

CRIBELLUM AND CALAMISTRUM ONTOGENY IN THE SPIDER FAMILY ULOBORIDAE: LINKING FUNCTIONALLY RELATED BUT SEPARATE SILK SPINNING FEATURES

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ABSTRACT. The fourth metatarsus of cribellate spiders bears a setal comb, the calamistrum, that sweeps over the cribellum, drawing fibrils from its spigots and helping to combine these with the capture thread's supporting fibers. In four uloborid species (*Hyptiotes cavatus*, *Miagrammopes animotus*, *Octonoba sinensis*, *Uloborus glomus*), calamistrum length and cribellum width have similar developmental trajectories, despite being borne on different regions of the body. In contrast, developmental rates of metatarsus IV and its calamistrum differ within species and vary independently among species. Thus, the growth rates of metatarsus IV and the calamistrum are not coupled, freeing calamistrum length to track cribellum width and metatarsus IV length to respond to changes in such features as combing behavior and abdomen dimensions.

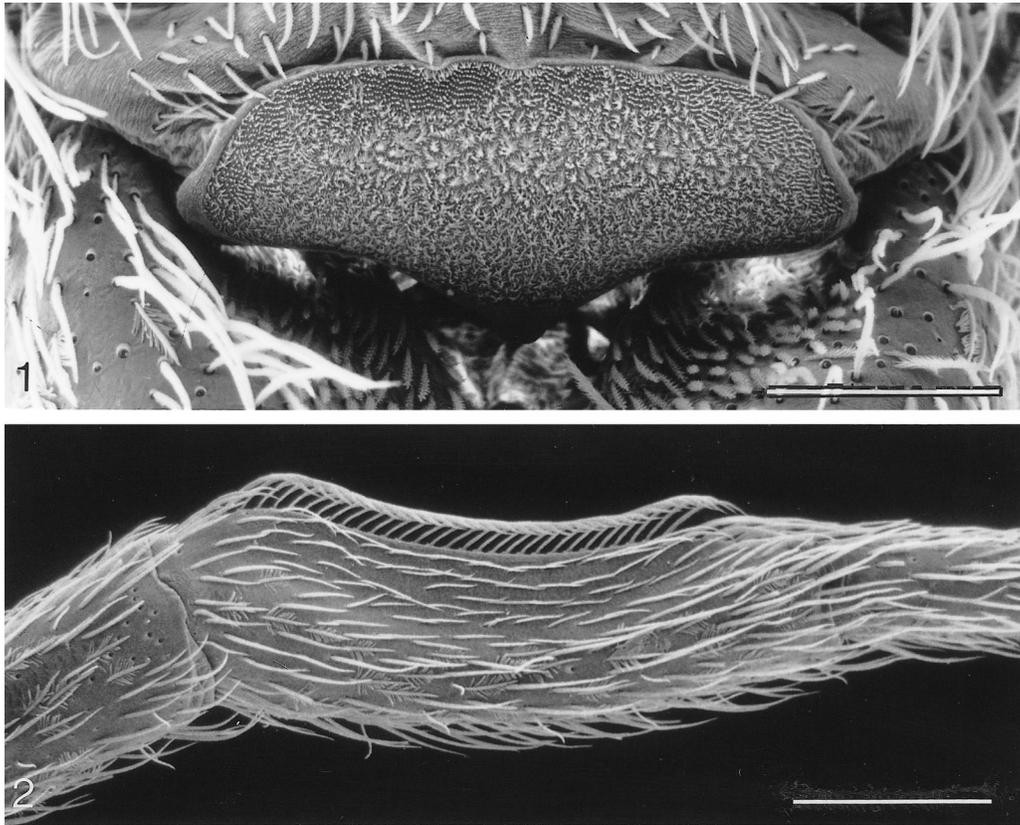
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Members of the family Uloboridae produce cribellar prey capture threads formed of a sheath of fine, looped fibrils that surround paracribellar and axial supporting fibers (Eberhard & Pereira 1993; Opell 1990, 1994, 1995, 1996, 1999; Peters 1983, 1984, 1986). Cribellar fibrils come from the spigots of an oval spinning field termed the cribellum (Fig. 1; Kooor & Peters 1988; Opell 1994, 1999), located on the ventral surface of the spider's abdomen, just anterior to its spinnerets. These fibrils are drawn from cribellar spigots by the calamistrum, a setal comb that is formed of a single row of long, slender, curved setae that extends along the proximal $\frac{1}{2}$ – $\frac{2}{3}$ of both fourth metatarsi (Fig. 2; Kullmann & Stern 1981; Opell 1979; Peters 1983, 1984). When drawing fibrils from the cribellum, uloborids brace the tarsus of the combing leg on the metatarsus of the opposite fourth leg (Eberhard 1988; Opell 1979; Peters 1984). Left and right legs are used alternately in short, vigorous bouts of combing (Eberhard 1988) and the resulting sheet of fibrils is compressed around supporting fibers by adductions of the posterior lateral spinnerets (Peters 1984).

In members of the family Uloboridae, spiderlings hatch from eggs, molt once within the egg sac, and emerge from the egg sac as sec-

ond instars (Opell 1979). However, their cribella and calamistra are not functional until they molt again to become third instars. Second instar orb-weaving uloborid species produce a juvenile web that lacks a sticky spiral and has many closely spaced radii (Lubin 1986). Members of the triangle-web genus *Hyptiotes* Walckenaer 1837 and the simple-web genus *Miagrammopes* O. Pickard-Cambridge 1869 do not construct capture webs until they become third instars. After emerging from the egg sac, second instar *Hyptiotes* rest on vegetation (Opell 1982a, b), whereas *Miagrammopes* cling to the outer surface of their cylindrical egg sac, which is still held by the female (Lubin, et al. 1978; Opell 2001). When spiders mature as sixth instars (Berland 1914; Opell 1982a, 1987), females retain a functional cribellum and calamistrum, but males do not (Opell 1989, 1995).

Complementary structures like the cribellum and calamistrum must develop in consort if they are to function throughout a spider's life. As the cribellum is borne on the abdomen and the calamistrum on the fourth legs, this requires a convergence in the developmental rates of structures on different body regions. If the growth rates of the calamistrum and metatarsus IV are linked, then both must de-



Figures 1, 2.—The cribellum (Fig. 1, scale bar = 150 μm), and calamistrum (Fig. 2, scale bar = 250 μm) of an adult female *Miagrammopes animotus*.

velop at a rate that equals or exceeds that of cribellum width. If these structures develop at different rates, then only calamistrum length must increase at a rate that equals or exceeds that of cribellum width. I hypothesize that the latter occurs, as this would not compromise other fourth leg functions or require compensatory changes in the lengths of other fourth leg articles.

I tested this hypothesis by comparing the developmental rates of structures within the orb-weaving species *Uloborus glomus* (Walckenaer 1841) and *Octonoba sinensis* (Simon 1880) and the reduced-web species *Hypitiotes cavatus* (Hentz 1847) and *Miagrammopes animotus* Chickering 1968. The orb is the plesiomorphic web form in the Uloboridae and the triangle-web and simple-web are derived forms (Coddington 1990; Opell 1979).

METHODS

I collected 102 *U. glomus* (39 of which were adult) from shrubbery on the Virginia

Tech campus in Montgomery County, Virginia during the spring and summer of 1989. *Octonoba sinensis* is an introduced Asian species. I collected 79 individuals (17 of which were adults) in greenhouses on the Virginia Tech campus during the spring and summer of 1989. I collected 136 *H. cavatus* (31 of which were adult) from Giles and Montgomery Counties, Virginia during the spring and summer of 1990. I collected 190 *M. animotus* (77 of which were female) from the Center for Energy and Environment Research's El Verde Research Station, Luquillo National Forest, Puerto Rico during the summer of 1990. Only one species of each genus was present at each locality, so there were no problems in determining the species of juvenile specimens. All instars of *M. animotus* were present at the same time. Successive instars of the other species were collected as they appeared during the spring and summer. These species were identified using the revisions of Chickering

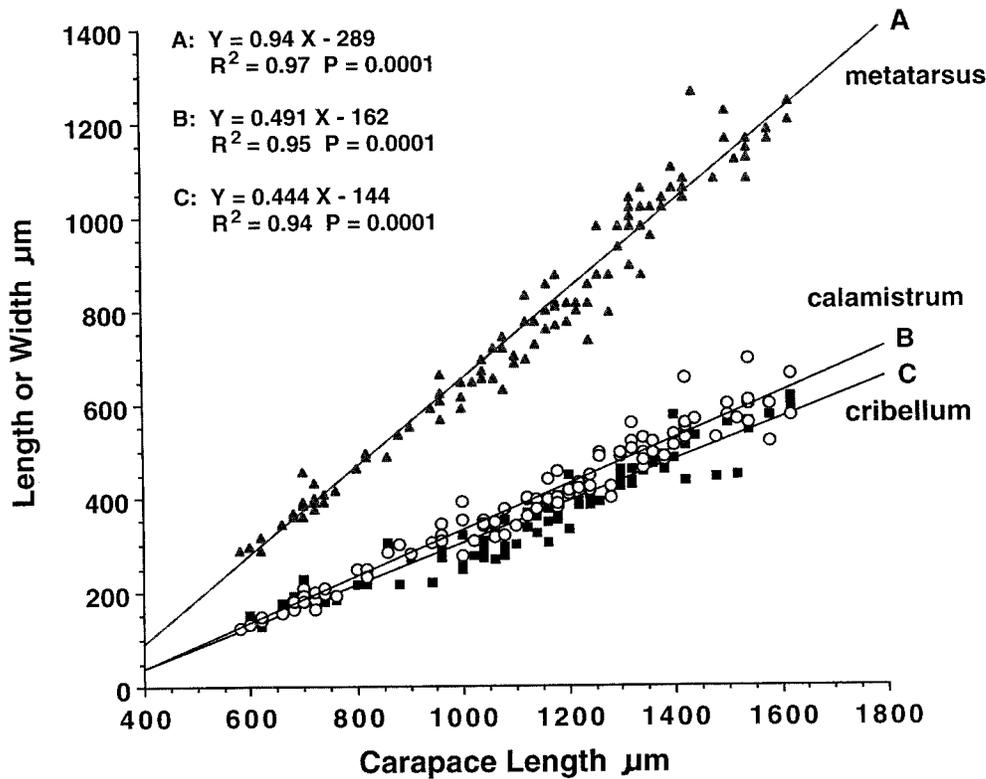


Figure 3.—Regressions of metatarsus IV length, calamistrum length, and cribellum width against carapace length in *Uloborus glomosus*. Sample size = 102.

(1968), Muma & Gertsch (1964), and Opell (1979). Voucher specimens are deposited in the Museum of Comparative Zoology.

Specimens were preserved in 80% ethanol. I measured the carapace length of each spider under a dissecting microscope. Each specimen's cribellum and fourth leg were then removed and mounted in water soluble medium under a cover slip on a microscope slide. Using a compound microscope, I measured cribellum width, fourth metatarsus length, and calamistrum length. All features were measured to at least the nearest 20 μm . I measured calamistrum length as the distance separating the proximal- and distal-most setal bases. This approach eliminates problems associated with missing setae and it does not make any assumptions about the deflection of calamistrum setae during cribellar fibril combing. Statistical tests were performed with SAS (SAS Institute Inc., Cary, North Carolina). P values of ≤ 0.05 were considered significant.

RESULTS

Figures 3–6 plot cribellum, calamistrum, and metatarsus IV lengths against carapace length in the four species studied. Each of these regressions is significant ($F = 584\text{--}2951$, $P = 0.0001$). As reflected by R^2 values, the variance of these features is greater in *H. cavatus* and *M. animotus* than it is in *U. glomosus* and *O. sinensis*. This may be the result of measurement precision, as *H. cavatus* and *M. animotus* are smaller than *U. glomosus* and *O. sinensis*. However, the smaller values of the axes of *H. cavatus* and *M. animotus* (Figs. 5, 6) tend to exaggerate the scatter of these species' points. Homogeneity tests show that, for each species, the slope of calamistrum length exceeds that of cribellum width ($F = 8.77\text{--}80.58$, $P = 0.0034\text{--}0.0001$) and the slope of metatarsus IV length exceeds that of calamistrum length ($F = 17.45\text{--}482.30$, $P = 0.0001$). In *M. animotus* the intercepts of cribellum width and calamistrum length differ (t

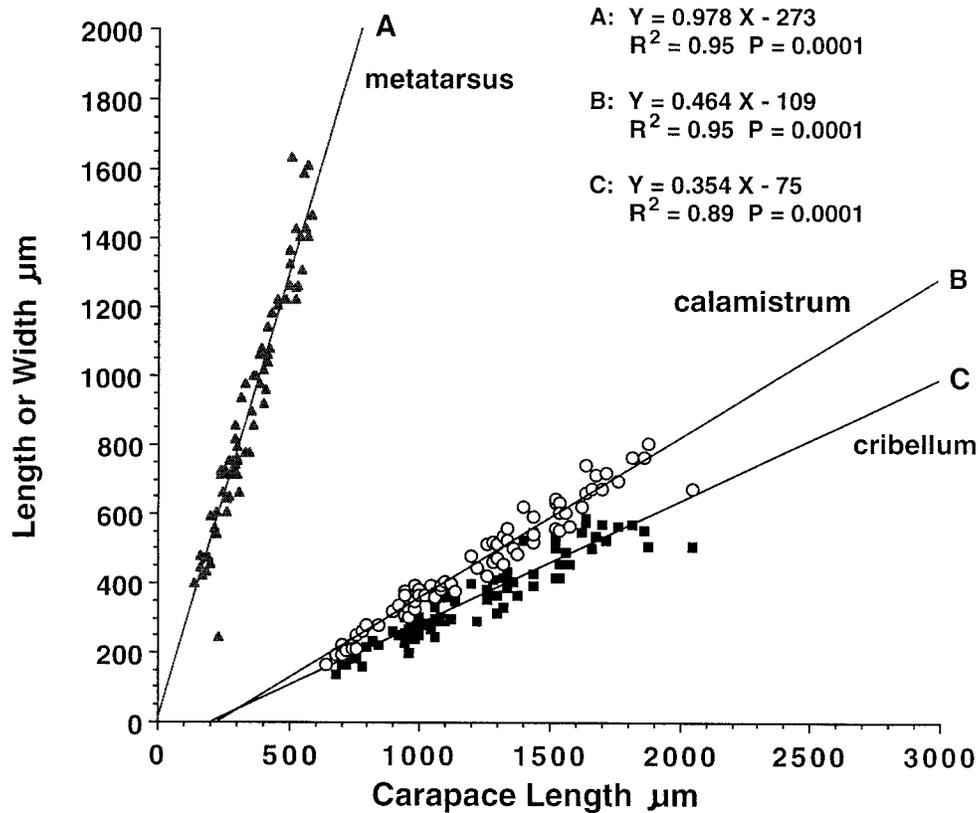


Figure 4.—Regressions of metatarsus IV length, calamistrum length, and cribellum width against carapace length in *Octonoba sinensis*. Sample size = 79.

= 2.558, $P = 0.015$), but in the other three species they do not ($t = 0.993\text{--}1.698$, $P = 0.100\text{--}0.285$). Thus, in each species, calamistrum length and cribellum width are initially very similar, but calamistrum length increases more rapidly than cribellum width.

Tests of the homogeneity of the regression slopes of metatarsus IV show the slopes of *U. glomosis* and *O. sinensis* do not differ ($F = 1.63$, $P = 0.204$). The slope of *U. glomosis* (the smaller of the two orb-web species' values) is greater than that of both *H. cavatus* ($F = 70.73$, $P = 0.0001$) and *M. animotus* ($F = 330.98$, $P = 0.0001$). Developmental rates of the calamistrum also differ but do not mirror differences in metatarsus IV development. If they did, calamistrum length would increase at a rate less than that of the cribellum in *H. cavatus* and *M. animotus*. However, as documented above, in all species calamistrum length increases more rapidly than does cribellum width.

The slopes of the calamistrum of *U. glo-*

mosus and *O. sinensis* do not differ ($F = 2.60$, $P = 0.109$). The slope of *U. glomosis* (the smaller of these values) is less than that of *H. cavatus* ($F = 11.94$, $P = 0.0007$) and greater than that of *M. animotus* ($F = 11.69$, $P = 0.0007$). The metatarsus IV of *H. cavatus* has a slope that is 0.229 less than that of *U. glomosis*, but its calamistrum has a slope that is 0.066 greater. In *M. animotus*, these values are -0.446 and -0.071 , respectively. This is further documentation that the slopes of metatarsus IV and its calamistrum are free to assume different trajectories.

DISCUSSION

The results of this study support the hypothesis that developmental rates of metatarsus IV and the calamistrum differ. By developing at a slower rate than the leg article that bears it, calamistrum length tracks more closely the development of the cribellum, with

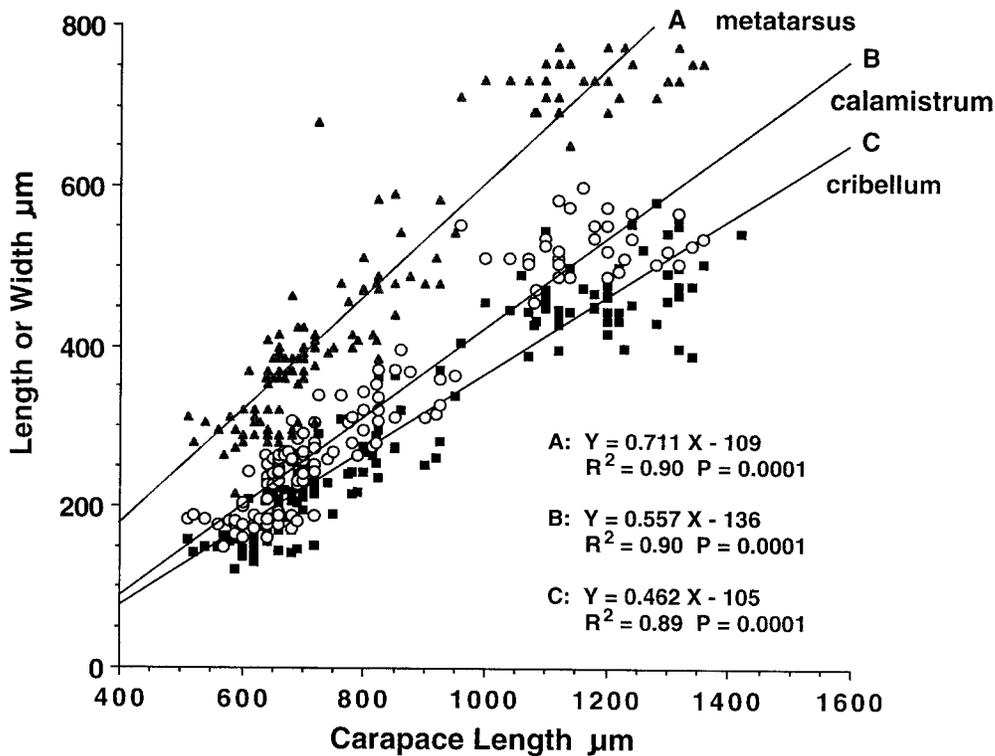


Figure 5.—Regressions of metatarsus IV length, calamistrum length, and cribellum width against carapace length in *Hyptotes cavatus*. Sample size = 136.

which it is functionally linked. I did not examine possible correlates of metatarsus IV length. However, changes in the lengths of the fourth leg articles may be associated with changes in abdomen length and may serve to maintain the proper alignment of the calamistrum as it passes over the cribellum. Calamistrum length and cribellum width are initially very similar, but calamistrum length increases at a slightly greater rate. If a calamistrum is to comb all the fibrils from cribellum spigots as it passes over the cribellum and is held with its length parallel to the transverse axis of the cribellum, then calamistrum length must equal cribellum width. As the angle formed by the calamistrum and the transverse axis of the cribellum increases, calamistrum length must increase if it is to completely span the cribellum. For example, at an angle of 15° , the calamistrum must be 4% longer, and at 30° , 16% longer than if it were held at an angle of 0° . If the calamistrum moves laterally as it sweeps across the cribellum, further increases in calamistrum length

would be necessary to ensure that the calamistrum completely spans the cribellum. Thus, the developmental increase of calamistrum length relative to cribellum width observed in this study may reflect increases in the angle at which the calamistrum passes over the cribellum or the lateral movement of its passage. These changes may be necessary to accommodate changes in the lengths of fourth leg articles or changes in abdomen length or width that require the fourth legs to assume different postures during the production of cribellar thread.

Within the family Uloboridae, web reduction is associated with a reduction in the length of metatarsus IV relative to the carapace length. In *U. glomosus* and *O. sinensis* adult females this ratio is 0.75 and 0.83, respectively. In *H. cavatus* and *M. animotus* this ratio is 0.63 and 0.56, respectively (Opell, unpubl. obs.). In contrast, the cribella of these two reduced-web species have greater numbers of spinning spigots than do the orb-weaving species (Opell 1994). Thus, unless meta-

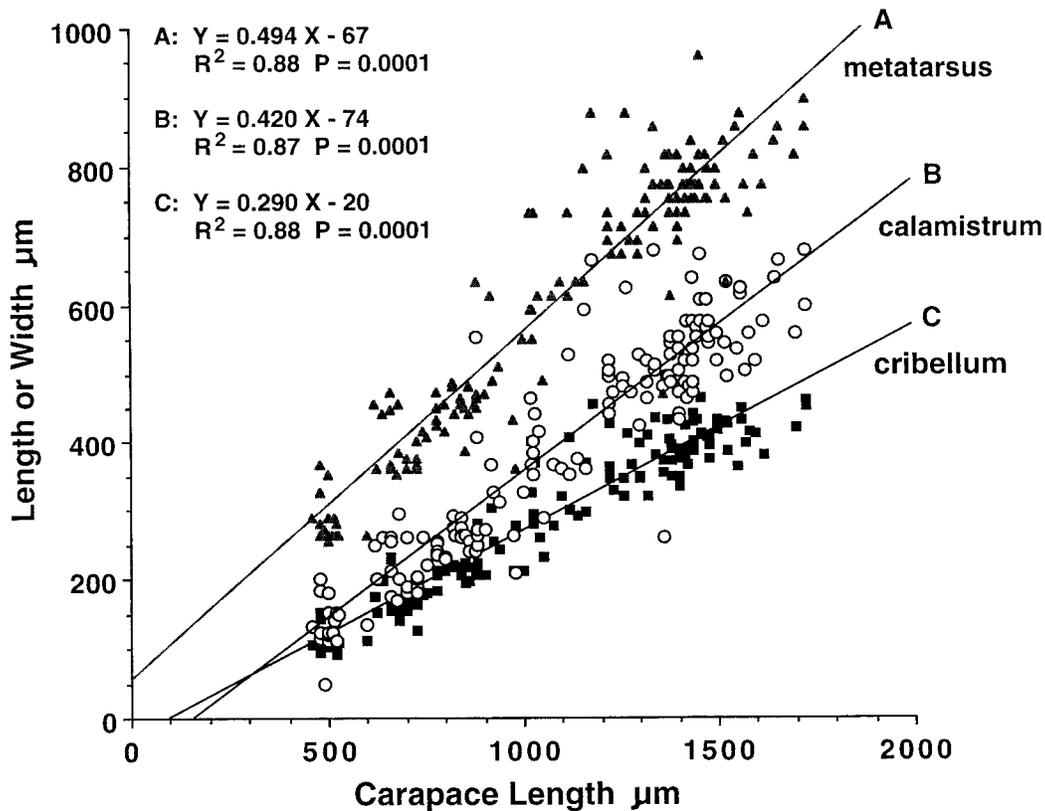


Figure 6.—Regressions of metatarsus IV length, calamistrum length, and cribellum width against carapace length in *Miagrammopes animotus*. Sample size = 190.

tarsus IV and the calamistrum have different developmental trajectories, increases in calamistrum length could not keep pace with the increases in cribellum width that are necessary to accommodate a greater number of spigots and produce wider, stickier cribellar threads (Opell 1995).

The strong ontogenetic linkage of cribellum width and calamistrum length observed in this study contrasts with the weak phylogenetic relationship between these features observed by Opell et al. (2000). In that study no correlation between cribellum width and calamistrum length could be demonstrated among representatives of different families or among genera of the family Uloboridae. Only among species of the dictynid genus *Mallos* O. Pickard-Cambridge 1902 was there an association between these features, and this regression had an R^2 value of 0.41 compared to a mean value of 0.93 for the developmental studies reported here. As Opell et al. (2000) point out,

differences in abdomen dimensions and cribellar thread combing behaviors among species probably explain the weak relationship between cribellum width and calamistrum length at more inclusive taxonomic levels.

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