

Cribellum, calamistrum and ventral comb ontogeny in *Hyptiotes cavatus* (Hentz) (Araneae: Uloboridae)

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Summary

Values and growth rates of fourth leg articles, calamistrum, ventral comb and cribellum were greater in female than in male *Hyptiotes cavatus* (Hentz). These differences plus disparity in growth rates of the fourth leg articles and similarity in cribellum, calamistrum and ventral comb values and growth rates appear necessary to allow the cribellum, calamistrum and perhaps the ventral comb to manipulate cribellar and wrapping silk. The two silk-handling combs must be able to pass in proper orientation over the calamistrum and/or spinnerets and must have lengths that will accommodate silk strands issuing from these structures. Cribellum size and the spacing of setae in the calamistrum and ventral comb increased during development, but cribellar spinning spigot density remained constant. This resulted in adult females having 4.1 times more cribellum spigots than third instars and producing webs with about 14 times more cribellar silk.

Introduction

Like other cribellate spiders (Berland, 1913), members of the largely orb-weaving family Uloboridae use a calamistrum on the proximal, dorsal surface of each fourth metatarsus to comb silk from the cribellum. In addition, members of this family and those of the Dinopidae have another comb (Opell, 1979), composed of straight, stout setae, found on the ventral surface of the fourth metatarsus and tarsus (Plate 1 b, c; Fig. 1). In Dinopidae this ventral comb is poorly developed, but in Uloboridae it is prominent and appears to be used to draw silk from the cribellum and/or spinnerets during prey capture. When wrapping a struggling prey, the spider faces away from it and, in rapid succession, uses alternate fourth legs to throw silk onto it from a distance. After the prey is encumbered the spider thoroughly

swaths it as it is held and rotated by the second and third legs (Eberhard, 1967; Marples, 1962).

Members of the genus *Hyptiotes* produce a unique vertical triangle-web, considered by many arachnologists to represent a reoriented sector of the family's common and primitive orb-web form (Opell, 1979). The *Hyptiotes* web consists of only four radii, between which cribellar threads extend. When *Hyptiotes cavatus* (Hentz) spiderlings emerge from the eggsac as second instars they lack a cribellum and calamistrum and produce only horizontal or diagonal resting lines. Third instars possess a cribellum, calamistrum and ventral comb and construct small triangle-webs. Nearly all laboratory-reared specimens matured as sixth instars, at which time males lost the cribellum and ceased constructing capture webs. Females continued to produce webs throughout adulthood (Opell, in press).

The purpose of this study is to examine development of the cribellum, calamistrum and ventral comb and to evaluate how growth of these structures and the fourth leg articles responsible for their alignment and use facilitates successful web construction and prey capture during each of the three male and four female instars in which a capture web is produced. Answers to these questions will provide insight into developmental relationships of three functionally associated structures responsible for prey capture.

Methods and Materials

Spiders were reared from eggsacs collected on 25 November 1978 from the lower limbs of a single hemlock tree, *Tsuga canadensis* (L.), near Newport, Giles County, Virginia. Eggsacs were refrigerated and, as specimens were needed, incubated at 23-25°C. Each spider was kept in a plastic box (measuring either 30 x 18 x 8.5 cm or 34.5 x 25.5 x 16.5 cm) into which wooden rods were cemented as attachment sites for webs. All containers were kept in a chamber where conditions of 23-25°C, 85-95% relative humidity and a 10:14 hour light:dark cycle were maintained. Laboratory studies were conducted from 14 January to 1 July 1979. Except for a few occasions, spiders were observed daily and fed one wild type *Drosophila melanogaster* for each web produced. Developmental times were similar to those observed in the field (Opell, in press). Exuviae and adults were placed into individually labelled alcohol

vials for later study. Male third, fourth and fifth instar measurements are each based on six to eight specimens; male sixth instar measurements on four or five specimens. Female third, fourth and fifth instar measurements are each based on 11 to 14 specimens; female sixth instar measurements on eight or nine specimens.

Carapace length and width of each specimen was measured with a dissecting microscope equipped with an ocular micrometer. The cribellum and left fourth leg were removed, mounted on a microscope slide in Hoyer's medium, and photographed with a differential interference contrast (Nomarski) compound microscope (Plate 1). All counts and measurements were made from projected colour slides using calibrations obtained from a projected slide of an ocular micrometer. Spacing of setae on both the calamistrum and ventral comb was determined by dividing the length of each structure by the number of its setae. Cribellum spigot spacing was determined by the number of spigots circumscribed by four triangles placed at random on the projected cribellum. The slide of each cribellum was projected at 1750 x, at which magnification each triangle encompassed an area equivalent to $100 \mu\text{m}^2$. Cribellum surface area is reported as the mean value of areas determined by formulae for a rectangle and for half an ellipse. The total number of cribellum spinning spigots was determined by multiplying cribellum surface area by spigot density.

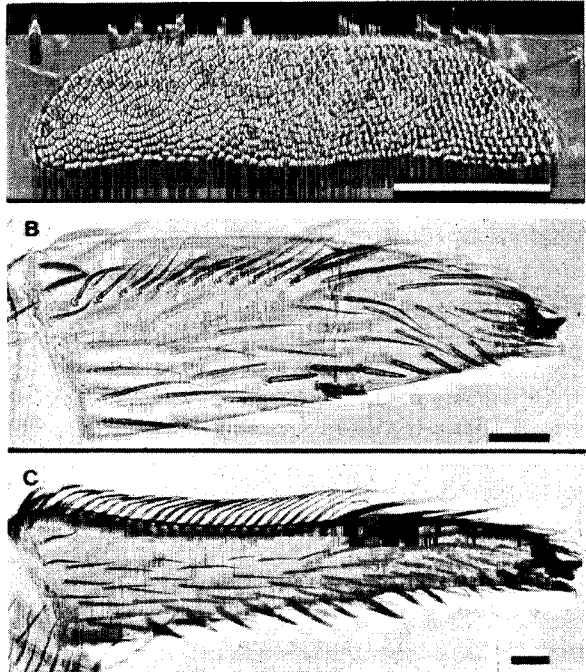


Plate 1: A. Cribellum of third instar female *Hyptiotes cavatus* showing spinning spigot bases. B. Pro-lateral surface of left fourth leg metatarsus and tarsus of a third instar female, showing calamistrum (upper comb) and ventral comb. C. Pro-lateral surface of left fourth leg metatarsus and tarsus of a sixth instar female, showing fully developed calamistrum and ventral comb. Scale lines = $50 \mu\text{m}$.

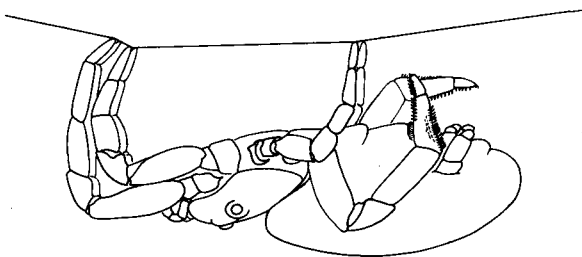


Fig. 1: Lateral view of the cribellar thread spinning posture of a *Hyptiotes cavatus* female, showing the right leg just after its calamistrum has passed over the cribellum. The cribellum is visible on the abdomen just anterior to the fourth leg, the ventral comb on the fourth leg's leading surface, and the calamistrum on its trailing surface.

Results

Female leg article, calamistrum and cribellum lengths and cribellum width exceeded those of males except during the third instar when values were similar (Table 1). This is the result of greater female growth rates shown in Figure 2. The rank order of the leg article growth rates was the same in males and females. Within each sex both the values and growth rates of the cribellum, calamistrum and ventral comb were similar.

Increases in the number of calamistrum and ventral comb setae did not parallel the growth of these structures (Table 1). This resulted in subsequent instars having more widely spaced setae, a trend that was more pronounced for the ventral comb than for the calamistrum. In females the increase in ventral comb setae was due largely to an increase in

tarsal setae from a mean of 2.0 in third instars to a mean of 5.6 in sixth instars (Plate 1 b, c). Both spinning spigot density and the cribellum width/length ratio remained fairly constant during development, the former showing an eight percent increase only in sixth instar females and the latter a three percent decrease in adult females. Except in sixth instar males, cribellum growth resulted in each instar having about 1.6 times more spigots than the previous one.

Discussion

Differences in growth rates of male and female leg articles appear related to abdominal growth. Based on measurements of nine third instars and six male and six female sixth instars, the slope of the carapace length/pedicle to cribellum distance regression line was 0.06 for males and 0.12 for females. The slope of the carapace length/maximum abdominal width line was 0.07 for males and 0.15 for females. This means that in order for the calamistrum and ventral comb to continue to pass across the cribellum (and/or spinnerets, Fig. 1) the growth rates of female leg articles must exceed those of males. In addition to abrupt changes which occur at moulting, there are also gradual increases in abdomen volume that occur within each instar. The latter may not greatly influence the pedicle to cribellum distance, but it does require the fourth femur of the leg whose calamistrum is being used to extend laterally a greater distance, thereby reducing its effective retraction.

The greatest disparity between growth rates of male and female leg articles (Fig. 2) occurs between femur and patella and the least between tibia and metatarsus. The former two articles have the greatest flexibility, both in literal and functional senses. In conjunction with coxa and trochanter articulations the femur establishes both the amount of lateral movement and retraction of the fourth leg. Patellar flexion further determines the effective length of the remaining leg articles, brings the metatarsus to the abdomen's midline, and provides for tibial rotation so that the metatarsus can be held parallel to and against the abdomen. Flexion of the metatarsus allows the calamistrum to become parallel to the cribellum. Tarsal flexion is probably very limited, but may be important for establishing contact with the opposite fourth leg. Therefore, proportionately

greater increases in female femur and patella lengths probably optimally facilitate greater posterior extension of the fourth leg and accommodation of a more rotund abdomen.

A second case of apparent functional linking of growth rates is seen in parallel increases in cribellum width and calamistrum length and perhaps also ventral comb length. The association of cribellum and calamistrum is clear and their alignment is apparently facilitated by the tip of the leg whose calamistrum is being used resting on the metatarsus of the opposite fourth leg (Gertsch, 1979; Opell, 1979; Fig. 1). This association is reflected by a cribellum width/calamistrum length ratio for both males (through the fifth instar) and females which remained between 0.90 and 0.95 throughout develop-

		3rd INSTAR	4th INSTAR	5th INSTAR	6th INSTAR
		X (SD)	X (SD)	X (SD)	X (SD)
CARAPACE	♂	570 (24)	678 (33)	810 (28)	928 (30)
LENGTH	♀	598 (122)	685 (53)	867 (89)	1027 (66)
FEMUR	♂	368 (31)	443 (12)	546 (54)	660 (22)
LENGTH	♀	370 (27)	464 (57)	616 (87)	762 (135)
PATELLA	♂	208 (17)	252 (11)	268 (41)	330 (54)
LENGTH	♀	212 (26)	271 (37)	346 (56)	409 (62)
TIBIA	♂	236 (16)	303 (15)	365 (30)	460 (8)
LENGTH	♀	233 (24)	324 (41)	415 (72)	511 (78)
METATARSUS	♂	259 (20)	308 (11)	358 (39)	455 (8)
LENGTH	♀	261 (27)	342 (43)	416 (58)	522 (81)
TARSUS	♂	184 (3)	210 (8)	234 (17)	267 (17)
LENGTH	♀	193 (9)	224 (15)	261 (21)	330 (84)
CALAMISTRUM	♂	184 (17)	222 (12)	273 (22)	320 (54)
LENGTH	♀	181 (16)	242 (29)	322 (55)	427 (91)
VENTRAL COMB	♂	182 (5)	211 (10)	271 (41)	333 (50)
LENGTH	♀	194 (22)	223 (17)	296 (66)	423 (141)
CRIBELLUM	♂	163 (3)	206 (4)	251 (24)	
WIDTH	♀	166 (8)	226 (27)	292 (46)	362 (50)
CALAMISTRUM	♂	11 (1)	14 (1)	16 (1)	15 (3)
SETAE NUMBER	♀	11 (1)	14 (1)	17 (2)	23 (5)
CALAMISTRUM	♂	17 (1)	16 (1)	17 (1)	21 (3)
SETAL SPACING	♀	16 (2)	17 (1)	18 (2)	19 (3)
VENTRAL COMB	♂	7 (0)	7 (0)	8 (1)	8 (1)
SETAE NUMBER	♀	7 (0)	7 (0)	8 (1)	10 (2)
VENTRAL COMB	♂	26 (1)	30 (1)	35 (5)	42 (6)
SETAL SPACING	♀	27 (2)	32 (3)	38 (6)	43 (6)
SPIGOT DENSITY	♂	12 (0)	13 (0)	13 (0)	
(#/100 μm^2)	♀	12 (0)	13 (0)	13 (0)	14 (0)
TOTAL SPIGOTS	♂	0.79 (.12)	1.46 (.17)	2.10 (.54)	
($\times 10^7$)	♀	1.10 (.51)	1.61 (.46)	2.68 (.80)	4.50 (.97)

Table 1: Developmental changes in the *Hyptiotes cavatus* carapace, leg IV articles, calamistrum, ventral comb and cribellum. All measurements are in μm .

ment. It is not known whether uloborids use cribellar silk for wrapping prey, but the cribellum width/ventral comb length was not constant, increasing from 0.88 to 0.98 in males and from 0.81 to 1.11 in females. During prey wrapping the ventral comb is not aligned in a manner similar to the calamistrum. Instead, it appears to move across the cribellum and spinnerets at an angle with both the sagittal and frontal body planes. Either this apparent lack of precision or the fact that cribellar silk is not used in prey wrapping may explain changes in the cribellum width/ventral comb length ratio.

More difficult to explain are changes in the spacing of calamistrum and ventral comb setae (Table 1), particularly in view of the constant cribellar spigot density. It may be that these changes are associated with the maintenance of a surface area whose resistance is just sufficient to allow silk to be drawn from the spigots, that they reduce tangling tendencies in older individuals forced to handle more threads, or that they allow a certain amount of slippage which may be necessary to establish the kinky nature of cribellar strands. However, there are no studies of the finer details of cribellar and wrapping silk handling upon which such conclusions might rest.

If all or a constant proportion of cribellar spigots spin silk, female fourth instars produce 1.5 times, female fifth instars 2.4 times, and female sixth instars 4.1 times as many cribellar strands as do female third instars. These ratios may be even greater if the paracribellar spigots described by Peters & Koor (1980) increase in a similar manner. Mean lengths of cribellar threads in field-produced *H. cavatus* female third, fourth, fifth and sixth instar webs were 41, 53, 113 and 145 cm respectively (Opell, in prep.). Therefore, female fourth instars probably produce 1.9 times, fifth instars 6.6 times, and sixth instars 14.5 times more cribellar silk per web than do third instars. Light and electron microscope photographs (Comstock, 1913; Friedrich & Langer, 1967; Kullmann, 1968; Opell, 1979) show that cribellar strands are convoluted and drawn into tufts so that individual cribellar strands in each cribellar thread are at least 1.5 times the length of the thread. Using these data and the total number of cribellar spigots (Table 1), one can calculate that third instar webs each contains 0.68 km of cribellar strands, fourth instar webs 1.28 km, fifth instar webs 4.54 km, and sixth instar webs 9.79 km.

The cribellate web thus seems to be an extremely

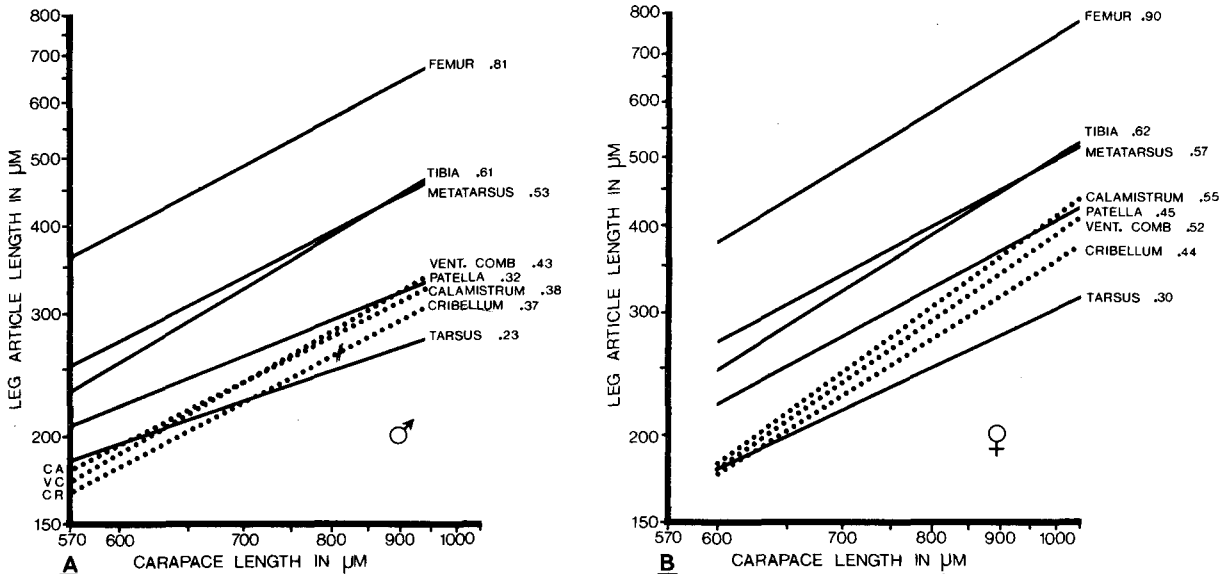


Fig. 2: Growth rates of fourth leg articles (solid lines) and cribellum, calamistrum and ventral comb (dotted lines) of *Hyptiotes cavatus* males (A) and females (B). Slopes are given after the identification of each line. Both horizontal and vertical axes are logarithmic. Although males do not have a functional cribellum upon reaching maturity (indicated by //), this line has been extended for comparative purposes.

costly method of prey capture, both in terms of silk output and labour required to comb and deposit cribellar silk. This study does not allow determination of the labour investment, but does permit estimation of material investment. Based on the previous information, coupled with Friedrich & Langer's (1967) finding that *Uloborus diversus* Marx cribellar strands were about $0.025 \mu\text{m}$ in diameter, a $10 \mu\text{m}$ length of adult female cribellar thread should contain approximately $33.1 \mu\text{m}^3$ of cribellar silk. When similar estimates of the adhesive material contained in the capture threads of cribellate spiders are obtained it will be possible to compare more precisely the material costs of the two web types.

Despite its production cost, cribellar silk must originally have enhanced prey capture by allowing a web to retain prey rather than simply signalling its presence or delaying its passage. This would have been particularly important to spiders which constructed aerial webs and captured flying prey. The similarity between cribellar silk production and prey wrapping suggests that the cribellum may have evolved from the anterior median spinnerets as a source of dense prey wrapping silk. This silk could also have been placed on the web to retard prey escape. The more effective that cribellar silk became for holding prey in the web the less need there would have been to use it for wrapping. The result would then have been a spider which produced an aerial web with cribellar capture elements, but no longer used wrapping silk. This prediction fits well with the biology of *Hypochilus* (Shear, 1969) which Platnick (1977) has shown to be the most primitive araneomorph. Although it produces an extensive web, *Hypochilus gertschi* Hoffman responds only to prey that comes into contact with the cribellar silk covered lampshade region of the web and there subdues prey only by biting. This is also consistent with Eberhard's (1967) conclusion that primitive web spiders did not subdue their prey by wrapping.

After cribellar silk became a component of the araneomorph web, the cost of producing it may have intensified selection for its more efficient (restricted) placement or for its loss. Evidence of the former is seen in several *Dictyna* species (Comstock, 1913; Wiehle, 1953) and *Eresus* (Wiehle, 1953) where cribellar silk is deposited only on peripheral threads extending from the retreat, and in Dinopidae and

Uloboridae where cribellar strands are laid down in parallel rows and in spirals respectively. The range in cribellum size and spigot number relative to the spider's size (Berland, 1913; Foelix & Jung, 1978; Kullmann, 1968) raises questions about the relative efficiency and importance of the cribellum and its silk among the cribellate groups. For example, did the cribellate orb-web evolve because uloborids had a proportionately larger cribellum than other cribellate groups (e.g. filistatids) and were, therefore, subjected to more intensive selection for economical use of cribellar silk, or do uloborids have a larger cribellum because their cribellar silk is more important for prey retention than that of filistatids?

Most groups which have lost the cribellum and its associated calamistrum rely on hunting, dense sheet webs, or webs with adhesive threads for prey capture. When cribellar and adhesive threads of orb-webs are compared, cribellar silk appears to be superior in two respects. Although less elastic than adhesive threads (Lubin, in press), cribellar threads are able to give when stressed. This is afforded by the sliding connections of spiral and radial web elements (Eberhard, 1976; Opell, 1979) and by the ability of the cribellar mat to pull free from its supporting axial threads (Eberhard, 1976). Additionally, cribellar silk appears to retain its holding properties longer and to be less affected by drying than adhesive thread (Eberhard, 1980). These properties suggest that there are features of cribellar silk that may compensate for the cost of producing it and may help explain the persistence of the cribellum and calamistrum.

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