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Functional Morphology of the Genitalia in the Spider *Spermophora senoculata* (Pholcidae, Araneae)

Bernhard A. HUBER

Zoological Research Institute and Museum Alexander Koenig, Bonn, Germany

Abstract. The reproductive biology of the spider *Spermophora senoculata* is investigated by microscopical observation, freeze-fixation of copulating pairs and preparation of semithin serial sections of the genitalia in functional contact. The mechanics of copulation is described in detail, revealing the functional significance of most genital structures. Before insertion, a pair of male cheliceral apophyses grasp a knob-like structure on the epigynum; the long bulbal apophyses are inserted into paired pockets on the rear of the female opisthosoma; the procursi and emboli are inserted into the uterus externus. The new data are placed in the context of data on other pholcids, and discussed with respect to morphology, function, and implications on pholcid phylogeny and sexual selection theory. The paired pockets on the female opisthosoma are interpreted to be derived from an unpaired pocket by subdivision due to space constraints. The complexity and interspecific variability of female internal genital morphology support the idea that previous models of sperm precedence patterns in spiders are overly simplistic. It is argued that grasping mechanisms may have an underestimated significance in the positioning of the genitalia. The rhythmical deformations of the female opisthosoma by the male palp agree with predictions from the hypothesis of genitalic evolution by sexual selection.

Key words. copulation, freeze-fixation, sperm storage, hematodocha, sexual selection, stimulation

1. INTRODUCTION

The pholcid spider *Spermophora senoculata* (Dugès, 1836) is a holarctic (PLATNICK 2000) species with published records for the United States, southern Europe, northern Africa, and East Asia (China, Korea, Japan). In the USA, this spider seems to be among the commonest macroscopic animals in human buildings, yet our knowledge about its natural history rests mostly on some basic observations of HENTZ (1850), EMERTON (1882), and KASTON (1948). The taxonomic literature provides a wealth of illustrations, mainly of the genitalia. These simple drawings are usually sufficient for species identification, but rarely provide any detail. Two recent publications have added some data on morphology (HUBER 2000: SEM photos of spigots and other characters used in phylogenetic analysis), and the first data on the functioning of the genitalia during copulation (SENGLET in press). The present paper adds behavioral, morphological and functional data, and places these in the context of recently accumulated data about pholcid (mainly reproductive) biology. The emphasis on genital functional morphology stems from the fact that this paper continues a series of works on genitalia in pholcid spiders (UHL et al. 1995; HUBER 1994, 1995, 1997, 1998b, c, 1999; HUBER & EBERHARD 1997). This series is intended to provide a basis for (1) experimental studies, for which several species of the family have proven to be exceptionally valuable (e.g., KASTER & JAKOB 1997; UHL 1998; and references therein); (2) a comparative analysis of the evolutionary transformations of genitalia and the significance of sexual versus natural selection (there is no comparable set of data on genital functional morphology for any arthropod family); (3) the evaluation of functional data for phylogenetic analysis.

2. MATERIAL AND METHODS

The spiders used in this study were collected from December 1999 until May 2000 in the basement of a house in New York City. Only adults and penultimate instar individuals were collected. They were kept individually in glass vials (55 mm high, 13 mm inner diameter) that were closed with cotton. The cotton was periodically moistened with tap water, and the spiders were fed a *Drosophila* fly each every 4-8 days.

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Behavior was observed under a dissecting microscope (Nikon SMZ-U). For observations of copulation, the cotton pads were removed and the vials placed with their openings facing each other, allowing the spiders to enter and leave the partner's vial without external force. Only virgin females were used. From eleven copulations, two were observed entirely (i.e., not interrupted).

The details of copulatory mechanics were studied by freeze-fixation of copulating pairs and subsequent preparation of histological serial sections. For fixation, the vial holding the copulating pair was placed in a Styrofoam container and liquid nitrogen was poured into the vial. The frozen pair was immediately transferred into 80% ethanol at about 25 °C below zero and kept at this temperature for about three weeks. Nine pairs were fixed in this way. Two of these pairs were critical point dried, gold sputtered, and examined in a Hitachi S-4700 cold emission SEM. Two others were dehydrated, embedded in ERL-4206 epoxy resin, and serially sectioned (1µm) with an ultramicrotome (Reichert OmU3) using a diamond knife. The sections were stained with a mixture of azur II (1%) and methylene blue (1%) in an aqueous borax solution (about 0.1%) at 70 ºC for about 30 s.

3. RESULTS

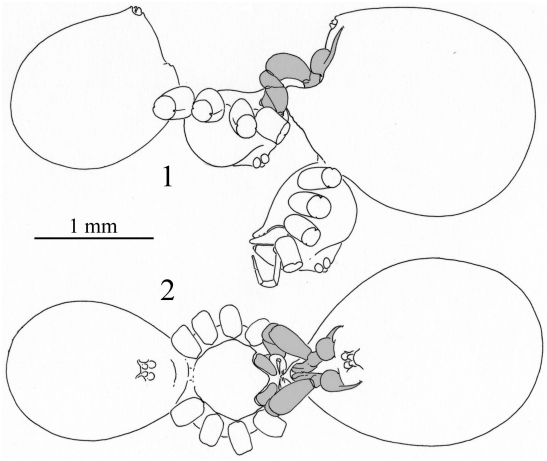
3.1. Courtship and Copulation

Successful courtship that resulted in copulation was observed eleven times (twelve further pairs were separated after about 2-4 hours of observation; in these, the males either failed to court or quickly stopped). The details of courtship varied considerably, ranging from a few minutes to two hours, and from barely any perceptible movements to elaborate sequences. In most cases the male entered the vial of the female, first gently vibrating his entire body and/or bobbing his opisthosoma, and usually moving around as if spinning some threads. Closer to the female, the male often shook his body violently for about 1 s each time, and started to tap the female with his front legs. Females kept motionless for most of the time, and finally either moved slightly back or assumed a receptive position, lowering their prosoma and spreading the legs more to the sides.

At this point, the male oriented his body precisely by placing each of his tarsi 1-3 on the respective female tarsi (male right tarsus 1 against female left tarsus 1, etc.). Shortly before or during this period the male rotated his palps 180º at the coxa-trochanter joint and kept them in this position until his chelicerae had grasped the female epigynum. As soon as this was accomplished (see below for details), the genitalia (procursi, emboli) were inserted into the female. This was usually followed by a period of variable length in which the male genitalia were moved in a seemingly exploratory manner until the tips of the long bulbal apophyses lodged in the pockets near the female spinnerets (see below). During this period, all or most of the matching tarsi lost contact and remained in the resulting position for the rest of copulation. The resulting copulatory position is shown in Figs. 1 and 2.

Immediately following this coupling stage, the male started to move his palps rhythmically (bold arrows in Fig 7). These movements were always symmetrical and simultaneous. The duration of cycles varied considerably among pairs but less within a pair (from about 6-13 s in one pair to about 13-19 s in another pair). There was no significant change in cycle length during copulation in the two pairs observed from beginning to end. Each cycle consisted of three phases. First was a forceful deep insertion of the genitalia into the uterus externus, lasting about 2-5 s (the resulting 'in'-position is shown in Fig. 7). This movement also resulted in the genital bulb being pressed against the ventral cuticle of the female opisthosoma. During the in-phase the female opisthosoma was considerably deformed (see below), but the movements became weaker towards the end of copulation. Secondly, a relaxation resulted in a partial withdrawal of the genitalia from the uterus externus (stippled in Fig. 7), lasting about 1-2 s. This was followed by a third phase, in which no movements were observed. No expansions of the membrane connecting the tarsus to the bulb were observed in any of the stages. The male chelicerae kept their grip on the female epigynum, and the long bulbal apophyses remained inserted into the female pockets.

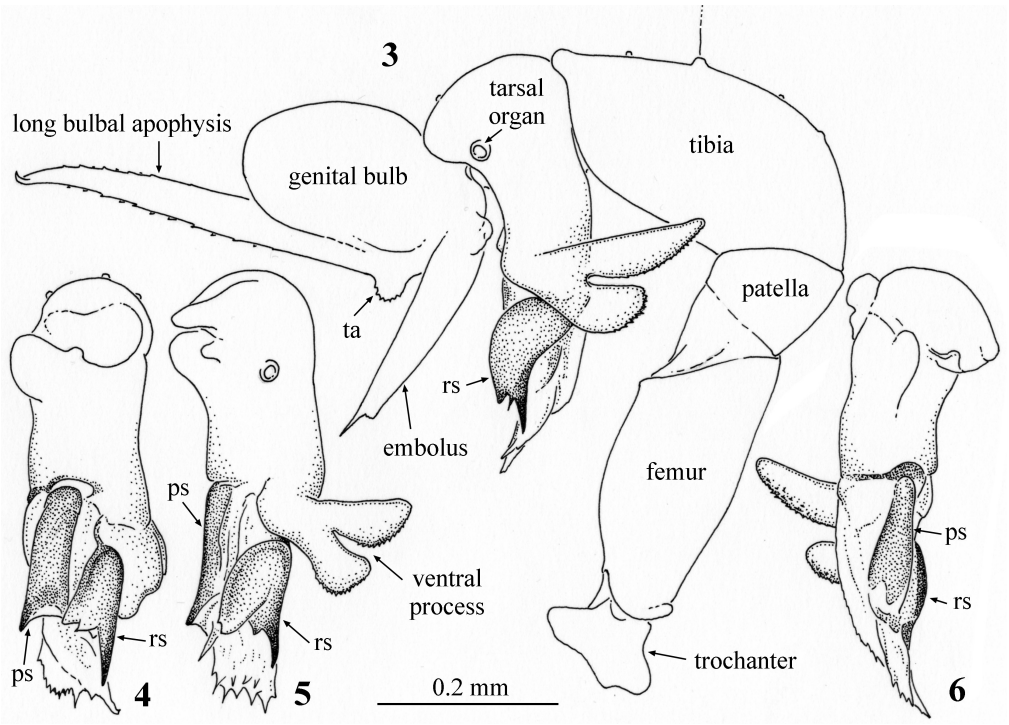
Other than the male palps, there were slight movements of the male legs and opisthosoma in phase 1, but



Figs. 1-2. *Spermophora senoculata*, copulatory position. Male palps grey; legs removed; male on the left. In the ventral view (Fig. 2), the female prosoma is mostly hidden and not drawn. The spiders are here shown in their natural upside-down position. All other illustrations are inverted to show the dorsal side up.

these seemed to be merely passive results of the forceful palpal movements. Both copulations ended suddenly without any preliminary sign, and the partners separated peacefully. Both males cleaned their procursi and emboli with their mouthparts, while the females hardly moved. Post-copulatory courtship was not observed.

Apart from these apparently "usual" sequences, some notable exceptions occurred. One male succeeded in placing his tarsi against those of the female and grasped her epigynum, but then failed five times to insert his genitalia (the sixth trial was successful). Two males succeeded in inserting their genitalia, but then failed to insert one of the two long bulbal apophyses into the respective female pocket (cf. Fig. 13). These



Figs. 3-6. Male copulatory organ. **3.** Left pedipalp, retrolateral view. **4-6.** Left procursus, dorsal (4), dorso-retrolateral (5), and ventral (6) views; ps: prolateral sclerite; rs: retrolateral sclerite; ta: toothed apophysis.

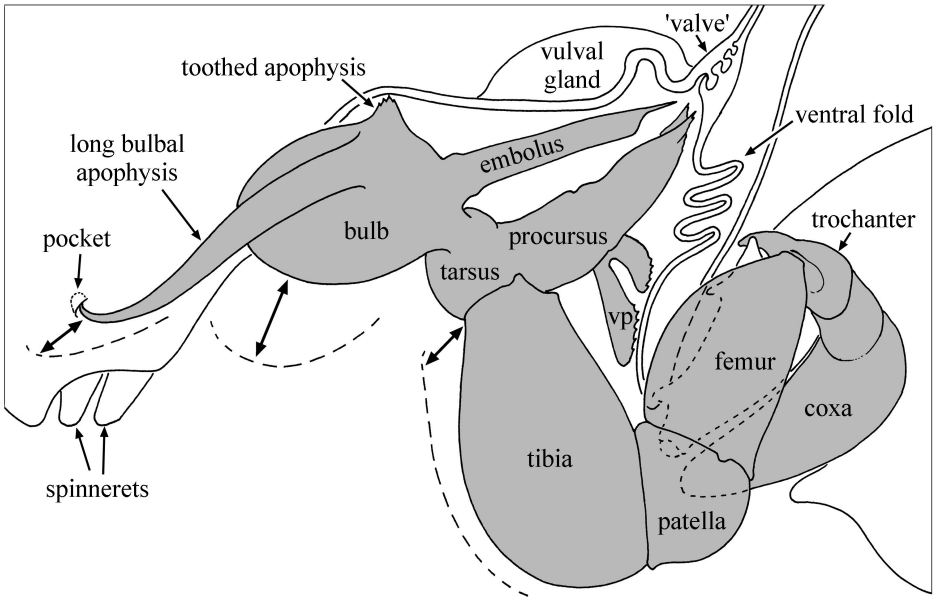


Fig. 7. Genitalia in functional contact, schematic. Male palp grey. Compare with Fig. 1 for orientation. Shown is the 'in'-position. The bold arrows indicate the direction and amplitude of the rhythmical palpal movements; vp: ventral process.

"copulations" never reached the stage involving rhythmical movements of the palps. Instead, the palps kept "searching" the pockets until the pairs were fixed in liquid nitrogen after 14 and 17 minutes respectively.

3.2. Genital Morphology and Mechanics

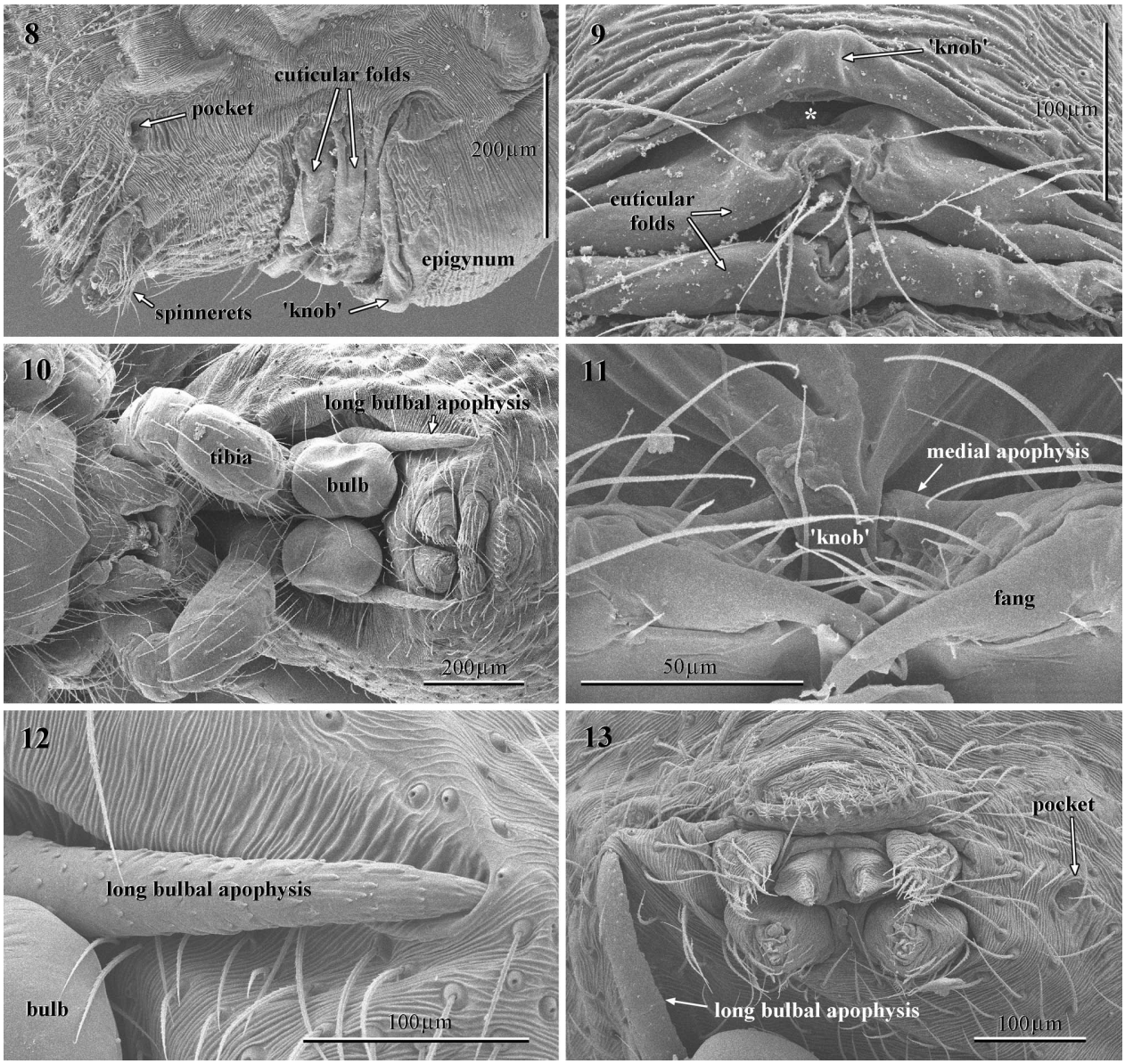
The genitalia of *S. senoculata* have been illustrated many times, but the terminology is inconsistent and even the best available drawings (DRESCO & HUBERT 1969; PAIK 1996) provide little detail. The male pedipalp is illustrated in Fig. 3, and various views of the procursus are shown in Figs. 4–6. The tarsus consists of a basal and a distal part. The basal part carries the genital bulb, the tarsal organ, and a bifurcated distal structure, here called ventral process. The basal part also houses one of the bulbal muscles (M30: Fig. 32). The distal part is only slightly demarcated from the basal part (the internal demarcation is more pronounced: Figs. 29, 32). It consists of two sclerites that are embedded into unsclerotized cuticle. They are here called the prolateral and retrolateral sclerites (ps and rs in Figs. 3–6). The genital bulb is connected to the tarsus by a simple membrane and carries three processes: the weakly sclerotized, hinged embolus that houses the sperm duct, a small toothed apophysis (ta in Fig. 3), and a long bulbal apophysis that ends in a hook. The other palpal segments are unmodified except for being packed with muscles. This is most notable in the tibia which carries the muscles that move the tarsus as well as the second bulbal muscle (M29, whose tendon traverses the tarsus: Fig. 34). The trochanter carries a short ventral apophysis.

The male chelicerae play an important part in copulation. Good illustrations have been published (SENGLET in press), including SEM photographs of the curiously sculptured modified hairs (HUBER 1999, 2000; SENGLET 2001). The terminology used here is simply positional: the medial apophyses carry the modified hairs (cf. Figs. 14–17; "apical apophyses" in SENGLET 2001; "frontal apophyses" in HUBER 1994); the lateral apophyses (cf. Fig. 21; term from HUBER 1995) are directed upward; and the anterior apophyses (cf. Fig. 19; term from SENGLET 2001) are directed forward and down.

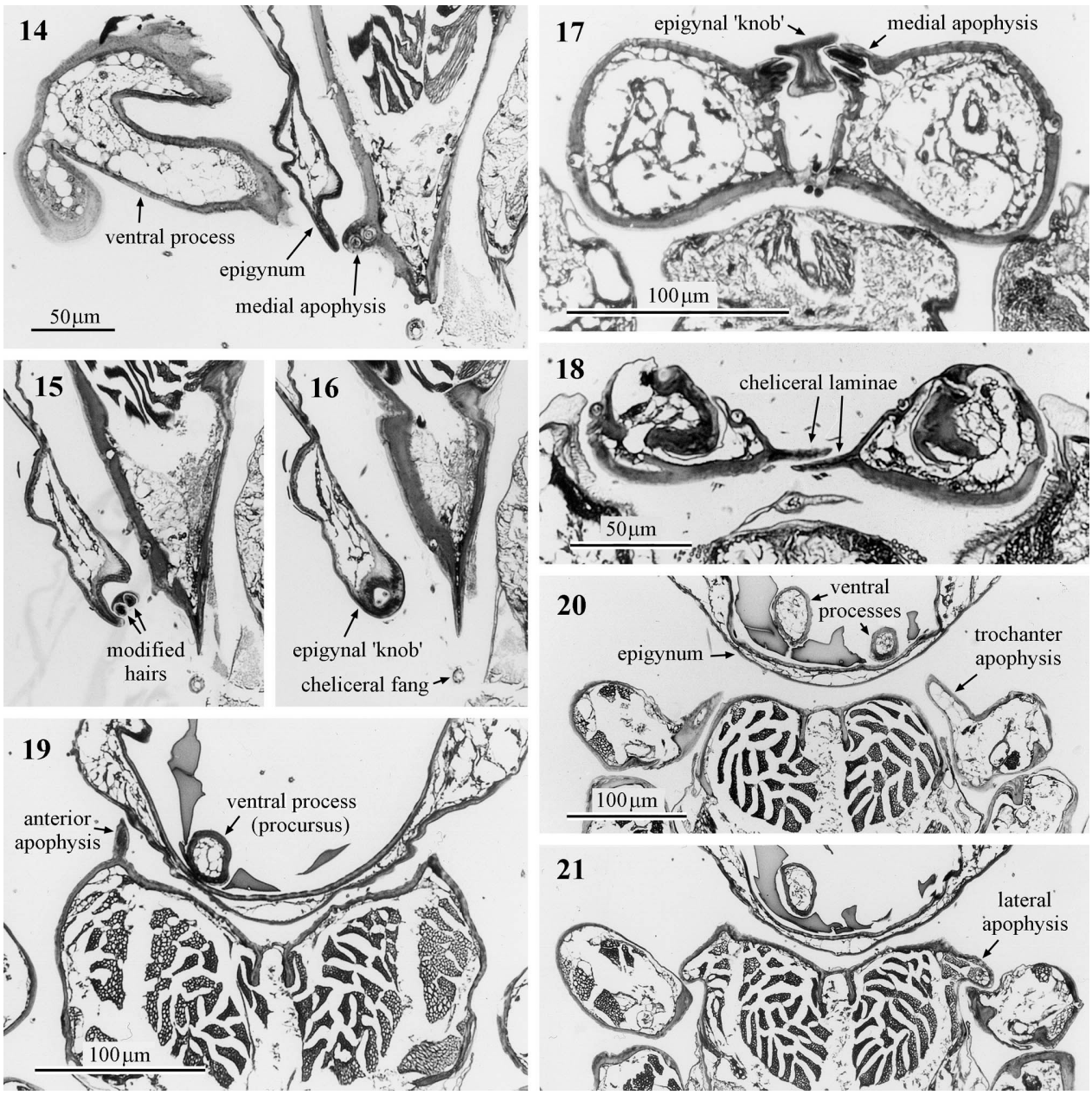
The female genitalia are comparatively simple. A large, weakly sclerotized "epigynum" (Fig. 8) covers the uterus externus. The rim of this epigynum carries medially an unsclerotized and poorly defined 'knob' (Figs. 8, 9). The area behind the epigynum is marked by large cuticular folds (Figs. 8, 9). Internally, there are the usual dorsal pore plates of the vulval glands (cf. UHL 1994), a pair of dorsolateral pouches or folds, the complicated "valve" that connects the uterus externus to the oviduct (Figs. 7, 31; see also fig. 2i in HUBER 1998c), and a series of ventral folds (Figs. 29, 32). In mated females, sperm is found primarily in the main cavity of the uterus externus, but also in the dorsal and ventral folds. Far back on the abdomen near the spinnerets sit a pair of weakly sclerotized pockets that are barely visible in light microscopy (Figs. 8, 13).

The sequence of events during coupling and copulation (see above) involves the following morphological interactions (overview: Fig. 7): First, the modified hairs on the male medial cheliceral apophyses grasp the knob on the rim of the epigynum (Figs. 11, 14–17; hidden by the femur in Fig. 7). Since the apophyses per se are not moveable, the chelicerae themselves make this gripping movement. Evidence for this action is found in the relative positions of the cheliceral laminae which lie side by side during rest but overlap considerably during copulation (Fig. 18). The anterior cheliceral apophyses are pressed against the epigynum in an unspecific way (no corresponding female structure seems to exist; Fig. 19). During this initial phase of coupling the palps are rotated 180° at the coxa-trochanter joint and held in this position by the interaction of the trochanter apophyses with the lateral cheliceral apophyses (Figs. 20, 21 – note that the trochanter apophysis lies dorsal of the cheliceral apophysis; the interaction can therefore not be shown directly in horizontal sections).

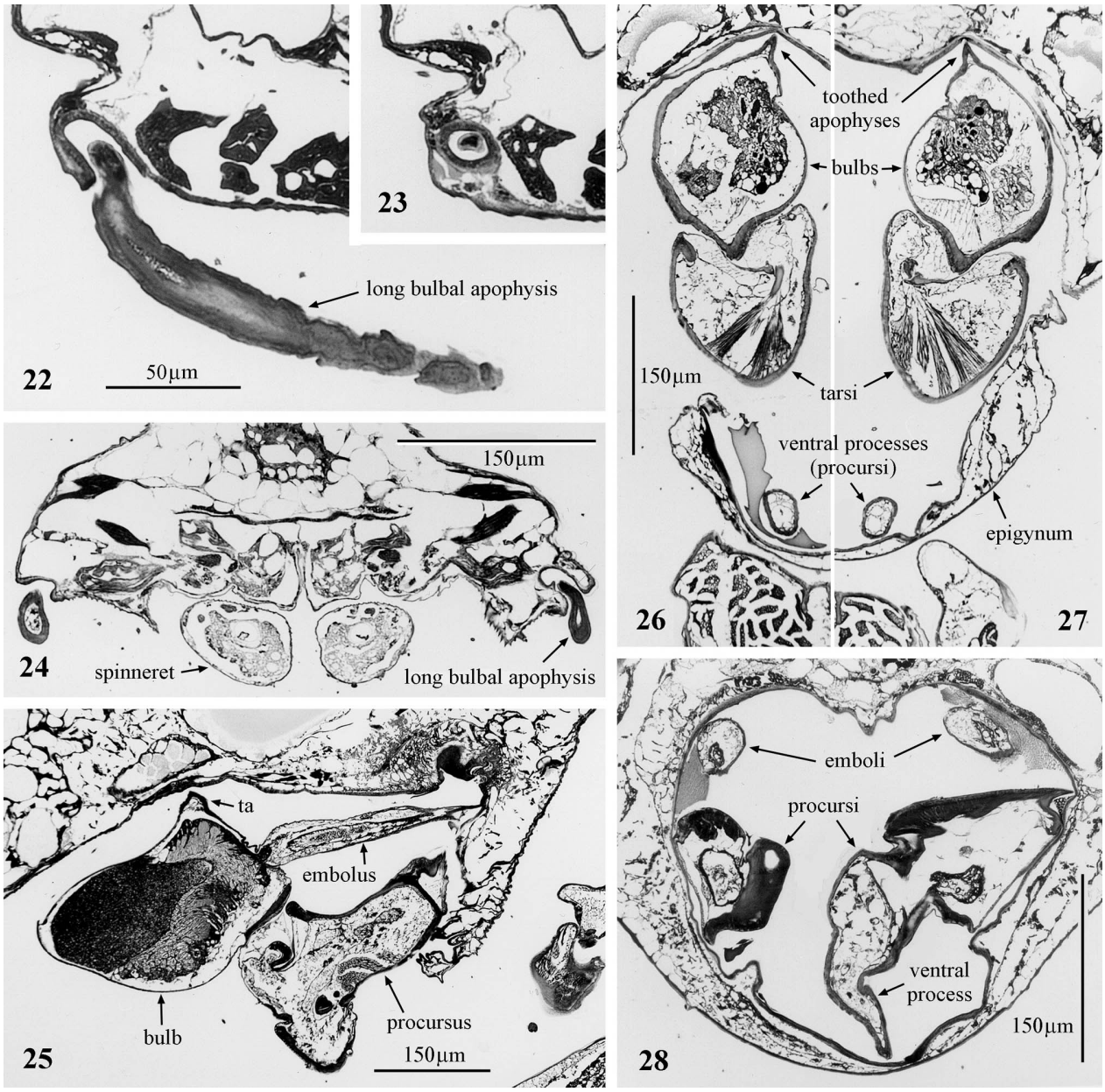
Second, the emboli and the distal parts of the procursi are inserted into the uterus externus. The toothed surfaces of the ventral processes of the procursi oppose the male cheliceral apophyses and squeeze the epigynum between them (Figs. 7, 14). The pro- and retrolateral sclerites on the distal parts of the procursi are inserted deep into the uterus externus, right up to the "valve" (Fig. 32). The emboli lie dorsal of the procursi (Figs. 25, 28), their sperm ducts opening near the female pore plates. The emboli are twisted about 90° from their position at rest (compare Figs. 3 and 7). This movement of the embolus against the bulb is passive and occurs after the insertion of the emboli when the bulbs are moved to insert the long bulbal apophyses into the tiny pockets at the sides of the female spinnerets (Figs. 12, 22-24). This seemingly delicate anchorage is a prerequisite for the forceful deformations of the female opisthosoma by the male bulb (Figs. 7, 13): it holds the posterior end of the opisthosoma while the toothed bulbal apophysis presses against the ventral cuticle between epigynum and spinnerets (Figs. 25-27). It is probably for this reason that the rhythmical palpal movements do not start until both long bulbal apophyses are inserted into the pockets. Surprisingly, there seems to be no significant thickening of the female cuticle in the area where the toothed bulbal apophyses press against the female opisthosoma.



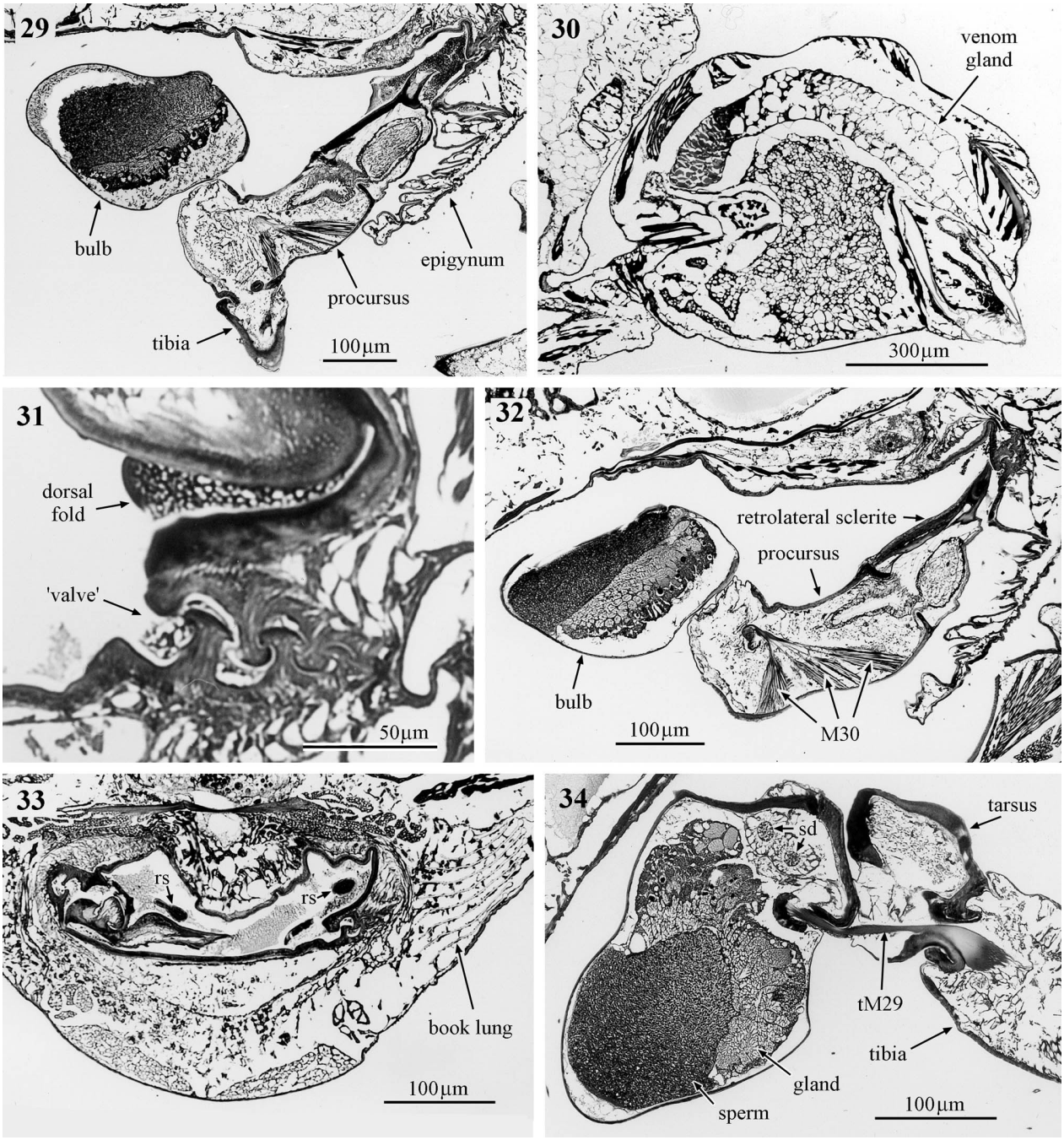
Figs. 8-13. SEM photographs. **8.** Ventral side of female opisthosoma, lateral view. **9.** Entrance to the uterus externus (asterisk), ventral view. **10.** Pair fixed in copulation, ventral view (compare with Fig. 2). **11.** Male chelicerae grasping the female epigynal knob. Note that it is not the fangs but the medial apophyses that grasp the knob. **12.** Long bulbal apophysis inserted into posterior pocket on female opisthosoma. **13.** Female spinnerets and male bulbal apophysis inserted into left female pocket. In this pair the male failed to insert the second bulbal apophysis. Note the deformation of the female cuticle by the male bulbal apophysis.



Figs. 14–21. Semithin sections: the male chelicerae during copulation. **14–16.** Series of sagittal sections (lateral to median) showing the medial apophysis grasping the female epigynal knob. Note also the ventral process of the procursus opposing the cheliceral apophysis. **17.** Horizontal section showing the medial apophyses grasping the female epigynal knob. **18.** Horizontal section showing the overlapping cheliceral laminae. At rest these laminae lie side by side. **19.** Anterior apophysis contacting the epigynum in a seemingly unspecific way. **20–21.** Series of horizontal sections (dorsal to ventral) showing the palpal trochanter apophyses interacting with the lateral cheliceral apophyses.



Figs. 22-28. Semithin sections: the male genital bulb during copulation. **22-23.** Series of sagittal sections (lateral to median) showing the long bulbal apophysis inserted into the posterior pocket on the female opisthosoma. **24.** Horizontal section through posterior tip of female opisthosoma, showing the long bulbal apophyses inserted into the female posterior pockets. **25.** Sagittal section through bulb and embolus, showing the toothed apophysis (ta) pressed against the dorsal wall at the entrance to the uterus externus. **26-27.** Composite horizontal section showing the toothed apophyses pressed against the dorsal wall at the entrance to the uterus externus (two sections were combined because the section plane was not perfectly horizontal). **28.** Horizontal section showing the emboli in the uterus externus, dorsal of the procursi.



Figs. 29-34. Semithin sections, miscellaneous structures. **29.** Genital bulb, and procursus in uterus externus. Note the internal division of the procursus (see also Fig. 32), and the mass of sperm in the uterus externus. **30.** Female prosoma, sagittal section, showing one of the two venom glands. **31.** 'Valve' connecting the uterus externus with the uterus internus, and dorsal fold with sperm. **32.** Genital bulb and procursus, showing the bulbal muscle M30. **33.** Horizontal section showing the retrolateral sclerites (rs) of the procursi reaching into the dorsal folds of the uterus externus. **34.** Genital bulb, tarsus, and tibia, showing the tendon of the bulbal muscle M29 (tM29) inserting in the bulb (its origin lies in the tibia); sd: sperm duct.

4. DISCUSSION

4.1. Female Posterior Pockets

The paired posterior pockets on the female opisthosoma into which the long bulbal apophyses are inserted during copulation are apparently unique to the present species. A similar structure, though unpaired, has been described in two Australian species that were assigned to the genus *Spermophora* for this and other reasons (HUBER 2001). Unpaired pockets seem to be quite common in the genus (HUBER 2001), but their unusual position, minute size, and lack of dark sclerotization has probably impeded their discovery. It is noteworthy that SENGLET (in press), who discovered the position of the tips of the long bulbal apophyses during copulation and studied the genitalia in detail (including SEM) nevertheless failed to see the paired pockets of *S. senoculata*. Obviously, only the conscious search for these functionally important structures will reveal their presence or absence. Previously published illustrations cannot be taken to prove the absence of pockets.

HUBER (2001) has treated the paired and unpaired posterior pockets in *Spermophora* as homologous, based on the exclusive occurrence of posterior pockets in spiders with very similar male palps. A prediction from this assumption is that the bulbal apophyses in other *Spermophora* are inserted into this pocket just as in *S. senoculata*. Another question concerns the polarity of transformation: is the paired condition primitive or derived? It seems reasonable to suppose that a short bulbal apophysis (the common situation in both Mediterranean, Asian, and Australian *Spermophora*) is primitive. If this is true, then the paired condition of the pockets is derived, resulting from the elongation of the bulbal apophysis. The female spinnerets were apparently the constraining factor impeding a further 'migration' of the unpaired pocket backwards and forcing it to spit up.

4.2. Sperm Storage and Sperm Precedence

In *S. senoculata* females, sperm are stored primarily in the uterus externus rather than in specific receptacles. This resembles the basic situation in other pholcids, but beyond this there is a confounding diversity in details. In *S. senoculata*, sperm are also deposited in a pair of dorsal folds close to the 'valve', and are also found in deep cuticular folds in the ventral wall of the uterus externus (how they got there is unknown). Some pholcid species have structures that appear to function as receptacles [dorsally in *Psilochorus simoni* (Berland, 1911), see HUBER 1994; ventrally in *Metagonia rica* Gertsch, 1986, see HUBER 1997], others seem to store sperm in a bewildering diversity of folds in addition to the main cavity of the uterus externus. Although the significance of this diversity in the morphology of the female internal genitalia is as yet unknown, it may be in accord with YOWARD'S (1996) idea that sperm precedence patterns cannot be deduced from a generalized morphology as envisioned by AUSTAD (1984) but may be diverse, even species-specific. Different sperm priority patterns within pholcids are also suggested by the varying occurrence of mate guarding. For example, no mate guarding was observed in *Pholcus phalangioides* (Fuesslin, 1775) (see UHL 1998), while mate guarding is the rule in some neotropical pholcids (EBERHARD & BRICEÑO 1983; HUBER 1998a). In addition to this predicted interspecific variation, intraspecific variation is also expected if sperm is stored in more than one compartment (e.g., uterus externus and folds in *S. senoculata*), and if males can access only one of these (e.g., the uterus externus in *S. senoculata*). P_2 values (the proportion of a brood sired by the second mating male) may vary for a number of further reasons, like cryptic female choice (EBERHARD 1996), copulation duration, and time between copulations (review in ELGAR 1998). Indeed, in the few studies so far, P_2 values in pholcids have been shown to vary conspicuously within species, sometimes from 0-100% (EBERHARD et al. 1993; YOWARD 1998; KASTER & JAKOB 1997).

4.3. Positioning Prior to Copulation

Obviously, successful copulation requires correct positioning of both partners (ROBINSON 1982). In spiders, this may be especially relevant because the intromittent genitalia are usually not innervated (in contrast to pterygote insects; EBERHARD & HUBER 1998b). In pholcids, the procursus is innervated and may provide information for the male about its position in relation to the female. Nevertheless, in *S. senoculata* pre-intromission positioning is achieved in three successive stages, each one requiring cooperation of both sexes: first, vibrations of silk threads provide a gross orientation of the bodies toward each other; second, the positioning of the tips of legs 1-3 against the respective legs of the partner; and finally, the grasping of the female epigynal knob by the male chelicerae, which assures an adequate position of the palps for insertion. Similar successive stages have been observed in other pholcids as well [e.g., in *Anopsicus zeteki* (Gertsch, 1939), see HUBER 1998b; *Pholcus phalangioides*, see BARTOS 1998] and also occur in distantly related spiders (e.g., EBERHARD & HUBER 1998a on a tetragnathid; COYLE 1986 on a diplurid). The impressive diversity of grasping organs in spiders (YOWARD & OXFORD 1997) might reflect multiple solutions to the common problem of correct orientation rather than (or in addition to) the "need to maintain contact more tightly than the pedipalps alone will allow" (YOWARD & OXFORD 1997). The positioning of the leg tips

against each other seems not be a general phenomenon in pholcids [apparently absent in *Pholcus phalangioides*, see UHL et al. 1995; *Physocyclus globosus* (Taczanowski, 1874), see HUBER & EBERHARD 1997; *Psilochorus simoni*, see HUBER 1994], but it may have been overlooked in other accounts of mating behavior. Moreover, leg tapping, which is almost omnipresent in spider courtship, has been interpreted to be primarily stimulatory, but probably also functions in orientation.

4.4. Haplogyne Hematodochae?

Whether haplogyne spiders (including Pholcidae) have a hematodocha or not is controversial. Most authors have followed COMSTOCK'S (1910) influential paper in restricting the term to folded membranes that are greatly expanded during copulation, and have not applied the term to the rather simple membranous connection between tarsus and bulb in haplogynes (e.g., GERHARDT 1927; HARM 1931; COOKE 1966; HAUPT 1978). However, some recent authors have rather emphasized the aspect of homology and applied the term hematodocha to haplogynes as well (e.g., SCHULT 1983a, b; UHL et al.1995). The question might be easily dismissed as purely semantical, depending just on the amount of volume increase during expansion that one considers sufficient to use the term hematodocha instead of membrane. Movements of the membrane connecting the tarsus with the bulb have been observed in some pholcids (GERHARDT 1924; UHL et al. 1995) and this has been taken as sufficient evidence to justify using the term hematodocha. However, from a functional perspective, pholcid 'hematodochae' are something very different form the typical entelegyne (basal) hematodochae. Entelegyne basal hematodochae actively produce the movement (usually rotation) of the bulb against the tarsus by hydraulics (e.g., HUBER 1993a). In contrast, pholcid bulbs are rotated by a muscle (the muscle M29 – see HUBER & EBERHARD 1997) and the 'hematodocha' is just a membrane allowing this movement. Later, when the bulb is anchored to the female during copulation (by the uncus and appendix in *Pholcus*: UHL et al. 1995, HUBER 1995; by the bulbal apophysis in *Psilochorus*, *Modisimus* and related genera: HUBER 1994, 1998b; by the embolic sclerite in *Physocyclus*: HUBER & EBERHARD 1997) the 'hematodochae' allow the movements of the tarsus (with procursus) against the bulb. These movements of the tarsus necessarily imply movements of the membrane connecting it to the fixed bulb, but the reason for these movements (at least for the forceful in-movement) is muscular again (the palpal muscles moving the tarsus; see HUBER & EBERHARD 1997). This should be kept in mind, no matter whether (basal) hematodocha is defined as the membrane connecting the tarsus to the bulb, or as hydraulically expanded membranes that move the bulb against the tarsus or parts of the bulb against each other.

4.5. Phylogenetic Implications

The most recent cladistic analysis of Pholcidae (HUBER 2001) was ambiguous with respect to the genus *Spermophora*: it was either placed within the *Pholcus* group sensu HUBER 1995, with this group being the sister taxon of *Metagonia*, or it was sister taxon of *Metagonia* + *Micromerys*, i.e., in a *Pholcus* group including *Metagonia*. The question can be simplified to: is *Spermophora* more closely related to *Pholcus* or to *Metagonia*? One potential solution would be to create an expanded matrix including more than the one *Pholcus* and two *Spermophora* species studied in the previous analysis. This is beyond the scope of the present paper. Instead, based on the functional analysis above, I will present a more detailed discussion of the data favoring one or the other alternative.

The following characters link *S. senoculata* to *P. phalangioides*: (1) The frontal cheliceral apophyses with their modified hairs grasping a knob-shaped structure on the female epigynum. This is a fairly complex character, never present in *Metagonia*. However, it must be noted that it is not present in all *Spermophora* species either. For example, *S. yao* Huber, 2001 is undoubtedly a close relative of *S. senoculata* but has a very different mechanism to lock the chelicerae to the epigynum (a pair of apophyses into a pair of pockets). Whether the mechanism in *S. senoculata* was lost in *S. yao* (and other congeners) or independently gained in *S. senoculata* and *Pholcus* remains open. The epigynal knob was coded as 'absent' in *S. senoculata* (HUBER 2001) but the new functional data suggest it is present, even though it is quite different morphologically from the 'real' *Pholcus* knob. Whether it should be treated as a separate character or not is another question, touching the controversial issue of character independence in cladistic analysis. (2) In *Spermophora* and *Pholcus*, the rotated palp is stabilized by the interaction of the lateral cheliceral apophysis with the trochanter apophysis (HUBER 1995). This is the character that was originally used to define the *Pholcus* group (HUBER 1995), and it is the one that is apparently the most consistently present in *Pholcus* and *Spermophora*, but absent in *Metagonia*. In *Metagonia*, a short trochanter apophysis is locked between chelicera and palpal coxa. (3) The shape of the male palpal tibia is similar in both genera ("spindle-shaped", HUBER 2000), but this character is difficult to quantify, and occurs also in other genera (e.g., *Physocyclus*).

What, on the other hand, links *Spermophora* to *Metagonia*? (1) The most obvious feature is the presence of a process ventrally on the procursus (the "ventral pro-

cess" above). The morphology varies widely within each genus, and the process is hinged in *Metagonia* but not in *Spermophora* (the structures were therefore coded as non-homologous in HUBER 2001). However, the position and the function during copulation are identical. Both in *S. senoculata* and in *M. rica* this process is pressed from inside against the ventral wall of the uterus externus, spreading it open (Fig. 7 herein, and fig. 28b in HUBER 1997). A similar structure (of unknown function) occurs in *Micromerys* (see HUBER 2001), but never in *Pholcus*. (2) A single long spine at the tip of the embolus occurs in *Spermophora* and *Metagonia*. However, the embolus of *P. phalangioides* is provided with a number of "teeth" (UHL et al. 1995) that might have been independently reduced to one in the other two genera.

The following characters are considered non-informative: (1) A toothed apophysis on the bulb is present in both *S. senoculata* and *P. phalangioides*, but absent in all known *Metagonia* species. However, in *Pholcus* this apophysis (the 'uncus') is pressed ventrally against the invaginated epigynal plate (UHL et al. 1995; HUBER 1995) while the toothed apophysis in *S. senoculata* is pressed dorsally against the cuticle at the entrance to the uterus externus. Thus, I disagree with SENGLET (2001) who tentatively suggested that the structures might be homologous. (2) *Spermophora* and *Metagonia* have lost the anterior median eyes (AME), which are present in *P. phalangioides*. However, the AME have also been lost in representatives of *Pholcus* (HUBER 2001), and within several other genera (HUBER 2000), suggesting multiple convergent reduction. (3) Finally, most representatives of *Pholcus* and *Metagonia* have a long opisthosoma, while most *Spermophora* species have a globular opisthosoma. Again, this is a character that has obviously gone through multiple convergent transformations, and the diversity of shapes makes unambiguous coding almost impossible (HUBER 2000).

In conclusion, the data suggest that *Spermophora* is closer to *Pholcus*. Considering the impact of taxon sampling for the outcome of phylogenetic analysis, it is worth noting that neither the genus *Spermophora* nor the genus *Pholcus* have ever been revised. As a result, simply sampling from the species included will just reveal paraphyly and polyphyly of the genera as presently delimited, but hardly solve the problem.

4.6. Sexual Selection and Stimulation

EBERHARD (1985) argued that male genitalia may function as courtship devices and be thus under sexual selection. However, in some spiders the female cuticle contacted by the male genitalia seems to be void of receptors, casting doubt on the importance of stimulation (HUBER 1993a, b, 1995). This potential problem was discussed by EBERHARD (1996), who pointed out the fact that "stimulation … might also occur on the basis of overall fit, perhaps signaled by pressing or twisting the entire epigynum or the female's entire abdomen …". This is indeed what might be happening in *S. senoculata*. During the rhythmical movements of the male palps, the entire ventral face of the female abdomen is strongly indented by the pressure of the toothed bulbal apophyses and the epigynum is squeezed between the ventral processes of the procursi and the male chelicerae (Figs. 7, 13, 14). Importantly, these pressures can only be applied if the genitalia and chelicerae are properly placed, including the insertion of the long bulbal apophyses into the tiny pockets at the rear of the female opisthosoma.

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Author's address: Bernhard A. HUBER, Zoological Research Institute and Museum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany;
e-mail: b.huber.zfmk@uni-bonn.de

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