Silk-producing organs of ecribellate and cribellate nymphal stages in *Austrochilus* sp. (Araneae: Austrochilidae): Notes on the transformation of the anterior median spinnerets into the cribellum

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ABSTRACT

During its life cycle, the cribellate spider *Austrochilus* sp. passes through the ecribellate nymphal, or spiderling stage (= the first instar, after leaving the egg sac), which has three pairs of spinnerets. According to the position and distribution of spigots on the spinnerets, these spigots are assumed to be connected to *glandulae ampullaceae major*, *glandulae ampullaceae minor*, *glandulae piriformes* and *glandulae aciniformes*. Such a spinning apparatus allows spiderlings to make draglines, attachment discs and silk for the molting platform. The cribellum, just like the calamistrum, is not developed in this stage. Instead the precribellum is present, which is similar to spinnerets in its shape (two protuberances divided by a groove and the presence of setae that look like spigots), but with a cuticle similar to the cribellum. The spinning apparatus of *Austrochilus* sp. shows one possible way in which the transformation of the anterior median spinnerets into the cribellum could have occurred during the evolution of silk-producing organs. In the following nymphal stage, the cribellum, the calamistrum and also the paracribellum are developed. Spiders in this stage are capable, after dispersal, of weaving complete webs, which serve as snares as well as retreats. The spigots of the paracribellum are on the posterior median and posterior lateral spinnerets.

KEYWORDS: Austrochilidae, morphology, cribellum, spinnerets, life cycle, ontogenesis, spider phylogeny.

INTRODUCTION

The silk-spinning apparatus of spiders consists of spinnerets and silk glands located in the opisthosoma. Spinnerets are highly modified opisthosomal appendages (Kautzsch 1910; Yoshikura 1954). Silk-producing glands originate from ectodermal invaginations from the embryonic spinneret limb buds, in relation to the morphogenesis of these buds (Hilbrant & Damen 2015). Silk glands are connected to sets of spigots (nozzles), which are generally regarded as modified setae (Foelix 2011). Three main groups (infraorders) of Araneae are distinguished, viz. Mesothelae, Mygalomorphae and Araneomorphae (Coddington & Levi 1991).

The Mesothelae are the most basal branched-off group within spiders (Wheeler *et al.* in press). The most thoroughly described genera are *Liphistius* Schiödte, 1849 from South and Southeast Asia, and *Heptathela* Kishida, 1923 from Japan, Vietnam and China. *Liphistius* has four pairs of spinnerets: two pairs of multiseg-

mental lateral (anterior lateral and posterior lateral) spinnerets and two pairs of monosegmental median (anterior median and posterior median) spinnerets. The presence of four pairs of spinnerets is a plesiomorphic character (Haupt 2003). Except for the Mesothelae, four pairs of spinnerets are never formed, since no anterior median pair is developed. The presence of functional, i.e. silk producing, anterior median spinnerets has not yet been found in any species belonging to Mygalomorphae and Araneomorphae (true spiders). The Araneomorphae, which include over 90% of the total number of 46,499 known spider species (World Spider Catalog 2017) possess three pairs of spinnerets and a cribellum or alternatively a colulus. Cribellar threads are made by members of 180 spider genera in 23 families (World Spider Catalog 2017).

A complex important synapomorphy of araneomorphs is the fusion and reduction of the anterior median spinnerets to a cribellum (Coddington 2005). The cribellum is a sieve-like, transverse plate and from its holes protrude thin spigots in the form of segmented tubes. The number of these tubes ranges from several dozen to several thousand in adult spiders of different species and different sizes; these tubes are external ducts of small spinning glands producing very fine, dry and extremely adhesive cribellate silk ('catching silk'). This silk is combed out by the calamistrum and mixed with silk produced by the spinnerets (Kovoor 1987; Opell 2013). The calamistrum is a comb-like row of curved setae on the metatarsus of the fourth legs, probably modifying the cribellate fibres when in contact with them by shaping the puffy structure of the cribellate thread (Joel *et al.* 2015).

A remarkable structure, which is a part of the spinning apparatus of certain cribellate spiders, including Austrochilidae, is the paracribellum. Peters and Kovoor (1980) used the name paracribellum for clusters of specialized spigots that occurred on the posterior median spinnerets in some of the cribellate spiders they studied. These spigots resemble those of the cribellum, but they are far fewer in number (Peters & Kovoor 1980). It is suggested that paracribellar fibrils impart the consistency of the fibrillar secretion of the cribellum (Peters 1983, 1987). The paracribellum is described in detail from the family Uloboridae, where paracribellar fibrils form, together with axial fibres and cribellar fibrils, one of the components of the capture thread (Opell 2013; Joel *et al.* 2015).

The colulus is a non-functional remnant of the anterior median spinnerets. It usually looks like a projection or protuberance and sometimes it is represented by a setal patch. In the past, the presence or absence of the cribellum in so-called labidognath spiders (= Araneomorphae) was, in spider taxonomy, the reason for dividing them into two suborders, the Cribellatae and Ecribellatae (Gerhardt & Kaestner 1937; Kaestner 1969). This concept was later abandoned (Lehtinen 1967; Platnick *et al.* 1991). At present, a web equipped with cribellate silk is considered to be plesiomorphic. With changes in lifestyle (vagabond hunters), many araneomorph lineages lost the cribellum (Coddington 2005).

The Paleocribellatae (incl. a single family Hypochilidae) are hypothesized as a sister group to all other araneomorphs (= Neocribellatae) (Forster *et al.* 1987;

Garrison *et al.* 2016; Wheeler *et al.* in press). Therefore, within the Neocribellatae (remaining spider lineages) there are families that include spider species, both with and without the cribellum.

The Austrochiloidea (infraorder Araneomorphae) comprise two families Gradungulidae and Austrochilidae (Forster *et al.* 1987). Platnick (1977) placed these families as an early branching lineage of the 'higher spiders', due their retention of the primitive arrangement of four book lungs. The study of the silk spinning behavior and scanning electron microscopy examinations have revealed derived characters in common with higher spiders (Wheeler *et al.* in press), thereby challenging their grouping near the araneomorph base (Garrison *et al.* 2017; Wheeler *et al.* in press).

The family Austrochilidae Zapfe, 1955 is divided into two subfamilies, Austrochilinae and Hickmaniinae. The subfamily Austrochilinae include two genera (*Austrochilus* Gertsch & Zapfe, 1955 and *Thaida* Karsch, 1880) endemic to the Andean forests of central and southern Chile and adjacent Argentina (Forster *et al.* 1987; Grismado *et al.* 2003; Griswold *et al.* 2005). The Austrochilidae share characteristics with more advanced araneomorphs and primitive spiders in the infraorders Mesothelae and Mygalomorphae (Doran *et al.* 2001). Austrochilines build conspicuous and horizontally oriented aerial sheet webs (Lopardo *et al.* 2004) in moist forests (Forster *et al.* 1987; Lopardo *et al.* 2004). At least some austrochilids have cylindrical gland spigots and card their cribellate silk in a supposedly derived manner (like entelegyne spiders, and unlike Hypochilidae and Filistatidae) using one leg IV braced against the other mobile leg IV (Lopardo *et al.* 2004). The ecribellate four-lunged 'bizarre family' (Wheeler *et al.* in press) Gradungulidae from Australia and New Zealand, appears related to the cribellate four-lunged sheet-web builder from Tasmania, *Hickmania troglodytes* (Wheeler *et al.* in press).

The silk producing organs of adult specimens of *Austrochilus melon* Platnick, 1987 were described in detail by Forster *et al.* (1987) and Platnick *et al.* (1991). The spinning apparatus of adults of *Thaida peculiaris* Karsch, 1880 and *Hickmania troglodytes* Higgins & Petterd, 1883 was described by Forster *et al.* (1987), Platnick *et al.* (1991), Griswold *et al.* (2005) and Ramírez (2014). The terms used by the above authors in their descriptions of the morphology of the silk-producing organs, including the names of spigots (and their abbreviations) connected with different types of glands, are also adhered to in this paper.

The aims of our study were:

(1) To examine and compare the spinnerets, spigots and spinning ability in two subsequent nymphal stages in the life cycle of the genus *Austrochilus*. These stages differ by the presence (or absence) of the cribellum and calamistrum and, in the life cycle, they represent the ecribellate and cribellate nymphal stages.

(2) To examine the structure immediately in front of the anterior lateral spinnerets of spiderlings. With respect to the fact that this structure occurs in the ontogenetic cycle before the cribellum, it is provisionally referred to as the precribellum.
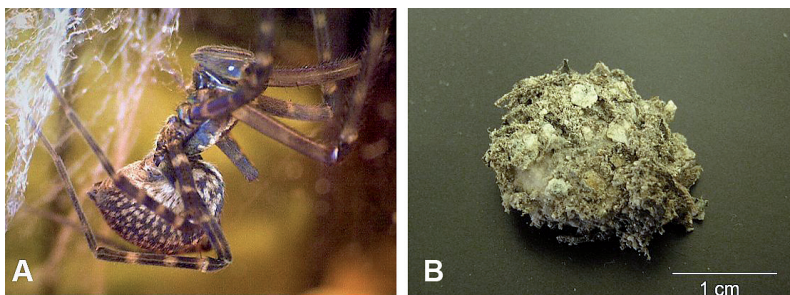
Fig. 1: *Austrochilus* sp.: (A) side view of male; (B) egg sac with surface covered (and therefore perfectly camouflaged) by dry plant debris and soil particles.

(3) To discuss implications of the transformation of anterior lateral spinnerets into the cribellum.

MATERIALS AND METHODS

Specimens of *Austrochilus* sp. (Fig. 1A) were collected at Los Lingues de Miraflores (33°22'43"S 71°02'00"W), Curacaví, Santiago, Chile by Dr Ivalů Maracena Herrera Ávila from the Department of Genetics and Microbiology, Faculty of Science, Charles University in Prague.

For the purpose of this study, we used young spiders in the first nymphal stage (N = 12) leaving the egg sac, i.e. spiderlings, and specimens in the subsequent nymphal stage (N = 11). The specimens of these two consecutive nymphal stages came from the same egg sac (Fig. 1B) produced in the laboratory by one of eight females kept in glass insectariums (35×35×40 cm). Spiderlings (Fig. 2) are 0.9–1 mm long (prosoma + opisthosoma) and remained on fibres of the maternal web in the vicinity of the egg sac (or on its surface) until their first ecdysis (i.e. for one or
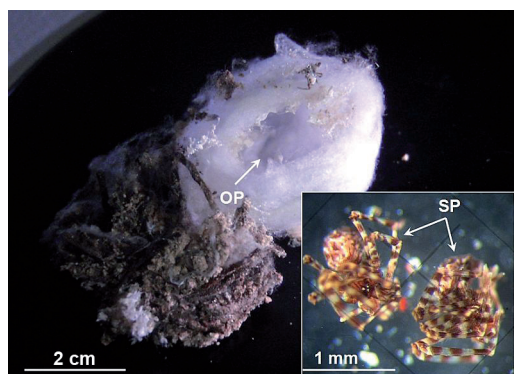

Fig. 2: Light micrograph of the egg sac and spiderlings (a framed picture). Abbreviations: OP – opening in the silken wall of the cocoon, SP – spiderlings.

two days). After ecdysis, specimens in the following nymphal stage (body length 1.1–1.2 mm) dispersed around the insectarium, where they started making their own webs.

Live spiders and their spinning activity were observed with a Novex stereo microscope, equipped with the INFINITY*lite* digital camera. The morphology of their spinnerets, in particular their spinning fields and spigots were studied under the TESCAN scanning electron microscope (SEM). For SEM studies, the spiders were killed by chloroform and dehydrated in ethanol and critical-point dried with carbon dioxide. After sputtering with gold, they were observed under the SEM. Voucher specimens were deposited at the Department of Biology, Faculty of Science, J.E. Purkinje University in Ústí nad Labem, Czech Republic.

<div align="center">

RESULTS
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Spinnerets and spigots of spiderlings

The spinning apparatus of this developmental stage consists of three pairs of distinctly segmented spinnerets (Fig. 3A), but unlike the following nymphal stage (Fig. 3B) spiderlings lack a cribellum and calamistrum. Spinnerets are equipped with four types of spigots. According to the position and distribution of spigots on the spinnerets it can be assumed, that these spigots are connected to *glandulae ampullaceae major*, *glandulae ampullaceae minor*, *glandulae piriformes* and *glandulae aciniformes*. The presence of ampullate glands allows spiderlings to produce draglines, which they attach to the substrate using attachment discs. The material for the attachment discs is produced by the piriform glands.
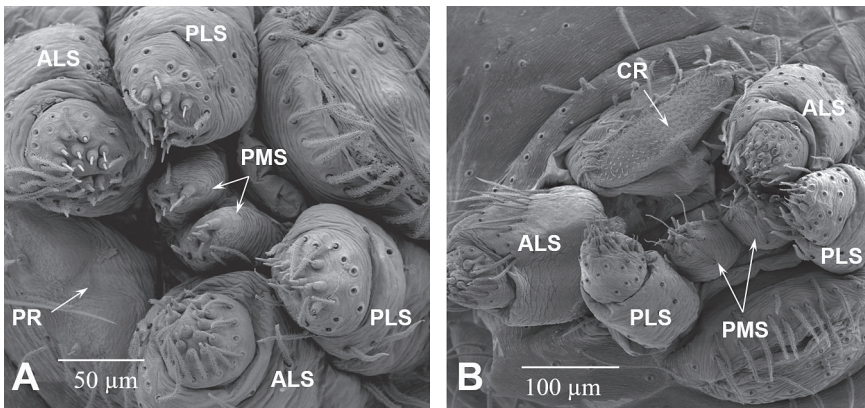

Fig. 3: Overviews of silk-spinning organs in two consecutive nymphal stages: (A) spiderlings (1st nymphal stage) that leaves egg sac. The spinning apparatus consists of three pairs of spinnerets, with precribellum being in place of undeveloped functional cribellum; (B) spinning apparatus of the second stage with a developed cribellum. Abbreviations: ALS – anterior lateral spinnerets, PMS – posterior median spinnerets, PLS – posterior lateral spinnerets, CR – cribellum, PR – precribellum.
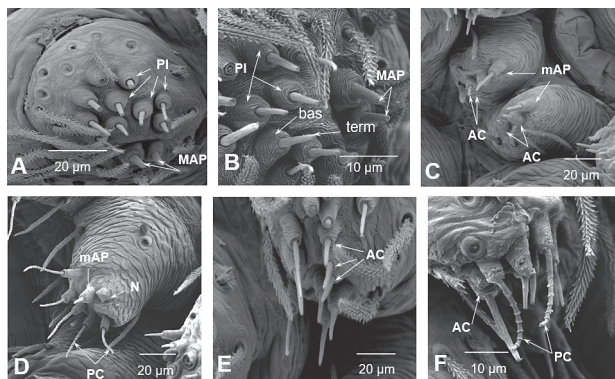
Fig. 4: Spigot placement on the spinnerets of first (A, C, E) and second (B, D, F) nymphal stages: (A) anterior lateral spinneret (ALS) of first nymphal stage (NI); (B) ALS of second nymphal stage (NII); (C) posterior median spinnerets (PMS) of NI; (D) PMS of NII; (E) posterior lateral spinneret (PLS) of NI; (F) PLS of the NII. Abbreviations: MAP – major ampullate gland spigot(s), PI – piriform gland spigot(s), AC – aciniform gland spigot(s), mAP – minor ampullate gland spigot(s), PC – paracribellar spigot(s), N – nubbin (tartipore) of mAP spigot, bas – basal part (socket), term – terminal part (shaft) of spigot.

The anterior lateral spinnerets (ALSs) (Figs 3A, 4A) are three-segmented; the spinning field of the apical segment of each of them is equipped with 11–12 piriform gland spigots and two major ampullate gland spigots located on the inner margin of the spinning field. When compared with the piriform gland spigots, the terminal part of the ampullate gland spigot (i.e. the 'shaft') is longer and thicker, and its basal part consists of a large socket. The sockets of ampullate and piriform glands bear distinct ridging.

The posterior median spinnerets (PMSs) are smallest of the three pairs of spinnerets (Figs 3A, 4C) and are only one-segmented. Each PMS is equipped with one minor ampullate gland spigot and two aciniform gland spigots. In total, there are only three spigots on each PMS.

The posterior lateral spinnerets (PLSs) are two-segmented (Fig. 3A); the spinning field of each of them is equipped with 14 aciniform gland spigots (Fig. 4E).

The cuticle surrounding the spinning fields of all the three pairs of spinnerets is covered with plumose setae, which emerge from less-developed sockets in contrast to spigots.

Precribellum

The precribellum of *Austrochilus* sp. is a plate-like structure situated between the anterior lateral spinnerets, i.e. at the place where the cribellum is located in the following nymphal stage (Figs 3A, 5A). A groove leads through the middle of the precribellum heading in the anteroposterior direction dividing it into two parts and giving this structure a distinctively bipartite appearance. Both parts look approximately like triangular protuberances and each of them is equipped with one seta, very similar to the spigots located on the spinning fields of spinnerets
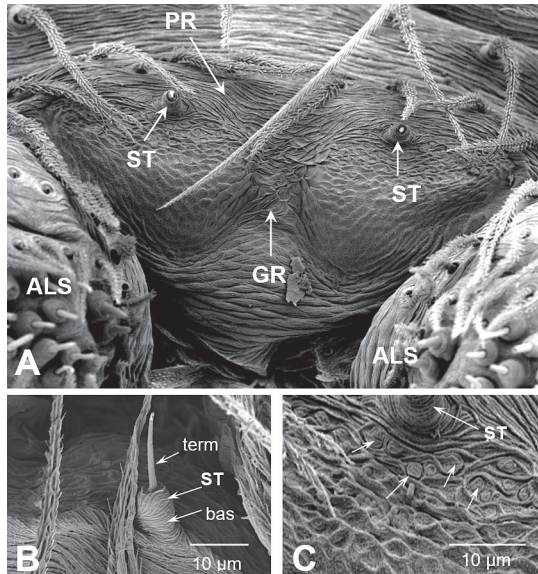
Fig. 5: Precribellum of spiderlings: (A) overview of precribellum; (B) detail of one spigot; (C) detail of the ultrastructure of the cuticle surface near the spigot where the microstructure of the surface, divided into bordered fields (marked with arrows), resembles the cribellum. No segmented spigots have developed here. Abbreviations: PR – precribellum, ST – setae (spigots?), GR – groove dividing the precribellum into two separate parts, bas – basal part (socket) of ST, term – terminal part (shaft) of ST.

(Fig. 5A). Similarly to the spigots, both setae also have a basal part (socket) that protrudes above the cuticle surface and is connected with the terminal part (shaft), which is almost identical in appearance to the shaft of the spigots (Fig. 5B). The sockets of these setae bear the same ridging as spigot sockets of the piriform and ampullate glands of the ALSs. It has not been proven yet whether both setae are functional spigots emitting silk secretion.

The cuticle has a conspicuous microstructure: at certain places (especially near the spigots) it is divided into small fields, similar to those that can be found on the surface of a functional cribellum (Fig. 5C). In the following nymphal stage, the precribellum is replaced with the cribellum.

Spinning apparatus of the second nymphal stage

Young spiders in the second developmental stage have silk producing organs consisting of three pairs of spinnerets (Fig. 3B), but unlike in the previous stage (Fig. 3A), they have developed a cribellum (Figs 3B, 6A) as well as a calamistrum (Fig. 6B). Their spinnerets are equipped with the same types of spigots and the same types of glands connected to them as in the previous stage. However, for the first time spinnerets of these spiders are equipped with segmented spigots, associated with the cribellum and paracribellum glands.
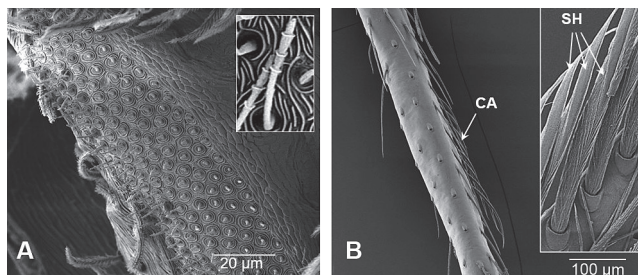
Fig. 6: Cribellum and calamistrum of the second nymphal stage: (A) detail of the surface of the cribellum, divided into small fields, from which segmented spigots arise (framed detail); (B) calamistrum – a row of specialized setae, whose shafts are flattened at their ends (see framed detail). Abbreviations: CA – calamistrum, SH – shafts.

As in spiderlings, the ALSs are each equipped with two spigots of major ampullae glands (Fig. 4B), but in comparison with the previous stage, the number of piriform gland spigots is greater (16–17).

Monosegmental PMSs (Figs 3B, 4D) are each equipped with one minor ampullate gland spigot and five paracribellar spigots. The presence of aciniform gland spigots was not detected here (unlike in spiderlings). Nubbins, located on the PMSs next to the major ampullate gland spigots (MAP) (Fig. 4D) represent so-called 'tartipores' *sensu* Townley and Tillinghast (2003) and Dolejš *et al.* (2014), which are non-functional structures that emerge after ecdysis from the minor ampullate gland spigot (mAP), functional in the previous instar; thus, they are missing in spiderlings. The presence of the paracribellum is a crucial qualitative change, which occurs in the ontogenesis of the PMSs (and also PLSs).

The PLSs are two-segmented; the spinning field of the apical segment of each of them is equipped with 12 aciniform gland spigots and 2 paracribellar spigots.

Cribellum

The perforated spinning area of this organ is entire, without visible vestiges of bipartition (Figs 3B, 6A). The area is divided into approx. 226–232 (N=6) small fields bordered by slats around their holes, wherefrom the same number of segmented tubes emerges.

Calamistrum

The calamistrum forms a single row of eight socketed setae with curved shafts (Fig. 6B). The proximal parts of setal shafts are ridged at the places where they connect with sockets, whereas their distal parts are flattened and smooth.

DISCUSSION AND CONCLUSIONS

During their ontogenesis, cribellate spiders of the genus *Austrochilus* pass through an ecribellate nymphal stage (spiderlings), when they have three functional pairs of spinnerets with spigots connected to ampullate, piriform and acini-

form glands. Such a spinning apparatus allows spiderlings to make (i) draglines, (ii) attachment discs, and (iii) silk for the moulting platform. Draglines, also referred to as lifelines (Osaki 1996), play a very important role in the life of spiders of the infraorder Araneomorphae. Anchored to the substratum by attachment discs, the silk track allows the spider to return safely to the starting point after a thrust at prey or following a free fall; it also allows spiderlings to maintain contact with the maternal web (Osaki 1996). The dragline material is produced by a pair of MAP, while the material of the attachment discs is secreted by piriform glands (Foelix 2011; Sahni *et al.* 2012). In *Austrochilus* sp., exactly as in other Araneomorphae, the spigots of both these glands are located on the surface of the anterior lateral spinnerets. Besides ampullate and piriform glands, the spinning apparatus of spiderlings of *Austrochilus* sp. is equipped with aciniform glands. Silk from these glands, whose spigots are located on PMSs and PLSs, is used by spiderlings for making molting webs. These glands have a similar role also in other families. After studying developmental changes in the spinning apparatus of wolf spiders (Araneae: Lycosidae), Dolejš *et al.* (2014) suggested that the function of aciniform silk is to serve as an ancillary 'scaffold' supporting the spider's body during ecdysis. Aciniform glands occur in all spiders of the infraorder Araneomorphae (Coddington 1989) and the silk they produce, together with the silk produced by tubuliform glands, is often used by adult females for building egg sacs (Foelix 2011).

Glands resembling aciniform glands were also found in some spiders of the infraorder Mygalomorphae, which led to the conclusion that aciniform silk was one of the earliest forms of silk to evolve (Blackledge 2013). The aciniform fibres of the Mygalomorphae and Araneomorphae may adhere to the substrate as well as to each other (Eberhard 2010; Hajer *et al.* 2013, 2016).

However, the nymphal stage of *Austrochilus* sp. that leaves the egg sac has neither cribellum nor calamistrum and cannot catch prey with the web fibres. Instead a precribellum is present, which appears like a pair of spinnerets rather than a proper cribellum mainly due to the groove that divides it in the anteroposterior direction into two protuberances. Furthermore, it also has setae, whose morphology is identical to the spigots of the three pairs of spinnerets through which silk is emitted. The function of these 'spigots' is unknown. If these setae would be external ducts of silk producing glands, then the precribellum could be considered to be functional, or at least not completely reduced AMSs, which bear a function in the early nymphal stages that has not yet been explained.

The development of the spinning apparatus of *Austrochilus* sp. reflects a possible scenario how the transformation of the AMSs into the cribellum could have occurred during the evolution of spiders. Ramírez (2014) described the similar intermediate morphology for *Thaida peculiaris* (Austrochilidae) and *Ectatosticta davidi* (Hypochilidae) and reported its absence in *Hypochilus pococki* (Hypochilidae) and *Filistata insidiatrix* (Filistatidae).

Based on the current state of knowledge, the precribellum can be considered a transitional structure, with two divided protuberances and the presence of a pair of

'spigots' resembling spinnerets, while its cuticular fine structure resembles those of the cribellum. In the development of *Austrochilus* sp., the precribellum is replaced in the second nymphal stage with the cribellum. A similar situation was reported for other cribellate genera that also lack a cribellum in spiderlings, for example *Amaurobius* L. Koch, 1837, *Eresus* Walckenaer, 1805, *Dictyna* Sundevall, 1833, *Nigma* Lehtinen, 1967, and *Titanoeca* Thorell, 1870 (Hajer 1988, 1990*a*, *b*). However, in these genera the protuberances, located at the future position of the cribellum, are equipped with no setae that resemble spigots. Instead, there are 'plumose hairs', i.e. setae, which bear many fine laminar extensions along the entire hair shaft. The same setae can be found not only on the surface of all segments of spinnerets, but also on other parts of the spider's body, e.g. on the surface of the legs. With their shape and the presence of the hairs, these protuberances resemble coluli and the microstructure of their cuticle surface does not resemble the cribellum (Hajer 1988, 1990*a*, *b*).

In the following nymphal stage of *Austrochilus* sp. the calamistrum and also the paracribellum occur together with the cribellum. As of this stage, juvenile spiders are able to build snares for catching prey. In comparison with the spiderlings the presence of the paracribellum changes especially in the PMSs, whose main function is clearly to provide one of the components of cribellar thread support lines. Besides paracribellar spigots, we found one minor ampullate gland spigot and tartipore on each PMS. The tartipores, vestigial structures corresponding to spigots of the previous instar, through which silk gland ducts pass during proecdysis, appear on the spinning field starting with the second instar (for explanation see Dolejš *et al.* 2014). Tartipore-accommodated glands also play roles during proecdysis and their evolution corresponds with how spiders secure themselves when molting (Townley & Tillinghast 2003).

The paracribellum is—from the perspective of the evolution of the spinning organs of cribellate spiders—just as important as the cribellum itself. Its segmented tube-like spigots are comparable in structure with those of the cribellum, and in cribellate spiders they are located on both PMSs and PLSs (Peters & Kovoor 1980; Peters 1983, 1987). The histological features of the associated glands are similar to those of the cribellar glands; histochemically, they seem closer to pseudoflagelliform glands (Peters & Kovoor 1980). Pseudoflagelliform glands, whose spigots are located on the PLSs, provide fibers, which work as axial supports of the cribellar wool. This kind of gland is undeveloped in all cribellate families and missing in, for example, Dictynidae and Filistatidae (Kovoor 1987). Paracribellar fibrils may impart consistency to the fibrillar secretion of the cribellum (Peters & Kovoor 1980) and they form part of the cribellar thread support lines system (Opell 2013).

A summary of cribellate families in which the presence (or absence) of a paracribellum has been detected is unavailable so far. However, it is certain that not all cribellate families have a paracribellum, as, for example, the cribellate families Eresidae and Oecobiidae. Indeed, the loss of the paracribellum is one of the

synapomorphies of the superfamily Eresoidea (Miller *et al.* 2012). The paracribellum is also missing in paleocribellate spiders of the family Hypochilidae. Austrochilidae are cribellate spiders whose PMS are equipped with paracribellar spigots. The presence of the paracribellum was demonstrated in three genera that belong to this family, i.e. *Thaida* Karsch, *Austrochilus* Gertsch & Zapfe and *Hickmania* Gertsch, 1958 (Platnick *et al.* 1991; Griswold *et al.* 2005).

Comparison of the spinnerets and spigots of two consecutive nymphal stages in the genus *Austrochilus* shows that the first stage (i.e. spiderlings) has a functional spinning apparatus (i.e. capable of silk production), but has not yet developed the cribellum, calamistrum or paracribellum. The following (second) nymphal stage has developed the cribellum and calamistrum and after dispersal it is thus capable of weaving complete webs that serve as snares and retreats.

Based on previous studies on cribellate spiders (Hajer 1988, 1990*a*, *b*), we are convinced that during their ontogenesis many of these spiders go through stages in which their spinnerets are capable of silk production, but no functional cribellum is developed. In such cases it is necessary to examine in great detail not only the structure of the spinning apparatus in juvenile spiders, but also the role of silk in the life of this ecribellate (or precribellate) stage. In addition to early nymphal stages, adult males should be studied, whose reduced cribellum loses its ability to produce 'catching silk' after the spider reaches sexual maturity. The silk-producing organs of adult males therefore represent the postcribellate stage of the spinning apparatus in the life cycle of cribellate spiders. Thus the ability of adult males to produce silk is comparable to that of spiderlings.

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