

Spotted dome-shaped webs of the pholcids *Crossopriza* sp. and *Holocnemus pluchei* (Araneae: Pholcidae)

Jaromír Hajer and Dana Řeháková

Department of Biology, Purkinje University,
České mládeže 8, 400 96 Ústí nad Labem,
Czech Republic

Summary

Holocnemus pluchei and *Crossopriza* sp. spiders can spin either non-spotted or spotted domed sheet webs. The spotted appearance of the domes is the result of puffs of silk. The material needed to produce the puffs of silk is provided by stretched skeleton and filling threads, or the threads which constitute the dome, onto which the spider applies loops of unstretched fibrils emitted by the spinning apparatus, using its fourth pair of legs. The ultrastructure of the surface differs between stretched and unstretched fibrils. The mass of the puffs largely consists of unstretched fibrils accumulated at one spot after the spider breaks off the stretched supporting threads. A spotted dome with shining white puffs, which increase its visibility, is always built during periods of the life cycle when the spider is vulnerable and easy to attack or unable to move, i.e. before moulting and egg-laying.

Spotted domes are also spun inside orb-weavers' host webs (by the kleptoparasite *Holocnemus pluchei*), and when skeletons of webs produced by several specimens of the same species interpenetrate. Spotted domes can be spun at all developmental stages of the spider, except the prenymphal stage, i.e. first-instar spiderlings.

Introduction

Webs referred to as “domes” or “dome-shaped webs” — the term reflects their shape — are spun by spiders belonging to several families. Vollrath (1987), for instance, used the term “dome shaped web” for webs constructed by spiders of the family Argyronetidae, and the term “space webs” for webs built by pholcids. Wise (1984, 1995) described fine domes produced by the filmy dome spider, *Neriene radiata* (Walckenaer, 1841) (Linyphiidae): the spider sits beneath the web, waiting for its prey. The same author pointed out the similarity in the shape of webs produced by *Neriene radiata* and those of the orb weaver *Mecynogea lemniscata* (Walckenaer, 1841) (Araneidae), also called the “basilica spider”; in his opinion, this similarity reflects convergent evolution, rather than close relationship.

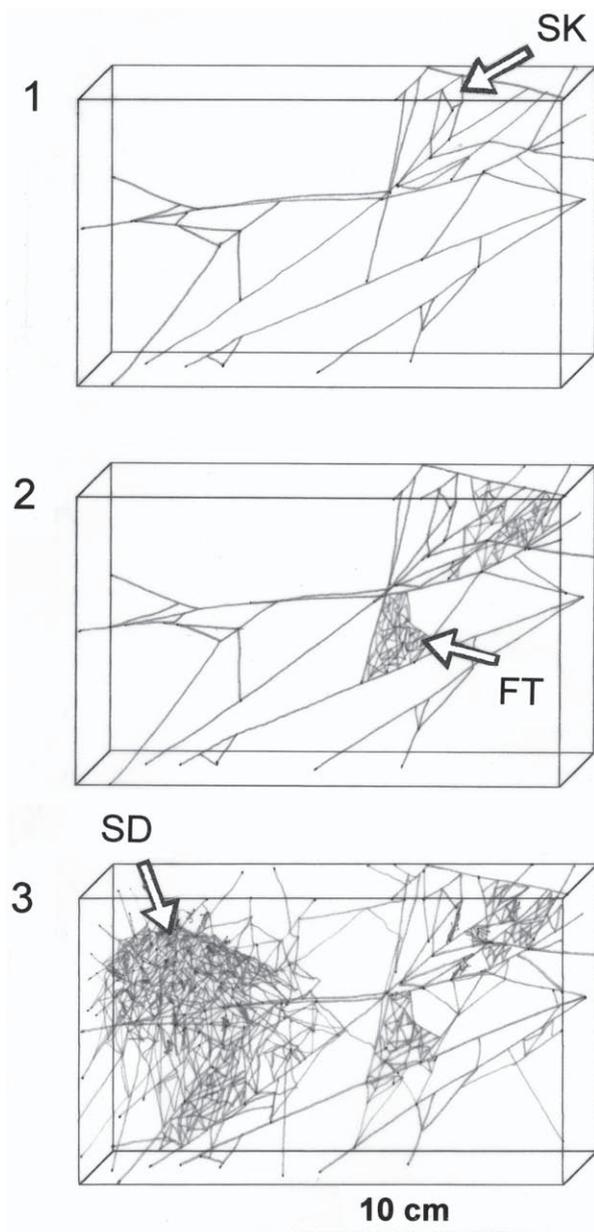
The family Pholcidae comprises approximately 570 hitherto described species, belonging to 40 genera. Spiders of this family have unusually long thin legs with long, flexible tarsi with false articulations. When hanging on the threads of their webs, they are suspended upside down; when disturbed, they can use their body and legs to vibrate the web, which makes the spider's body invisible to the invader or difficult to hit. The relatively large number of species in this family, living in diverse biotopes, has allowed the development of a diversity of web forms, including unique special structures. This diversity has been confirmed especially by the works of Kirchner (1986), Deeleman-Reinhold (1986), Eberhard & Briceño (1985) and Eberhard (1992a, b).

Research into the spinning activity of pholcid spiders has shown that some of them build dome-shaped webs. Wiehle (1933) was the first to notice that some domed webs woven by *Holocnemus hispanicus* Wiehle, 1933 have a spotted appearance. Sedey & Jakob (1998) described an “unusual dome web occupied by egg-carrying *Holocnemus pluchei*”; although the authors did not pay special attention to either the micro- or ultrastructure of threads constituting this web, they mentioned that silk strands were occasionally clumped into small balls on the surface of the dome, and a photograph, which shows the shape of the web they describe, clearly proves the presence of such puffs. Eberhard (1992a) described in detail the construction of domed sheet webs by *Modisimus* sp. spiders, but did not describe spots on the dome. Our research focused on webs containing domed sheets which have a spotted appearance as a result of the presence of white puffs of silk. Our aim was, on the one hand, to describe the microstructure and ultrastructure of the threads in these puffs and, on the other hand, to explore the formation of the puffs and to establish under what circumstances the spiders construct webs of this type.

Material and methods

The subjects of the study were the Mediterranean species *Holocnemus pluchei* (Scopoli, 1763) and an unidentified species probably belonging to the genus *Crossopriza*. The latter were identified as *Crossopriza* sp. by B. A. Huber. Voucher specimens are deposited at the Department of Biology, J. E. Purkinje University in Ústí nad Labem, Czech Republic.

In 1992, 17 live adult females and 4 males of the kleptoparasitic species *Holocnemus pluchei* were collected in Catania (Sicily, Italy). This species, like the theridiid *Argyrodes argyrodes* (Walckenaer, 1841), occurs there in the peripheral parts of webs of the orb-weaver *Cyrtophora citricola* (Forskål, 1775) built on *Opuntia* cacti. A further 11 adult females and 6 adult males of *H. pluchei* were collected, also from webs of *C. citricola*, in August 1995 near Valencia, Spain. Kleptoparasitism is not the only method of obtaining food for this species. Brignoli (1971) reports that single webs or web aggregations built by this species may often be found in southern Europe both in trees and bushes near human dwellings and inside buildings. In the USA this introduced species lives in similar locations (Sedey & Jakob, 1998). Throughout our nine years of observation, these spiders were kept in enclosed cages, with basically three methods being used: (1) together with *C. citricola* in 80 × 45 × 60 cm (length × width × height) glass insectaria, with either a fertilised adult female or a pair of adults of *H. pluchei* of both sexes being placed in an insectarium inhabited by one adult or sub-adult female *C. citricola*; (2) in insectaria of the same size, but in web aggregations built by spiders of the same species yet at different stages of development; (3) singly (in cages of different sizes) in isolation from all other spiders. We also observed hundreds of webs built outside cages at various locations at the Department of Biology of J. E.



Figs. 1–3: The process of web building by an adult female *Crossopriza* sp. in an insectarium measuring $20 \times 7 \times 11$ cm. **1** After 2 days; **2** After 7 days; **3** After 13 days. FT=threads filling space between skeleton threads, SD=spotted dome, SK=skeleton. The web at the stage shown in Fig. 2 was sufficient to intercept small insects placed in the insectarium. The entire spotted dome-shaped web (Fig. 3) was spun in one night (11–12 August 2000).

Purkinje University in Ústí nad Labem. Under laboratory conditions the females produce 2–8 egg-sacs between April and October (pers. obs.).

Spiders of the other studied species, *Crossopriza* sp., came from Larache near the city of Lixus in northern Morocco. Twenty-two adult females and 14 adult males were collected on 2 September 1997 from a wet wall partly covered by vegetation on the edge of a phosphate mining pit. The spiders weave domed sheet webs and form communities of up to several hundred individuals. Another 26 females and 8 adult males were collected at the same site on 11 September 1998. We bred and observed *Crossopriza* sp. under the same conditions as *H. pluchei*. During less than four years, until June 2001,

we reared dozens of specimens through all stages of development. As with *H. pluchei*, we studied webs constructed by spiders both inside and outside glass insectaria.

The microstructure and ultrastructure of threads constituting the spotted dome was studied using an ECLIPSE E600 NIKON phase contrast light microscope, a TESLA BS-340 scanning electron microscope (Figs. 6–7, 12, 20), and a METRIS 2001 NC Atomic Force Microscope (Burleigh Instruments Inc.) with the following parameters: X&Y Range $25 \mu\text{m}$, X&Y Resolution $<17 \text{ \AA}$, Z Range $4 \mu\text{m}$ and Z Resolution 2 \AA (Figs. 13–16).

To study the web construction behaviour for the spotted parts of the webs and, in particular, the phenomenon which we consider critical to formation of the spotted dome, i.e. biting off the silk threads (see Figs. 1–3, 8–11, 17–18), four *Crossopriza* sp. females were placed separately in three insectaria measuring $20 \times 7 \times 11$ cm (length \times width \times height). Between 18 January and 21 February 2000 and between 13 July and 24 August 2000 a video microscope (and a separate video camera mounted on a tripod) were used to record 44 hours of details of the spinning activity related to web construction and prey capture. Those sequences of the footage which showed the above activities were copied to CDs and relevant pictures were printed on photographic paper. Figures showing the spiders or their organs in motion, and therefore not always perfectly distinct, were processed using an ACC (Adaptive Contrast Control) Image Structure and Object Analyser (by SO FO). With ACC it is possible to increase the contrast of imaged structures in a precise and controlled manner, depending on the size and density of the structure. This software was used to process Figs. 8–11, 17–18 and 23–24. During observation of the spinning activity of spiderlings, 25 young *Crossopriza* sp. and 15 young *H. pluchei* after hatching, i.e. in the prenympal stage, were placed separately into small cylindrical vials 80 mm long and 10 mm in diameter. Before observation of the spinning activity in the next stage, i.e. first nymphal instar, 24 hours after ecdysis the same number of spiders were isolated in vials 160 mm long and 45 mm in diameter. All the vials were positioned vertically. While studying these small webs, the use of a stereoscopic microscope equipped with a CCD (Charge Coupled Device) camera proved beneficial; this device enables the microscope image to be transmitted to a TV screen.

Results

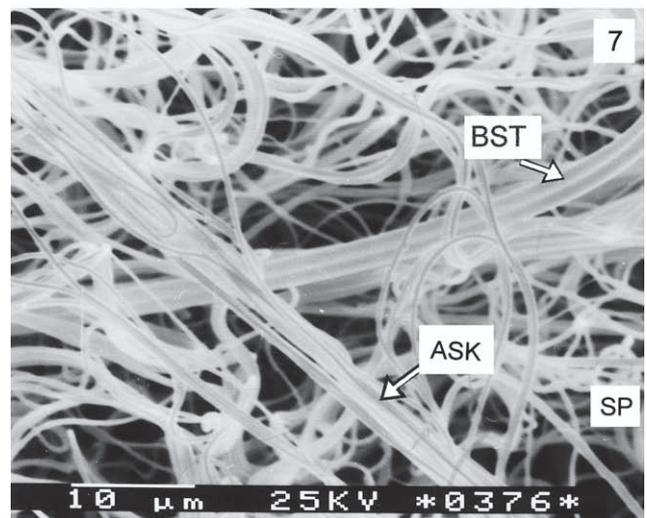
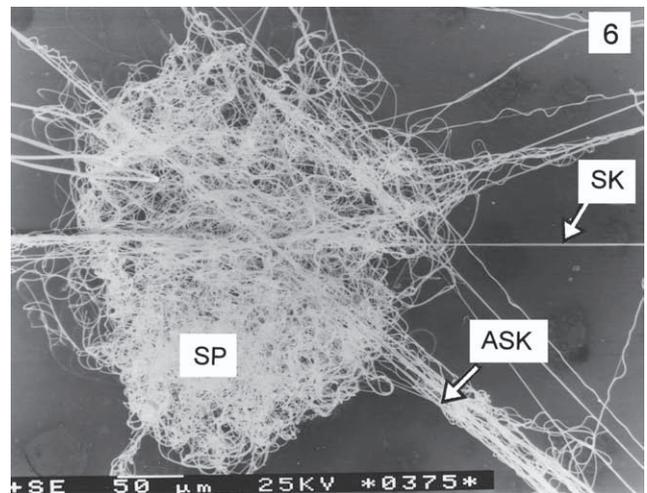
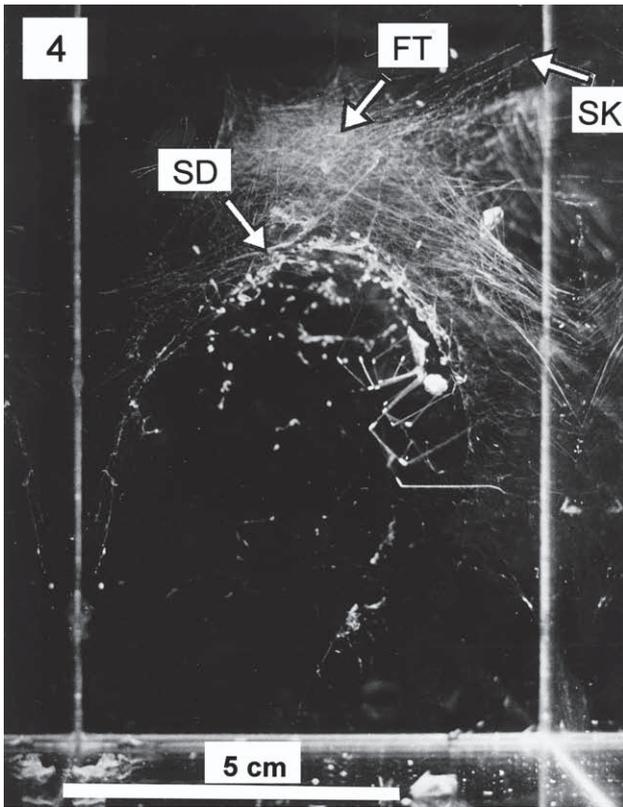
Spotted domed sheet web

This term refers, in both species of pholcids we studied, to a web whose domed sheet (or “dome”, the term being used as a synonym) always contains puffs of fine silk, giving it a typical spotted appearance (Figs. 3, 4). Unless disturbed, the spider is suspended upside down on the web threads within the upper part of the dome (Figs. 5, 19, 23). The empty space inside the dome,

i.e. the space which lacks any threads, results from the spider breaking off most of the threads in the dome. The spinning of the spotted dome is a continuous activity, including the final stage of forming the puffs, which is an integral part of the process. In other words, spotted domes are not formed by adding puffs to non-spotted domes, nor do puffs build up in spotted domes over the long term (several days); rather they are all formed by the spider within one night as the dome is built.

Nature of threads used to construct the spotted dome, and the process of forming silk puffs

Both *H. pluchei* and *Crossopriza* sp. use the same method of building webs containing a spotted dome (Figs. 1–3). First, a skeleton is built (Fig. 1), which serves as scaffolding. The stretched skeleton threads (Figs. 1, 14, 25) are the thickest of the web construction elements. They are attached to the substrate by means of attachment discs (Fig. 13), similar to those of *Pholcus phalangioides* (Fuesslin, 1775) described by Schütt (1996). These threads are largely made up of bundles (or more exceptionally, pairs) of fibrils (Fig. 14), which appear to be nearly smooth when studied by means of the AFM (Fig. 15). The thickness of the entire bundle of fibrils is 5–6 μm, with the diameter of one fibril being approximately 1.2 μm. If the skeleton is destroyed soon after it is completed, the spider builds a new one; however, the patterns of the two skeletons built under the same conditions by the same spider are not identical. In the next stage, the spider fills the space between the



Figs. 4–5: **4** Lateral view of completed web woven by a *Crossopriza* sp. female in an insectarium measuring 20 × 7 × 11 cm; FT=dense tangle of threads filling space between skeleton threads above spotted dome, SD=spotted dome with white puffs of silk, SK=skeleton threads; inside the dome, a female tends an egg-batch. **5** Close-up of female suspended upside down, hanging on internal threads of dome; the female holds embryos in its chelicerae. Scale line=0.5 cm.

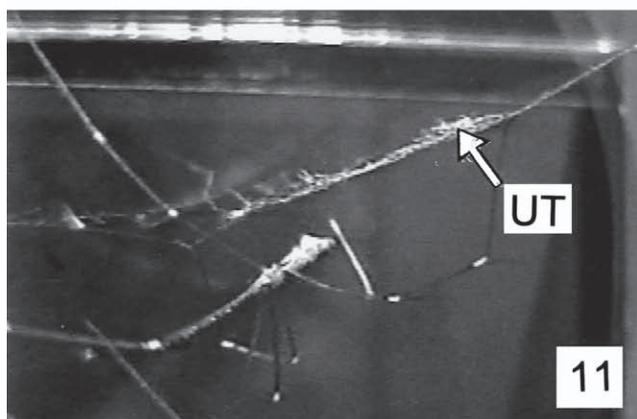
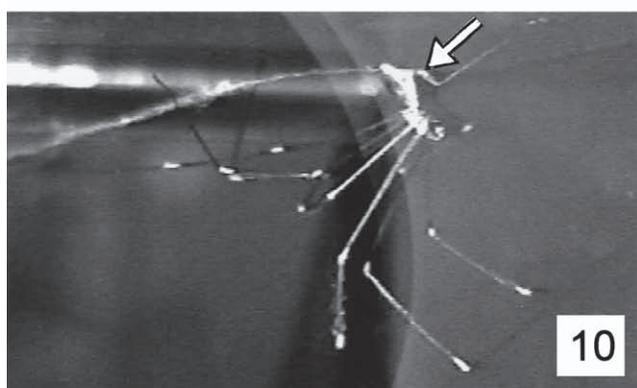
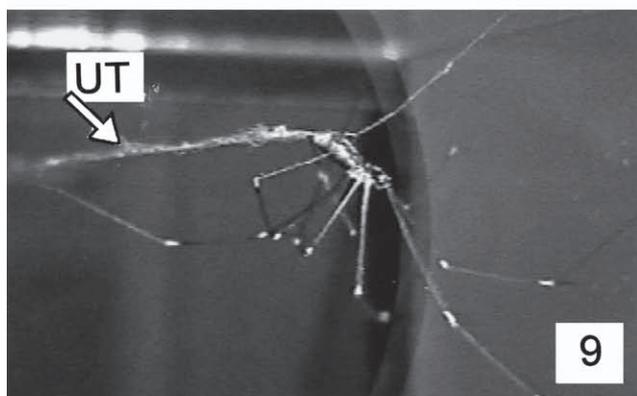
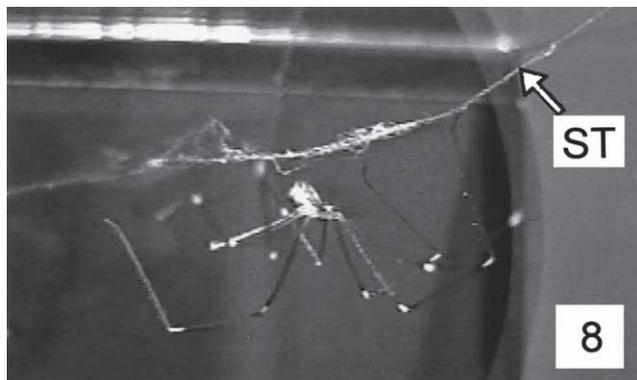
Figs. 6–7: Puffs of silk in detail. Threads of different thicknesses can be observed in the puffs, since they are formed by biting off stretched threads of the dome, onto which loose, i.e. unstretched, fibrils of very fine silk had previously been applied. ASK=untorn skeleton threads with loops of loose fibrils, BST=a previously stretched, now bitten-off thread, SK=skeleton thread, SP=silk of loose fibrils accumulated in puffs.

threads of the skeleton with occasional tangles of stretched threads (Figs. 2, 4), attached to the skeleton threads and to one another by means of small attachments made of amorphous secretion (Fig. 12). These filling threads are thinner than skeleton threads and invariably consist of a single pair of fibrils, each of them 0.8–0.9 μm in diameter. The ultrastructure of the surface of the fibrils in these filling threads is smooth, as for the

skeleton lines. The web, constructed in this manner, is irregular in shape and is similar to the three-dimensional permanent web of *Pholcus phalangioides* described by Kirchner (1986).

The spotted dome itself is a product of spinning activity following a pause of several hours to several days. As mentioned above, a complete spotted domed sheet is always built in one night. The process of construction starts with the building of an additional skeleton that will support the dome. Once this second skeleton is completed, the spider fills the spaces between the skeleton threads with a tangle of fine lines, and then produces the domed sheet. When spinning the domed sheet, the spider always proceeds from the centre to the periphery. The skeletal tangle is always at its densest above the dome (Fig. 4). All the stretched threads which constitute the dome, fixed to one another with small attachments, have an important feature: their surface carries loops of unstretched, very fine silky fibrils, which are the main building material for puffs of the spotted dome. The method employed by the spider to spin threads for the dome and to apply the above-mentioned loose fibrils onto the stretched threads using its fourth pair of legs is illustrated in Figs. 8–11. Loops of loose fibrils are similarly applied to those sections of skeleton lines which run through the dome and onto which filling threads are attached. The jagged and grooved surface of the loose fibrils (Fig. 16) differs considerably from the smooth surface of stretched fibrils, skeleton and filling threads (Fig. 15).

Puffs are formed by biting off stretched threads (Fig. 17), both filling and skeleton threads, bearing on their surfaces loose fibrils. As a result of the contraction of bitten-off threads, a mass of loose fibrils accumulates at one spot (Figs. 6–7). Thus, the puffs consist of accumulated loose fibrils and of bitten-off, previously stretched, supporting threads. Sporadically, we also observed the spiders to bite off clusters of loose fibrils (Fig. 18). Puffs are also sometimes a product of biting off threads inside the dome, which results in an empty space, i.e. a space which is not filled with any threads. The process of biting off the threads as such is not quite clear as yet. Figs. 17–18 clearly show that the spiders always hold the threads in their chelicerae, and subsequently tear them off. However, an anonymous reviewer of this paper suggested that the process of biting off the threads most likely involves an enzymatic reaction, in which the



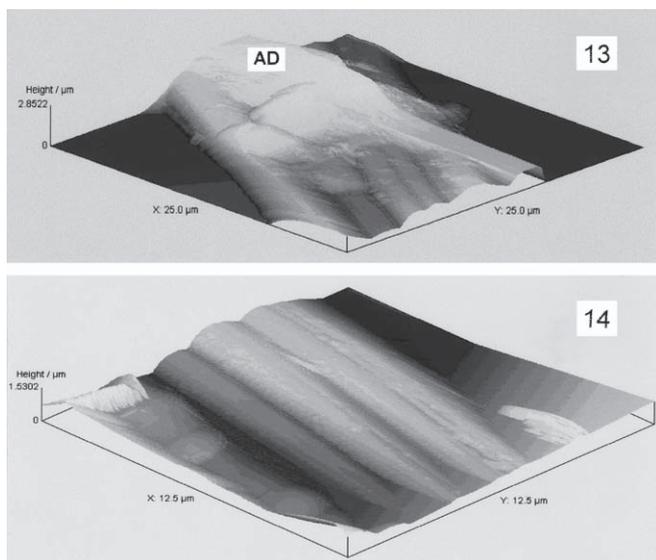
Figs. 8–11: Production of silk necessary for construction of dome-shaped webs and silk puffs (enhanced by ACC). **8** An adult *Crossopriza* sp. female applies clumps of loose, i.e. unstretched, fibrils on a stretched and firmly fixed thread using its fourth pair of legs; **9–10** A female touches the support thread with its spinning apparatus (the spot indicated in Fig. 10 by an arrow) and uses a drop of secretion (for details see Fig. 12) to apply to it another stretched thread, which is then attached to another thread of the dome in the same manner; **11** The thread dragged by the female behind itself when photographed in this stage was invisible, given the angle of the light. ST=stretched thread, UT=clumps of unstretched fibrils. Length of spider's body=12 mm.



Fig. 12: An attachment formed of amorphous secretion at a spot where several filling threads cross. Analogous drops of solidified secretion are used to interlink filling threads of the dome and to attach filling threads to skeleton lines. After removing a sample of threads from the web and preparing them for scanning electron microscopy the previously tense fibrils became loose.

chelicerae hold the thread and “press it against the mouth area where enzyme cuts the thread”. Nevertheless, we are unable to confirm this opinion even though a thorough analysis of slow-motion sequences of the video footage has been carried out.

Throughout our long-term observations we concluded that an important role of the spotted dome is to provide protection. In the species we studied, all stages except first-instar spiderlings were capable of producing this type of web. Spotted domes are always spun by these spiders before moulting, and before egg-laying in the case of females. Between 12 September 2000 and 16 March 2001 we observed a group of 18 *Crossopriza* sp. spiders living separately outside cages, on window sills or between window frames and strips of Venetian blinds; the spiders had no contact with other specimens of the



Figs. 13–14: AFM study of the surface of stretched skeleton threads. **13** Skeleton threads are firmly fixed by attachment discs (AD) to the substrate; **14** Each thread is made up of a bundle of longitudinally oriented fibrils.

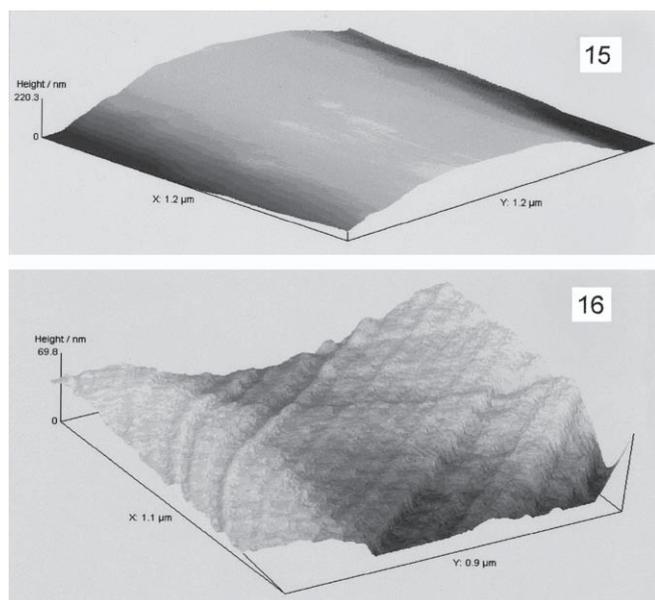
same species. In the course of five consecutive stages of the life cycle (from second nymphal stage to adults) each of the spiders under observation spun five permanent non-spotted domed sheet webs and four spotted domes. Those domes which featured a spotted dome always appeared next to the existing web 3–4 days before ecdysis, and exuviae always remained in them after moulting (Fig. 25). After moulting, the spiders always built a new non-spotted domed sheet web.

Females tending eggs stay inside the dome throughout the embryonic and larval development (Fig. 5). In addition, we observed spinning of spotted domes whenever webs woven inside insectaria by several spiders of the same species came into contact or their skeletons interpenetrated. Of course, the latter circumstance requires further ethological research including field studies; at present we do not know what stimuli occasion such behaviour in these spiders.

Spotted dome sheet and protection of females tending an egg-batch or spiderlings

Crossopriza sp.

Following their fertilisation, and before egg-laying, *Crossopriza* sp. females always spin a spotted domed sheet (Figs. 4–5). The group of 14 fertilised females under observation was kept in the same number of glass boxes measuring 20 × 7 × 11 cm (length × width × height), under natural diffused light. They gradually spun 26 webs, which contained spotted domes, in all cases horizontal. All of them were primary webs, i.e. their production did not follow the construction of non-spotted dome webs. Before egg-laying, females which were not kept in insectaria and which lived and mated in non-spotted dome webs, were observed to spin an additional small spotted domed sheet inside or at the



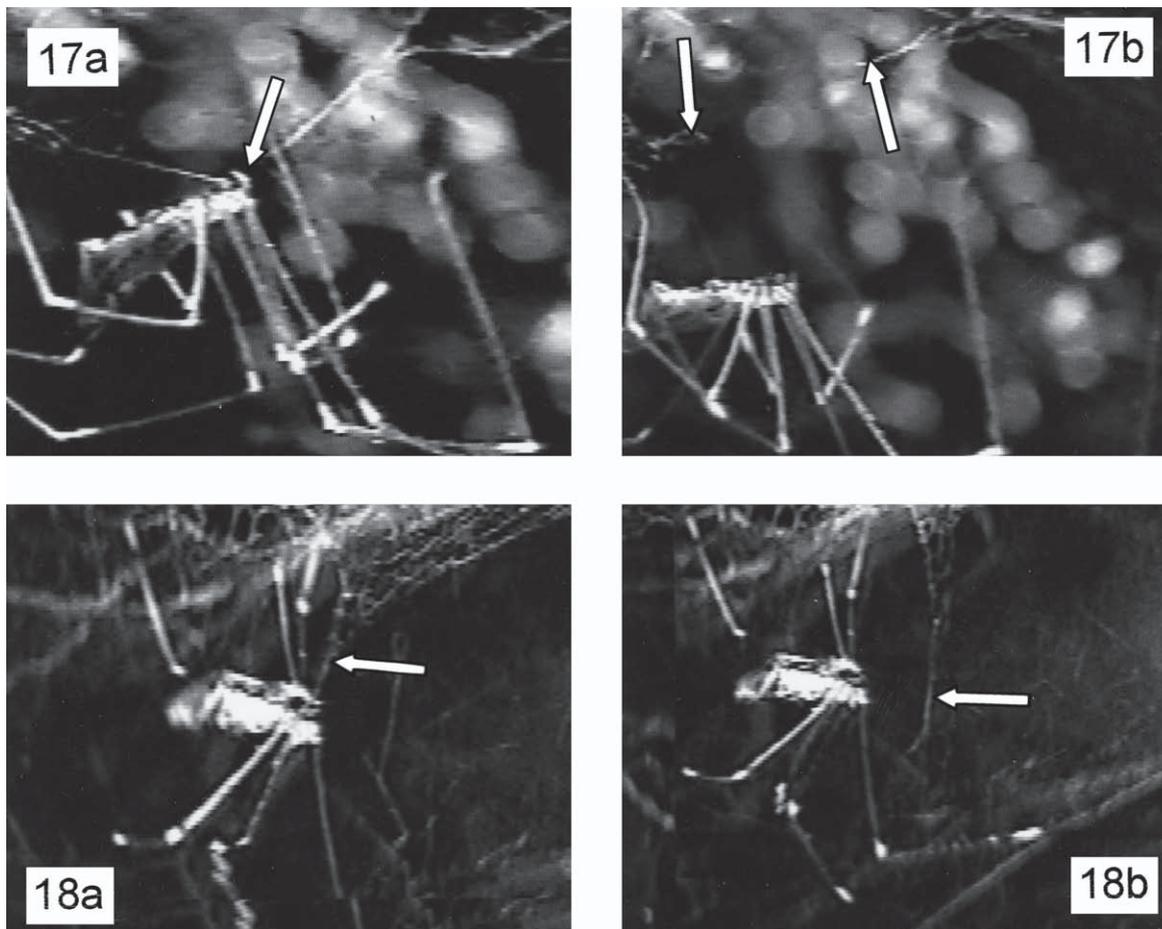
Figs. 15–16: AFM study of the surface of stretched and unstretched fibrils. **15** The almost smooth surface of a fibril from a stretched skeleton thread; **16** Grooved surface of an unstretched fibril; fibrils of this type make up much of the mass of silk puffs.

edge of the web, using the skeleton threads. The sole purpose of these “secondary” sheets is probably the protection of developing eggs; the female is suspended upside down on the threads in the upper part of the dome and holds the egg-batch in her chelicerae. Whenever we touched with forceps the skeleton threads which ran through the dome, the female used its body and legs to vibrate the spotted sheet. The dome, which is hollow and has an opening at the bottom, enables the female (unlike that of *H. pluchei*) to leave the dome when attacking prey. When attacking prey that is entangled in the web above and around the dome, the female attaches the eggs to the dome and then returns with the prey. Females tolerate the presence of males inside the spotted dome (Fig. 23), and they also repeatedly copulate with them, while still holding the egg-batch (Fig. 24). During copulation, the eggs, scantily wrapped in silk threads, occasionally move to the dorsal part of the female’s cephalothorax. Even then, the female still holds the threads in her chelicerae. The spiderlings hatch at a developmental stage which Platel (1989), in his study of *Pholcus phalangioides*, refers to as “pre-nymphs”. In this first stage with free movement, the spiders are capable only of spinning drag lines, and they do not attack prey. Another mass ecdysis occurs after approximately 48 hours. Until that point all the spiderlings stay together with the female (and sometimes also with the male)

inside the spotted dome (Fig. 19). The spiderlings remain on the part of its wall which contains puffs on the surface, and this is also where they moult (Fig. 20). The adults stay inside the dome, upside down on the threads. However, soon after this ecdysis is completed, the female cuts most of the dome threads (basically destroying the dome), and both the female and the young leave it. Prenymphs isolated in glass vials produced a thin structure of drag lines fixed by attachment discs to the glass walls. All the pre-nymphs, suspended on the threads, died, failing to accomplish ecdysis. However, young specimens of the next stage, i.e. first nymphal instar, isolated in the same manner first spun a web containing a non-spotted domed sheet. In the vertical vials, domed sheets containing puffs were first observed just before the next ecdysis, i.e. after 17–22 days; they were built beneath the existing, i.e. original, domes.

Holocnemus pluchei

Fertilised *H. pluchei* females, together with males of the same species, were kept as pairs, each in an 80 × 45 × 60 cm glass insectarium together with a female of *C. citricola*; other specimens were kept isolated in glass boxes measuring 20 × 7 × 11 cm. Before laying eggs, *H. pluchei* females spin hollow ball-shaped shelters (Fig. 21), using the following procedure. First, they spin

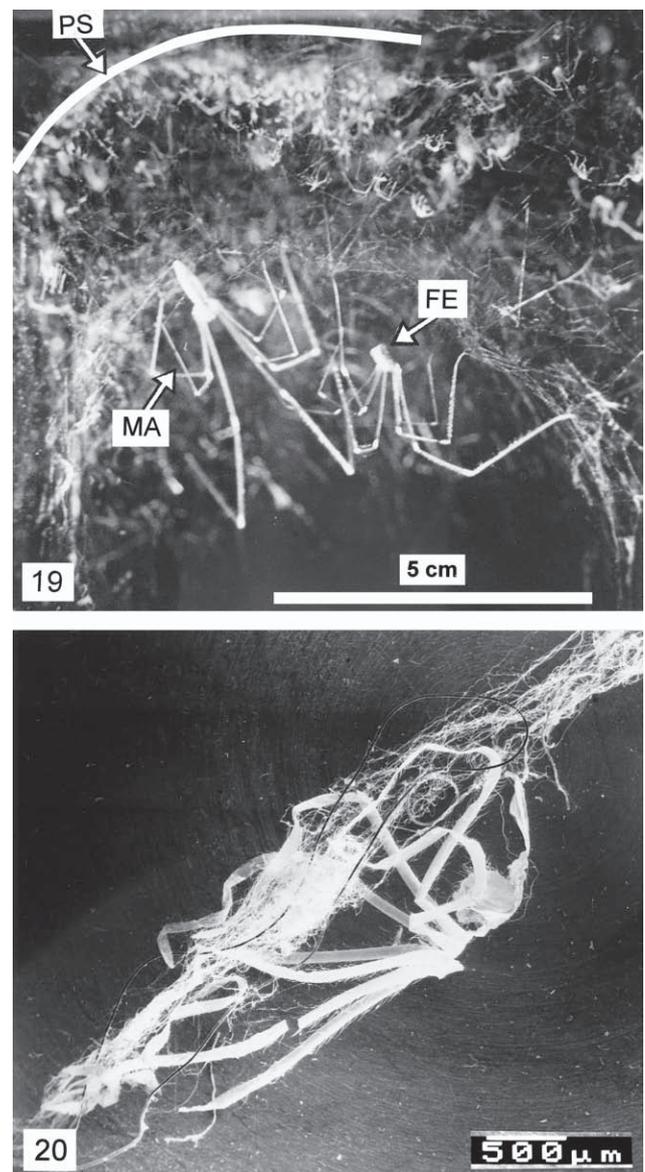


Figs. 17–18: *Crossopriza* sp. females biting off threads in the process of producing puffs in spotted dome-shaped webs (enhanced by ACC). **17** Biting-off a stretched thread. **17a** Chelicerae with stretched thread, being bitten off, indicated by arrow; **17b** Both ends of torn thread (arrows). **18** Biting off loops of unstretched fibrils applied onto stretched threads. **18a** Bunch of fibrils held in chelicerae (arrow); **18b** Torn-off fibrils (arrow).

a small spotted dome, identical to the dome spun by *Crossopriza* sp. females for egg-caring. This dome forms the upper part of a spherical shelter. Domes averaged 5.22 cm in diameter (SE=1.26, $n=18$); in six domes which were removed from the webs and spread on a glass plate placed on millimetre graph paper there were 42–51 puffs within an area of 48.4–52.1 cm². Then, the female spins the bottom part, which is not spotted and rarely contains any puffs, thus completing the spherical shelter. Where the female cohabited as a kleptobiont with the orb-weaver, it used the threads of the host web as scaffolding, and spun the spherical shelter on its periphery. Unlike *Crossopriza* sp., *H. pluchei* females hold their eggs continuously in their chelicerae throughout the whole course of egg development. The female is enclosed in the shelter the whole time, and it does not mate or attack prey. If the host orb-weaver comes too close when pursuing prey, or if an insect is caught nearby in the web, the female *H. pluchei* uses its legs to vibrate the whole shelter. In *H. pluchei*, we also observed whether the spatial positioning of the dome and the concentration of puffs depended on the direction of the light, by covering all but one of the sides of the glass insectaria with black paper. Six isolated females were kept in these conditions. Between 22 May and 6 September 2000, they spun a total of 21 spherical shelters (and thus produced 21 egg batches). None of the upper parts of the spherical shelters (i.e. the spotted domes) spun under these conditions was in the usual horizontal position with the top up; almost all of the spotted parts of the hollow spherical shelters were built so that the tops touched (or nearly touched, within a few mm) the only uncovered side wall. In all cases practically the entire spotted part of these hollow spherical webs was tilted into a more or less vertical position, oriented towards the incoming rays of light (Fig. 21). When “freeing” the spiderlings from the hollow shelter, the females bit off only the “lower” non-spotted part (Fig. 22). The spinning abilities of *H. pluchei* and *Crossopriza* sp. at the prenymphal and first nymphal stages are identical.

Discussion

The construction of two types of web by one species, differentiated by presence or absence of decoration by means of special silk structures, is not a feature peculiar to pholcids. In this respect, some orb-weavers of the families Araneidae and Uloboridae are better known and described more thoroughly; the webs built by these species may or may not contain stabilimenta, formed of secretions from the aciniform glands in the case of araneids and of the same secretions together with those of the piriform glands in the case of uloborids (Peters, 1993). The specification of the secretion forming the stabilimenta is the only certain and generally accepted attribute of stabilimenta, described first by Simon (1892). The function of these zigzag silken bands added to the hub and neighbouring radii has been the subject of dozens of published studies and controversial conclusions. The secretion from the aciniform glands is



Figs. 19–20: **19** Spotted dome constructed by *Crossopriza* sp. female. Suspended on the threads inside the dome are, upside down, a female (FE) and a male (MA). White curve indicates section of dome with highest concentration of bright white puffs (PS); moulting of first-instar spiderlings takes place in this part of the web. **20** Exuviae of first-instar spiderlings under puffs of silk.

used by orb-weavers not only to build the stabilimentum, but most importantly in wrapping behaviour, which is related to attacks on prey. Clumps of loose fibrils which pholcids use in decorated webs to produce puffs are in the case of non-spotted, and thus non-decorated, webs a part of a thread system intended for prey capture, and similar clumps of fibrils are thrown onto the prey during wrapping behaviour (pers. obs.). The decorated webs of orb-weavers and pholcids differ in the manner in which these “decorations” are produced and in the fact that in pholcids they form a part of three-dimensional domes. An important shared feature, however, is that decoration by puffs in domed sheet webs or by stabilimenta in orb webs is produced only under certain circumstances and it is not essential to prey capture. On the other hand, the presence of a stabilimentum may function as a prey attractant

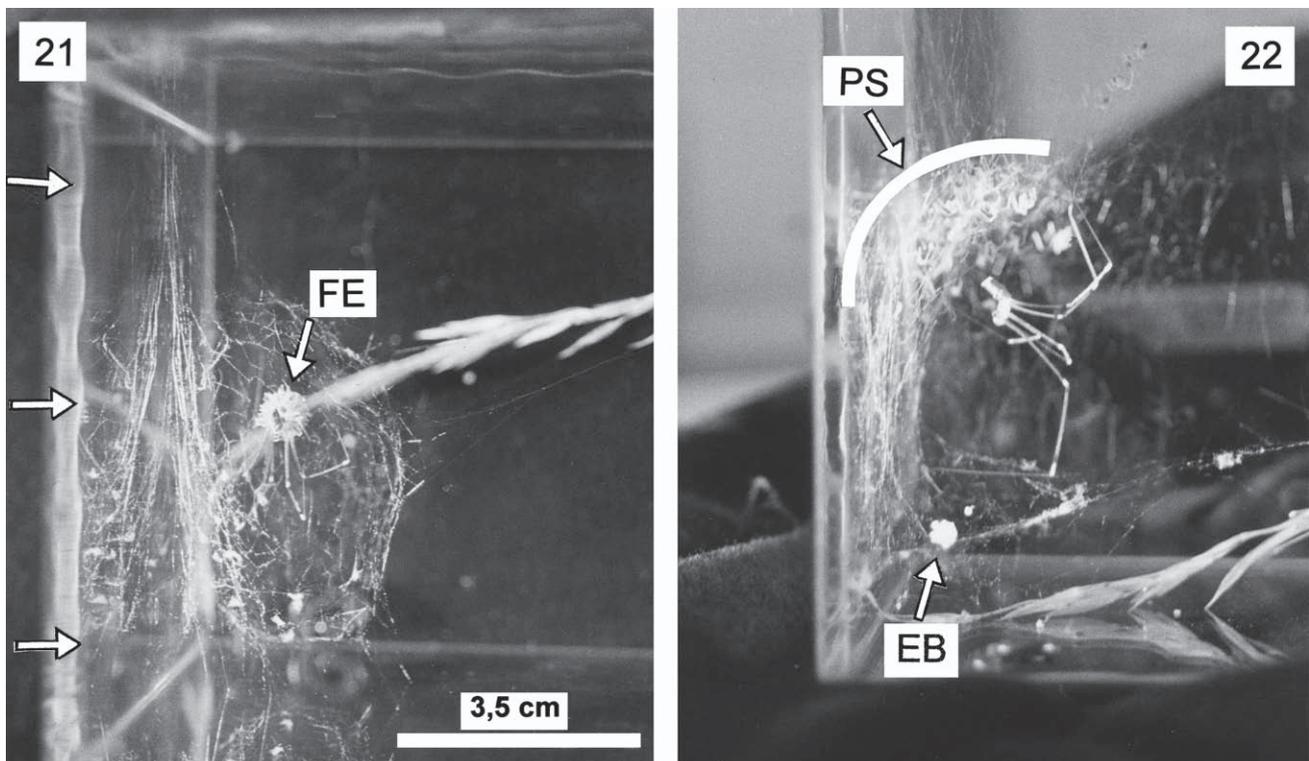
for certain groups of flying insects (Tso, 1996) and increase insect interception by webs (Tso, 1998). Likewise, Blackledge (1998) and Herberstein (2000) have demonstrated in their studies on foraging behaviour of orb-web spiders that web decorations may increase prey capture success. However, Blackledge also concludes that stabilimenta can warn predators of the presence of a noxious web, preventing damage to webs and spiders, which is in our opinion one of the possible functions of pholcids' decorated domes.

Eberhard (1992a) concluded "the functional significance of the domed form is not clear". This statement remains valid for a number of reasons. It is known that dome-shaped webs are constructed by several families, yet we do not know their *modus operandi*.

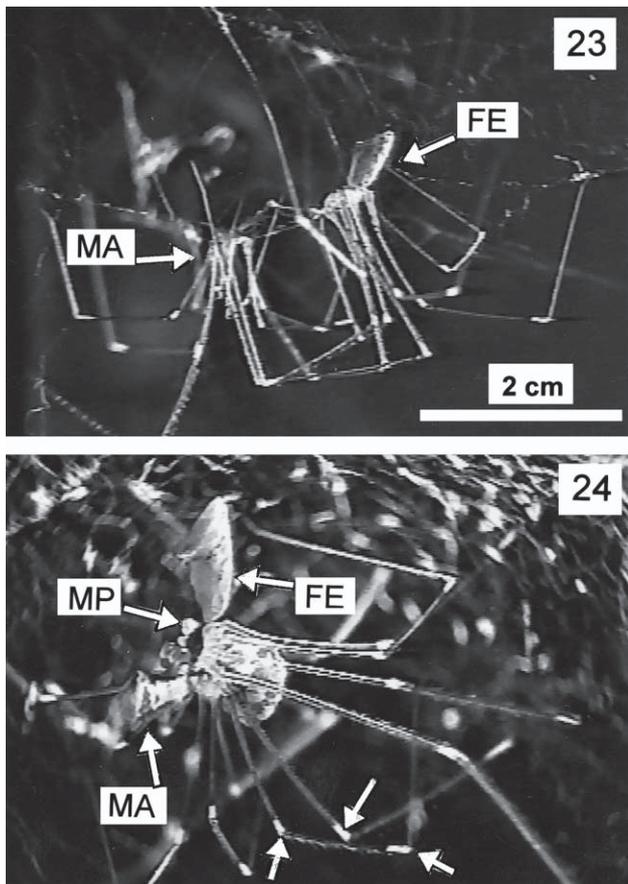
The results of previous studies on pholcid webs, achieved by diverse research techniques, do not provide sufficient evidence either for mutual comparisons or for a conclusive homologisation of silk products by different species within the family; the same applies to comparisons of domed webs spun by species belonging to different families. The general shape, i.e. the macrostructure, of the domed web of *Neriene radiata* (Linyphiidae) as described and drawn by Wise (1995), or *Hypochilus thorelli* Marx, 1888 (Hypochilidae), a good photograph of which was published by Comstock (1948), and *Hypochilus gertschi* Hoffman, 1963, described by Shear (1969), is very similar to that of the domed webs of pholcids, although phylogenetic analyses (Coddington & Levi, 1991; Griswold *et al.*, 1998) show that they are

unrelated taxa. In addition, the Hypochilidae represent plesiomorphous araneomorphs (Coddington & Levi, 1991) retaining the cribellum, i.e. a functional homologue of the anterior median spinnerets, the glands of which produce highly adhesive silk.

No study has been published hitherto describing the microstructure or ultrastructure of threads in spotted domed sheet webs spun by pholcids. Eberhard (1992a), who studied the construction of the domed sheet web of *Modisimus* sp., distinguished three types of construction behaviour in this species: (1) extension of the skeleton web; (2) filling in the skeleton web; (3) filling in the sheet. Both species in our study, *H. pluchei* and *Crossopriza* sp., spin two types of domes, one of them being non-spotted domes, identical with those described by Eberhard (1992a). Both pholcids we studied proceeded in their spinning activity in the same manner and, apparently, there is no difference between the domed sheet of *Modisimus* sp. and the non-spotted dome of *H. pluchei* and *Crossopriza* sp. Eberhard's study does not describe spotted sheets or webs in which spiders of all instars stay during ecdysis and in which females tend their eggs. We consider it as a proven fact that some pholcids can produce both non-spotted and spotted domed sheets. Spotted domed sheet webs were first described by Wiehle (1933) in his study of the biology of *Holocnemus hispanicus*. He also observed that spiders of this species copulate inside the spotted dome. In our observation of *H. pluchei* we never witnessed copulation inside the spotted dome. Most copulations occur on the



Figs. 21–22: **21** A spherical, fully enclosed shelter built by an isolated female of *Holocnemus pluchei* in a glass insectarium. Arrows on left show direction of light coming through the only uncovered wall; other walls covered with black paper. Highest number of puffs occurs on threads attached or adjacent to the uncovered wall. FE=female tending egg-batch at beginning of hatching. **22** The same web 48 hours later. During hatching the female holds the egg-batch in her chelicerae and, after the last spiderling hatches, drops the remains of the eggs (EB). The female tears the stretched threads of the shelter so that an open dome-shaped web is formed, the highest concentration of silk puffs (PS) being near the glass wall of the insectarium which lets in light.



Figs. 23–24: **23** A fertilised female of *Crossopriza* sp. tolerates the presence of a male inside the spotted dome. **24** A female tending eggs repeatedly copulates with a male; however, the threads wrapping the eggs are constantly held in the chelicerae even if the egg-batch moves to the dorsal part of the female's cephalothorax during copulation. Both photographs (enhanced by ACC) show clearly that light is reflected not only by the puffs of silk but also by the unpigmented distal parts of the femora and tibiae (indicated by arrows). FE=female, MA=male, MP=male palpus.

periphery of host orb-webs or the individual's own webs. Moreover, males cannot approach females tending eggs, enclosed in spotted spherical shelters.

However, in *Crossopriza* sp. repeated copulations of the same pair occur both outside and inside the spotted domed sheet. Inside the dome, females tolerate the presence of males and copulate with them even while they tend egg-batches. The "unusual dome web" described by Sedey & Jakob (1998) is undoubtedly identical to the spotted spherical shelter we observed, which is constructed by the originally Mediterranean, kleptoparasitic *H. pluchei* invariably before egg-laying, whether living in isolation or in webs of the orb-weaver *C. citricola*. Our data support the assumption of the above authors that this variation of domed sheets protects spiderlings and allows them to moult. We believe that by reflecting sunlight (including ultraviolet radiation) the silky puffs protect the young from overheating and damage, increasing the likelihood of their survival. Prenymphs, i.e. first instar spiderlings, can spin only drag-lines: they cannot spin domed sheets. Spiderlings in the next nymphal stage, i.e. second instar, can construct both non-spotted and spotted domed sheets.

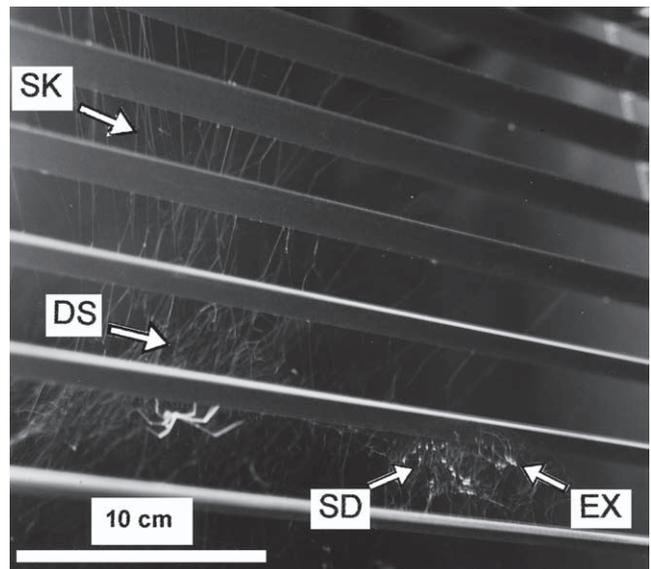


Fig. 25: Two types of domed sheet webs, constructed by the same *Crossopriza* sp. spider in the third nymphal instar, between a window frame and strips of a Venetian blind. On the left is a non-spotted domed sheet web (DS), on the right a spotted dome (SD), built before ecdysis. SK=skeleton, EX=exuviae.

In the webs of the spiders we observed we did not find any sticky balls of a liquid nature, described by Briceño (1985) for *Modisimus* sp. On the other hand, loops of loose fibrils attached to the tense lines of dome-shaped webs produced by the pholcids we studied resemble closely the "screw threads" described by Kirchner (1986) in three-dimensional irregular webs of *Pholcus phalangioides*.

It is evident that spotted domes with white puffs which reflect light and conceal the darker body of the spider are built periodically in critical situations, when the spider is vulnerable or temporarily immobile and unable to attack its prey, i.e. before moulting and before the egg-laying stage and during the subsequent stage of egg development including moulting in the pre-nymphal stage. We do not believe, therefore, that a possible function of decorated domes is prey attraction, which is one of the suggested and often tested functions of stabilimenta. The bright white puffs of silk in a domed sheet, when not vibrating, may enhance visibility of the web both for flying insects and predators, and reduce the risk of damage to it. A similar role, i.e. web protection through visual advertisement, is attributed to stabilimenta by Eisner & Novicky (1983).

A spider which shelters inside this type of dome becomes almost invisible to an intruder once it vibrates the whole web with its body and legs. However, any pholcid becomes invisible as a result of similar vibrations, irrespective of the type of web it occupies; this can be best demonstrated in the behaviour of the well-known *P. phalangioides*, which does not construct either of the two types of domed sheet. Under laboratory conditions, both species of pholcids studied also constructed spotted domes whenever at least two specimens were kept together in the enclosed space of an insectarium and the skeletons of their webs came into contact. Also, when collecting *Crossopriza* sp. specimens at

Larache, Morocco, we noticed that all the domed sheets were spotted wherever the concentration of spiders was such that the skeletons of their webs touched one another. On the other hand, non-spotted domes formed part of those webs built in isolation. Further research is needed to answer the question of what stimulates pholcids to leave non-spotted domed sheets to build spotted domes.

Acknowledgements

We are grateful to Dr Peter Merrett and an anonymous reviewer for providing many useful comments and suggestions, which have helped to improve this article. This research was supported by grant No. 206/98/0092 of the Grant Agency of the Czech Republic. Our thanks to Bernhard A. Huber for determination of *Crossopriza* sp.

References

- BLACKLEDGE, T. A. 1998: Stabilimenta and predator-prey trade-offs in *Argiope*. *XIV International Congress of Arachnology, 22nd Annual Meeting of the American Arachnological Society. Oral Presentation Abstracts*: 1–78.
- BRICEÑO, R. D. 1985: Sticky balls in webs of the spider *Modisimus* sp. (Araneae, Pholcidae). *J. Arachnol.* **13**: 267–269.
- BRIGNOLI, P. M. 1971: Beitrag zur Kenntnis der Mediterranen Pholcidae (Arachnida, Araneae). *Mitt. zool. Mus. Berl.* **47**(2): 255–267.
- CODDINGTON, J. A. & LEVI, H. W. 1991: Systematics and evolution of spiders (Araneae). *A. Rev. Ecol. Syst.* **22**: 565–592.
- COMSTOCK, J. H. 1948: *The spider book*. Comstock Publishing Company, Ithaca, New York.
- DEELEMEN-REINHOLD, C. 1986: Leaf-dwelling Pholcidae in Indo-Australian rain forests. In W. G. Eberhard, Y. D. Lubin & B. C. Robinson (eds.), *Proceedings of the ninth International Congress of Arachnology, Panama 1983*: 275–279. Washington, DC: Smithsonian Institution Press.
- EBERHARD, W. G. 1992a: Web construction by *Modisimus* sp. (Araneae, Pholcidae). *J. Arachnol.* **20**: 25–34.
- EBERHARD, W. G. 1992b: Notes on the ecology and behaviour of *Physocyclus globosus* (Araneae, Pholcidae). *Bull. Br. arachnol. Soc.* **9**(2): 38–42.
- EBERHARD, W. G. & BRICEÑO, R. D. 1985: Behavior and ecology of four species of *Modisimus* and *Blechnoscelis* (Pholcidae). *Revue arachnol.* **6**: 29–36.
- EISNER, T. & NOVICKY, S. 1983: Spider web protection through visual advertisement. Role of stabilimentum. *Science, N.Y.* **219**: 185–187.
- GRISWOLD, C. E., CODDINGTON, J. A., HORMIGA, G. & SCHARFF, N. 1998: Phylogeny of the orb-web building spiders (Araneae, Orbicularia: Deinopoidea). *Zool. J. Linn. Soc.* **123**: 1–99.
- HERBERSTEIN, M. E. 2000: Foraging behaviour in orb-web spiders (Araneidae): do web decorations increase prey capture success in *Argiope keyserlingi* Karsch, 1878? *Aust. J. Zool.* **48**: 217–223.
- KIRCHNER, W. 1986: Das Netz der Zitterspinne (*Pholcus phalangioides* Fuesslin) (Araneae: Pholcidae). *Zool. Anz.* **216**: 151–169.
- PETERS, H. M. 1993: Über das Problem der Stabilimente in Spinnennetzen. *Zool. Jb. (Physiol.)* **97**: 245–264.
- PLATEL, T. G. H. 1989: The egg laying and larval development of *Pholcus phalangioides* (Fuesslin) (Araneae: Pholcidae). *Tijdschr. Ent.* **132**: 135–147.
- SCHÜTT, K. 1996: Wie Spinnen ihre Netze befestigen. *Mikrokosmos* **85**: 274–278.
- SEDEY, K. A. & JAKOB, E. M. 1998: A description of an unusual dome web occupied by egg-carrying *Holocnemus pluche* (Araneae, Pholcidae). *J. Arachnol.* **26**: 385–388.
- SHEAR, W. 1969: Observations on the predatory behavior of the spider *Hypochilus gertschi* Hoffman (Hypochilidae). *Psyche, Camb.* **76**: 407–417.
- SIMON, E. 1892: *Historie naturelle des Araignées* **1**(1): 1–256.
- TSO, I. M. 1996: Stabilimentum of the garden spider *Argiope trifasciata*: a possible prey attractant. *Anim. Behav.* **52**: 183–191.
- TSO, I. M. 1998: Stabilimenta increase insect interception of webs spun by *Cyclosa conica* (Pallas). *J. Arachnol.* **26**: 101–105.
- VOLLRATH, F. 1987: Kleptobiosis in spiders. In W. Nentwig (ed.), *Ecophysiology of spiders*: 274–286. Berlin, Springer-Verlag.
- WIEHLE, H. 1933: *Holocnemus hispanicus* n. sp. und die Gattungen *Holocnemus* Simon und *Crossopriza* Simon. *Zool. Anz.* **104** (9/10): 241–252.
- WISE, D. H. 1984: Phenology and life history of the filmy dome spider (Araneae: Linyphiidae) in two local Maryland populations. *Psyche, Camb.* **91**: 267–288.
- WISE, D. H. 1995: *Spiders in ecological webs*. Cambridge University Press.