

# Silk gland morphology of the net-casting spider *Deinopis spinosa*

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## Research Article

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## Additional Declarations:

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20

21 **Abstract.** Net-casting spiders (Deinopidae) are cribellate spiders that spin a rectangular, sticky  
22 net that is held stretched between the claws of their first two pairs of legs. Deinopids produce  
23 eight distinct silk types, but knowledge of the silk-producing morphologies is mostly limited to  
24 the spigots associated with different fibers. As there have been no studies of deinopid silk gland  
25 structure, we dissected all the silk glands from *Deinopis spinosa* and document their number and  
26 morphology. We found silk gland position and morphology consistent with the type and number  
27 of silk spigots described for Deinopidae. Notably, for the first time, we describe the silk glands  
28 associated with cribellate silk: paracribellate, pseudoflagelliform, and cribellar silk glands. Our  
29 findings support the homology of pseudoflagelliform glands with araneoid flagelliform glands  
30 and will have importance for informing our understanding of spider web evolution.

31

32 **Keywords:** Deinopid, cribellate silk, silk glands, spigot, spinneret

33

34 Net-casting spiders (Deinopidae C. L. Koch, 1851) are skilled nocturnal hunters. These cribellate  
35 spiders spin an unusual type of orb-web: a rectangular, sticky net that the spider holds stretched  
36 between the claws of its first two pairs of legs. Suspended, the spider hovers motionless at night,  
37 then when prey is detected, it rapidly expands its net and flings it over prey moving on the  
38 substrate beneath them or flying above them (Coddington & Sobrevila, 1987). Studies on  
39 *Deinopis spinosa* Marx, 1889 (Marx, 1889) have shown that this unique foraging strategy  
40 involves multiple specializations, including extremely sensitive night-vision to capture prey off  
41 the ground (Stafstrom & Hebets, 2016) and extremely extensible silk (Blackledge & Hayashi,  
42 2006).

43

44 Deinopids use a dry, Velcro-like adhesive in their prey-capture web, composed of cribellar silk  
45 surrounding a pair of supporting fibers, a pair of undulating fibers, and a mat of connecting  
46 fibers. Cribellar silk is produced from a specialized plate called the cribellum. The cribellum is  
47 densely covered with thousands of miniature spigots from which nanofibrils emerge and then are  
48 teased into highly-coiled, cloudy masses of fibers. The supporting fibers are produced in the  
49 pseudoflagelliform glands, the undulating fibers in the minor ampullate silk glands and the  
50 connecting fibers in the paracribellate silk glands (Peters, 1984, 1992). While the external  
51 spinning apparatus (spinnerets and their spigots) has been characterized in a few works

52 (Coddington, 1989; Griswold et al., 1998, 2005; Murphy & Roberts, 2015; Peters, 1992), to our  
53 knowledge, there are no previous morphological studies of the silk glands associated with  
54 deinopid spigots.

55

56 Here, we document all silk gland types present in the net-casting spider *D. spinosa* and describe  
57 their position, size, and morphology, drawing comparisons with current knowledge about their  
58 spigots, as well as silk gland morphology outside of deinopids. Our findings are consistent with  
59 the number and variety of spigot morphologies and for the first time for any spider, we describe  
60 the morphology of the silk glands used in the cribellate capture silk.

61

62 Mature female *D. spinosa* were collected in Florida (2021 and 2022). All spiders were  
63 anesthetized with CO<sub>2</sub> and dissected under a stereomicroscope with forceps in saline sodium  
64 citrate buffer. Images of all tissues were collected from two individual females using a ZEISS  
65 Axiocam 105 Color Microscopy Camera mounted on a ZEISS 435063-9010-100 Stemi 305  
66 Stereo Microscope with the ZEN Blue software. We identified eight types of silk glands:  
67 aciniform, cribellar, major ampullate, minor ampullate, paracribellate, pseudoflagelliform,  
68 pyriform, and tubuliform (Fig. 1), which correspond to the eight types of silk spigots described  
69 for deinopid spiders (Fig. 2) (Coddington, 1989; Griswold et al., 1998; Murphy & Roberts, 2015;  
70 Peters, 1992). Each gland type was confirmed by tracing its duct to the spinneret on which it  
71 terminated. An additional mature female was anesthetized with CO<sub>2</sub> and the abdomen was  
72 severed at ~30% anterior of the spinnerets. The spinnerets were prepared following (Townley &  
73 Harms, 2017). In short, spinnerets were submerged in 2X SDS-PAGE running buffer  
74 (ThermoFisher) for 3 days, then dehydrated in an ethanol series: 30%, 50%, 70%, 85%, 95%,  
75 and then twice in 100% (24 hour each). Spinnerets were critical-point dried using a Tousimis  
76 Samdri CPD, mounted on SEM stubs, sputter-coated with a Denton Vacuum Desk IV, and  
77 examined in a JEOL 6390 scanning electron microscope.

78

79 The major ampullate and minor ampullate glands were astonishing in number and shape. There  
80 were ten pairs of major ampullate glands (Fig. 1A), corresponding to the ten major ampullate  
81 spigots on each anterior lateral spinneret (ALS; Fig. 2A and 2B) (Coddington, 1989; Peters,  
82 1992). By contrast, most mature araneoids have only one pair of major ampullate glands

83 (Coddington 1989). Many non-araneoid spiders, such as eresids, nicodamids, desids,  
84 amaurobiids, agelenids, and lycosoids, have been described as having more than one pair of  
85 major ampullate silk spigots as mature individuals (Griswold et al., 1998, 2005; Řezáč et al.,  
86 2017). Similarly, most juvenile spiders have multiple major ampullate spigots which have been  
87 proposed to be used alternatively during molting. That is, one spigot functions in even-numbered  
88 instars and the other in odd-numbered instars (Townley et al., 1993). The silk glands associated  
89 with these spigots also undergo changes during ecdysis: larger ampullate glands (usually those  
90 that stay through maturity) become non-functional pre-ecdysis while the smaller ampullate silk  
91 glands become functional, thus allowing for continuous use of ampullate silk.

92  
93 We also found the elongated *D. spinosa* major ampullate glands to vary in size within an  
94 individual, a phenomenon rare among araneid and theridiid spiders (Berger et al., 2021; Chaw &  
95 Hayashi, 2018; Coddington, 1989). However, such variation has been described for some  
96 agelenid and cribellate amaurobiid species (Řezáč et al., 2017). In the case of agelenids, (Řezáč  
97 et al., 2017) showed that they have a system of three pairs of glands, in which by following the  
98 Townley *et al.* (1993) model, each silk gland will function at a different time during the molting  
99 cycle. In general, major ampullate silk glands have three distinct parts: a secretory tail (Fig. 1A,  
100 star), an ampule-shaped storage sac, and an elongated spinning duct (Fig. 1A, arrow) (Chaw &  
101 Hayashi, 2018; Vollrath & Knight, 1999). In *D. spinosa*, all major ampullate silk glands have an  
102 ampule-shaped sac and an elongated spinning duct, with the three longest glands (Fig. 1A, left  
103 group) also having a long tail similar to other species (Chaw & Hayashi, 2018; Clarke et al.,  
104 2017; Vollrath & Knight, 1999). The other seven major ampullate silk glands have shorter tails,  
105 tend to be clustered together, and are smaller, approximately one-fourth the size of the longest  
106 glands (Fig. 1A, right group). We also found differences in the size of the ampullate spigots on  
107 the ALS (Fig. 2A) associated with these glands: there are three larger spigots on the inner side  
108 closer to the pyriform spigots and a cluster of seven smaller major ampullate spigots on the outer  
109 side (Fig. 2B). Given the presence of additional glands in juvenile spiders (data not shown), the  
110 current understanding of molt-related changes in silk glands (Townley et al., 1993), and our  
111 observation that all major ampullate glands are filled with silk dope, we posit that all ten major  
112 ampullate silk glands found in mature *D. spinosa* are fully functional. Whether the

113 morphological differentiation in *D. spinosa* major ampullate silk glands translates into usage or  
114 functional diversification of major ampullate fibers is unclear.

115

116 Historically, minor ampullate silk glands were named due to their morphological similarity to  
117 major ampullate silk glands, albeit smaller in size. In *D. spinosa*, the minor ampullate silk glands  
118 were not found to be ampule-shaped, as in other orb-weaving spiders, but instead were identified  
119 based on their location, by following their ducts to the minor ampullate spigots on the anterior  
120 median edge of each posterior median spinneret (PMS; Fig. 2A and 2D). We observed only one  
121 minor ampullate spigot on each PMS. Moreover, we found no evidence of a second pair of minor  
122 ampullate spigots. By contrast, Peters (1992) found two ampullate spigots in *Deinopis subrufus*  
123 (Koch, 1878): a large one corresponding to minor ampullate and a smaller one that was difficult  
124 to observe. Following Peters (1992), Griswold *et al.* (2005) reported *Deinopis* as having two  
125 minor ampullate spigots, although only one minor ampullate spigot was visible in their  
126 micrographs of *Deinopis*. It may be that *D. spinosa* and *D. subrufus* differ in the number of  
127 minor ampullate silk glands. In *D. spinosa*, minor ampullate silk glands are bifurcated in the sac  
128 (or secretory section), have a very long secretory duct, and a short tail compared to major  
129 ampullate silk glands (Fig. 1B). Bifurcation of minor ampullate silk glands has also been  
130 observed exclusively in other cribellate spiders (Řezáč *et al.*, 2017), suggesting that bifurcation  
131 could be functionally paired with the production and/or function of the undulating fibers in  
132 cribellate silk.

133

134 The other silk glands that do not have any function in cribellate capture threads are the  
135 aciniform, pyriform, and tubuliform (also known as cylindrical) silk glands. We found the  
136 aciniform and pyriform silk glands to be among the smallest gland types (Fig. 1C, D). The  
137 aciniform silk glands lack morphologically distinct tails and were tightly packed in a grape  
138 cluster-shaped formation (Fig. 1C). There were two pairs of clusters (one on each side): a cluster  
139 of ~47 aciniform glands attached to the posterior lateral spinneret (PLS) and a cluster of ~96  
140 aciniform silk glands attached the PMS (Fig. 1C, D). Moreover, morphological differences in  
141 aciniform silk glands and spigots in *D. spinosa* were not observed as with other spiders (Kovoor  
142 & Peters, 1988; Peters & Kovoor, 1980).

143

144 Pyriform silk glands were also tightly clustered, with ~100 glands arranged in a “baseball-glove”  
145 shape (Fig. 1D). It was not possible to separate individual aciniform or pyriform silk glands  
146 without destroying them. Both aciniform and pyriform silk glands were found in the hundreds  
147 and have very small and thin ducts. Tubuliform silk glands were long, with a yellow-orange  
148 color, and take on the previously described noodle-shape of tubuliform glands from other  
149 Entelegynae species (Fig. 1E). We found the tubuliform silk glands to be extraordinarily  
150 numerous, ~90 pairs, compared to araneoid spiders, which possess only three pairs of tubuliform  
151 glands (Coddington, 1989; Griswold et al., 1998, 2005; Murphy & Roberts, 2015). Deinopids  
152 construct very densely woven and hard egg cases (Barrantes et al., 2014), and these properties  
153 likely result from their large number of tubuliform glands.

154  
155 Prey capture silk in deinopids is a composite of multiple components, including the ultrafine  
156 cribellar fibrils, the extensible core pseudoflagelliform silk fibers and connective paracribellate  
157 fibers. A fourth component of deinopid cribellate silk is minor ampullate silk which is used in  
158 the undulating fibers as mentioned above. The morphologies of the glands associated with these  
159 three silks are largely unknown for any species. We identified a single noodle-shaped silk gland  
160 attached to a single large spigot present on the lateral edge of the PLS (Fig. 2A and 2C). This  
161 spigot has been considered to be homologous to the flagelliform silk spigots of ecribellate orb-  
162 web weavers because of similarity in position and shape and was thus called the  
163 pseudoflagelliform spigot (Alfaro et al., 2018; Coddington, 1989; Peters, 1992). It follows that  
164 the silk gland attached to this spigot is the pseudoflagelliform silk gland (Fig. 1F). Like the  
165 flagelliform silk gland, the pseudoflagelliform silk gland is elongated ampule-shaped, with a  
166 distinct tail and a small kink towards the duct (Fig. 1F). As for the second component of  
167 cribellate silk, the paracribellate silk glands were identified by tracing the glands to the  
168 corresponding spigots on the PMS (Fig. 2D). The paracribellate silk glands are ampule-shaped  
169 with thin elongated ducts and short tails. Paracribellate glands are numerous ~120 (~60 silk  
170 glands on each side), tightly arranged in clusters (Fig. 1G), and separating them was challenging  
171 (but see Fig. 1H). The final silk type, cribellar silk glands, are attached to a special plate-like  
172 organ called the cribellum (Fig. 1I, brown line), which is an identifying feature of cribellate  
173 spiders. The cribellar silk glands were so snugly clustered together that it was impossible to  
174 isolate a single gland (Fig. 1I). The number of glands was also so vast that they were impossible

175 to count. However, a study of *D. subrufus* estimated that there were ~25,000 spigots on the  
176 cribellum, suggesting ~25,000 cribellar silk glands (Peters, 1992). Histological studies shows  
177 that cribellar glands are arranged as a compact mass widespread above and around the PLS and  
178 PMS (Kovoor & Peters, 1988) which is consistent with the morphology and the number  
179 described in this work. When the cluster of *D. spinosa* cribellar glands was torn apart, thin ducts  
180 were observed and the glands appeared to be ovoid, with no visible tails. The glands were  
181 arrayed in tightly packed rows that folded back on themselves, almost giving the appearance of a  
182 box pleated skirt.

183  
184 We show for the first time the morphology of the complete complement of silk glands from a  
185 cribellate spider. Moreover, we describe the previously unknown morphology of the  
186 paracribellate, pseudoflagelliform, and cribellar silk glands. Confirmation of the presence of a  
187 pseudoflagelliform gland in a deinopid, exhibiting morphological and positional similarity to  
188 araneoid flagelliform glands has special significance for our understanding of spider silk  
189 evolution and the origin of the iconic orb-web. Early debates centered on whether the orb-web  
190 evolved convergently in different spider lineages or if it had a single origin (Shear, 1986).  
191 Coddington (1989) proposed homology of the pseudoflagelliform and flagelliform silk spigots,  
192 implying that cribellate spiders spinning orb-webs and orb-web derivatives (Uloboridae and  
193 Deinopidae) were the sister group of Araneoidea (ecribellate orb-weavers), and that the orb-web  
194 traced to a single origin in their most recent common ancestor. However, recent phylogenomic  
195 reconstructions of the spider tree of life are contentious: several have repositioned deinopids,  
196 uloborids, and araneoids in different ways; and they disagree as to whether the orb-web had a  
197 single, but more ancient origin (e.g., Coddington et al., 2019; Garrison et al., 2016), versus  
198 multiple, convergent origins (e.g., Fernández et al., 2018; Kallal et al., 2020). Adding to this,  
199 (Eberhard, 2022) recently argued that a suite of several web-building behaviors shared across  
200 cribellate and ecribellate orb-weavers are homologous, and strongly favors a single origin of this  
201 web architecture. Like these behavioral characters, the positional and morphological similarity of  
202 the pseudoflagelliform and flagelliform silks glands in deinopids and araneoids, reinforces that  
203 they are homologous (Alfaro et al., 2018; Correa-Garhwal et al., 2022). Given that silk extruded  
204 from these glands is predominantly used in the orb-web capture spiral (for both cribellate and  
205 ecribellate orb-weavers) or in deinopid capture silk supporting fibers, resolution of the



206 phylogenetic positions of these spider lineages will not only inform the number of times the orb-  
207 web evolved, but also the number of times the pseudoflagelliform/flagelliform glands have been  
208 lost, as well as how silk fibers extruded from their spigots have functionally transformed over  
209 evolutionary time. Beyond the importance of the pseudoflagelliform gland, future studies are  
210 needed to understand the function and evolution of the entire suite of silk glands that allow  
211 deinopids to capture prey with their remarkable, hyper-extensible capture nets.

212

213 **Figure 1.** Silk glands of the net-casting spider *Deinopis spinosa*. Silk glands are oriented with  
214 the ducts (arrow) up and tails (star) at the bottom. A. Major ampullates, B. Minor ampullate, C.  
215 Aciniform cluster, D. Pyriform cluster, E. Tubuliform single, F. Pseudoflagelliform, G.  
216 Paracribellate cluster, H. Paracribellate single, and I. Cribellar cluster. Major ampullate, minor  
217 ampullate, aciniform cluster, pyriform cluster, pseudoflagelliform, and paracribellate are paired  
218 inside the spider and only one side is depicted. Scale bar = 500  $\mu\text{m}$ .

219

220 **Figure 2.** Cribellum and spinnerets of adult female *Deinopis spinosa*. A. Overview of spinnerets  
221 B. Anterior Lateral Spinneret (ALS), C. Posterior Lateral Spinneret (PLS), D. Posterior Median  
222 Spinneret (PMS) E. Cribellum, with close-up inset on upper left. Abbreviations as follows: Cr  
223 cribellum and spigot types, Py: pyriform, Ma: major ampullate, Tu: tubuliform, Ac: aciniform,  
224 Pflag: pseudoflagelliform, Mi: minor ampullate, Pcr: paracribellate.

225

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230

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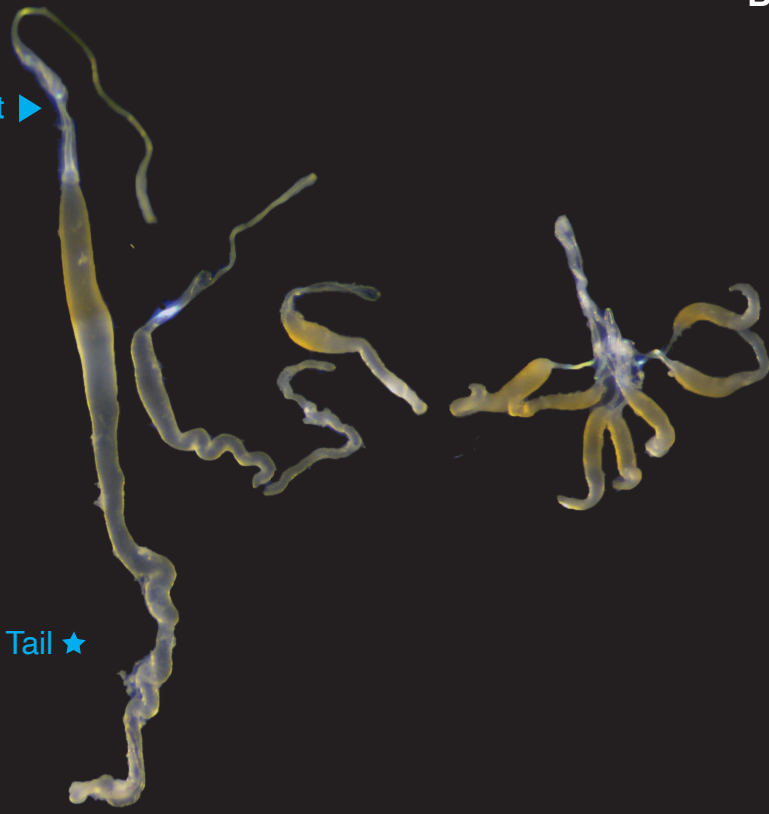
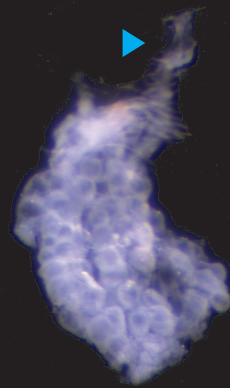
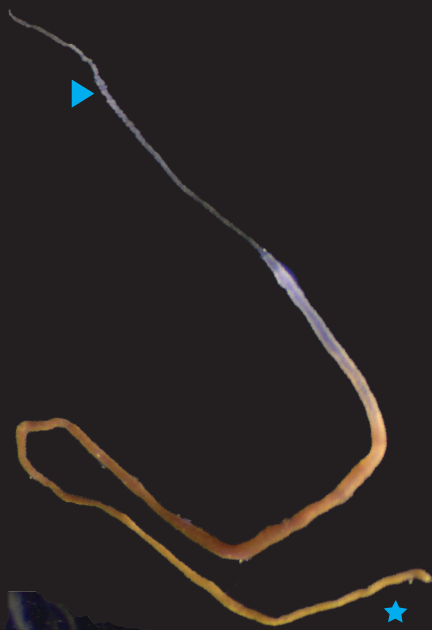
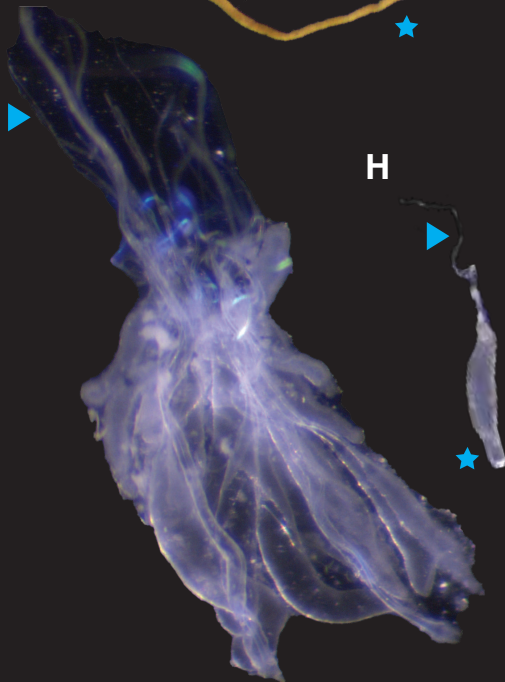
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**A**

Duct ▶

Tail ★

**B****C****D****E****F****G****H****I**