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Web-building behavior of the odd-clawed spider *Progradungula otwayensis* (Araneae: Gradungulidae) and implications for the evolution of combing behavior in spiders

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Abstract. This study explores the web-building behavior of Gradungulidae for the first time, using the Otway odd-clawed spider *Progradungula otwayensis* Milledge, 1997. The web consists of a signal line leading to a retreat, an upper scaffold and a cribellate catching ladder connected to the substrate. The construction sequence and final structure of the catching ladder are highly stereotyped, especially in the initial segments of the cribellate capture thread. Two vertical rail lines—made of thin cribellate silk that is not combed with the calamistrum—are connected by looping segments of combed, much thicker cribellate capture threads. Small juveniles make a relatively larger non-sticky supporting scaffold with some cribellate silk on it. Microscopic analysis of the silk revealed that the cribellate bands have a pair of axial lines and a pair of reserve warps; the cribellate fibrils have nodules. The non-sticky structural lines are made of straight or coiling lines, changing gradually from straight to coiling; each of these structural lines is composed of tightly appressed fibrils, probably associated with the occurrence of multiple ampullate gland spigots. During combing behavior both legs IV are used synchronously. The same combing behavior is performed by the Tasmanian cave spider *Hickmania troglodytes* (Higgins & Petterd, 1883). We conclude that both type I and type II combing behaviors are monophyletic, although it is unclear which one is ancestral. Given the phylogenetic position of *Progradungula* Forster & Gray, 1979, we suggest that the ability to measure with precision and produce repetitive, stereotyped silk structures made of specific silk types may have arisen close to the ancestor of araneomorph spiders.

Keywords: Silk, cribellum, Austrochiloidea, web

Spiders are well known for their ability to produce silk and many of them construct webs with sticky threads to catch prey. In general, two main types of sticky threads can be distinguished—dry, *cribellate* capture threads produced by minute cribellar spigots and viscid, *ecribellate* capture threads characterized by droplets of sticky glue produced by the aggregate gland spigots (Foelix 2011). The structures used to produce cribellate silk evolved early in Araneomorphae and have been suggested to be a synapomorphy of this largest spider group (Lehtinen 1967; Platnick 1977; Wheeler et al. 2017). Although most araneomorph lineages lost the cribellum and use ecribellate capture threads for prey catching or developed web-less predatory strategies, around one fourth of the araneomorph families still have cribellate representatives (e.g., Eberhard & Pereira 1993; Griswold et al. 1999; Griswold et al. 2005).

Cribellate silk is highly-effective (Opell & Schwend 2009) and consists of a wooly mass of nanofibers which are supported by two axial fibers, and in most cases, two additional curly strands called reserve warps (Kullmann 1975; Eberhard & Pereira 1993) or undulating fibers (Peters 1987). Cribellum threads are pulled from the cribellum using a comb of setae (the calamistrum) on the posterior metatarsi (Joel et al. 2015). Based on a comparative study, Eberhard (1988) described two basic and distinct behavior patterns with which cribellate silk is combed from the cribellum. In *type I*, the combing leg IV rests on the contralateral leg III, whereas in the *type II* the combing leg IV rests on the contralateral leg IV and both legs move synchronously as a rigid unit. The type I combing behavior is known only for the closely related lampshade weavers (Hypochilidae) and crevice weavers (Filistatidae), which together are the sister-group to Synspermiata (Bond et al. 2014; Garrison et al. 2016; Wheeler et al. 2017; Fernández et al. 2018). All other groups with cribellate representatives investigated so far are characterized by the type II combing behavior. Even though there is considerable information on combing behavior within the highly diverse Entelegynae, only one study addressed the web-building behavior in the enigmatic superfamily Austrochiloidea (Lopardo et al. 2004, see below). This taxon was considered to be the sister-group of all higher araneomorph spiders (Platnick 1977; Ramirez 2000; Griswold et al. 2005), but based on target gene as well as phylogenomic analyses this clade of austral spiders seems to be more closely related to leptonetids, and all together to palpimanoid and Entelegynae spiders (Wheeler et al. 2017; Fernández et al. 2018). In either case, because of their pivotal placement among the most ancestral branches of aerial web building spiders, the behavior of austrochiloids is crucial to reconstruct the evolution of web-building in araneomorph spiders.

Austrochiloids are represented by two families, Austrochilidae and Gradungulidae, consisting of only few genera and species (World Spider Catalogue 2019). Austrochilidae occur in Chile, Argentina (*Austrochilus* Gertsch & Zapfe, 1955 and *Thaida* Karsch, 1880, subfamily Austrochilinae) and Tasmania (*Hickmania* Gertsch, 1958, subfamily Hickmaniinae), whereas Gradungulidae are restricted to East and Southeast Australia (*Progradungula* Forster & Gray, 1979, *Macrogradungula* Gray, 1987, *Kaiya* Gray, 1987 and *Tarlina* Gray, 1987) and the South Island of New Zealand (*Gradungula* Forster, 1955, *Spelungula* Forster, 1987 and *Pianoa* Forster, 1987). In contrast to the large sheet webs of Austrochilidae, two gradungulid genera, *Progradungula* and *Macrogradungula*, build webs with a very peculiar cribellate prey-catching ladder (Forster & Gray 1979; Gray 1983; Forster et al. 1987; Milledge 1997; Michalik et al. 2013). While the web-building behavior of gradungulids has never been observed, a detailed study by Lopardo et al. (2004) on the South American austrochilid species *Austrochilus forsteri* Grismado, Lopardo & Platnick, 2003 and *Thaida peculiaris* Karsch, 1880 showed a type II combing behavior for austrochilines and their evolutionary reconstruction suggested that this type might be characteristic for the superfamily.

In this paper we addressed the following questions – (1) How does *Progradungula* builds its cribellate catching ladder; (2) How do *Progradungula* and *Hickmania* comb their silk; and (3) what are the implications for the evolution of combing behavior in Araneomorphae?

METHODS

Specimen data.—We investigated the web-building behavior of the Otway odd-clawed spider, *Progradungula otwayensis* Milledge, 1997, which is endemic to the Otway Ranges in Victoria (Australia). The Otway odd-clawed spider received its common name from the dissimilar superior claws of the first and second legs (one of them raptorial, long and strongly developed), and from its highly restricted distribution in the humid forests of the Great Otway National Park in Victoria, Australia (Michalik et al. 2013). We observed 66 specimens and their respective webs in the Great Otway National Park at the following localities in the following types of habitat: Little Aire Cascade Trail, E. of Lavers Hill, 38.67032°S, 143.49810°E (GPS, ±100 m), elev. 330 m, 11 February 2013, *Nothofagus*, *Eucalyptus*, tree ferns wet forest (MJR-Loc-125); Triplet Falls Trail, E. of Lavers Hill, 38.67188°S, 143.49673°E (GPS, ±300 m), elev. 300 m, 10 February 2013, *Nothofagus*, *Eucalyptus*, tree ferns wet forest (MJR-Loc-124); Maits Rest Trail, W. of Apollo Bay, 38.75492°S, 143.55495°E (GPS, ±200 m), elev. 240 m, 13–14 February 2013, *Nothofagus*, tree ferns, wet forest (MJR-Loc-126); Melba Gully Trail, 38°41.726′S, 143°22.312′E (GPS, ±200 m), elev. 328 m, 15 February 2013, *Nothofagus*, tree ferns wet forest (MJR-Loc-128). Web-building behavior was observed during the night using headlamps with red LED light. The combing behavior of the Tasmanian cave spider, *Hickmania troglodytes* (Higgins & Petterd, 1883), was observed in two localities and habitats in Tasmania (Australia): Bates Creek rainforest, Francistown, 43.30487°S, 146.98983°E, elev. 137 m, 22 February 2013, under big logs; Honeycomb Cave, Mole Creek, 41.59983°S, 146.40813°E, elev. 313 m, 24 February 2013. Vouchers are deposited in the Museo Argentino de Ciencias Naturales (MACN, Buenos Aires, Argentina) and the Zoological Institute and Museum of the University of Greifswald (ZIMG).

Silk collection and imaging.—Web samples of *P. otwayensis* were taken in the field using a frame of thick adhesive tape on a glass slide as described in Ramírez et al. (2013). Approximate measures of signal threads were taken with a measuring tape from the upper scaffold to the entrance of the hollow or resting site. Incident light images of silk samples were obtained with the BK PLUS Lab system (Dun Inc., USA) with a customized microscope lens (Ocellus) using a 10x Mitutoyo objective mounted on a Canon 7D Mark II camera. Image stacks were processed using Zerene Stacker and Adobe Photoshop CS6. Transmitted light images were taken with a Leica DM2500 microscope and a DFC7000 T camera. Extended focal range images were obtained by combining focal planes with Zerene Stacker or Helicon Focus. Scanning electron microscope images were obtained with a FEI XL30 TMP or a field emission Zeiss Supra 40 in high vacuum, after sputter coating the whole slide with AuPd. Images of spigots were obtained with a Leica M165 stereomicroscope. For the description of the web and silk elements we followed the terminology of Eberhard & Pereira (1993).

Evolutionary reconstruction.—The evolution of characters was traced by parsimony using TNT on a summary phylogenetic tree combining the results from Garrison et al. (2016), Wheeler et al. (2017) and Fernández et al. (2018), following the later study in cases of discrepancies.

RESULTS

Web structure and building.—The webs of *P. otwayensis* resemble the description given by Gray (1983) for *P. carraiensis* Forster & Gray, 1979. The main regions of the web can be summarized as (1) an upper scaffold, (2) a pair of suspensor lines, and (3) a catching region, which lies between the upper and lower bridge lines (Fig. 1B). The *upper supporting scaffold* is connected by a single, sturdy *signal line* to a retreat area, usually in a hollow tree (Fig. 1; Michalik et al. 2013). The signal lines vary substantially in length (80 ± 52 cm, range 10–260 cm, $n = 31$). Most of the specimens were found in hollows of myrtle beech trees (*Nothofagus cunninghamii*), but also in hollows of mountain ash trees (*Eucalyptus regnans*), bases of large tree ferns (*Dicksonia antarctica*), or miscellaneous structures of the low vegetation or wooden bridges on trails (*Nothofagus* 47, *Eucalyptus* 7, tree ferns 6, misc. 2, $n = 62$) (see also Milledge 1997; Michalik et al. 2013). One large hollow *Eucalyptus* tree hosted five specimens; there were no traces of elaborate resting refuges or silk-lined areas.

The web is composed of structural, non-sticky threads supporting a catching ladder of sticky cribellate silk (Figs. 1–3). The upper scaffold is attached to the signal line on top, and two or more lateral attaching points on the ground or on the surrounding vegetation. The simplest upper scaffold is a single line (Fig. S1C, online at http://dx.doi.org/10.1636/JoA-S-18-104.s1) while the more irregular take advantage of twigs as attachment points (Fig. S1A). Small immatures seem to build more regular, approximately triangular upper scaffolds between the signal line and two lateral attachment lines (Figs. 3C, S1B, S2A, online at http://dx.doi.org/10.1636/JoA-S-18-104.s2; $n = 3$). From the upper scaffold come the two *suspensor* lines whose lower ends connect to the vertical *rail* lines of the catching ladder. The rail lines are held parallel by the *upper and lower bridges*. The *catching ladder* of cribellate silk begins in an *upper diagonal* segment leading to a *lower cross*, and then up again into several *looping segments* attached to the rails and crossing from side to side (8.1 ± 2.4 crossing segments, $n = 15$; Figs. 2, 3A,B).

All 6 observed specimens used both fourth legs for combing, with the stereotyped type II behavior (Fig. 6D). Combing an entire ladder took about half an hour (27–34 minutes) in two specimens observed. We observed a complete sequence of ladder construction of a penultimate male. We first removed the entire ladder, leaving just a small remnant of it at 21:27 hours. The spider stayed up on the signal line. At 21:36, the spider descended into the ladder area, facing down, grasping a previous line with at least one extended leg IV. The spider

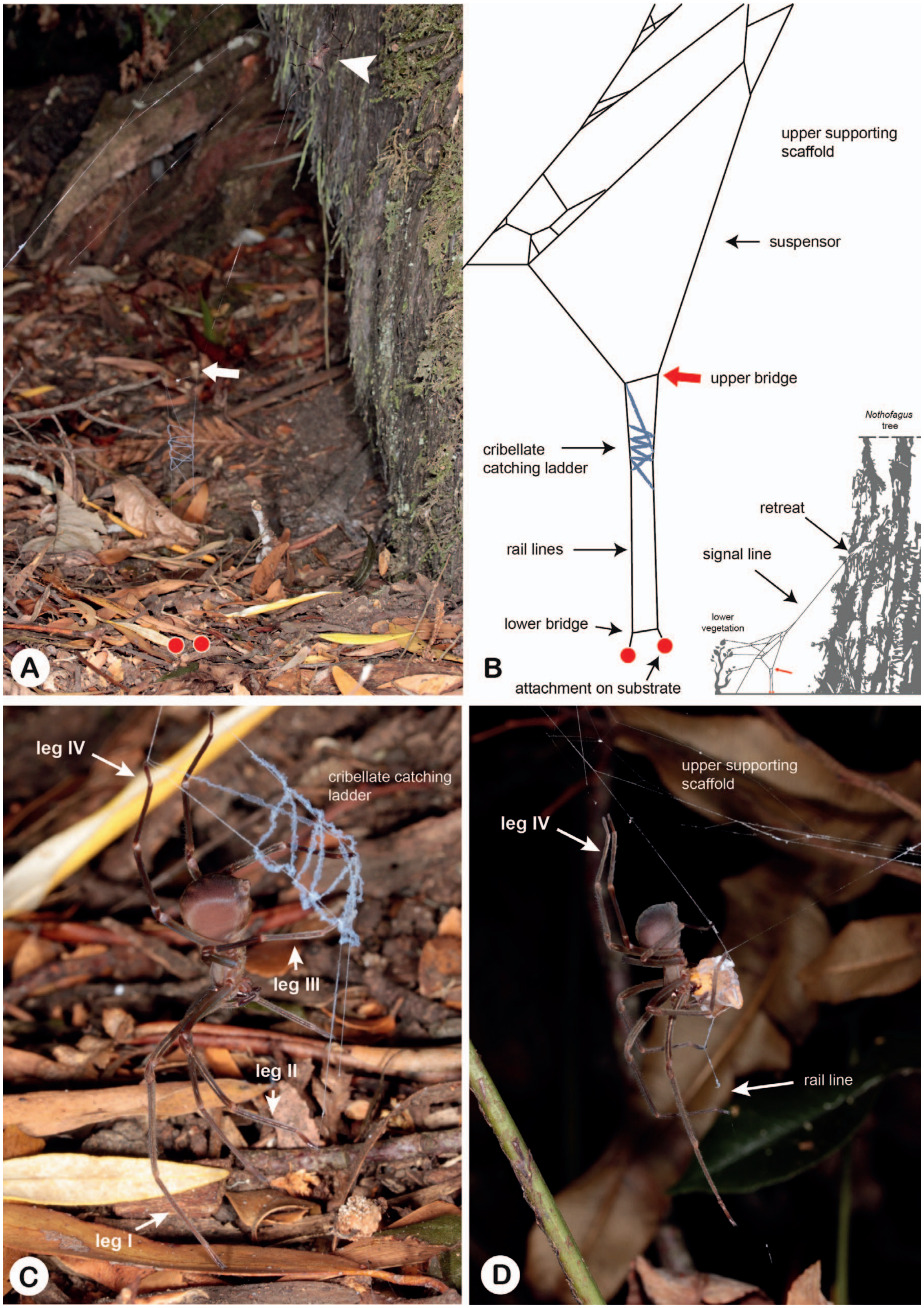

Figure 1.—A. Catching ladder and upper scaffold of a penultimate male of *P. otwayensis* (arrowhead to spider, arrows to upper bridge and red dots mark attachment to substrate). B. Schematics of the web. C. Same, specimen in stalking position. D. Another penultimate male feeding on a crab spider.

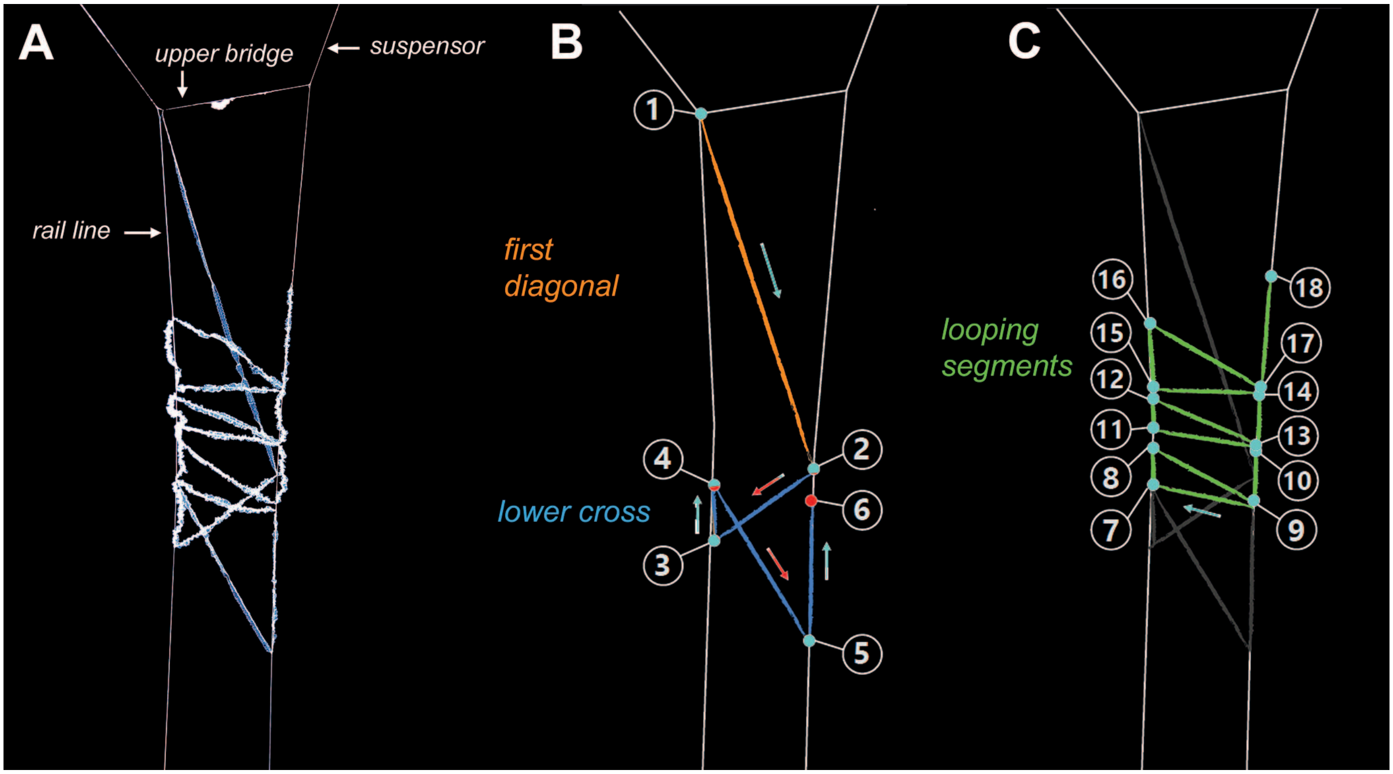

Figure 2.—A. Detail of catching ladder (same as Figs. 1A-C). B, C. Schematics of sequence of construction.

encountered the small remnant, made a ball, and brought it near its mouth, while facing downward. This ball remained in the upper bridge (Fig. 2A). Then the spider went up to the scaffold and down to the soil surface three times, making attachments to lay the rail lines of the ladder, without combing. Upon reaching the soil, each time the spider waved the anterior legs, as if exploring the surface. We could not distinguish the making of the lower bridge. At 21:43, the specimen started combing the first ladder segment (the upper diagonal) from attachment point 1 (top left in Fig. 2B), facing down, gradually combing laterally and finally attaching on the other rail line (point 2). The spider moved up about 3 cm and started combing a new segment face up, then attached it to the opposite rail line (point 3) thus making the second diagonal, part of the lower cross. From here, all segments were about the same length while in the process of combing; the vertical segments on the rail lines were not tense, with attachment points close to each other, while the transversal segments were under more tension. The combing legs irregularly alternated between segments (from attachment points 11 to 17, the combing legs were right, left, left, left, [not seen], right). After 34 minutes (22:10), the ladder was completed (Figs. 1A, 2A), and the spider took the waiting position (Fig. 1C). The original scaffold lines are visible in Fig. 1A. Four additional partial sequences of ladder construction were observed, all conforming to the same sequence just described (see intermediate stages in Fig. 3A, B). There was no lateral preference of the starting point (5 ladders started on left side, relative to the position of 11 stalking spiders), and no preference either on when to end the ladder (in 12 times out of 19, the last combed segment ended on the opposite rail line, relative to the initial attachment point 1 of the ladder, binomial test $P = 0.92$). Of two consecutive ladders constructed by the same spider, one started on each side.

All elements of the ladder (suspensors, rail lines, upper and lower bridges, upper diagonal, lower cross and looping segments) were present in all webs, differing only in the number of looping segments. In only a single case did a ladder lack half of the lower cross (Fig. S1D). Most ladders were vertical or slanted; we found only one completely horizontal. We did not find ladders of small immature specimens in the open; presumably they build their snares inside the hollow trunks. We had access to the interior of a large hollow *Eucalyptus* tree, and found two small spiderlings with complete webs and rather triangular supporting scaffolds (e.g., Figs. 3C, S1E). Both webs had irregular loops of cribellate silk on the scaffold (Figs. 3C, S2), reminiscent of those found in austrochilids (see below).

Hunting and prey.—The hunting position is similar to that reported for *P. carraiensis* by Gray (1983). Leg I stays free, gently contacting the substrate or occasionally just above it. Leg II holds the rail line, just below the lower bridge. Legs III push and tense the rail lines, on the sides of the ladder. Leg IV holds the suspensor, just above the upper bridge. Three specimens were observed feeding on tipulid flies and one on a crab spider (*Sidymella* sp.), in both cases hanging head down from the hind legs while consuming the prey (Fig. 1D). Several individuals stalked on worn ladders (Fig. S1A); it is unclear how those were damaged.

Silk structure.—The web of *P. otwayensis* is made of two basic types of threads, for simplicity referred to as structural and capture threads. The signal line is a thick cable made of

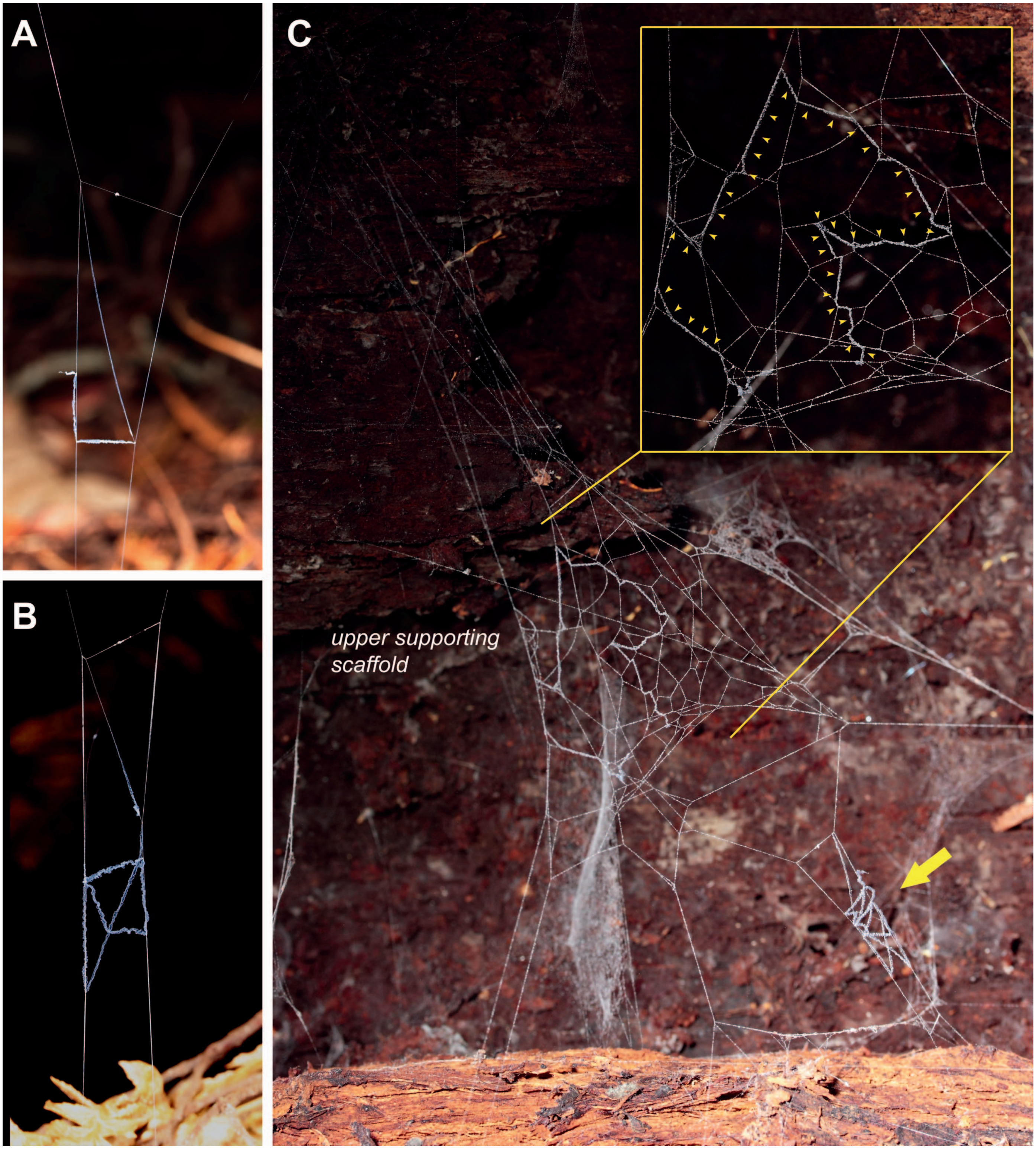

Figure 3.—A, B. Catching ladders interrupted in early stages of construction. C. Complete web of a small immature in the interior of a hollow *Eucalyptus* tree (arrow points to the catching ladder). The inset shows the cribellate silk in the upper scaffold (arrowheads; see also Fig. S2B).

several parallel fibers (Fig. 4A). Each fiber is composed by tightly appressed filaments, which sometimes separated and coiled, probably as an effect of our tearing the signal line while collecting the sample (Figs. 4B, S3A–C, online at http://dx.doi.org/10.1636/JoA-S-18-104.s3). The upper scaffold is made of similar silk as the signal line, with straight and coiled segments (Fig. 4C); the same continuous fibers were included in both straight and coiled segments (Figs. S3D–G). The

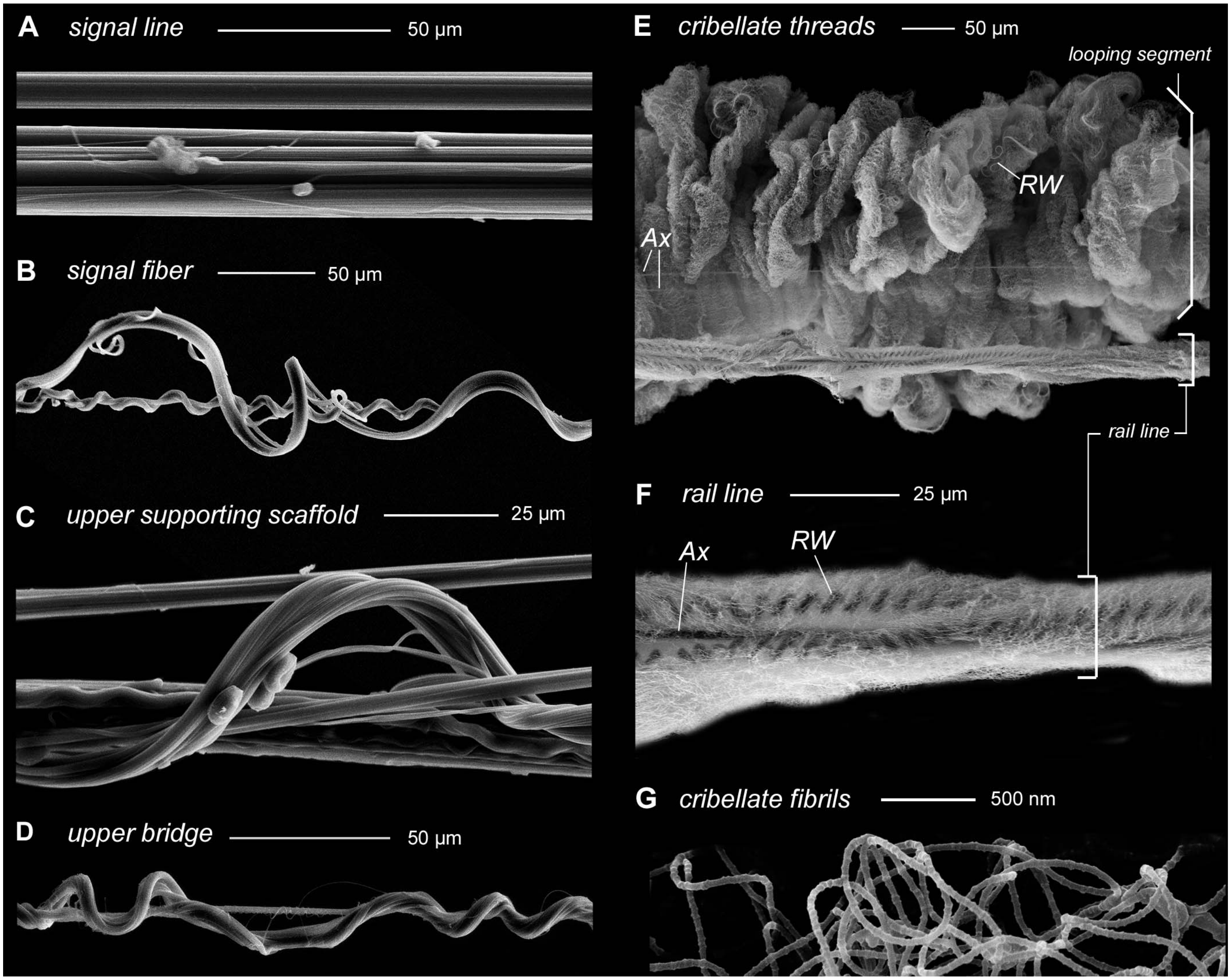

Figure 4.—Scanning electron microscope images of silk of *P. otwayensis*. A. Signal line, composed of several parallel silk threads; note the fibrous structure of each thread. B. A single thread of the signal line, decomposed into several coiling fibers. C. Silk threads of the upper scaffold; note the coexistence of straight and coiling threads, and the fibrous composition of each thread. D. The upper bridge. E. A combed cribellate looping segment (top) running parallel to the rail line. F. Close-up of the not combed cribellate rail line; note the thin fibrils and the coiling reserve warps.

suspensor lines and the upper bridge (and presumably the lower bridge as well) are coiled threads, like the coiled segments of the upper scaffold (Fig. 4D), and sometimes have remains of cribellate silk adhering to them (Figs. 2A, S3I). The looping segments of the cribellate capture silk have two parallel axial lines, two reserve warps and a heavily folded, flat mat of combed nanofibers (Figs. 3B, 5B; see also description in Michalik et al., 2019). In the reserve warp, segments that are tightly coiled alternate with others that are only weakly coiled (Fig. 5B). The nanofibers of the cribellar mat have irregularly spaced nodules (Fig. 4G). The rail lines are thin threads only identified as cribellate with magnification (Fig. 4F), with two axial lines, two coiled reserve warps and a tightly appressed mat of nanofibers (Fig. S4, online at http://dx.doi.org/10.1636/JoA-S-18-104.s4). The reserve warp in the rail line is sometimes uniformly coiled and sometimes has alternating segments with weaker coils (Fig. S4A, C), as in the looping segments.

Anterior lateral spinnerets morphology.—The spinning field of the anterior lateral spinnerets shows the typical morphology of gradungulids (Platnick et al. 1991; Griswold et al. 2005), with a mesal field of ampullate spigots, of which 6 are larger, and a marginal row of ca. 12 smaller spigots (Fig. S5B, online at http://dx.doi.org/10.1636/JoA-S-18-104.s5).

Web-building behavior in *Hickmania troglodytes* (Austrochilidae).—The Tasmanian cave spiders build large sheet webs in hollow logs or in caves (Fig. 6A). The webs are similar to those of Chilean austrochilines (Lopardo et al. 2004), and consist of a non-sticky ecribellate scaffolding that is laid first (Fig. 6B), and irregularly looping cribellate

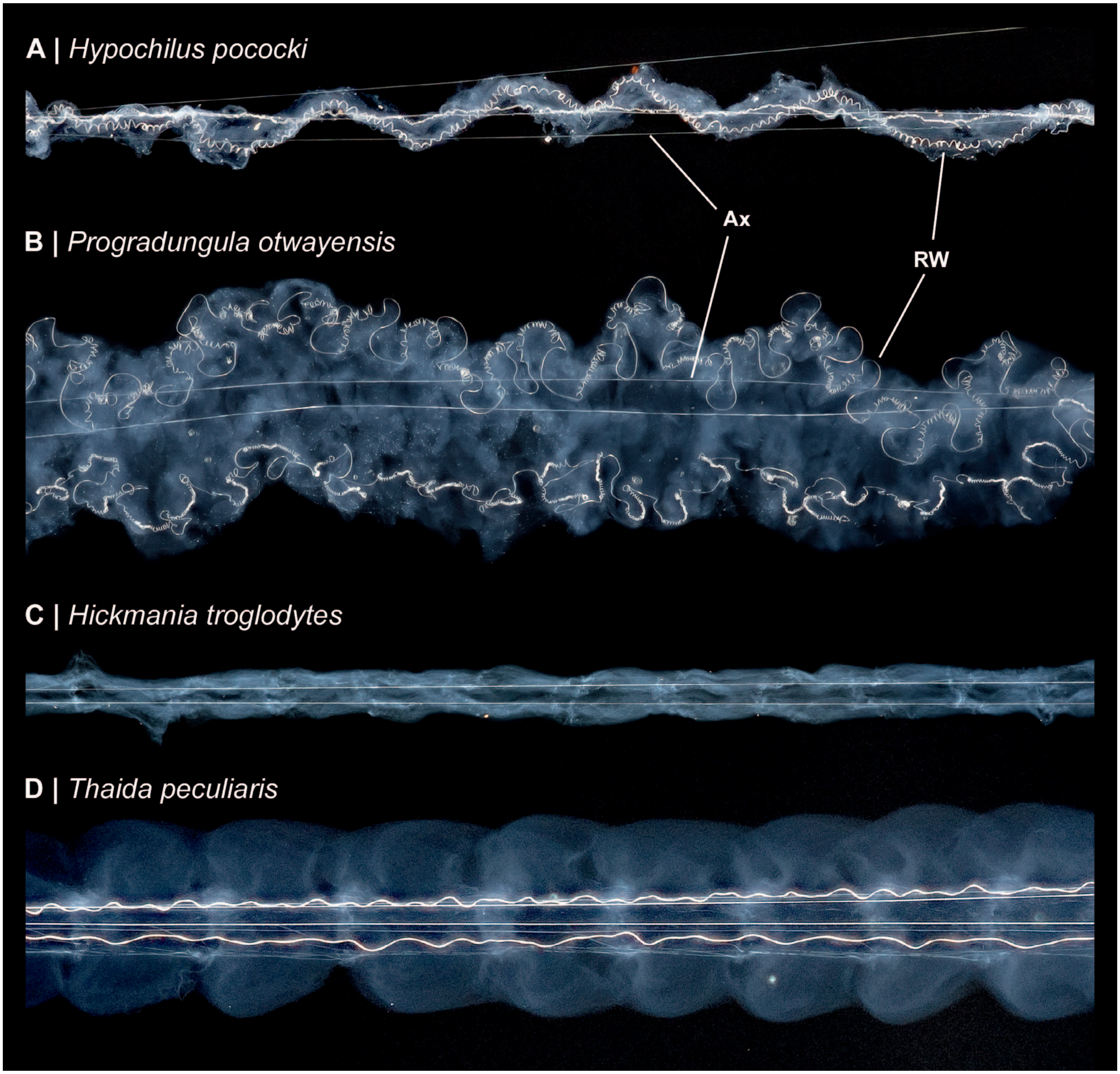

Figure 5.—Incident light images of cribellate bands produced by (A) *Hypochilus pococki* Platnick, 1987 (Hypochilidae), (B) *Progradungula otwayensis* Milledge, 1997 (Gradungulidae), (C) *Hickmania troglodytes* (Higgins & Petterd, 1883) (Austrochilidae) and (D) *Thaida peculiaris* Karsch, 1880 (Austrochilidae). Ax = axial line, RW = reserve warp.

threads that are added later (Fig. 6C). The cribellate bands are combed using the type II behavior (Fig. 6E). The cribellate band has two axial lines and a moderately scalloped cribellar mat (Fig. 5C); there are no reserve warp lines (see also Griswold et al. 2005).

Phylogenetic analysis.—The mapping of the cribellate thread spinning behavior indicates that both types I and II have no homoplasy, although the ancestral state in the common ancestor of Araneomorphae is ambiguous (Fig. 7).

DISCUSSION

The cribellate catching ladder portions of the webs of *P. otwayensis* consistently had a very regular structure constructed in a highly stereotyped sequence. In contrast, only the general positions of the supporting scaffold and signal thread are stable, and their detailed construction and lengths are variable, each adapted to the position of nearby twigs that serve as attachment points and to the relative position of the

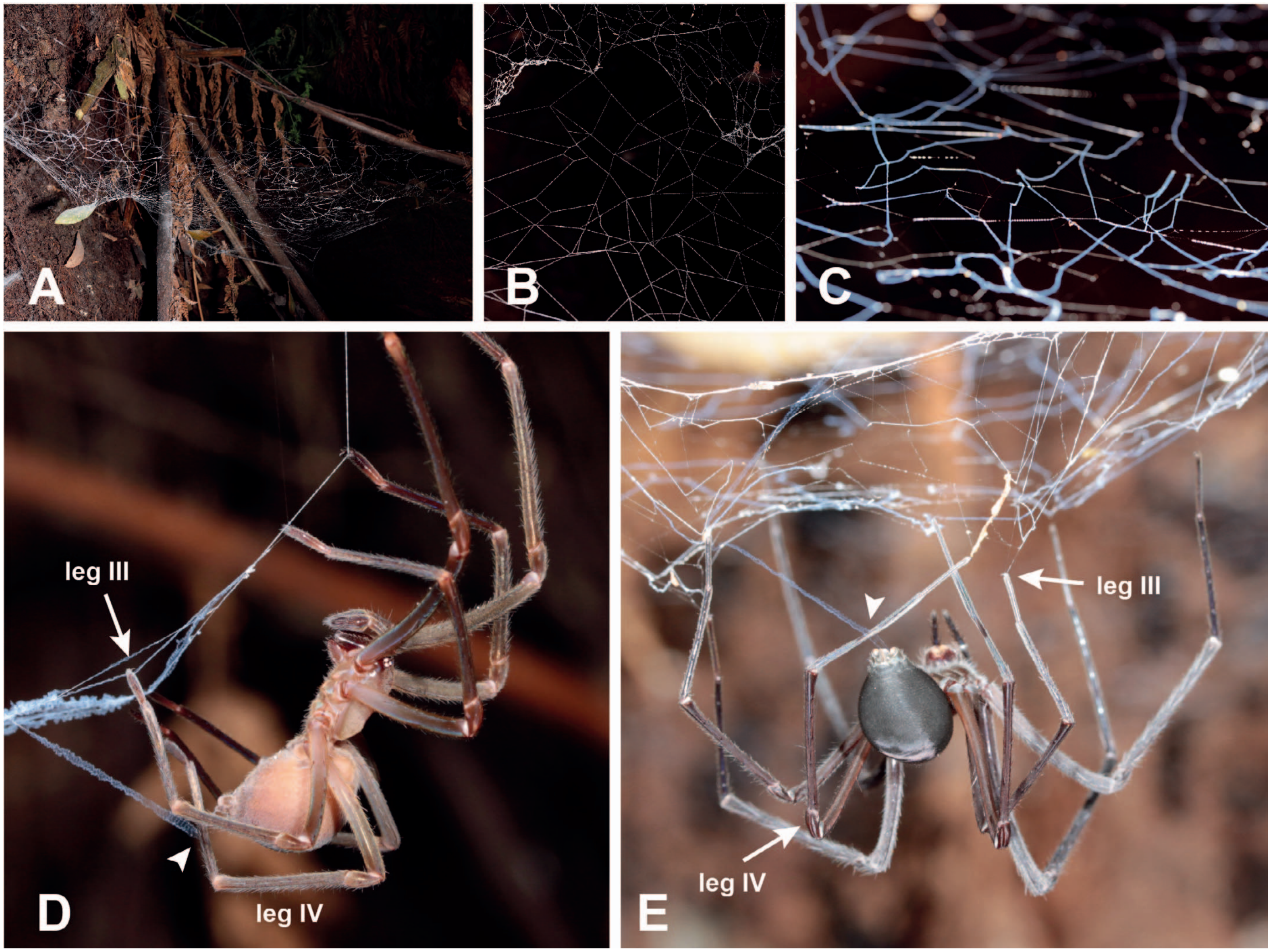

Figure 6.—A–C. Web of the Tasmanian cave spider *Hickmania troglodytes*. A. Complete web, the thick lines are cribellate bands. B. Repaired sector of web, showing the non-sticky ecribellate scaffolding. C. Same, after the application of cribellate threads. D. Penultimate male of *P. otwayensis* combing a cribellate segment using leg IV as support (type II combing behavior). E. Female of *Hickmania troglodytes* in type II combing behavior.

refuge. The catching ladder is very similar in *P. carraiensis* (see Gray 1983) and *Macrogradungula moonya* Gray, 1987 (see Forster et al. 1987), and may be an evolutionary novelty (and synapomorphy) of these three gradungulids. The webs made by early instars of *P. otwayensis* have a section of structural scaffold plus cribellate capture threads, probably an atavism of a generalized capture web like that of austrochilids and many Entelegynae. In contrast, Forster et al. (1987) reasoned that, since the enormously enlarged claws of the anterior legs are key for the function of scooping the prey into the cribellate ladders, they must have evolved in the ancestor of all gradungulids, and adapted later to the cursorial lifestyle of the ecribellate species. A detailed phylogenomic study of gradungulids, as well as the hunting strategies of the ecribellate species, will help elucidate which of those scenarios is more reasonable.

Along with these cribellate gradungulids, other spiders known to construct highly repetitive or geometrically regular web units are the prithine filistatids (Lopardo & Ramirez 2007), some pholcids of the genus *Belisana* Thorell, 1898 (Huber 2005), the desids of the genus *Matachia* Dalmas, 1917 (Opell 1999), and of course the orb-weavers. Their wide taxonomic distribution suggests that the ability to measure with precision and construct highly stereotyped webs may trace back to the ancestors of Araneomorphae. Our data clearly demonstrate a stereotyped combing behavior with both legs IV synchronously (type II) in *Progradungula* and *Hickmania* which agrees with phylogenetic results linking these austrochiloids with the higher araneomorph spiders (Fig. 7; Wheeler et al. 2017). Thus, a monophyletic origin can be assumed for the type II behavior, without subsequent transformations except for those lineages that lost the cribellum altogether (Fig. 7). Recent genomic data (Garrison et al. 2016; Fernández et al. 2018) group the cribellate families Filistatidae and Hypochilidae, both with the alternative behavior (type I), as sister groups. Consequently, type I behavior has a monophyletic origin as well (Fig. 7). The morphology of the cribellar fibrils has exactly the same

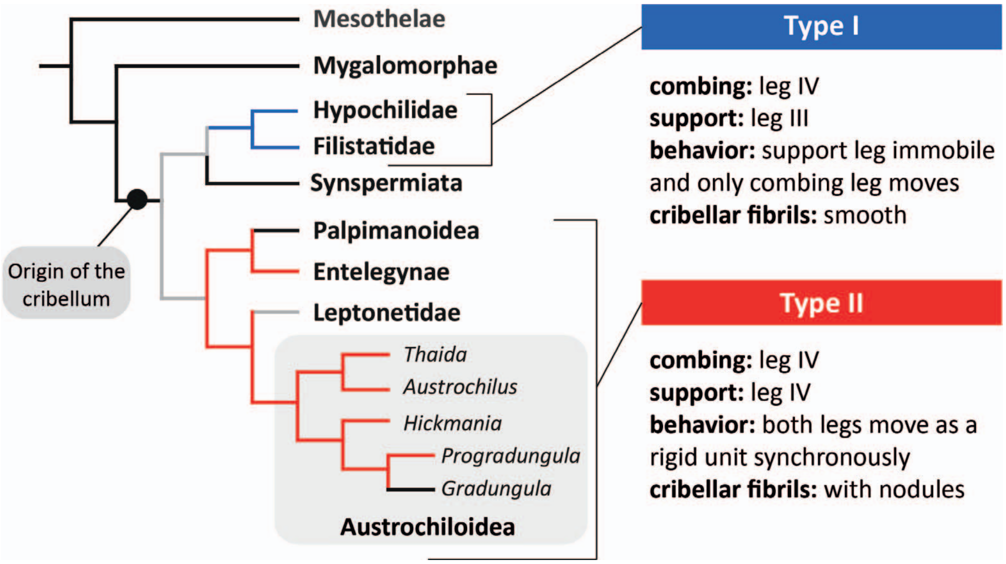

Figure 7.—Evolution of cribellum and combing behavior in a summary tree of main clades of spiders.

taxonomic distribution: all smooth cribellar fibrils come from species using the type I behavior, and all fibrils with nodules from species using the type II. Taking into account that the cribellum evolved before either clade, probably in the common ancestor of Araneomorphae, how did the earlier cribellate araneomorphs comb their cribellate silk? Given current knowledge of the spider tree of life, we see no reason to believe that either behavior is more primitive than the other. Despite this ambiguity, we find it remarkable that only two rigidly stereotyped combing behaviors evolved and maintained unchanged in the 300 million years of araneomorph evolution. This contrasts with the diversity of web architectures among cribellate spiders, including orb webs (Uloboridae), highly modified and extensible snares (Deinopidae, Gradungulidae), and radial capture lines or half-split cribellate bands (Filistatidae; Lopardo & Ramirez 2007).

According to our observations, the cribellate rail lines were laid at once in a single pass, without intervention of the calamistrum, and have the exact composition of a regular cribellate band, just thinner. The uncombed rail lines probably provide more elasticity for the deformation of the ladder (for details see Michalik et al. 2019). Embryological studies demonstrated that the cribellum develops from the buds of anterior median spinnerets (Montgomery 1909), but it is difficult to conceive what may have been the evolutionary intermediates that led to a highly modified cribellum functionally correlated with the calamistrum. Our finding of a spider that spins cribellate threads without the intervention of the calamistrum opens the possibility that the cribellum may have originated before the calamistrum. Conversely, some ecribellate spiders are known to pull silk with the aid of combs of setae in the hind tarsi (e.g., theridiids, nesticids and pholcids; see Foelix 2011), thus it is also possible that the calamistrum may have originated before the cribellum acquired its nano-scale spigots.

A second unique characteristic is the fibrous nature of the structural silk, where each thread may split into several coiling fibers. What glands may produce such a silk? Structural silk in spider webs is usually made of ampullate silk, but this was described as one or two pairs of fibers, each as a uniform cylinder and coming from a single major or minor ampullate gland spigot (see Yarger et al. 2018). *Progradungula otwayensis*, however, has a primitive configuration of several major ampullate gland spigots, in contrast with the one or two pairs in more derived araneomorphs (Platnick et al. 1991; Griswold et al. 2005), and this may be the explanation of the multiple fibers of the structural thread. A similar configuration of multiple fibers is found in the ampullate threads made by the filistatid *Kukulcania hibernalis* (Hentz, 1842) (pers. obs.; W. Eberhard and A.-C. Joel, pers. comm.), which also has three pairs of major ampullate spigots (Platnick et al. 1991; Griswold et al. 2005). Our observations of *P. otwayensis* silk show that the same thread may start straight as a single compact cable, to become coiled in several fibers. It remains to be studied whether the coiling and splitting is a result of the stretching and release of tension, or due to the incorporation of minor ampullate fibers, which coil spontaneously. The artificial coiling and splitting of the signal threads suggests that the first is a plausible mechanism, while the observations of building of catching ladder indicates that the spider produces the coiled segments as it spins the web.

SUPPLEMENTARY FILES

Supplementary Figure S1.—Catching ladders and scaffolds of *P. otwayensis*. (A) Complex scaffold; note the partially damaged but still functional ladder. (B) A regular ladder made by an immature; the ladder is worn out. (C) A simple scaffold made by a single line. (D) Rare variant of a catching ladder with incomplete lower cross. (E) Close-up of the catching ladder of an early immature (same as Fig. 2F). Online at http://dx.doi.org/10.1636/JoA-S-18-104.s1

Supplementary Figure S2.—Early immature webs if of *P. otwayensis*. (A) Specimen in hunting position on a complete web. Note that the upper scaffold has three attachment areas (triangles), one is the signal line (top) and two are placed laterally (sides). The upper scaffold also has irregular loops of cribellate silk (arrows). (B) Same web as in Figure 2F, but before dusting with cornstarch. Note the strand of cribellate silk on the upper scaffold (arrows). Online at http://dx.doi.org/10.1636/JoA-S-18-104.s2

Supplementary Figure S3.—Scanning electron microscope images of silk structures in the web of *P. otwayensis*; yellow fans show the location of close-ups. (A) Signal line. (B) Decomposition of four threads of the signal line near the end torn off while taking the sample. (C) Detail of a single signal thread decomposed in several coiling fibers. (D) Sector of the upper scaffold showing straight and coiling segments. (E, F) Details of the upper scaffold showing the same fibers participating in straight and coiled segments. (H) Same as Fig. 3D. (I) Connection of upper bridge, suspensor and rail line, showing continuity of fibers in suspensor and upper bridge. (J, K) Same as Figure 3E, F. Online at http://dx.doi.org/10.1636/JoA-S-18-104.s3

Supplementary Figure S4.—Transmitted light images of silk structures in the web of *P. otwayensis*. (A) Top, a combed cribellate looping segment, note the reserve warp with alternating segments weakly and heavily coiled; bottom, the rail line, note the uniformly coiled reserve warp. (B) Connection of upper bridge, suspensor and rail line; note the remains of cribellate silk on upper bridge. (C) Closeup of the not combed cribellate rail line. Online at http://dx.doi.org/10.1636/JoA-S-18-104.s4

Supplementary Figure S5.—Spinnerets of female *P. otwayensis*. (A) Overview. (B) Detail of spinning field of right anterior lateral spinneret. ALS = anterior lateral spinneret, Cr = cribellum, maAmp = major ampullate spinning field. Online at http://dx.doi.org/10.1636/JoA-S-18-104.s5

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