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Copulatory Mechanism in *Holocnemus pluchei* and *Pholcus opilionoides*, With Notes on Male Cheliceral Apophyses and Stridulatory Organs in Pholcidae (Araneae)

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Abstract

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The pholcid spiders *Holocnemus pluchei* (Scopoli, 1763) and *Pholcus opilionoides* (Schränk, 1781) are investigated with respect to functional morphology of their genital organs using freeze-fixation of spiders during copula in liquid nitrogen and subsequent preparation of histological serial sections of the copulatory organs in functional contact. Special attention is paid to the mode of male pedipalpal arrestation before copulation, which is achieved in two quite different ways: in *Pholcus* by contact of the lateral cheliceral apophysis with the pedipalpal trochanter-apophysis, in *Holocnemus* by locking the pedipalpal trochanter between chelicera and pedipalpal coxa. The condition in *Pholcus* is considered to be apomorphic and to present a synapomorphy of about a dozen genera for which the name "Pholcus-group" is proposed. The stridulatory apparatus of *Holocnemus pluchei* is described, its biological significance discussed and an overview of accounts on stridulation in Pholcidae given.

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Introduction

In comparison to the increasing number of works treating copulatory mechanisms in entelegyne spiders (e.g. Osterloh 1922; Melchers 1963; Loerbroks 1983, 1984; Grasshoff 1968, 1973; van Helsdingen 1965, 1969; Huber 1993, 1994a, in press a, b) little is known about the functional morphology of the genitalia in haplogyne spiders (e.g. Cooke 1966). The recent paper of Uhl *et al.* (in press) on the haplogyne *Pholcus phalangioides* (Fuesslin, 1775) provides for the first time detailed information on the function of various elements of the copulatory organs. A comparable investigation of the pholcid *Psilochorus simoni* (Berland, 1911) (Huber 1994b), revealed a very different type of copulatory mechanism, thus adding to the diversity of such mechanisms among the otherwise rather uniform Pholcidae. The present study adds data on two further pholcid species to the previously described species and corroborates the hope that characters from functional morphology may contribute considerably to the investigation of pholcid phylogeny.

Materials and Methods

Holocnemus pluchei (Scopoli, 1763) was collected in Sicily (Italy), from crevices in walls and various types of shrubs in Syracuse and Taormina. *Pholcus opilionoides* (Schränk, 1781) was collected from a heap of stones at the bank of a brook in the Mühlviertel near Linz (Austria). The penultimate-stage specimens of both species were reared individually at room temperature in plastic boxes (11 x 8 x 5 cm).

Two pairs of each species were freeze-fixed in liquid nitrogen during copulation. The copulatory organs of these pairs were embedded in Spurr's medium and serially sectioned in functional contact (for methodological details, see Huber 1993). The copulatory organs were further studied with a scanning electron microscope (Jeol JSM-35CF).

Courtship and copulation behaviour of *Holocnemus pluchei* were observed at bright daylight. Attempts to record airborne sound produced by the stridulatory organs, using a microphone (AKG 1200), a ultrasound detector (Pettersson D940) and a tape recorder (UHER Report Monitor 4000), were not successful.

Results

Copulatory organs

The male copulatory organs, the genital bulbs, are situated distally on the pedipalpal tarsi (Fig. 1). In both species, the tarsus is provided with a conspicuous appendage, the procurus. This is a massive structure that bears distally a number of complex lamellae, fringes and apophyses (Figs 2A, 3A). The genital bulb consists of a globulous part that contains the sperm reservoir (spermophor) with associated glands,

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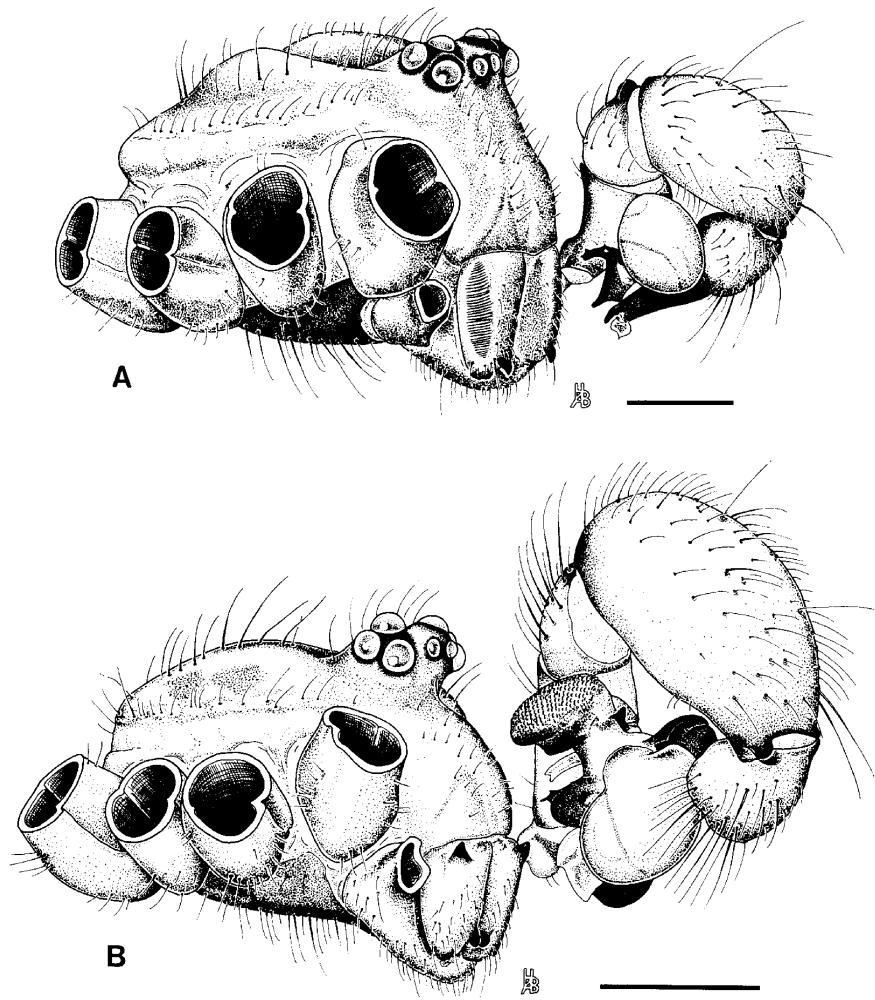


Fig. 1. Males of *Holocnemus pluchei* (A) and *Pholcus opilionoides* (B). Opisthosoma and extremities removed except of left pedipalps. Scale lines = 0.5 mm.

and bears distally appendages which can so far not be homologized unambiguously between the two genera. In *Holocnemus pluchei*, there are two bulbal appendages, the dorsal and the ventral bulbal apophysis (Fig. 2B). The sperm reservoir opens between these apophyses without forming an embolus. In *Pholcus opilionoides*, the bulbal appendages are named (in accordance with previous authors, e.g. Gerhardt 1927; Wiehle 1953) unculus, appendix and embolus (Fig. 3B).

Apart from the thickening of all pedipalpal segments, only the male trochanter in *Pholcus opilionoides* is further modified, bearing a long apophysis (Fig. 3A). Other non-pedipalpal male structures that are modified in the context of copulatory mechanics are the chelicerae. In *H. pluchei* (Fig. 4) only a frontal cheliceral apophysis (*fca*) is present (in addition to the usual armature found in both sexes). It bears a single cone (sensillum?) at its apex (see Fig. 8A). In *Ph. opilionoides* (Fig. 5) each chelicera carries distally a frontal apophysis with two cones, basally a lateral apophysis (*lca*) and a frontal prominence (*fp*).

The female copulatory organ in both species corresponds well with the condition found in most Pholcidae (cf. Deeleman-Reinhold 1986; Uhl 1994). In *H. pluchei* the transversal slit that opens into the uterus externus is bordered by conspicuous bulges anteriorly and posteriorly (Fig. 6C). In *Ph.*

opilionoides the female copulatory organ is marked externally by a highly sclerotized, triangular plate (epigyneal plate) which is provided with an anterior sclerotized hook. In both species the uterus externus is characterized by a pair of dorsal pore plates (Fig. 6D) through which the vulval glands discharge their products (cf. Uhl 1994). A complex valve apparatus separates the uterus externus from the uterus internus (see Figs 8C, 9C).

Genitalia coupling

Prior to intromission, the males of both species rotate the pedipalps for about 180° in the coxa-trochanter joint (compare Fig. 1 to Fig. 6B). In *H. pluchei*, the pedipalpal trochanter and basal parts of the femur are locked between the chelicera and the pedipalpal coxa (Fig. 8B). In *Ph. opilionoides* a completely different mechanism is realized: the pedipalp becomes arrested in the rotated position by the pedipalpal trochanter-apophysis that is hooked into the lateral cheliceral apophysis (Fig. 9A).

Correct positioning of the male relative to the female is achieved with help of the frontal cheliceral apophyses. In *H. pluchei* they are brought into contact with a specially sculp-

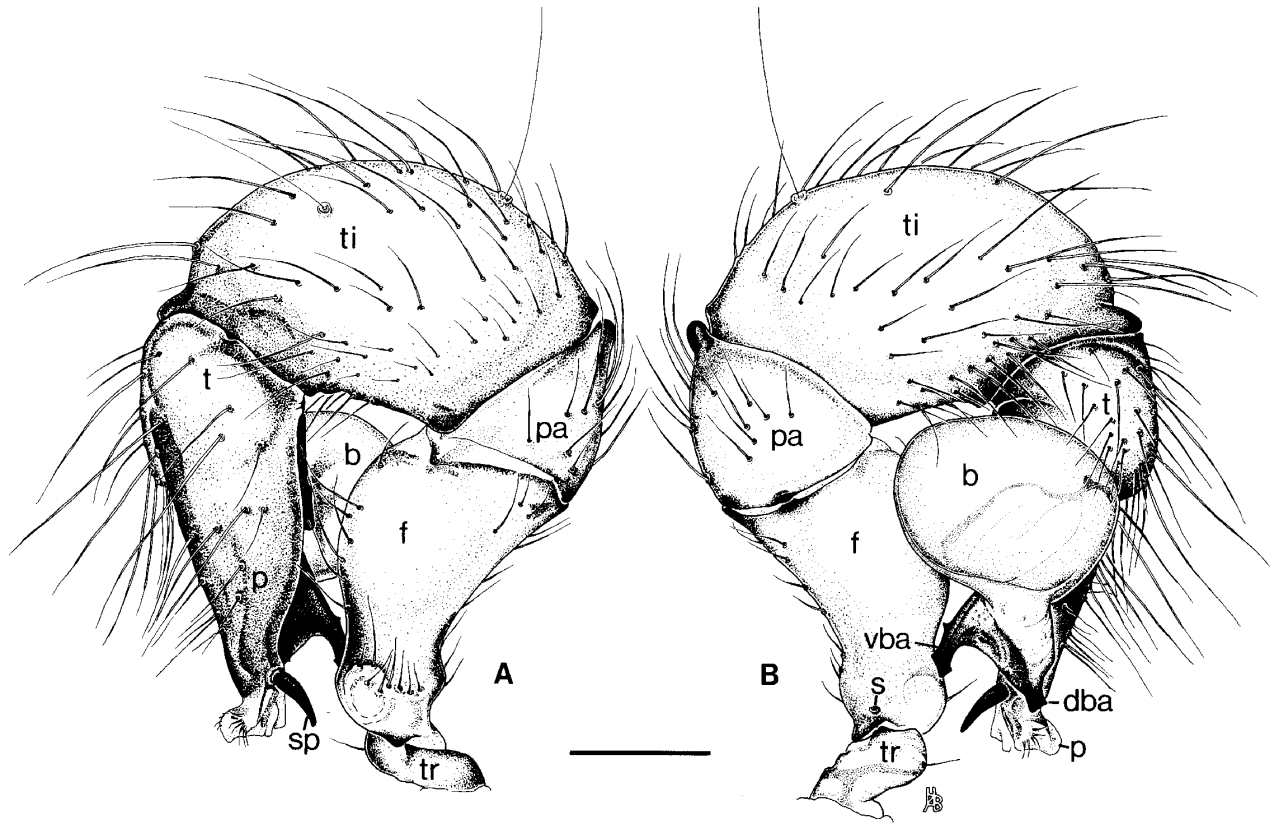


Fig. 2. Left male pedipalp of *Holocnemus pluchei*, retrolateral (A) and prolateral (B) view. Scale line = 0.3 mm.

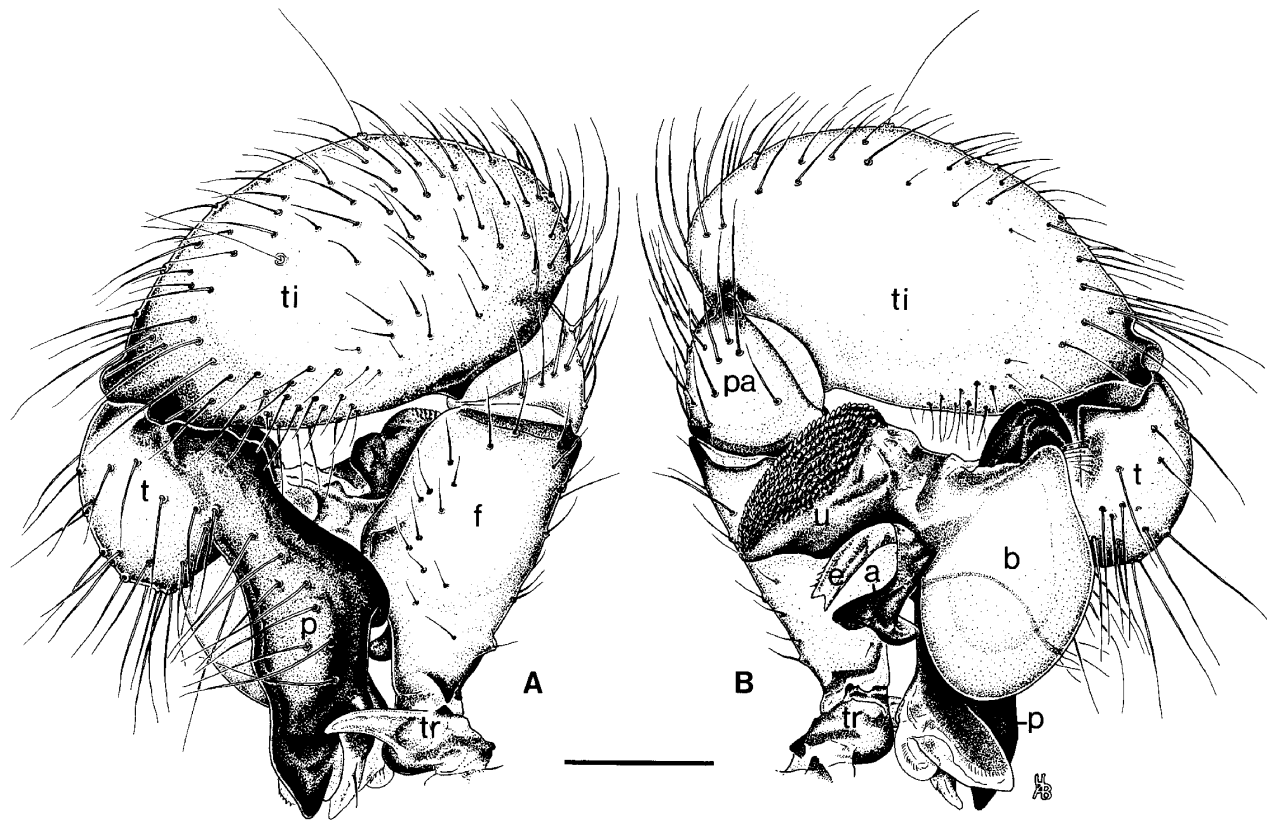


Fig. 3. Left male pedipalp of *Pholcus opilionoides*, retrolateral (A) and prolateral (B) view. Scale line = 0.3 mm.

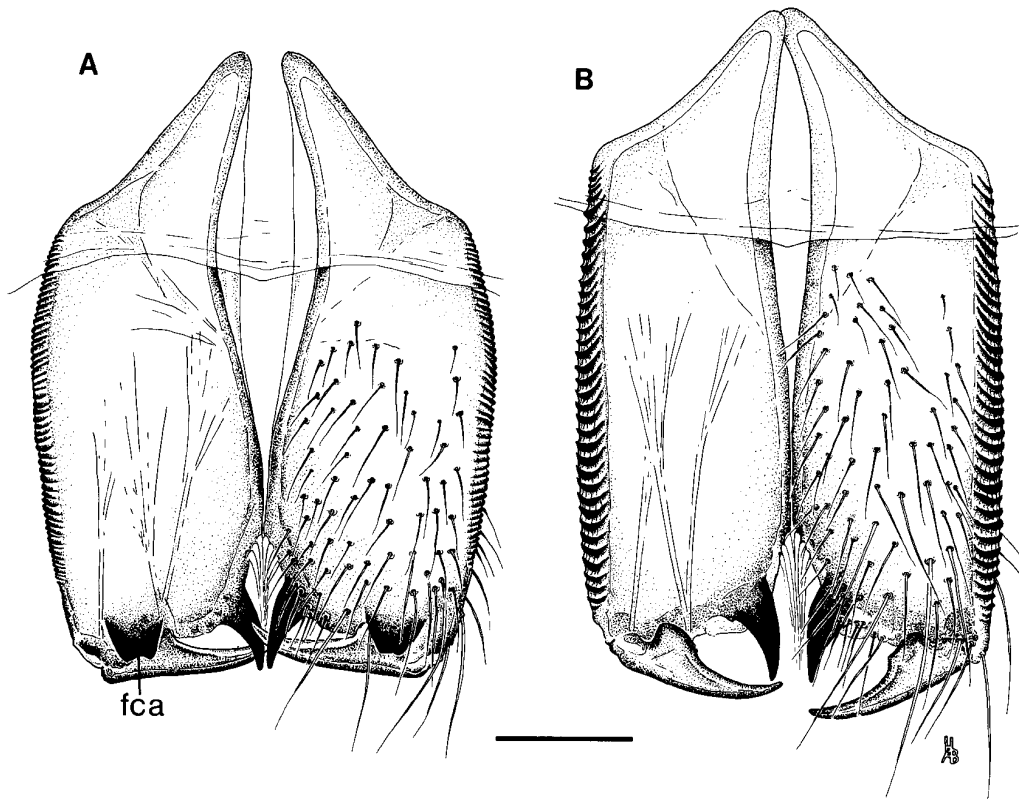


Fig. 4. Chelicerae of male (A) and female (B) *Holocnemus pluchei*, frontal view, hairs of left side not illustrated. Scale line = 0.2 mm.

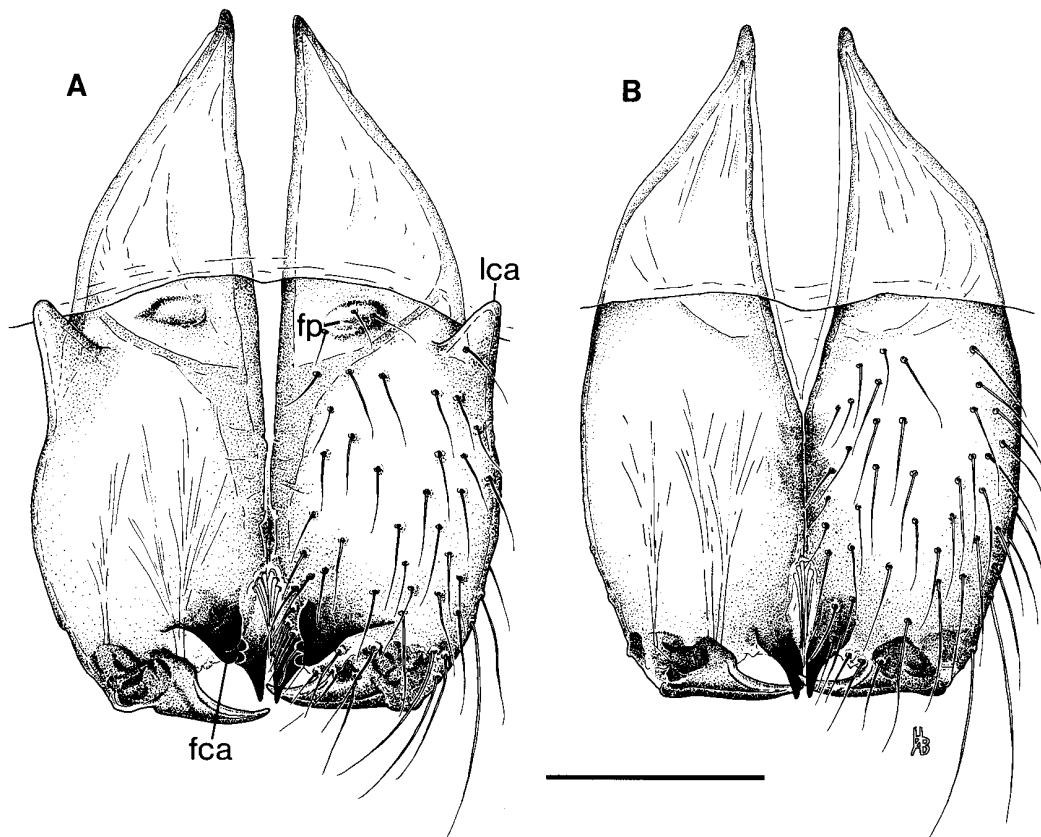
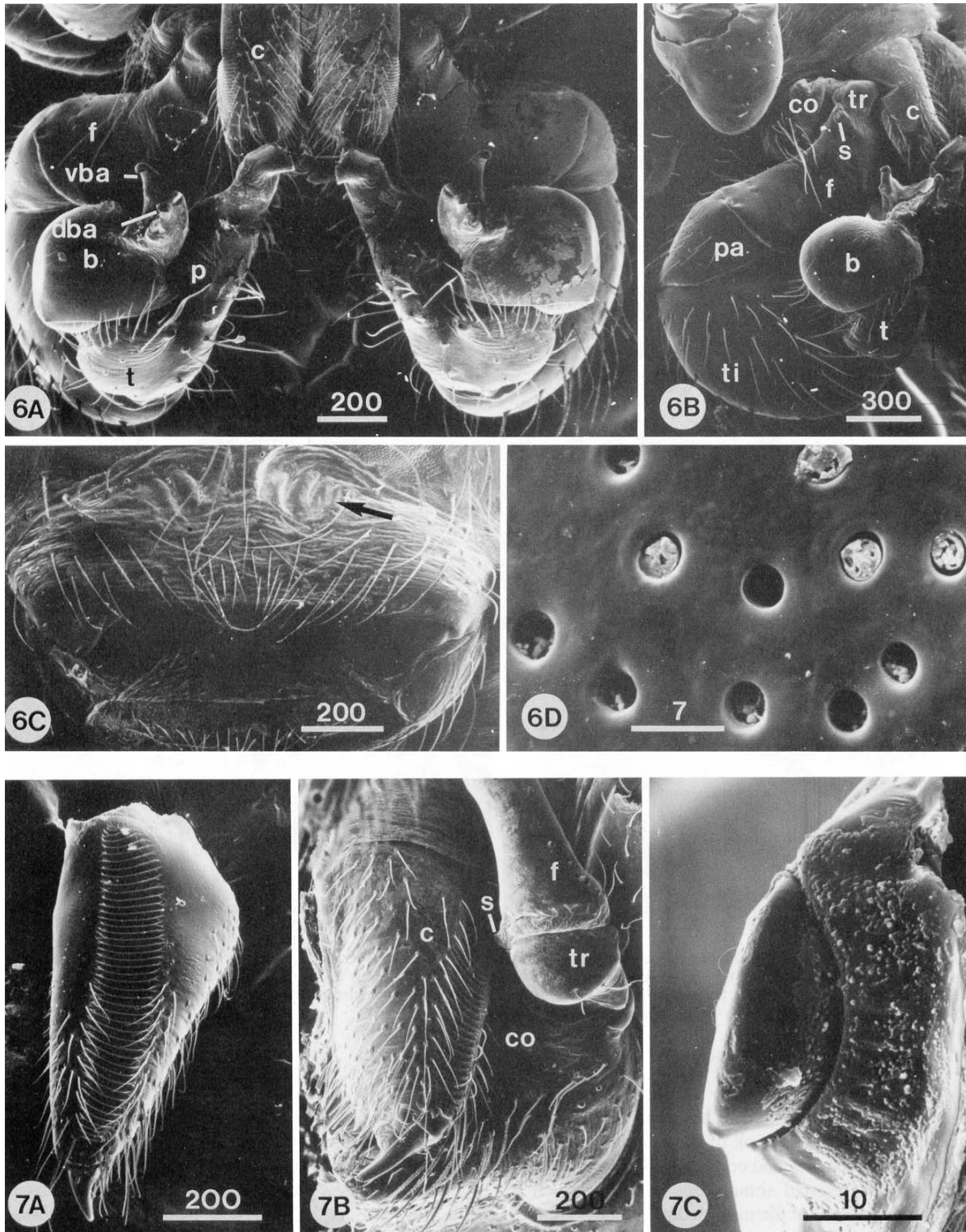


Fig. 5. Chelicerae of male (A) and female (B) *Pholcus opilionoides*, frontal view, hairs of left side not illustrated. Scale line = 0.2 mm.



Figs 6-7—Fig. 6 *Holocnemus pluchei*, copulatory organs (SEM).—A. Male pedipalps in copulatory position, i.e. rotated for 180°, frontal view.—B. The same in lateral view, note position of pedipalpal trochanter between chelicera and pedipalpal coxa.—C. Female epigyne, arrow marks area that is contacted by male frontal cheliceral apophysis during copulation.—D. Detail of female pore plate. Scale lines in μm .—Fig. 7. *Holocnemus pluchei*, female stridulatory organ (SEM).—A. Left chelicera, lateral view.—B. File and scraper in natural position.—C. Scraper. Scale lines in μm .

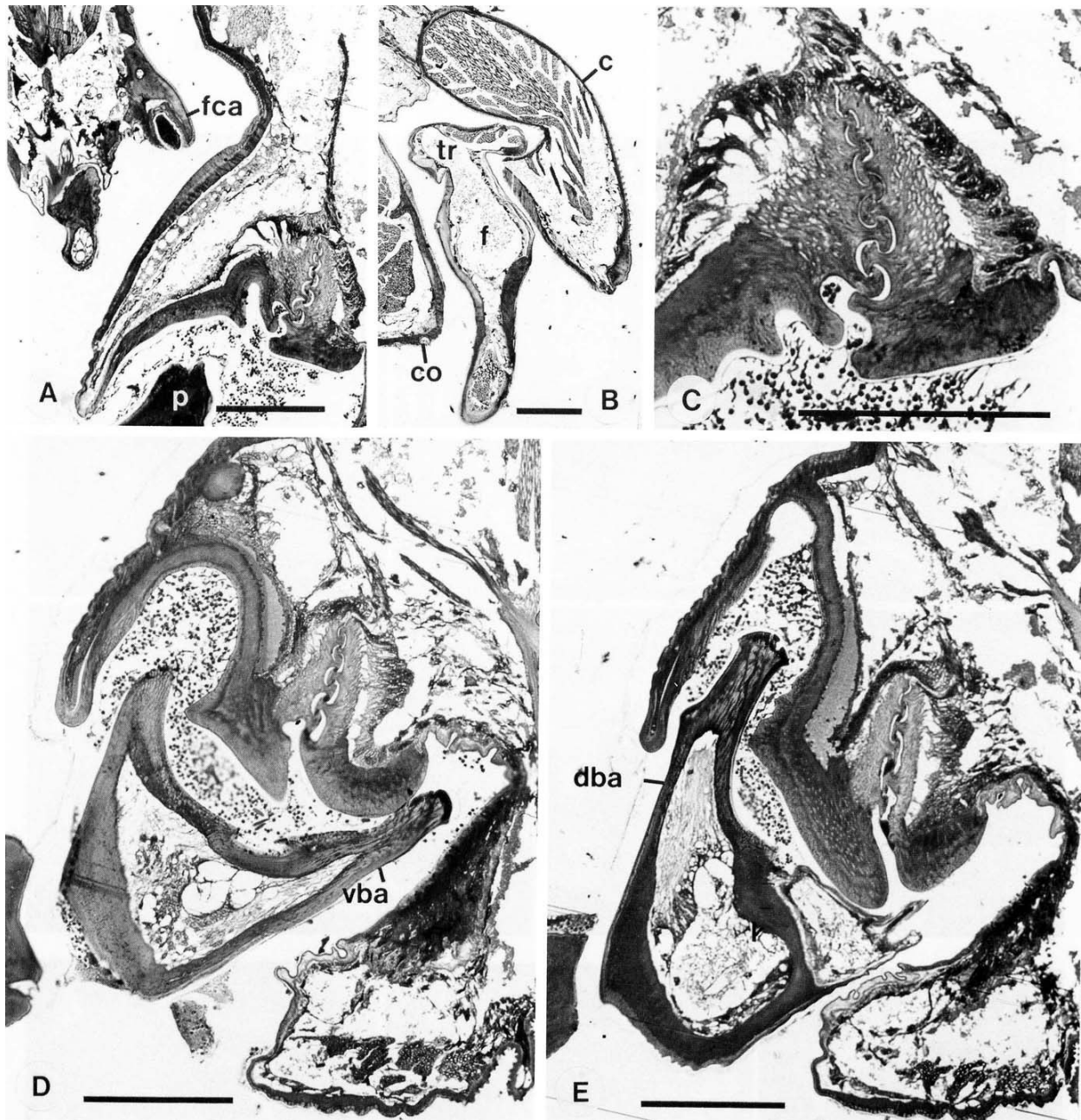


Fig. 8. *Holocnemus pluchei*. Sagittal semithin sections through copulatory organs in functional contact, for an overview see Fig. 10. —A. Male cheliceral apophysis in contact with female during copulation (the space between apophysis and female is an artefact). —B. Male trochanter-apophysis and basal parts of femur, locked between chelicera and pedipalpal coxa. —C. Valve, separating uterus externus from uterus internus. —D, E. Dorsal and ventral bulbal apophyses in corresponding uterine cavities. All scale lines = 100 μ m.

tured area anterior to the epigyneal bulges (Fig. 6C). In *Ph. opilionoides*, they clasp the hook of the epigyneal plate.

After pedipalpal rotation and correct positioning, the copulatory organs are inserted simultaneously and coupled to the female. The procursi of the male pedipalpal tarsi are then situated medially, the bulbal apophyses are inserted laterally in the uterus externus (Fig. 6A). In *H. pluchei*, the strong spur at the apex of the procurus is bent backwards in the uterus externus. The dorsal and ventral bulbal apophyses are inserted into corresponding cavities (Fig. 8D, E).

In *Ph. opilionoides* the appendix is hooked into a dorsal fold at the entrance into the uterus externus (Fig. 9B), the embolus is directed to the dorsal pore plate and the uncus with its denticles is pressed against a ventral sclerotized plate (Fig. 9E). This is the epigyneal plate that lies externally at rest (see above) and is inverted at the beginning of copulation. This inversion is produced by the male that clasps the hook of the epigyneal plate with the frontal cheliceral apophyses and draws it backwards. During copulation, the hook is still situated between the cheliceral apophyses and

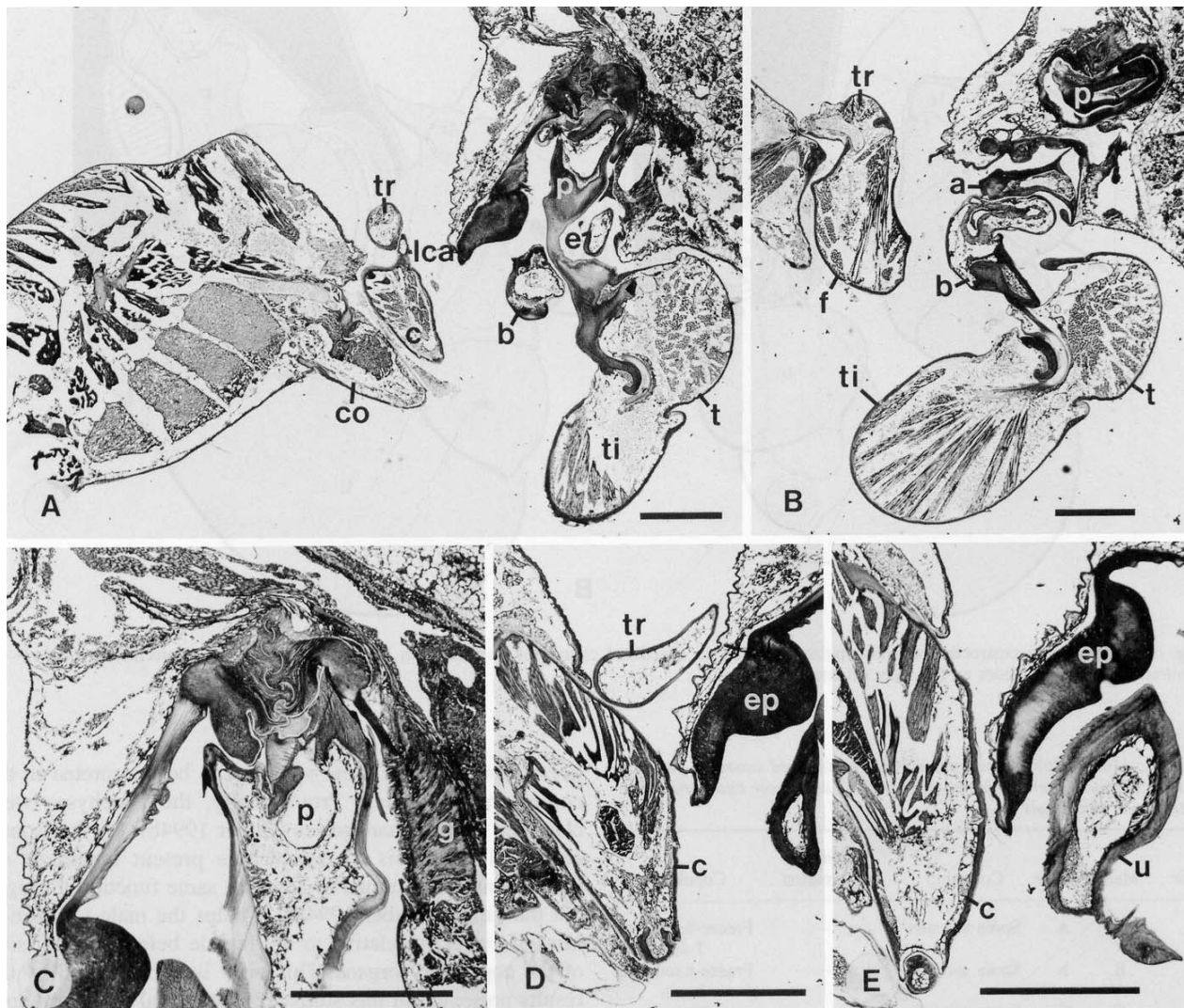


Fig. 9. *Pholcus opilionoides*. Sagittal semithin sections through the copulatory organs in functional contact, for an overview see Fig. 10. —A. Trochanter-apophysis hooked into lateral cheliceral apophysis, procurus inserted into uterus externus, embolus points towards dorsal pore plate. —B. Appendix hooked into a dorsal rim at the entrance into uterus externus. —C. Tip of procurus exactly matches uterus externus. —D. Tip of trochanter-apophysis contacts female. —E. Uncus pressed against epigyneal plate, thus opposing trochanter-apophyses. All scale lines = 200 μ m.

the membranous area anterior to the epigyneal plate is highly expanded. The tips of the trochanter-apophyses are pressed against this membranous area, thus opposing the pressure of the uncus (Fig. 9D).

Stridulatory organ in Holocnemus pluchei

Both sexes in *H. pluchei* have stridulatory organs that are composed of a file of cuticular ridges on the chelicera (Figs 1A, 4, 7A, B) and a scraper at the basis of the pedipalpal femur (Fig. 7B, C). The male file consists of 50-55 ridges with a mean distance between them of 8.8 μ m, while the female file has only 34-38 ridges with a mean distance of 16.4 μ m. The signal produced with these organs during courtship (see below) is not audible with unaided ears. Attempts to record airborne sound were not successful.

In order to examine a possible correlation between the

female stridulatory organ and the highly thickened distal pedipalpal segments, serial semithin sections of female pedipalps were prepared. Their investigation revealed that the thickened segments are filled with a simple filling-tissue; they contain no glands or air-sacs.

Courtship and copulation in Holocnemus pluchei

Courtship behaviour resulting in copulations was observed in seven pairs (Table 1). In three pairs, courtship lasted a few seconds, the males jerking their bodies and directly approaching the females which immediately attained the mating position (opisthosoma vertical, legs sideways). In the other four pairs the female (same individual in all four pairs) appeared less receptive and vigorously bounced against the males, sometimes rubbing the pedipalps against the chelicerae (thus presumably stridulating). The males responded with

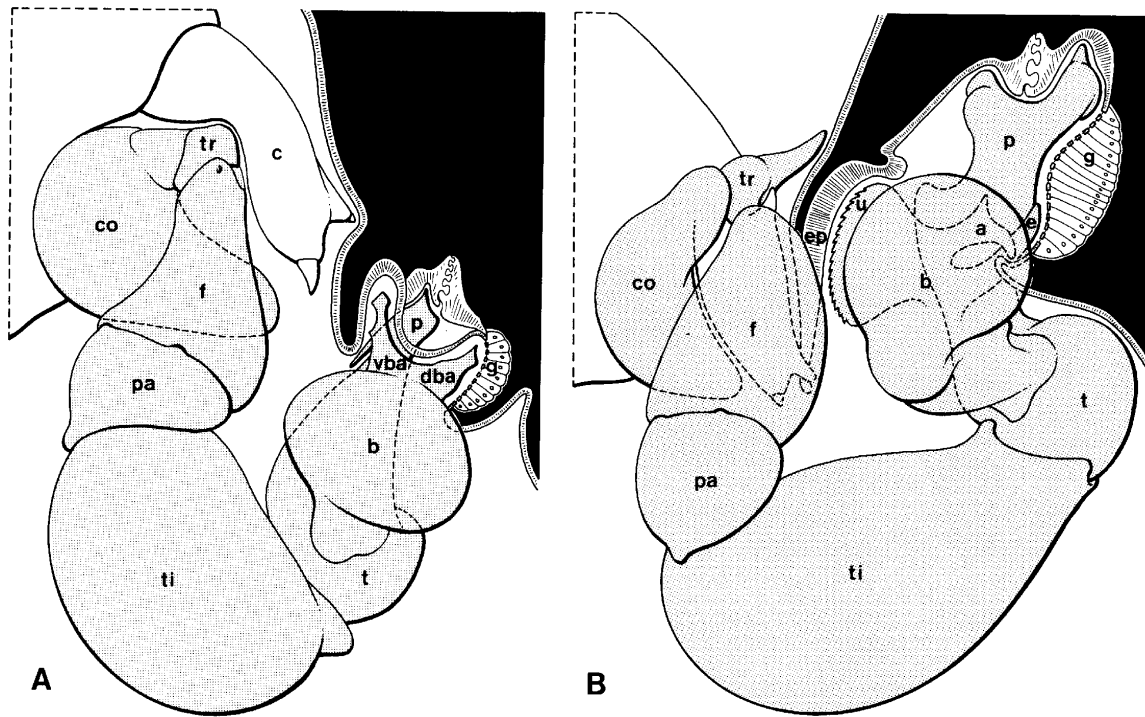


Fig. 10. Schematic reconstruction of the copulatory organs in functional contact as derived from the serial sections. —A. *Holocnemus pluchei*. —B. *Pholcus opilionoides*. Males on left side, oriented as in Fig. 1.

Table 1. List of *Holocnemus pluchei* pairs observed courting and copulating. Capital letters indicate virgin individuals, lower case letters indicate mated individuals

Pair	Male	Female	Courtship	Female aggression	Copulation
1	A	A	Some seconds	-	Freeze-fixed after 7 min
2	B	b	Some seconds	-	Freeze-fixed after 5 min
3	C	C	Some seconds	-	20 min
4	D	D	25 min	+	32 min
5	E	d	24 min	+	16 min
6	d	d	3 min	+	50 min
7	F	d	3 min	+	46 min

gentle opisthosoma vibration and pedipalp movements (= male stridulation?) which increased in intensity until the next female's attack. This was repeated several times until the female finally accepted the male. In a few other pairs (not included in Table 1), the males left the female webs after unsuccessful courtship and aggressive female behaviour.

Entire copulations were observed in five pairs. During insertion the males continuously performed very gentle opisthosoma-vibrations and hardly visible movements with the pedipalps.

Discussion

Male cheliceral apophyses and the monophylum "Pholcus-group"

Recent investigations into the copulatory mechanism in *Pholcus phalangioides* by Uhl *et al.* (in press) and *Psilochorus simoni* by Huber (1994b) have indicated that the che-

liceral apophyses of these species can be interpreted in the context of copulation. Provisionally, the apophyses were classified into two categories (Huber 1994b): (1) the frontal cheliceral apophysis (*fca*) which is present in almost all pholcids and is assumed to have the same function throughout the family (Huber 1994b). It helps the male to position himself correctly relative to the female before intromission of the copulatory organs. This view is corroborated by the results presented in this study; (2) the lateral cheliceral apophysis (*lca*) which is present only in some genera and which was found to be correlated functionally with the trochanter-apophysis in *Ph. phalangioides* (Uhl *et al.* in press) and *Ph. opilionoides* (this paper). This correlation may presumably be generalized for at least most of the genera that have a *lca* and a trochanter-apophysis. A survey of suitable illustrations given by previous authors revealed the fact that almost all species which have one of these structures, also have the other one (for references see below). Problems arise from the high number of (mainly older) works in which the trochanter and/or the chelicera are not illustrated.

The presence or absence of these two structures has been found to entail different modes of pedipalpal arrestation following precopulatory rotation of the pedipalps. The rotated pedipalp is either arrested by the contact of *lca* and pedipalpal trochanter-apophysis (in *Pholcus*: Uhl *et al.* in press; this paper) or by locking the trochanter between the chelicera and the pedipalpal coxa (in *Holocnemus*: this paper; *Psilochorus*: Huber 1994b).

Locking of the rotated pedipalp by contact of the pedipalpal trochanter-apophysis and the lateral cheliceral apophysis (as well as the presence of these two structures) is considered to be a synapomorphy of a group of pholcids (the name "Pholcus-group" is proposed) including the following genera (references refer to works illustrating or mentioning

the *lca* and/or the trochanter-apophysis): *Pholcus* (e.g. see Mello-Leitão 1918; Millot 1941; Senglet 1971, 1974), *Micropholcus* (see Deeleman-Reinhold & Prinsen 1987), *Leptopholcus* (see Millot 1946; Timm 1976; Brignoli 1980), *Micromerys* (see Deeleman-Reinhold 1986), *Paramicromerys* (see Millot 1946), *Calapnita* (see Deeleman-Reinhold 1986), *Panjange* (see Deeleman-Reinhold & Deeleman 1983; Deeleman-Reinhold 1986; Deeleman-Reinhold & Platnick 1986), *Smeringopina* (see Millot 1941: sub *Smeringopus*, see below; Kraus 1957), *Spermophora* (see Simon 1893; Millot 1946), *Belisana* and *Uthina* (C. L. Deeleman-Reinhold personal communication).

In Brignoli's (1981) provisional division of the family into a largely American and a largely Old World group, these are all genera of the Old World group. The remaining genera of the Old World group (including *Holocnemus*) share with the American group (including *Psilochorus*) the arrestation mechanism of locking the trochanter between chelicera and coxa. This is in contrast with Simon's (1893) classification, in which the Pholceae include both representatives of the "Pholcus-group" (*Pholcus* and *Spermophora*) and of the "Holocnemus-group" sensu Timm 1976 (*Holocnemus*). Further evidence for the monophyly of the "Pholcus-group" has been found in bulbal morphology by Deeleman-Reinhold (personal communication).

It is remarkable in this context that it was exactly the presence or absence, respectively, of a *lca* and a pedipalpal trochanter-apophysis which originally caused Kraus (1957) to divide the genus *Smeringopus* into: (I) *Smeringopus* (*lca* and trochanter-apophysis absent); and (II) the new genus *Smeringopina* (*lca* and trochanter-apophysis present). The present study confirms this division but also entails that the taxon *Smeringopodinae sensu* Kraus (1957) is in fact polyphyletic. It further indicates the necessity to place *Smeringopus pulcher*, *S. guineensis* and *S. bineti* (all: Millot, 1941) into the genus *Smeringopina* Kraus, 1957.

Stridulation in Pholcidae

In their review article on acoustic communication in spiders, Uetz & Stratton (1982) give a list of "families known to produce sound or to possess organs that are presumably capable of making sounds". Only one reference is given in this article in respect to Pholcidae (Gertsch 1979b: *Physocyclus*). *Physocyclus* is also the only pholcid genus listed in the more recent work of Starck (1985) who claims to give a complete list of all known stridulating spiders. Since stridulation is apparently much more common in Pholcidae, it appears appropriate to include a (certainly still incomplete) supplement to the existing lists in the present paper (Table 2). Stridulatory organs have been found in at least 11 pholcid genera and according to the classification of Legendre (1963) they are all of type d (pedipalp rubs against chelicera) or of type a (opisthosoma rubs against prosoma; only in females).

In three pholcid genera (*Holocnemus*, *Hoplopholcus*, *Holocneminus*) there are type d stridulatory organs in both sexes (in the female sometimes reduced or even absent). Intersexual differences in the space between the ridges have only been described for *Holocneminus* (Marples 1955), although such differences should be generally predicted

Table 2. List of the pholcid genera for which stridulatory organs have been described or illustrated. Stridulatory organ types correspond to the classification of Legendre (1963); see text

Genus	Stridulatory organ type		Reference
	Male	Female	
<i>Anopsicus</i>		a	Gertsch (1979a)
<i>Psilochorus</i>		a	Gertsch (1979a); Deeleman-Reinhold (in press)
<i>Crossopriza</i>	d	a	Millot (1941, 1946)
	d		Wiehle (1933)
<i>Physocyclus</i>	d		Brignoli (1981); Chamberlin (1924); Gertsch (1979b)
	d	a	Gertsch (1979a)
<i>Gertschiola</i>	d		Brignoli (1981)
<i>Artema</i>		d	Millot (1941)
<i>Ninetis</i>	d		Kraus (1957)
<i>Holocnemus</i>	d	d	Kulczynski (1908); Wiehle (1933); Kratochvil (1940)
<i>Hoplopholcus</i>	d		Brignoli (1971, 1978, 1979a,b)
	d	d	Kulczynski (1914)
	d	d	Senglet (1971); Kratochvil (1940)
<i>Holocneminus</i>	d	d	Marples (1955); Deeleman-Reinhold (1993, in press)
<i>Trichocyclus</i>	d		Deeleman-Reinhold (in press)

from the high probability of different functions of male and female signals respectively. Wiehle (1933), for example, specified the space in *Holocnemus pluchei* as 17 µm; he obviously only measured the female chelicera.

As in many spiders (Uetz & Stratton 1982) the male stridulatory organs in *Holocnemus pluchei* are used in courtship. As to the female stridulatory organs, the observations of courtship (see above) rather suggest a defensive or even aggressive function, since females that readily accepted the male never rubbed the pedipalps against the chelicerae. This was also hypothesized for *Micrathena*-species (Araneidae) by Hinton & Wilson (1970). The thickening of the distal pedipalpal segments in the female may probably be interpreted in the context of vibratory signal intensification.

Abbreviations Used in the Figures

<i>a</i>	appendix (<i>Pholcus</i>)
<i>b</i>	genital bulb
<i>c</i>	chelicera
<i>co</i>	coxa
<i>dba</i>	dorsal bulbal apophysis (<i>Holocnemus</i>)
<i>e</i>	embolus (<i>Pholcus</i>)
<i>ep</i>	epigyneal plate (<i>Pholcus</i>)
<i>f</i>	femur
<i>fca</i>	frontal cheliceral apophysis
<i>fp</i>	frontal prominence on chelicera (<i>Pholcus</i>)
<i>g</i>	vulval glands
<i>lca</i>	lateral cheliceral apophysis (<i>Pholcus</i>)
<i>p</i>	procursus
<i>pa</i>	patella
<i>s</i>	scraper of the stridulatory organ (<i>Holocnemus</i>)
<i>sp</i>	spur on procursus (<i>Holocnemus</i>)
<i>t</i>	tarsus
<i>ti</i>	tibia
<i>tr</i>	trochanter
<i>u</i>	uncus (<i>Pholcus</i>)
<i>vba</i>	ventral bulbal apophysis (<i>Holocnemus</i>)

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