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Silk spinning apparatus and silk microstructure of *Silhouettella loricatula* (Araneae, Araneomorphae, Oonopidae)

Jaromír Hajer*, Michaela Czerneková# and Dana Řeháková$

Department of Biology, Faculty of Science, J. E. Purkinje University in Ústí nad Labem, České mládeže 8, 400 96 Ústí nad Labem, Czech Republic

ABSTRACT

The spinning apparatus of *Silhouettella loricatula* is made up of three pairs of spinnerets and colulus. Bisegmental anterior lateral spinnerets possess a single spigot each, monosegmental posterior median spinnerets possess two spigots, and bisegmental posterior lateral spinnerets possess three spigots. No differences in the spinnerets between both sexes were found. Only two types of silks, used for the construction of webs, are released from two types of spigots. During retreat construction, the emitted silk, that hardens when exposed to air, is processed only by movements of the opisthosoma and spinnerets, i.e. none of the four pairs of legs is used. Due to the probable absence of piriform glands, the threads are not attached to the ground by means of attachment discs. The microstructure of webs built by *S. loricatula* resembles the microstructure of webs produced by the Dysderidae. The opisthosoma of *S. loricatula* is equipped with a ventral and dorsal scutum. Spinnerets are extended from the expanded opisthosoma only during the spinning activity. When the spider is outside the retreat and when it attacks prey, the opisthosoma is contracted and dorsoventrally flattened. The edges of the broader dorsal scutum of the contracted opisthosoma cover the narrower ventral scutum. In such instances, the spinnerets are retracted into the opisthosoma, with the two scuta functioning as a bivalval case.

KEYWORDS: spiders, spinnerets, Haplogynae, Oonopidae, silk microstructure

INTRODUCTION

Spiders belonging to the family Oonopidae (goblin spiders) are typically characterized as free-living nocturnal ground dwellers which spend the daytime in a silken retreat [1]. Most goblin spiders live in the litter of tropical rain forests [2] and show an enormous species diversity [3, 4]. The family Oonopidae currently comprises of 97 genera with 1,325 species [4], which have adapted in the process of evolution to a wide variety of ecological niches [5, 6, 7, 8].

Goblin spiders are among the target taxa of the Planetary Biodiversity Inventory Program (PBI), 'because the distribution range of the species tends to be extremely small, and the group has the potential to provide substantial amounts of information on areas of endemism on a worldwide scale' [9].

Oonopidae are small spiders, the body size of adult specimens ranging between 1 and 3 mm [5]. *Silhouettella loricatula* (Roewer, 1942), whose silk spinning apparatus has been studied, reaches a body length of 1.3-2.1 mm in males and 1.5-2.4 mm in females [10]. The retreat of the spider

*Corresponding author: Jaromir.Hajer@ujep.cz
#CzernekovaM@seznam.cz
$Dana.Rehakova@ujep.cz

species *Silhouettella loricatula* was for the first time briefly described by Burger and Carrera [11]. It typically consists of a tube with two opposite openings. The tube is overlaid with long oblique additional threads functioning as signal threads [11].

The haplogyne (for explanation of this term see Burger *et al.* [12] and Foelix [13]) family Oonopidae was generally divided into two subfamilies, Oonopinae and Gamasomorphinae [1, 11]. The subfamily Gamasomorphinae, also called dwarf armoured spiders [1], comprises oonopids with hardened plates (scuta) on the dorsal and ventral sides of their opisthosoma. The traditional classification into two subfamilies has been superseded by a new classification by Platnick *et al.* [14], who recognized three subfamilies, the Orchestininae, Sulsulinae and Oonopinae. The subfamily Oonopinae contains the majority of oonopid genera, including those previously placed in Gamasomorphinae (such as *Silhouettella*).

The research presented in this paper focuses on the silk-producing apparatus in spiders (Araneae), which is made up of spinnerets and sac-like spinning glands, whose epithelial cells produce different types of silk secretions. Spinning glands are connected to excretory ducts running into jet-like spigots on spinnerets. Spiders of the infraorder Araneomorphae, which also includes the family Oonopidae, possess three pairs of spinnerets, namely the anterior lateral, posterior median and posterior lateral spinnerets. The Araneomorphae can have a colulus or, alternatively, a cribellum (see [13]) in place of the anterior median pair of spinnerets. The colulus is a nonfunctional remnant of the anterior median spinnerets, reduced to varying degrees [15]. In the family Oonopidae, it is represented by at least one pair of setae [16, 17].

The present study provides the results of a study on spinnerets, spigot placement on the spinnerets, silken web microstructure and silk spinning behavior of *Silhouettella loricatula*. The findings are compared in the Discussion section with the results of relevant studies focusing on the silk spinning organs of other Oonopidae and families belonging to the superfamily Dysderoidea [8]. No histological or histochemical studies of the spinning glands of the Oonopidae have been conducted to date. On the other hand, there are a number of studies describing the external morphology of the spinnerets of oonopids (e.g. [7, 15, 17, 18, 19]). These studies typically provide the number of spigots through which the different categories of spinning glands are discharged on the surface of spinnerets. None of the species of the family Oonopidae studied so far has been found to possess more than three types of spigots, from which it may be assumed that no more than three categories of spinning glands occur in this family. Spigots of anterior lateral spinnerets are, as in most spiders belonging to the infraorder Araneomorphae, referred to as major ampullate and piriform gland spigots [7, 18, 20, 21, 22, 23]. For spigots of posterior median and posterior lateral spinnerets, the authors above did not give the names of the glands to which they are connected, but state only the numbers of spigots. The same approach was chosen by the authors of the present paper; however, the Discussion section considers the probable homology of these glands with glands/spigots which have been described for the Dysderidae family by Glatz [16].

MATERIALS AND METHODS

Eighteen adult females and twelve males of the reddish-brown colored species *Silhouettella loricatula* were collected in August 2012 from approx. 2 km east of the coastal city of Igoumenitsa in north-western Greece by sieving the humid leaf and tree litter layer.

The spiders were kept in the laboratory in small glass test tubes (10 × 50 mm); either small pieces of the moss *Tortula muralis* Hedw. or strips of polyurethane bath sponge, moistened daily with 1-2 drops of water, were placed inside. The vials were closed using balls of cotton wool. The spiders were fed with Collembola (*Folsomia candida* Willem, 1902). The silk of retreats constructed in the moss was frequently contaminated with detritus and fungal hyphae. The pieces of bath sponge mentioned above proved to be a particularly suitable substratum for obtaining webs for studying the silk by means of scanning electron microscopy (SEM). The webs built by the spiders in the small cavities of this porous material with pores 2-7 mm in diameter remained entirely intact upon removal of the sponge from the vials.

Live spiders and their spinning activity were observed with a Novex stereo microscope, equipped with an INFINITY*lite* digital camera. The morphology of spinnerets, in particular their spinning fields and spigots, and the microstructure of silk threads constituting the web was studied by means of a Leica DMLB light microscope equipped with a Canon Power Shot S50 camera (Figs. 1A, 2B, 4A-D) and by a scanning electron microscope (Figs. 2A, 3A-D, 5A-D, 6A-B). For scanning electron microscopy studies, the spiders were dehydrated in ethanol and critical-point dried with carbon dioxide. After sputtering with gold, they were observed with a TESCAN SEM.

It was necessary to use the light microscope in order to enable a reliable count of spigots, which were often covered with hardened silky secretion, just like the setae surrounding them. In this case, the spinnerets were separated from the rest of the opisthosoma and partially digested with a KOH (approx. 10%) solution to dissolve the soft tissues, embedded in Hoyer's medium and slide-mounted.

RESULTS

Opisthosoma, opisthosomal scuta and position of spinnerets

As in the other dwarf armored spiders of the subfamily Gamasomorphinae, the opisthosoma of *Silhouettella loricatula* was equipped with a ventral and dorsal scutum (Figs. 1A-B, 2A).

While the retreat was constructed, i.e. during the spinning activity, the spinnerets were extended from the expanded opisthosoma (Fig. 1B). By contrast, when the spider was outside the retreat or when attacking its prey, the opisthosoma was contracted and dorsoventrally flattened. In this case, the spinnerets were retracted inside the opisthosoma, with both scuta (dorsal and ventral) functioning as a bivalval case protecting the opisthosoma with its spinning apparatus drawn inside (Fig. 2A). The edges of the broader dorsal scutum of the contracted opisthosoma covered the narrower ventral scutum (Fig. 2A). As the opisthosoma contracted and the spinnerets retracted, the apical segments of anterior lateral and posterior lateral spinnerets were 'telescopically' drawn into the basal segments (Fig. 2A-B). As a result of this, all of the retracted spinnerets appeared as if they were monosegmental.

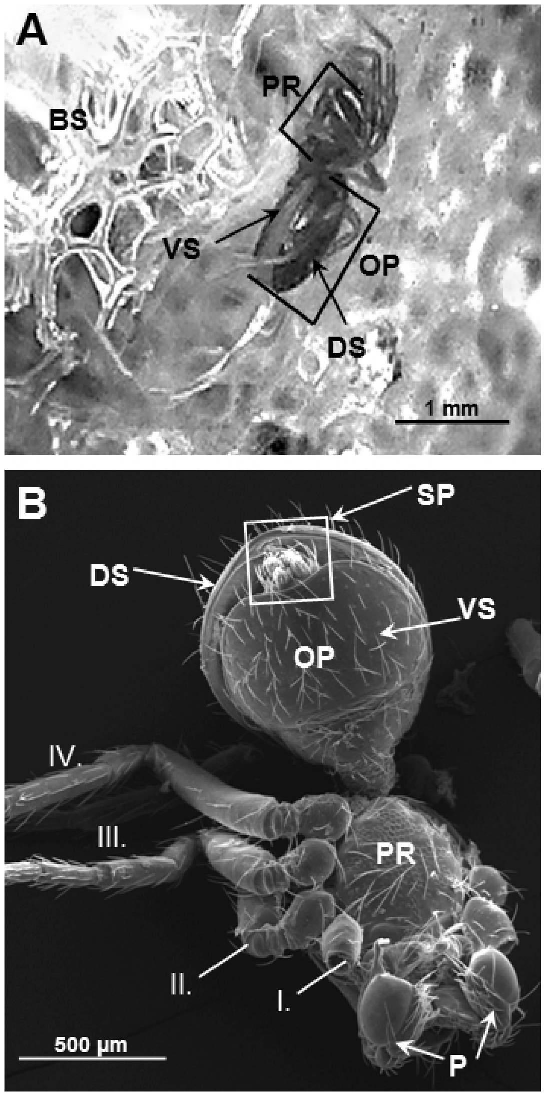

Fig. 1A-B. *Silhouettella loricatula* and its retreat. **(A)** Adult female when building a retreat inside a glass vial in which a piece of bath sponge was placed. At the time of retreat spinning, the opisthosoma was always dorsoventrally expanded and the scuta did not touch each other with their edges. **(B)** View of ventral side of the body of an adult male. Abbreviations: PR = prosoma; OP = opisthosoma; VS = ventral scutum; DS = dorsal scutum; BS = bath sponge; SP = spinning apparatus; P = pedipalps; I-IV = four pairs of legs. Parts of legs obscuring the ventral part of the body were removed prior to scanning.

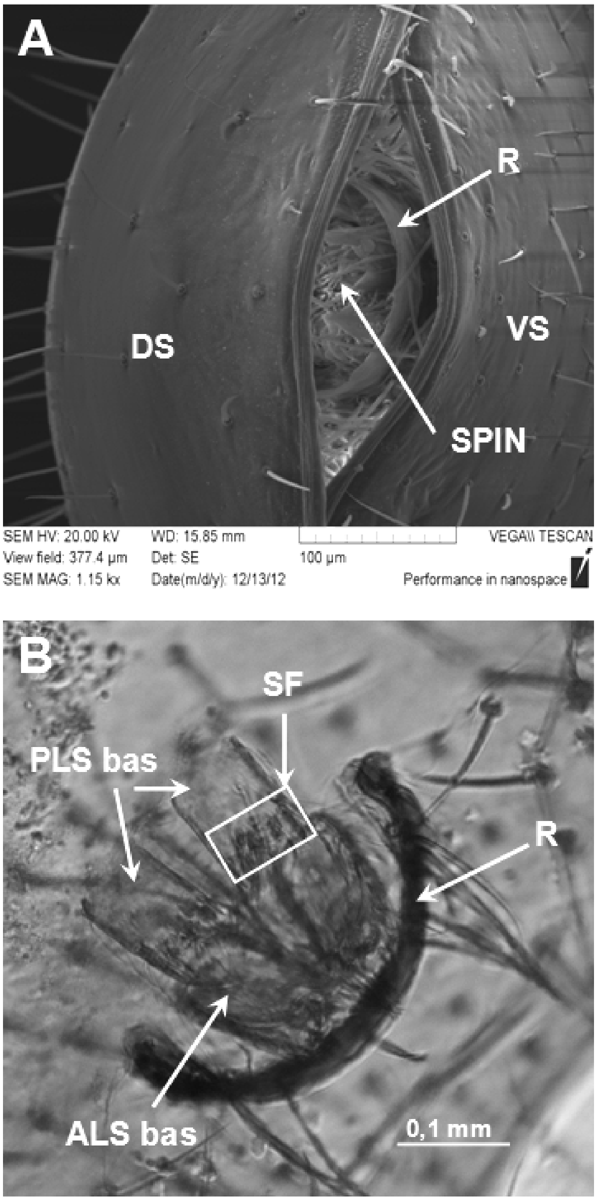

Fig. 2A-B. (A) SEM and **(B)** light microscopy picture of retracted spinning organs. Abbreviations: DS = dorsal scutum; VS = ventral scutum; R = ring; SPIN = spinnerets; PLS bas = basal segments of posterior lateral spinnerets; SF = spinning field of the apical segment retracted inside the basal segment; ALS bas = basal segment of anterior lateral spinneret.

Spinnerets and spinneret spigot morphology

The spinning apparatus of *Silhouettella loricatula* consisted of three pairs of spinnerets (Figs. 3A-D, 4A-D) and a colulus (Fig. 4D), which had the appearance of a small cylindroid protuberance with two setae on its apex. The spinnerets were surrounded by a ring shaped sclerite, called the spinneret scutum (Figs. 2A-B, 3A-B).

Anterior lateral spinnerets (ALS) (Figs. 2B, 3A-B, 4A) were bi-segmented. The larger basal segment was almost cylindrical in shape, while the smaller apical segment was conically tapered toward its apex. There was only a single spigot (Fig. 3B, 4A) in the small spinning field (an area equipped with spigots) at the top of the apical segment. The sockets (basal parts) of these spigots were 2 µm high and 5 µm in diameter. The shafts (terminal parts) reached a length of approx. 25 µm. The spinning fields of ALSs were, like the spinning fields of posterior median and posterior lateral spinnerets, surrounded by setae (Figs. 3C-D) which resembled the tactile hairs of spiders (see Foelix 2011).

Posterior median spinnerets (PMS) (Figs. 3A, 3C, 4B) were the smallest of the three pairs and consisted of one segment only. The spinning field of each PMS, both in males and females, was equipped with two spigots (Figs. 3C, 4B).

Posterior lateral spinnerets (PLS) (Figs. 3A, 3D, 4C) were made up of two segments. The spinning fields of their apical segments were equipped, both in males and females, with three spigots. There were no morphological differences between the spigots of posterior lateral and posterior median spinnerets. The sockets (Figs. 4C-D) of posterior lateral and posterior median spinnerets were approx. 5 µm high and 15-20 µm in diameter. The shafts reached up to 25-30 µm.

Webs and their microstructure: role of spinnerets in silk processing

The webs had the appearance of silky tube-like chambers (Fig. 1A), which served as retreats but were not used for prey hunting. The walls of the chambers had the appearance of densely spun sheets with a microstructure resembling fishing nets (Figs 5A-B). The fibers were formed by the hardening of the liquid silken secretion, emitted through the spigots of posterior median and posterior lateral spinnerets. Both the size of web mesh loops and the thickness of the fibers increased toward the edges (Figs. 5C-D). Each fiber was a complex of parallel-arranged fibrils, emitted by spigots of the same pair of spinnerets.

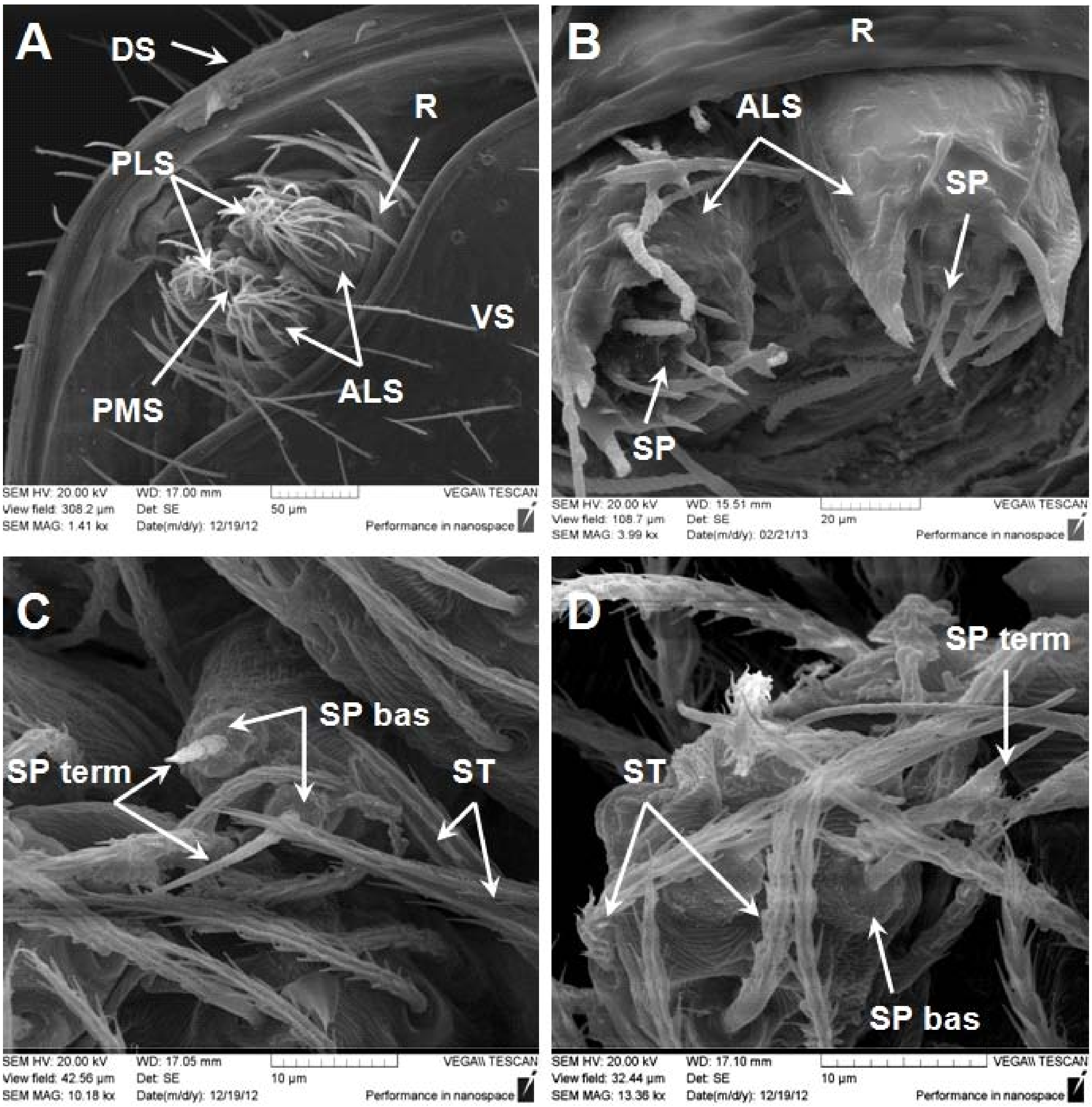

Fig. 3A-D. SEM micrographs of spinnerets of an adult female. (**A**) View of all three pairs of spinnerets when opisthosoma is expanded. Detailed scans of **(B)** anterior lateral, **(C)** posterior median and **(D)** posterior lateral spinnerets. Abbreviations: DS = dorsal scutum; VS = ventral scutum; ALS = anterior lateral spinnerets; PMS = posterior median spinnerets; PLS = posterior lateral spinnerets; R = ring; SP = spigot; SP bas = basal parts (i.e. sockets) of spigots; SP term = terminal parts (i.e. shafts) of spigots; ST = setae.

During spinning activity, spinnerets of the same pair moved either synchronously (touching when silk was emitted) or asynchronously (the spinnerets did not touch and their spinning fields faced in different directions when emitting silk). The synchronous/asynchronous movement of the spinnerets of the same pair during silk production affected the thickness of the fibers. The thickest fibers were the result of applying bundles of new fibrils to existing fibers.

Anterior lateral spinnerets produced fibers referred to as draglines (Fig. 6A). Anchored to the substratum, the "silk track" allows the spider to return safely to the starting point after a thrust at its prey or following a free fall; it also allows spiderlings to maintain contact with the parental web. The dragline material (i.e. extracellular fibrous protein called spidroin) is produced by a pair of major ampullate glands and emitted from spigots, one of which is located on each anterior

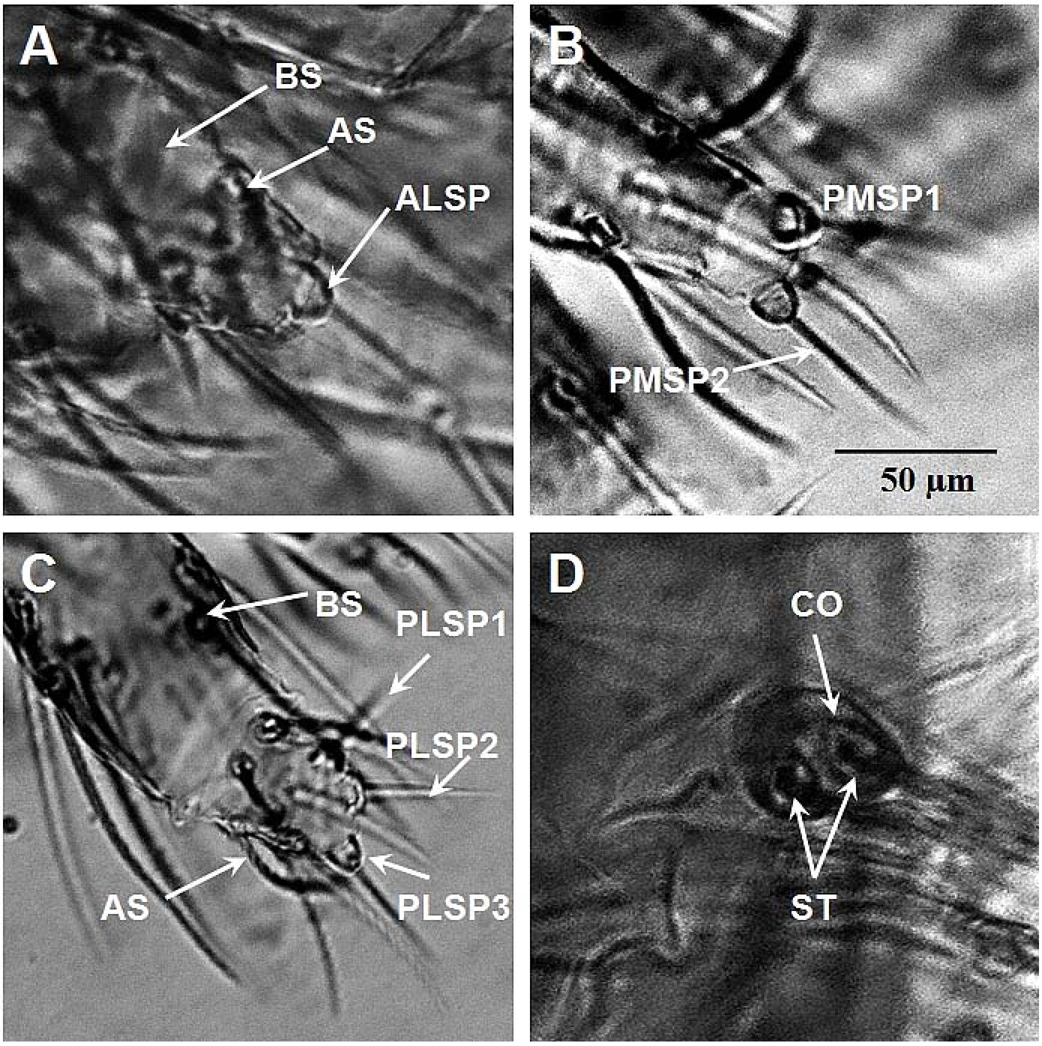

Fig. 4A-D. Spigot placement on spinnerets of an adult female. Light microscope micrographs of **(A)** anterior lateral, **(B)** posterior median, **(C)** posterior lateral spinnerets and **(D)** colulus. Abbreviations: BS = basal segment; AS = apical segment; ALSP = anterior lateral spinneret spigot; PMSP1, PMSP2 = two spigots of posterior median spinneret; PLSP1, PLSP2, PLSP3 = three spigots of posterior lateral spinnerets; CO = colulus; ST = setae.

lateral spinneret (Figs. 3B, 4A). The movements of anterior lateral spinnerets during spinning activity were always synchronized, and spigots located in the inner side of both anterior lateral spinnerets touched as they emitted draglines. The taut dragline fibers, unlike those of most spiders from the infraorder Araneomorphae, were not connected to the substratum (Fig. 6B) with the protein secretion, used to bind materials or cement threads, produced by piriform glands. This type of gland (and spigot), facilitating the attachment of web fibers to the ground, has not developed in *Silhouettella loricatula*.

DISCUSSION

Silhouettella loricatula is one of those goblin spiders of the family Oonopidae whose opisthosoma is equipped with hardened plates, referred to as scuta, which operate like a bivalval case, expanding during spinning activity and contracting when spinning activity stops. The opisthosoma was observed to be invariably contracted when the spider wandered around its retreat or lunged at its prey. As the opisthosoma contracts, the spinnerets retract. The retraction of the bisegmental anterior lateral and posterior lateral spinnerets into the

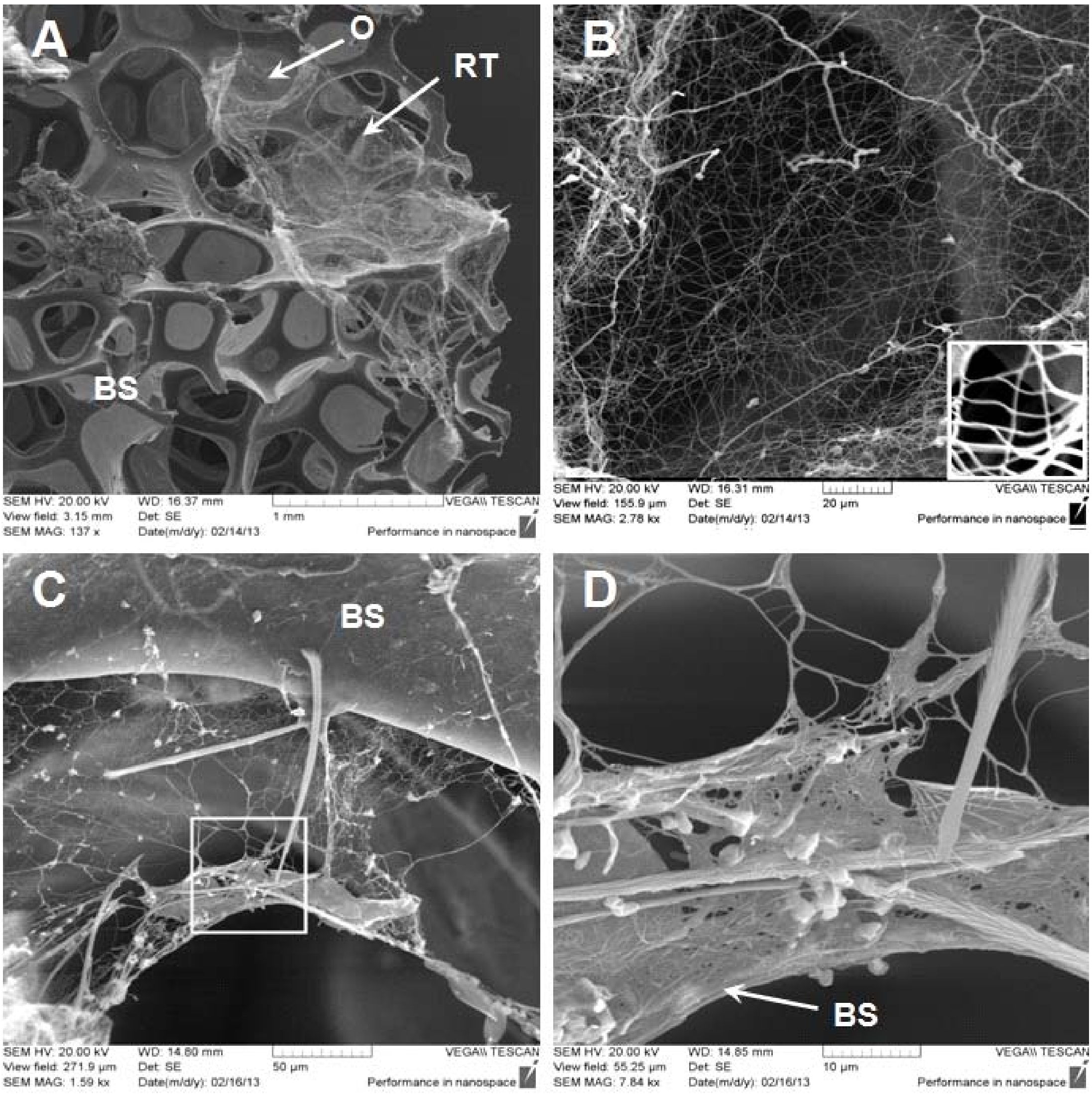

Fig. 5A-D. SEM micrographs showing the silk of a retreat built by an adult female inside a glass vial. **(A)** View of an entire web covering a part of the substrate, in this case a piece of bath sponge. **(B)** Central part of densely spun sheeted webs. A detail of this part of the web is framed in the bottom right corner of the picture. **(C)** Microstructure of the web along its edge. **(D)** Enlarged view of framed section in **(C)**. Abbreviations: RT = retreat; O = opening; BS = bath sponge.

opisthosoma is accompanied by a telescopic retraction of their apical segments into the basal segments, which is an interesting and as yet undescribed phenomenon. The retraction of spinnerets into the opisthosoma (as well as their extension) is through a sclerite (spinneret scutum), which has the shape of a sclerotized ring surrounding the spinnerets.

The movement of spinnerets described above may, at least in several species, be related to one of the probable functions of scuta, namely to conserve moisture, i.e. to reduce the loss of water from the spider's body in dry times [24]. In such a case, retraction of the spinning apparatus into the opisthosoma is necessary as extended spinnerets would make complete closure of the 'bivalval case' on contraction of the opisthosoma impossible. Whether this type of spinneret movement also occurs in soft-bodied 'Oonopides moles' [25] of the subfamily Oonopinae [3], where both the

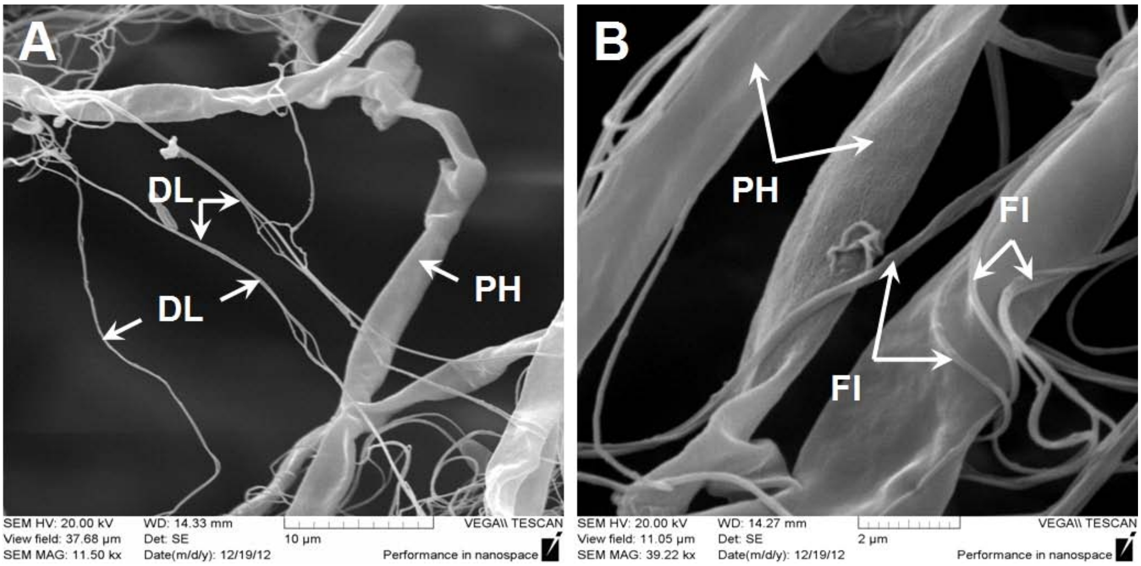

Fig. 6A-B. SEM scans showing the manner of attachment of fibers onto the substrate, in this case phyloids of moss. **(A)** Draglines drawn between phyloids around the retreat. **(B)** Details of the attachment of fibers onto the surface of phyloids. Abbreviations: PH = phyloids; DL = draglines; FI = fibers.

dorsal and ventral scuta only cover the opisthosoma partially or are missing completely [7], is still unknown.

Considering the structure and composition of their spinning glands, and correlatively the specific use of the silk produced, spiders may be divided into two groups - generalists and specialists [15]. The generalist spiders produce one to three kinds of fibers, which are used indifferently for the construction of their retreats or burrows as well as cocoons or sperm webs [15]. In contrast, the silk glands of the specialists [15] - the best described being the Araneoidea (in sensu [26]) - are more diversified. Specialist spiders produce four to nine kinds of fibers, while each type of construction has its characteristic fiber composition and they include several types of proteins [27]. The Oonopidae, like the related Dysderidae, belongs to the generalists (in sensu Kovoor [15]). The spinning glands of spiders belonging to the family Dysderidae have been described by Glatz [16], who found adult females of *Dysdera erythrina* (subfamily Dysderinae) to have only three types of spinning glands (*Glandulae ampullaceae*, *Glandulae piriformes*, and *Glandulae pseudaciniformes*). The same types of glands have been found in the species *Harpactea rubicunda* (Harpacteinae) by Hajer *et al.* [28]. The presence of only three types of spigots has also been observed in several other species of the genus *Dysdera* [29, 30, 31, 32] and *Rhode* (Dysderidae, Rhodinae) [33]. Three types of spigots, with the same arrangement on the surface of spinnerets as in the Dysderidae, are also found in spiders of the genus *Loxosceles* (Sicariidae) [34]. The maximum number of categories of spinning glands found in the Oonopidae (deduced from the presence of their spigots) is three: *Glandulae ampullaceae*, *Glandulae piriformes*, and glands which have not been given a name in any study on the Oonopidae published to date, whose spigots are located on the posterior median and posterior lateral spinnerets (see, for example, [19, 22, 35]. The authors of this paper believe that these 'unnamed' glands (and their spigots) are homologous to *Glandulae pseudaciniformes* of the family Dysderidae [23]. Glatz coined this term for glands that resemble in shape to *Glandulae aciniformes*, which are found in nearly all species of the infraorder Araneomorphae. Spigots of these glands are located on the posterior median and posterior lateral spinnerets. The same *Glandulae pseudaciniformes* are also found in the haplogyne family Segestriidae [16], which is also a part of the superfamily Dysderoidea. However, unlike the Dysderidae, Oonopidae and Sicariidae, spiders of the family Segestriidae possess two pairs of *Glandulae ampullaceae*, with the second pair of these large glands being discharged through posterior median spinnerets. At any rate, the role of the pseudaciniform glands in the Dysderidae and Oonopidae is identical: in both families they provide silks intended for the construction of retreats of a similar microstructure [28]. Silk secretions emitted from the spigots of *Silhouettella loricatula* spiders during the construction of retreats are not, as in the case of the Dysderidae [28], processed by the legs in the subsequent hardening process.

In *Silhouettella loricatula*, only two categories of spinning glands have been identified on the basis of the presence of two spigot types, as *Glandulae piriformes* are not developed in this species. The absence of these glands in certain oonopids means that these spiders cannot attach their draglines, also called lifelines [36], to the substrate using attachment discs (i.e. the thread-like secretion of pirifom glands). A similar reduction of piriform glands has also occurred in the process of evolution in certain other oonopids [7, 9, 21, 18]. The spinning apparatus of *S. loricatulla*, possessing only two types and a small number of spigots/ spinning glands, supports the hypothesis of a tendency toward spinning apparatus reduction within the family Oonopidae [7]. This manifests itself in some oonopid species by the reduction of posterior lateral spinnerets, for example, having the appearance of minute remnants that are hard to recognize [7], or by a reduction, fusion or absence of posterior median spinnerets [9].

CONCLUSION

Scanning electron microscopy and light microscopy were used to study the silk spinning apparatus and silks of *Silhouettella loricatula* spiders. Two types of silk secretions that are produced by two kinds of silk spinning glands (ampullate and pseudaciniform) and released through two types of spigots, were confirmed for adult spiders. Silks for the construction of spider retreats are produced by the pseudaciniform silk glands. This article is the first to describe silken threads produced by the Oonopidae. It also describes the construction of retreats, the behavior during spinning, and the movements of the spinnerets when the silk fibers are secreted. The results show the need for a thorough examination of the dragline-associated behaviour of spiders. This study expands our knowledge of the family of Oonopidae and may also be used in the analyses of phylogenes of Araneoidea.

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CONFLICT OF INTEREST STATEMENT

The authors certify that there is no conflict of interest with any financial organization regarding the material discussed in the manuscript.

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