appeared to originate from the female, and sometimes females tapped briefly with their anterior legs. One female twice began moving her legs, and each time the male vibrated his abdomen several times and she became immobile again, A more consistent movement was an alternate dorsoventral pedipalp movement that occurred once every 5-20 s and may have resulted in stridulation (see below). The conspicuous peak on the female carapace (Fig. 3D) did not interact with the opposing sclerotized plate on the abdomen during copulations.

Termination of copulation: copulations ended when the male released his clamp with the palps and the spiders sprang apart. In all cases it appeared that the male rather than the female ended the copulation. In nearly all pairs the male then moved away and the female moved after him, either immediately or after a pause. Often the male turned away to avoid her whenever they met. In two cases the male left the web and walked away, while in others he stayed on her web but became motionless, as did the female (males and females are often found together on webs in the field; Eberhard 1992). All pairs were observed for 20-30 min after copulation ended, and in no case did the male give any sign of sexual interest in the female nor did he recharge his palps with sperm. In one female that remained immobile for about 3 min after copulation ended, the swollen membraneous area posterior to the epigynurn repeatedly pulled rearward and then sagged forward, gradually becoming less swollen; eventually it folded anteriorly to cover the rear margin of the epigynum.

The sexually dimorphic stridulatory apparatus

Both male and female *P. globosus* have a stridulatory apparatus corresponding to type *d* of Legendre (1963), in which a pick (plectrum) on the basis of the pedipalpal femur scrapes over ridges (pars stridens) on the lateral surface of the chelicera. In females the spaces between the ridges were more or less uniform, while the ridges of the male were farther apart in the central area (Fig. 8). Such sexual dimorphism has not been reported previously in pholcids.

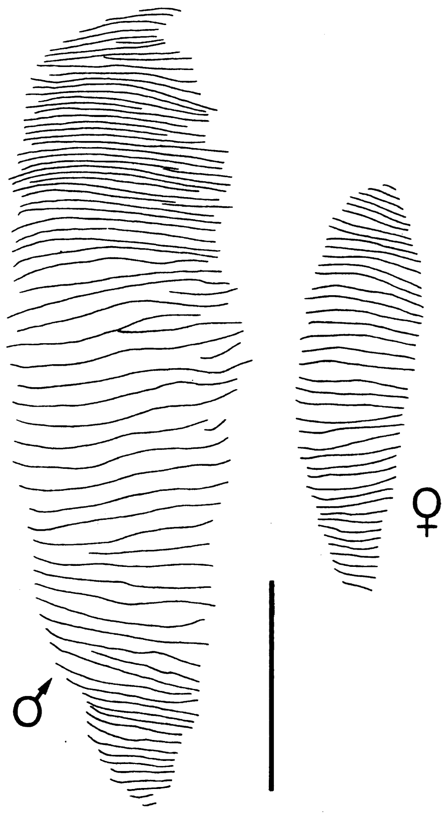
Discussion

Pedipalp movements prior to and during copulation in pholcids

The conspicuous rotation and twisting movements of the pedipalps prior to copulation seem to be a general character in pholcids. They have been observed both in Old World pholcids (Gerhardt 1924*a*, 1927, 1933; Uhl et al. 1995; Huber 1995*a*) and New World pholcids (Huber 1994*a*, 1997*a*, 1997*b*; B.A. Huber, unpublished data on *Anopsicus zeteki*, *Metagonia rica*, *Modisimus* spp., and "*Coryssocnemis*" cf. *viridescens*). Differences of systematic importance occur in the way the pedipalps are locked against the chelicerae in the final position (Huber 1995*a*). *Physocyclus globosus* shows the plesiomorphic condition of locking the rotated trochanter against a sclerite on the rear side of the chelicera (Fig. 6A). The precopulatory rotation of the bulb has not been reported previously, but this may be a methodological problem, since it occurs within about 1-2 s and is synchronous with the much more conspicuous movements of the pedipalp and easily missed except in videotaped pairings.

During copulation, rhythmic movements of the pedipalps have been observed in all pholcids studied. In *Pholcus phalangioides* (Gerhardt 1927; Uhl 1994; Uhl et al. 1995) the pedipalps alternately made lateral twists that primarily resulted in in-and-out movements of the procursi. Movements slowed gradually during copulation from 7.5 to 200-600 s/cycle. Male *Hoplopholcus forskalii* and *Holocnemus rivulatus* (= *H. pluchei*) made "the same rotating movements of both palps as in *Pholcus*" (Gerhardt 1924*a*, 1927). Male *A. zeteki* performed simultaneous movements, also directed laterally and resulting in in-and-out movements of the procursi (B.A. Huber, unpublished data). Movements slowed from 2 to about 10 s/cycle. Several species of *Modisimus* (sp. indet.) made rhythmic pedipalpal movements (B.A. Huber, unpublished data). In "*Coryssocnemis*" cf. *viridescens* (B.A. Huber, unpublished data), squeezing movements similar to those described in this study were observed; movements barely slowed (from 2–3 to 3–4 s/cycle). In *Hedypsilus culicinus* (Huber 1997*b*), movements were alternate outward thrusts once every 4–7 s throughout copulation. Rarely did the males also make simultaneous movements. Male *Psilochorus simoni* repeatedly changed between simultaneous and alternate rhythmic movements (Huber 1994*a*). Male *Metagonia rica* first moved their procursi nonrhythmically in the female genital cavity, then changed to a rhythmic pattern in which a pair of successive lateral twists alternated with simultaneous inward thrusts of the emboli (not the procursi!) (Huber 1997*a*). Movements slowed during copulation, from 5 to 9 s/cycle.

Fig. 8. Stridulatory files on the chelicerae of a male and a female. For the position of the files see Fig. 3. Scale bar = 0.1 mm.



Although these observations are fragmentary, they indicate that rhythmic pedipalpal. movements during copulation are both common and diverse in pholcids. In the following two sections we discuss the possible significance of such movements, in spiders in general and pholcids in particular.

Revisiting the genitalic movements of spiders

Pedipalpal and bulbal movements are one of the most characteristic aspects of spider copulation (e.g., Gerhardt 1921–1933). One central purpose of palpal mobility is certainly to aid the process of intromission (Gerhardt 1921, p. 117), which is often accompanied by complicated internal movements that stabilize the male genitalia internally and lock them to the female (e.g., Huber 1993). A second purpose, which is central in the present context, must be found for rhythmical movements of the palp during insertion. These movements have often been interpreted as a part of the mechanism by which sperm are ejaculated. In non-entelegyne spiders, ejaculation is thought to be accomplished by secretions from glands in the genital bulb that are discharged into the sperm duct (Harm 1931). In entelegynes, the hemolymph pressure that causes hematodochal expansion and bulb movements has often been thought to be responsible for ejaculation also (e.g., Gerhardt 1923; Gering 1953; Helsdingen 1965; Grasshoff 1968; Loerbroks 1984). Conclusive evidence for this claim is lacking, however, and morphological data argue against it. If the spider were squeezing sperm out of the sperm duct by increasing the pressure within the palp, a different design would be appropriate: the sperm duct would have thin and (or) soft walls rather than the thick, sclerotized cuticle that is typical of most entelegyne sperm ducts; and the bulb would be rigid, so that pressure could build up, instead of having expanding hematodochae that buffer increases in pressure. On the other hand, there is some evidence that entelegynes also use secretions within the bulb to expel sperm (Osterloh 1922; Lamoral 1973; Lopez 1987). We know of no reason to suppose that entelegynes should need hemolymph pressure to activate bulbal glands (as suggested by Osterloh 1922; but see Lamoral 1973).

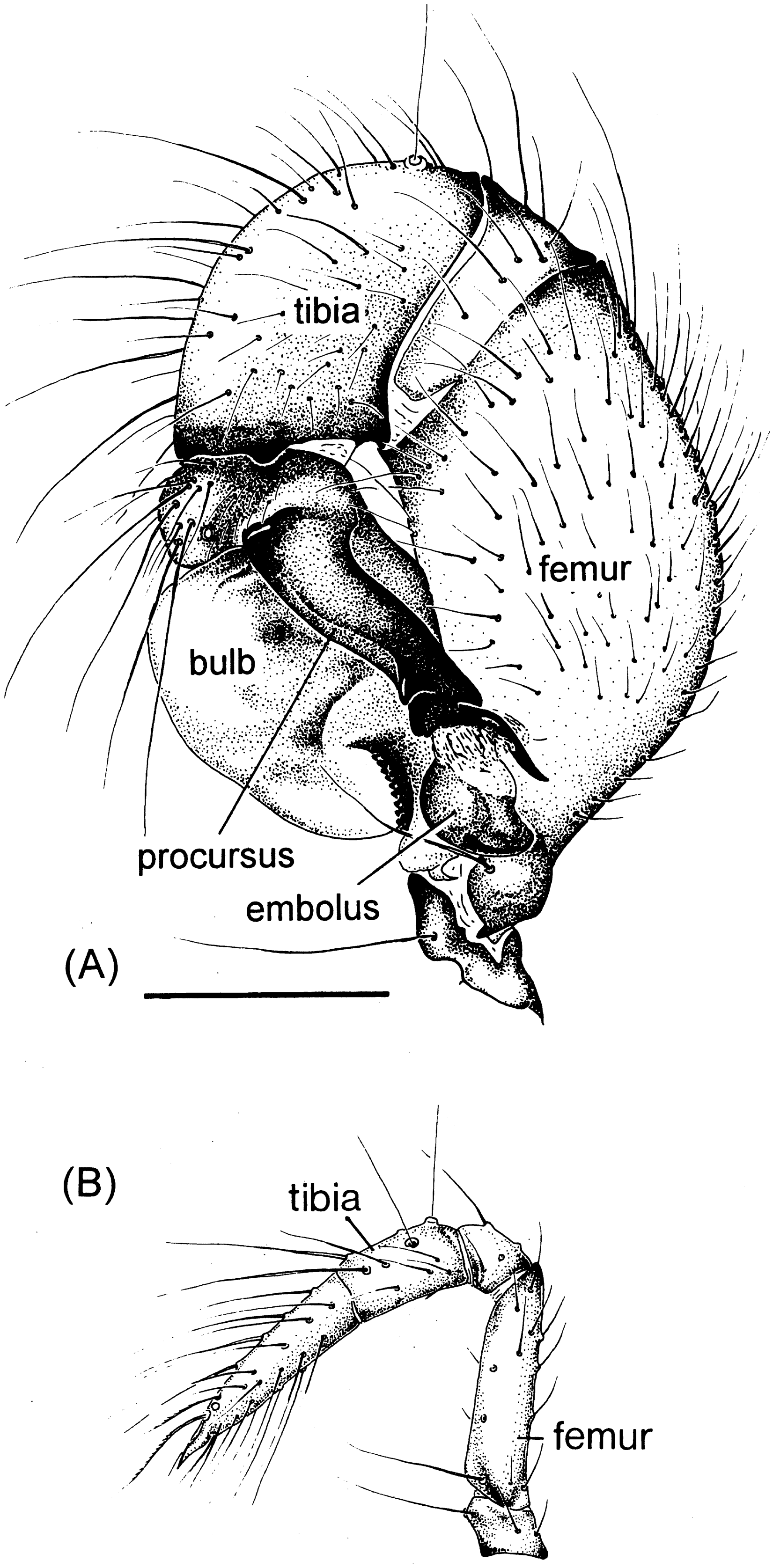
Another purpose of the rhythmic palpal movements could be removal of the sperm of previous males (cf. the “pumping” movements of male odonates during sperm removal; Waage 1984). However, the details of male and female morphology argue against sperm removal as a general or even widespread explanation of the rhythmic palpal movements in spiders. In many entelegyne spiders the male genitalia do not reach the spermathecae (Gering 1953; Melchers 1963; Helsdingen 1969, 1971; Wiehle 1967; Grasshoff 1968, 1973; Martin 1981; Loerbroks 1983, 1984; Huber 1993, 1994*b*, 1995*b*, 1995*c*). And in species in which they do, a thin, threadlike embolus is inserted through a narrow insemination duct (Wiehle 1961, 1967; Helsdingen 1969, 1971; Blest and Pomeroy 1978; Schult and Sellenschlo 1983; Huber 1994*b*, 1995*b*), a situation that makes sperm removal by means of in-and-out movements of the male’s genitalia mechanically unrealistic. Haplogyne males often have better access to the site of sperm storage in the female. In *P. globosus*, the distal structures on the procursi (especially the tuft of hairlike projections) might indeed seem appropriate for sperm removal, but two sets of evidence argue against this. First, the masses that were observed on the abdomens of female *P. globosus* appeared to emerge gradually rather than in step with rhythmic movements of the male palps. In fact, in some cases most of the sperm emerged after the male had withdrawn. Second, while sperm extrusion occurred only in copulations with non-virgin females, it is not clear whether the sperm belonged to the first or. second male (or both). Since there was no correlation between sperm extrusion and sperm precedence (males in copulations with sperm extrusion achieved 0–100% precedence), sperm extrusion is, obviously not a reliable indicator of sperm precedence patterns. In *P. phalangioides*, Uhl (1994) found that sperm extrusion also occurred in copulations with virgin females. Thus, sperm extrusion in this species also does not seem to result from the male trying to remove the sperm of a previous male.

These considerations lead us to conclude that instead of sperm ejaculation or removal, rhythmic palpal movements during insertion may rather serve to stimulate the female in an attempt to influence her to perform post-intromission behaviours and processes that can increase the male’s chances of fathering her offspring (see Jackson 1980; Thornhill 1983; Eberhard 1996). One critical point in favour of this argument concerns the presence of sensory structures in the female that could sense such male stimuli. Sensilla have not been found in the area of male-female contact in studies of the cuticular surfaces of the female genitalia in spiders (e.g., Huber 1993). They have not been sought in membraneous structures, however, so the possibility that internal stretch receptors do occur cannot be confidently dismissed. In *P. globosus*, a large area around the epigynum is deformed by the male pedipalpal movements, which could cause stimulation of stretch receptors, if any, in this area.

Sexual selection and male vigour

Many behaviour patterns of males during copulatory courtship seem poorly designed to give the female information regarding the male’s overall vigour (Eberhard 1994, 1996). *Physocyclus globosus* and many other pholcids may be an exception. The highly swollen pedipalpal femora and tibiae of this species (Fig. 9) are filled with muscle tissue; the rhythmic squeezing movements of the pedipalps that we have described are produced by the strongest muscles in the whole body. The asymmetrical insertion of the procursi and their locking to form a single mechanical unit may also be a mechanism to further increase the force of the male’s genitalic movements, since the male may thus be able to concentrate the power of the two palps on one critical region. How the male gains from exercising this power in terms of fertilization success remains to be established. The squeezing movements do not seem to be appropriate for extending the female’s uterus externus (which is the sperm-storage site). In freeze-fixed pairs the sclerotized uterus externus did not differ perceptibly in form from that of noncopulating females. Nor does the power seem to be used to squeeze the previous male’s sperm out of the female (see above). One intriguing possibility is indicated by the strong “valve” between the uterus externus and uterus internus whose function is as yet unknown. Relative to other pholcids, both the strength of the male pedipalps and the complexity and size of the female valve of *P. globosus* are well developed. The male’s main cheliceral frontal apophyses are pressed against the female at a position exactly external to that of the valve (Fig. 6B), suggesting a functional correlation. However, there are indications against this idea. In some pholcids (e.g., *P. phalangioides*, *P. opilionoides*, *Holocnemus pluchei*; Uhl et al. 1995; Huber 1995*a*), females have a strong valve but the male’s frontal apophyses are positioned far away from it during copulation. In others (e.g., *Psilochorus simoni*, Huber 1994*a*; *M. rica*, Huber 1997*a*), the junction between the uterus internus and uterus externus is not developed as a valve but the male apophyses (in *M. rica* they are on the clypeus) are pressed nearby. Moreover, in some pholcids in which the female junction is not developed as a valve (e.g., *Metagonia* and American “*Micromerys*” species; Huber 1997*a*), the males have extremely strong pedipalps. Finally, in the two female *P. globosus* that were freeze-fixed during copulation and then sectioned, the valve was closed as in resting females (Fig. 6B). It seems likely that the male pedi-

Fig. 9. (A) The male's strongest organ, his genitalia. The swollen femur and tibia of the pedipalp (seen here in retrolateral view) are full of muscles. (B) The unmodified female pedipalp, at the same scale, illustrating the extreme sexual dimorphism. Scale bar = 0.5 mm.



palps of *P. globosus* forcefully stimulate the female when they deform the epigyneal area, and the functional significance of pedipalpal strength may be related to increasing such stimulation. We cannot dismiss the possibility of a functional correlation between male palpal strength and the female valve.

The idea that forceful genitalic movements are favoured in pholcids may be in accord with the observations of Uhl (1994) on *P. phalangioides*. She found that a higher rate of palpal twisting movements early in a copulation correlated positively with copulation duration. The assumption, however, that longer copulations per se increase the male's chances of fertilizing the female's eggs were unconfirmed. Longer copulations were correlated with larger numbers of offspring, but this may have resulted also from the positive correlation between female size and copulation duration.

Finally, a morphometric study (Huber 1996) revealed a negative correlation between the diameter of the male pedipalpal tibia of *P. globosus* and its fluctuating asymmetry: the largest palps were most symmetrical. Such a correlation may mean that males with larger tibiae have especially good viability genes (e.g., Møller 1990, 1993; Møller and Pomiankowski 1993), since greater symmetry may result from a superior genetically based ability of the male to cope with stresses during ontogeny (Leary and Allendorf 1989; Parsons 1990).

Species-specificity of contact structures

In.pholcids, taxonomists primarily use three sets of structures in the male to distinguish species (e.g., Millot 1941, 1946; Kraus 1957; Gertsch 1971, 1977, 1982; Senglet 1971, 1972; Deeleman-Reinhold 1986, 1994):

(1) The male chelicerae with their frontal armature of spines, teeth, modified hairs, and warts. As in most other pholcids examined (Huber 1994*a*, 1995*a*, 1997*a*; unpublished data on *A. zeteki*, *Modisimus* spp., *Hedypsilus* spp.; Uhl et al. 1995), male *P. globosus* also press the frontal face of their chelicerae against the ventral body surface of the female. The details of the mesh vary: in some pholcids the apophyses are inserted into corresponding cavities in the female epigynum (Kraus 1984; Huber 1994*a*, 1995*a*); in *Pholcus* spp. the male grasps an apophysis of the female epigynum with his frontal pair of apophyses (Uhl et al. 1995; Huber 1995*a*); in *P. globosus* the tooth-like processes are pressed against the sclerotized bulges of the epigynum; in *A. zeteki* the extraordinarily long apophyses contact the female's sternum (B.A. Huber, unpublished data). In genera such as *Modisimus* and *Metagonia*, the usual cheliceral modifications are hairs of various forms, and these are pressed against the externally flat epigynum (Huber 1997*a*; B.A. Huber, unpublished data) and probably have a sensory or stimulatory rather than a mechanical function. The common theme is that the species-specific and sexually dimorphic chelicerae of male pholcids are brought into contact with the female during copulation. In one notable exception ("*Coryssocnemis*" cf. *viridescens* Kraus, 1955), the male does *not* bring the frontal side of his chelicerae in contact with the female; this is one of the rare pholcid species whose chelicerae are sexually monomorphic (B.A. Huber, unpublished data).

(2) The genital bulb with its appendages and apophyses. Since the bulb is the actual sperm container, contact of the bulb with the female is obviously the general condition. In many pholcids (representatives of *Psilochorus*, *Anopsicus*, *Modisimus*, *Hedypsilus*) the bulb is equipped with a species-specific hook that locks the bulb into the female (Huber 1994*a*; unpublished data); *Pholcus* spp. have both a hook (appendix) and a massive apophysis (uncus) with denticles that may function to spread open the female genital cavity (Uhl et al. 1995; Huber 1995*a*); in *P. globosus* the bulb lacks a hook but has a sclerotized structure (embolic sclerite in Fig. 7B) fused to the embolus (possibly a homologue to the uncus in *Pholcus* spp.) that contacts the female.

(3) The procursus, an apophysis of the distal pedipalpal segment. The procursus is inserted into the female in all pholcids studied (Uhl et al. 1995; Huber 1994*a*, 1995*a*, 1997*a*; unpublished data on *Modisimus* spp., *Hedypsilus* spp., *A. zeteki*, "*Coryssocnemis*" cf. *viridescens*). Again, the details of the mesh vary. Asymmetric insertion has not been reported for any other pholcids, but is apparently common in *Physocyclus* spp., as several species have the projections and hoods on the procursi (Fig. 7A) that allow them to lock together (see Gertsch 1971). In general, the procursi of pholcids seem to be inserted and moved within the female genital cavity.

The fact that all these taxonomically important structures contact the female during copulation is in accord with the hypothesis that cryptic female choice has been responsible for the rapid and divergent evolution of genitalia and non-genitalic contact structures (Eberhard 1985).

The details of the mesh between the male chelicerae and the female epigynum in *P. globosus* accord better with this model of selective female cooperation with males during copulation than with an alternative hypothesis: that such species-specific structures are the result of conflict between males and females in which males attempt to force their attentions on females and females resist indiscriminately (Alexander et al. 1997). Contrary to the male-female conflict of interest explanations, female *P. globosus* take an active role both morphologically and behaviourally in bringing about precopulatory coupling with males. The protuberance that binds the male and female together (the bifurcate apophysis of the epigynum) is on the female, not the male. The same is apparently true for other species of this genus (see Gertsch 1971). In addition, the female protuberance is brought into position to engage the male as a result of behaviour by the female herself (swelling of the membraneous area posterior to the epigynum), rather than being taken forcefully by the male. These morphological and behavioural interactions seem more appropriately described as selective cooperation by the female rather than a struggle by the male to forcefully control coupling in spite of female resistance. The female's cooperation is selective in the sense that coupling is facilitated for males with more appropriate cheliceral morphology (i.e., a cavity of the appropriate size and shape to receive and hold the female apophysis).

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